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THE UNIVERSITY OF ALBERTA

PHYSIOLOGICAL ASPECTS OF LATE SUMMER PRODUCTIVITY OF SEVERAL TEMPERATE GRASSES

BY

GEORGE ALOYSIUS VAN ESBROECK

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND
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Abstract

Poor late season productivity of pastures is a serious problem in western Canada. The problem is especially acute with smooth bromegrass (*Bromus inermis* Leyss.), one of the most extensively grown species. The objectives of this study were to examine the pattern of late season regrowth of several temperate grasses in the field and to investigate the effects of temperature and photoperiod on aspects of regrowth in controlled conditions. A growth analysis experiment was carried out from late July to mid September of 1985 and 1986 at Lacombe Alberta on smooth bromegrass cv. Carlton, meadow bromegrass, (*Bromus riparius* Rhem and Schult.) cv. Regar, an interspecific cross between smooth and meadow bromegrass (SS9044) and meadow foxtail (*Alopecurus pratensis* L.), "common". Regrowth parameters of these species as well as orchard grass (*Dactylis glomerata* L.) cv. Kay and tall fescue (*Festuca arundinacea* Shreb.) cv. Alta was evaluated in cabinets at a 14 and 18 h photoperiod and at a 15/5 and 25/15°C day/night temperature regime.

Smooth bromegrass had lower dry matter yields in the field than the other species. Crop growth rates in all species peaked after 21-35 days of regrowth which coincided with leaf area indices and interception of incident light ranging from 1.3 to 2.4 and 90-95% respectively. Yields of all species thus appeared limited by less than complete light interception early in regrowth and then a low critical leaf area index at complete light interception. In controlled conditions dry matter yields were greater at the high compared to the low temperature for all species. Lengthening the photoperiod however increased the dry matter yields of only smooth bromegrass (39%) and S9044 (22%). Photoperiodic yield enhancements were associated with increases in shoot weight and shoot:root ratios. In smooth bromegrass photoperiod extension increased both leaf (+25%) and stem (+94%) extension rates. The lower productivity for smooth bromegrass in the field, in comparison to the other species studied, appeared to be related to its slow growth under short daylengths.

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Definition of frequently used Abbreviations

Term	Definition	Units
LAI	leaf area index (leaf area per ground area)	$cm^2\ cm^{-2}$
LER	leaf lamina per tiller extension rate	$cm\ tiller^{-1}\ week^{-1}$
LAT	leaf area per tiller	$cm^2\ tiller^{-1}$
LYT	leaf yield per tiller	$mg\ tiller^{-1}$
SYT	stem yield per tiller	$mg\ tiller^{-1}$
TN	tiller number per pot	$tillers\ pot^{-1}$
TD	tiller density	$tillers\ dm^{-2}$
TW	weight per tiller	$mg\ tiller^{-1}$
CGR	crop growth rate	$g\ m^{-2}\ d^{-1}$
RGR	relative growth rate	$g\ g^{-1}\ d^{-1}$
NAR	net assimilation rate	$g\ m^{-2}\ d^{-1}$
LAR	leaf area ratio (leaf area per total plant weight)	$m^2\ kg^{-2}$
LWR	leaf weight ratio (leaf weight ratio)	$kg\ m^{-2}$
SLA	specific leaf area (leaf area/leaf weight)	$m^2\ kg^{-1}$
PPFD	photosynthetic photon flux density	$mol\ m^{-2}\ s^{-1}$

1. INTRODUCTION

Forage crops are of considerable importance to the economy of Alberta since approximately 38% of farm income in Alberta is derived from ruminant livestock. Forages provide 60 to 80% of the feed for ruminant livestock and 24% of the improved farmland in Alberta is used for hay and pasture production (Anonymous 1985). Poor seasonal yield distribution has long been a major limitation to the use of pastures for livestock. Grass production in most temperate regions declines as the season progresses and often over half of the total annual yield is obtained by early June (Jung et al. 1974). Livestock requirements however increase as the season progresses and producers must therefore resort to supplementary feeding, reduce the herd size, or suffer reduced animal gain. Therefore improvements in late season pasture yields could considerably increase the profitability of livestock enterprises.

The most widely grown forage grass species in Alberta for both hay and pasture is smooth bromegrass (*Bromus inermis* Leyss) but other species such as meadow bromegrass (*Bromus riparius* Rhem. and Schult.), orchard grass (*Dactylis glomerata* L.), meadow foxtail (*Alopecurus pratensis* L.) and tall fescue (*Festuca arundinacea* Schreb.) are also grown. Smooth bromegrass was first introduced into North America in the 1880's from Europe but probably originated in central Asia (Heath et al. 1978). This long lived grass has a deep root system and is heat and drought tolerant and is thus well adapted to the Canadian prairies. Its major limitation for use as a pasture grass is its elevated growing point which if removed by defoliation can result in a lag period before regrowth is initiated (Sheard and Winch 1966). A second weakness is its poor late season growth (Anonymous 1984). Meadow bromegrass, introduced to the USA from Turkey in 1948, is adapted to similar conditions as smooth bromegrass (Knowles and Folkins 1980). Its advantages over smooth bromegrass are that it has a lower growing point which enables it to recover rapidly after defoliation and it has good late season regrowth (Knowles and Folkins 1980). S9044 is an experimental F_2 hybrid from a cross between Carlton smooth bromegrass and Regar meadow bromegrass (Knowles and Armstrong 1984). Baron and Van Esbroeck (1986) found S9044 to yield equal to smooth bromegrass for hay production and intermediate between smooth and meadow bromegrass for pasture production. Tall fescue is grown extensively in the midwestern USA and eastern Canada but is not winter hardy in all areas of Alberta (Anonymous 1984). Orchard grass was introduced from Europe in the 1760's (Heath et al. 1973). It is adapted to the warm moist areas of Alberta and is a very productive species under irrigation It regrows rapidly following defoliation and hence is an excellent pasture grass. Its major limitation under western Canadian conditions is its variable winter hardiness (Anonymous 1984). Meadow foxtail, native to temperate Europe and Asia is adapted to cool moist conditions (Heath et al. 1978). It has very good early season growth but is intolerant of heat and drought. In Alberta it is predominantly grown on the Grey Luvisol and peat soils (Anonymous 1984).

Yields of all pasture grasses decline as the season progresses. The problem of poor late season production is however particularly severe in smooth bromegrass, which is currently the most extensively grown grass species in Alberta. Recent studies show that it produces less than 10% of its total annual yield in the final third of the growing season (Baron and Van Esbroeck 1986; Knowles and Sonmore 1985). During this same period some of the less commonly grown species such as meadow bromegrass and orchard grass can yield twice as much as smooth bromegrass (Knowles and Sonmore 1985).

Response to high temperatures and soil moisture deficits is frequently reported as the cause of summer dormancy (Baker and Jung 1968; Evans 1984; Jung et al. 197[illegible] Norris 1985). However, these factors are probably not the principal causes of the low late season yields of smooth bromegrass in central Alberta because high temperatures do not normally occur at the time of yield reduction, and because similar results are reported under irrigation (Knowles and Sonmore 1985). A major difference between spring and late summer growing conditions in central Alberta is that temperature declines and photoperiod is reduced from a peak of 18 h in late June to 14 h by mid September. Recent studies indicate that daylength and temperature can exert considerable influence on the vegetative growth of certain species or ecotypes. In high latitude ecotypes of certain species short daylengths and low temperatures can result in an early cessation of growth and the subsequent development of winter hardiness (Cooper 1964; Eagles 1971; Kelebesadal 1971; Robson and Jewis 1968). In addition long photoperiods can increase growth in a number of species, but more so in high latitude ecotypes, and may explain why dry matter production of northern ecotypes is skewed to the early part of the season (Hay 1985; Hay and Pederson 1986).

The extent and the manner in which temperature and photoperiod influence the late season growth of commonly grown species in Alberta has not been determined. The objectives of this study were to examine the pattern of late season regrowth of several temperate grasses in the field, and to investigate the effects of temperature and photoperiod on regrowth under controlled conditions, in an attempt to determine if yield differences between species were related to these factors.

2. LITERATURE REVIEW

2.1 Introduction

In order to improve forage yields an understanding of the physiological characteristics related to herbage yield is necessary so that limiting factors can be identified and overcome. Forage production involves the conversion of light energy, CO_2, water and soil minerals into plant dry matter. The efficient conversion of light energy into harvestable dry matter in the absence of moisture and nutrient limitations depends on the amount of light energy available, the pattern of light interception, photosynthetic rate and dry matter partitioning (Cooper and Wilson 1971). Techniques used to study the physiological characteristics related to yield and the relative importance of these characteristics include yield component analysis and growth analysis. Studies on yield components may be used to determine the relationship of traits such as tiller weight, tiller size and tiller morphology to yield. Growth analysis can be used to determine the relative importance of leaf area, net photosynthetic rate and partitioning in explaining variation in productivity between species and genotypes.

In frequently clipped pastures, where less than 100% of the incident light energy is intercepted, the size of the total leaf surface available for light interception limits the crop growth rate (Nelson 1982; Rhodes 1973). Hence, the faster the total leaf surface area is increased the faster will be the growth rate of the crop (Edwards 1967). Pearson (1984) considered the generation of leaf area to be the most important aspect of crop development. The growth of forage crops in temperate regions varies considerably throughout the year with growth rates highest in spring and then declining as the season progresses. Kemp (1985) related high spring growth rates to daylength induced flowering which resulted in higher leaf area expansion rates and greater light penetration into the canopy. Subsequent growth in summer and fall is predominantly vegetative and has lower growth rates (Leafe et al. 1974). Differing seasonal patterns of growth between species have been attributed to a response to temperature and daylength mediated through a range of yield components and growth processes (Eagles and Ostgard 1971; Ryle 1966a).

2.2 Leaf growth

In forages leaves not only intercept the light energy necessary for photosynthesis but are also the harvestable product and thus a knowledge of how leaf area is generated is of paramount importance in understanding the limitations to pasture productivity. Langer (1972) has extensively reviewed leaf area development in grasses. In grasses leaves are initiated by the apical meristem located at the shoot apex. The apical meristem, or growing point, on vegetative grasses is normally located close to the soil surface, below defoliation height, allowing for rapid regrowth following defoliation. Leaf primordia are produced alternately along opposite sides of the apical dome and at any one time a number of leaf primordia exist on the growing point, each at various stages of development. Young leaf primordia are initially meristimatic, but are soon divided by parenchyma cells into an upper and lower portion, forming the leaf lamina and sheath, respectively. Extension of the intercalary meristem (meristem at the base of the new leaf) causes the leaf to push up inside the sheath of the previous leaf and eventually out into the light. Lamina extension of the leaf is complete when the ligule is differentiated but the sheath may continue to elongate until the ligule is exposed. At this point no further leaf growth occurs and the next younger leaf above it on the apical dome begins to rapidly elongate (Edwards 1967).

The number of leaves elongating at any one time is relatively constant for a particular species and environment (Langer 1972), and ranges from 1 up to 3 for most temperate grasses (Jones 1985). Often, however, only a single leaf elongates and when it stops the next leaf will begin to elongate (Nelson 1978). Rates of primordia initiation and rates of leaf appearance are usually similar for C_3 grasses although exceptions are possible (Jones 1985). The rates of leaf appearance in vegetative grasses are fairly constant for a constant environment and therefore the rate of leaf appearance can be determined by regressing leaf number with time (Silsbury 1970). The reciprocal of the rate of appearance or initiation is the interval between successive leaves and is termed the phyllochron interval. Leaf extension rate in monocotyledonous plants is nearly linear over time (Edwards 1967) and thus can be measured by regressing leaf length with time (Wilhelm and Nelson 1978).

Final leaf size is the product of the rate of expansion and the duration of expansion and can be influenced by temperature (Cooper and Tainton 1968) and daylength (Stuckey 1942). The total leaf area of a tiller depends on the number of existing leaves (determined by the leaf appearance rate) and leaf size (Cooper and Edwards 1961). An inverse relationship was found between final leaf size and rate of leaf appearance in ryegrass, such that plants had either a slow production of large leaves or a rapid rate of production of small leaves (Cooper and Edwards 1961). Nelson (1978) also observed this phenomenon in tall fescue and found that when leaves were long the rate of leaf appearance declined. This phenomenon can be explained by the fact that at any one time the number of leaves elongating is constant (Edwards 1967). To attain long leaves requires a longer duration of extension and subsequently a longer period of time before the next leaf begins to elongate. This inverse relationship between leaf size and rate of leaf appearance led to the suggestion that selection for an increase in total leaf area increase may be more important than selection for leaf size (Cooper and Edwards 1961; Edwards 1967). Yields of tall fescue were found to be positively correlated to both leaf area expansion rate (Robson and Jewis 1968) and to leaf extension rate (Horst et al. 1978). Although both an increase in width and length contribute to the final size of a leaf, the increase in length is considerably more important (Nelson et al. 1977). The higher yields achieved by genotypes with rapid leaf extension rates may be due to their ability to rapidly achieve a large light interception surface and high canopy photosynthetic rates (Zarrough and Nelson 1980). The leaf area expansion rates of individual tillers were found to be highly correlated with post flowering yields in tall fescue (Nelson et al. 1977), and an important determinant of winter productivity in Phalaris tuberosa L. (Hoveland et al. 1974). Robson and Jewis (1968) found yield differences in tall fescue cultivars to be due to differing rates of leaf area expansion.

Wilhelm and Nelson (1978) concluded that leaf area expansion rates were a more important determinant of yield than individual leaf photosynthetic rates. There is evidence that in vegetative pasture grasses the photosynthetic rate is limited by the rate at which the sinks (meristematic regions) can accept assimilate. In addition to a high photosynthetic rate, plants should have an active sink to utilize photosynthate (Nelson et al. 1982). Wong and Randel (1985) suggested that the higher photosynthetic rates in polyploid genotypes of tall fescue were due to a higher sink activity. A high leaf area expansion rate represents a strong sink and the positive correlations observed between yields of tall fescue and leaf area expansion rates may be due to the fact that a high leaf area expansion rate provides the active sink necessary for the utilization of the photosynthate (Nelson et al. 1982).

2.3 Pattern of light interception

As more and more leaves are produced and expanded, the leaf area of the canopy increases, causing more and more of the incident light to be intercepted. Brougham (1956) found that growth rate increases until 95% of the incident light is intercepted. After this point crop growth slows because of shading and leaf senescence, and a ceiling yield is attained when increases in leaf growth on the canopy surface are matched with leaf senescence at the base of the canopy (Robson 1973).

Leaf area index (LAI) is a measure of the leaf area of a sward per unit of ground area. The LAI at which 90-95% of the incident light is intercepted is termed the critical LAI (Brougham 1956). Once the critical LAI is attained, leaf area is no longer the major limitation to crop growth, but rather the amount of leaf area that can be illuminated above the light compensation point (Beadle et al. 1985). Two distinct responses of crop growth rate to LAI once critical LAI (95% light interception) is attained have been reported. Brougham (1956) observed that CGR attained its maximum at critical LAI and then remained stable over a wide range of LAI. Watson (1958) reported an increase in crop growth rate as LAI increased up to a certain LAI and then a decline, and termed the LAI at maximum CGR "optimum LAI".

At critical LAI lowermost leaves fall below the light compensation point. If leaf production at the top of the canopy is greater than leaf death at the base of the canopy than a stable crop growth rate can be maintained (Robson 1973). However, when critical LAI is attained in canopies where new leaves are produced at the base of a canopy, as in vegetative swards of orchard grass (Pearce et al. 1965), the situation is different. New leaves import photosynthate from fully expanded leaves, and when they are not able to attain rates of photosynthesis in excess of respiration the new leaves remain consumers and the crop growth rate of the sward rapidly declines (Gardner et al. 1985). In such situations, or if for other reasons respiration losses of the canopy exceed the photosynthetic gains, crop growth rate declines after an optimum LAI is attained (Gardner et al. 1985).

The higher the critical leaf areaattained the greater will be the sward's photosynthetic potential, and hence the sward's growth potential depends on the ability of light to penetrate the canopy (Rhodes 1973). Light penetration into a canopy follows Beer's law with ln I/Io= -kL where Ln is the natural log, I = light interception below a LAI of L , Io = incident light interception above the canopy, and k = the extinction coefficient(Brown and Blaser 1968). This implies a logarithmic decline in light intensity as one moves down the canopy with k a measure of the rate of decline. If light penetrates the canopy poorly a small leaf area will intercept all the incident light giving a low critical LAI and k will be high. When light penetrates deeply into the canopy, a large leaf area will be illuminated above the compensation point, k will be low, and a high critical LAI can be attained. Leaf size, arrangement and internodal elongation are factors which can affect light attenuation into canopies and hence influence the potential growth of the crop (Rhodes 1973). The ideal canopy structure however is not the same for frequently versus infrequently clipped stands. Under frequently clipped systems where light interception is limiting genotypes with prostrate tillers and high basal leaf areas gave the highest yields (Rhodes 1973; Zarrough and Nelson 1980). With infrequently clipped stands (where critical LAI is attained) genotypes with elevated canopies and long, erect, rigid leaves allow greater light penetration. This results in more leaf area being illuminated and hence a higher critical LAI which contributes to a potentially higher canopy photosynthetic rate and crop growth rate (Rhodes 1973).

Selection for canopy characteristics which improved light interception and produced a higher critical LAI has in a number of cases resulted in increased yields (Wilson et al. 1980). Leaf arrangement is however considered to be relatively unimportant when LAI is below 3 (Duncan 1971). For frequently clipped pastures, factors such as leaf elongation rate, leaf area expansion rate, and tiller density have been suggested as selection criteria (Nelson et al. 1977). Leaf elongation rate or leaf area expansion rate influence the leaf area of a tiller, and combined with tiller density determines the LAI. Although size of the total photosynthesizing surface (LAI) rather than the photosynthetic rate of individual leaves is the major determinant of growth rate of a sward, in comparisons between species the growth rate may not be directly related to LAI (Rhodes 1973). In such situations features such as a higher specific leaf weight or chlorophyll content per unit of leaf area, which influence the photosynthetic rate of the leaves, may also have a large influence on growth rates (Hunt and Cooper 1967).

Vegetative yield of forage grasses has been reported as a function of tiller weight and tiller density (Nelson et al. 1977). Several researchers have investigated the relative importance of tiller weight and tiller density to herbage yield in tall fescue. At low levels of competition or early in regrowth tiller density was found to be of greater importance to yield than tiller weight (Sleper et al. 1977), while at later stages of regrowth, when tiller number stabilizes, tiller weight was concluded to be the most important yield determinant (Zarrough et al. 1983).

2.4 Response to defoliation

The ability of a sward to rapidly regenerate leaf area and continue growth following defoliation depends on a combination of factors, including environmental conditions, species, genotype, height of defoliation, height of the growing point, residual leaf area, and root carbohydrate reserves (Heathe et al. 1973). Regrowth following defoliation is initiated utilizing photosynthates produced in the residual leaf area and from carbohydrate reserves. Carbohydrate reserves are however considered to be important for regrowth for only a short time (possibly only several days) with subsequent growth dependent on photosynthate produced from existing leaf area (Davidson and Milthorpe 1966; Richards and Caldwell 1985). Ward and Blazer (1961) found that a large residual leaf area reduced the dependence on reserves. The larger the leaf area that remains after clipping the greater will be the light interception, photosynthesis and regrowth potential (Brown and Blaser 1968). Low growing species with many basal tillers are therefore less dependent on reserves than the more erect types with few leaves below the cutting height (Smith et al. 1985). Rhodes (1973) reports that prostrate tillers with a dense tillering habit are ideal for frequent clipping as this allows for a large residual leaf area and ensures rapid regrowth. A delay of several weeks in regrowth of smooth bromegrass was reported when elevated growing points were removed during internodal elongation (Sheard and Winch 1966).

2.5 Response to temperature

Temperature and photoperiod can independently affect the growth of pasture grasses or may act together to trigger the cessation of growth of some species in autumn

(Kelebesadal 1971). The optimum temperature for dry matter increase for C_3 grasses ranges from 20-25°C, with growth ceasing above 30-35°C and [illegible] $^{\circ}$C (Cooper and Tainton 1968). Temperature exerts a greater influence on react[illegible] involving the products of photosynthesis (maintenance respiration and growth) than on photosynthesis itself (Kemp 1985). The optimum temperature for dry matter increase shifts downward as the plant ages since the requirement for maintenance respiration (which rises considerably with temperature) increases with age (Kemp 1985).

The 20-25°C optimum for dry matter increase is constant for a wide variety of species (Cooper 1968), however there is considerable variation between and within species to both high (Baker and Jung 1968) and low temperatures (Eagles 1967; Nelson 1978; Robson and Jewis 1968). An inverse relationship between the ability to grow at low temperatures and winter survival has been observed (Cooper 1964; Robson and Jewis 1968), and thus cool weather dormancy has been regarded as an important aspect of winter hardiness. Response to low temperatures has been related to latitude of origin with northern adapted strains of the same species showing dormancy at low temperatures while more southern strains are able to maintain growth (Cooper 1964; Eagles 1967; Robson and Jewis 1968). Wilson et al. (1980) produced hybrids between European and Mediterranean ecotypes of orchard grass that were intermediate to the parents in low temperature growth and winter hardiness.

For most C_3 grasses photosynthesis has an optimum in the 18-20°C range, while leaf extension rates peak in the 20-25°C range (Kemp 1985). This combined with the fact that extension growth rates decline more rapidly than extension growth rates with declining temperature, results in an accumulation of carbohydrates in leaf, stem and root tissue under cool temperatures. (Eagles 1967; Levitt 1972). At high temperatures nearly all the products of photosynthesis are utilized in growth or respiration and the accumulation of sugars is minimal (Levitt 1972). Eagles (1967) found that winter dormant orchard grass stored carbohydrate while a non-dormant type utilized carbohydrate for new leaf growth. Brown and Blazer (1970) and Peacock (1975) concluded that carbohydrate accumulation occurs whenever growth is restricted. In general carbohydrates accumulate whenever growth is restricted more than photosynthesis, which occurs under cool temperatures or moisture stress (Brown and Blazer 1970; Pollock and Jones 1979).

Since temperature optima differ for various aspects of growth and morphology, temperature can exert considerable influence on sward characteristics. Optimum temperatures for root growth, tillering, and specific leaf weight are lower (in the 10-20°C range) than optima for shoot growth and leaf area (in the 20-30°C range) (Langer 1972). Therefore under cool conditions swards would have low leaf areas, low shoot:root ratios, abundant tillering, high specific leaf weights and high carbohydrate levels. High temperatures conversely would result in high shoot:root ratios, high leaf areas, low specific leaf weights, low tillering, and low carbohydrate levels.

2.6 Response to photoperiod

Vince-Prue (1982) has described the physiological basis of the photoperiod response in plants. When exposed to light plants produce a chromophoric protein called phytochrome in the young leaves. Phytochrome exists in two isomeric forms Pr and Pfr. During the day Pr is converted to Pfr (the active form) by the action of red light. In the dark no new Pfr is synthesized and the existing Pfr is slowly broken down to Pr, the inactive form, or destroyed. The conversion of Pr to Pfr is very rapid while reversion of Pfr to Pr is slow so that during the night Pr slowly accumulates. Studies show that it is the duration of the night (period with low Pfr levels) that determines the plants physiological response. Short light breaks during the night rapidly convert Pr to Pfr, reduce the time that phytochrome is in the Pr form, and hence are able to simulate long days. Very low levels of light are able to convert Pr to Pfr. Therefore, extending daylength with low levels of light allows the effects of photoperiod to be assessed without confounding the effects of a longer period of active photosynthesis.

Response to light breaks or daylength extension depends to some extent on the light spectrum, with incandescent light better than fluorescent in producing photoperiodic effects (Ryle 1966b).

Most temperate grasses are long-day plants. Within this group there are species with an obligate requirement (need a critical daylength to flower), and with a quantitative requirement for flowering (flowering is hastened under long days). In addition to the well documented effects of photoperiod on floral development, there may also be an effect on vegetative growth and development (Vince-Prue 1975). These responses are often confined to specific ecotypes (Hay 1985) and may be influenced by temperature (Heide et al. 1985a, 1985b). Response to photoperiod is usually determined by comparing growth at a long photoperiod with growth at a short photoperiod and may therefore be a combination of short day dormancy and long day stimulation. Greatest responses have been observed in high latitude ecotypes which experience large daylength changes (Hay and Pederson 1986).

Typical effects of long photoperiods include increases in; dry matter production, leaf area, stem height, and shoot:root ratios, leaf length and width,. and reduced tillering (Cooper and Tainton 1968; Eagles 1971; Eagles and Ostgard 1971; Heide et al. 1985a, 1985b; Ryle 1966a). Heide et al. (1985a) reported the greatest yield enhancement at intermediate temperatures for smooth bromegrass. Eagles (1971) reported ecotype differences to be more evident at 5 than at 15 or 25^{o}C in orchard grass. The physiological basis for higher dry matter production under extended daylength appears to be a greater partitioning into leaf area. Eagles (1971) found that higher yields at extended photoperiods in orchard grass were associated with higher relative growth rates. These were associated with higher leaf area ratios that resulted from higher shoot:root ratios, and specific leaf areas. Heide et al. (1985b) also concluded photoperiodic yield enhancement to result from a greater partitioning into leaf area, but found that the increase in leaf area was associated with a decrease in leaf photosynthetic rate. The increase in leaf area, however more than compensated for the decrease in leaf photosynthetic rates and canopy photosynthesis was increased (Heide et al. 1985b).

2.7 Growth analysis

Whereas direct measurements of yield or traits associated with yield give information about a crop at a given point in time, growth analysis gives information over an extended period and thus has become a useful tool in identifying yield influencing processes. Two distinct types of growth analysis can be carried out and have been described in detail by Hunt(1982). In the classical type, measurements of dry weight and leaf area are taken at intervals and the mean growth rates for the period between the harvests calculated. In the more recent functional approach data are collected at frequent intervals and mathematical functions are fitted to the data. Instantaneous values are then derived from the equations that were fitted to the observational data. The form of the mathematical function is of no physiological significance as long as the resulting curve describes the data in a convenient way. Inferences are made from the fitted curve, not the original data and therefore it is essential that the functions adequately describe the data.

Often a polynomial in the form of $Y= b_0 +b_1X + b_2X^2 + ... + b_nX^n$ is used with Y the ln transformed plant weight or leaf area and X as time. The higher the order of polynomial used the more accurately the function will represent the data. Since it is unlikely that any curve will provide a complete biologically satisfying picture of the operation of a complex system over a period of time it is not necessary to obtain a perfect fit (Milthorpe and Moorby 1979). The object of growth analysis is to exact general trends and ignore short term fluctuations (Milthorpe and Moorby 1979). Hunt (1979) suggests that the experimenter select the simplest model possible that is consistent with the degree of smoothing required and his own mechanistic insight into the process that is being modelled.

Growth parameters determined in growth analysis include crop growth rate (CGR), relative growth rate (RGR) and net assimilation rate (NAR). The CGR is defined as the gain in weight of a community of plants on a unit of land in a unit of time. It is the slope of the yield versus time plot or the first derivative of the yield function, i.e. CGR = dW/dT. Biomass production in most crops (i.e. CGR) is generally a linear function of light interception until canopy closure (Beadle et al. 1985). The maximum observed short term CGR rates in C_3 species are 34-39 g m^{-2} d^{-1} (Gardner et al. 1985). In closed ryegrass swards in the Netherlands and England a maximum CGR of approximately 20 g m^{-2} d^{-1} occurs in May and June, but as the season progresses CGR declines to less than 10 g m^{-2} d^{-1} by early September (Alberda 1968, Leafe et al. 1974). The maximum spring CGR for smooth bromegrass in Nebraska was reported to be 18.8 g m^{-2} d^{-1} (Engel et al. 1987). Mid-season growth rates for irrigated alfalfa in Washington state were similar, ranging from 10.8 to 20.7 g m^{-2} d^{-1} (Evans and Peaden 1984).

The RGR is the growth rate per existing dry matter and can be determined as the slope of the plot of the ln W against time or as 1/W x dW/dT (Hunt 1982). It is essentially the same as the "interest" rate since it is a measure of yield gained per existing yield. As plants grow, the proportion of structural material increases and the proportion of material contributing to further yield declines, and therefore RGR declines with age. The decline in RGR with age may however be affected by an improvement in the environment (Milthorpe and Moorby 1979). Typical RGR values for pasture grasses are around 0.1 g g^{-1} d^{-1} (MacColl and Cooper 1966).

NAR is the increase in yield per unit of leaf area and is calculated as 1/leaf area x dW/dT. Since less than 5% of the dry matter in plants is in the form of minerals NAR may be viewed as a direct measurement of net photosynthetic rate (photosynthesis less respiration) and is a measure of assimilatory efficiency of the canopy (Beadle et al. 1985). Although in general NAR is more stable than RGR it also declines as plants mature (Hunt 1982). This occurs because leaves age and because shading reduces light levels and photosynthetic efficiencies of the leaves. This downward drift with ontogeny may be considerably altered by favorable or unfavorable environments (Hunt 1979). At low levels of light below 500 μmol m^{-2} s^{-1} the photosynthetic rate is limited by light energy only and the leaf can fix about 12-15% of the incoming light energy. At higher light intensities other factors become limiting and less than 2-3% of the light energy is fixed (Cooper 1970).

Another parameter that may be determined in growth analysis is leaf area ratio (LAR) which is the ratio of leaf area to plant weight and is an expression of the ratio of photosynthesizing tissue to total respiring tissue (Gardner et al. 1985). The LAR of a plant or community may be subdivided into its two components: specific leaf area (SLA) and leaf weight ratio (LWR). The SLA is the area per weight of leaves or a measure of the leaf density. The density of leaves n [illegible] expressed as the specific leaf weight, defined as the weight per area of leaf. [illegible] ight ratio (LWR) is the ratio of leaf weight to total plant weight and is a measure of the proportion of leaves in a plant.

A number of interrelationships between growth analysis parameters exist. The CGR of a canopy can be expressed as the product of the photosynthetic efficiency of the leaf area and the total leaf area or CGR= NAR x LAI. Variation in CGR can therefore be attributed to variations in NAR or LAI (Lambers 1987). CGR can also be expressed as the product of RGR and yield (i.e. CGR= RGR x Biomass), with differences in CGR then attributable to variation in RGR or accumulated yield (Lambers 1987).

The RGR can be expressed as the product of NAR and LAR. In other words, RGR is the product of the photosynthetic rate per leaf area and the fraction of a plant that is leaf area. Differences in RGR between species have been attributed to differences in the physiological component (NAR) or to the morphological component (LAR) (Lambers 1987). The LAR is the product of SLA and LWR and thus variation in LAR may be due to variation in investment in leaf dry matter (LWR) or to investment in leaf area (SLA) (Lambers 1987).

Hunt (1979) points out several considerations that are needed to assure proper interpretation of functionally derived growth variables. If fitted errors are systematic then distortions from the truth are introduced and inferences made from the fitted function may not be valid. A curve with the highest r^2 value may therefore not necessarily be the best. The form of the derived functions (i.e. CGR, RGR) will depend on the nature of the fitted function. For example a 1st order polynomial will always result in a linear CGR and a constant RGR while a 2nd order polynomial will produce a CGR that peaks and a linear RGR.

To understand limitations to late season pasture productivity the influence of environmental factors (temperature and photoperiod) on the factors influencing growth should be examined. Numerous studies of this kind have been carried out in Europe (Eagles and Ostgard 1971; Ryle 1966a). Few have been carried out that are directly applicable to the western Canadian situation.

3. LATE SEASON REGROWTH OF FOUR GRASSES: GROWTH ANALYSIS AND YIELD COMPONENTS

3.1 INTRODUCTION

A knowledge of the growth processes and yield components of pasture grasses may indicate physiological traits limiting to late season regrowth of pastures. Under favorable conditions dry matter production is limited by the efficiency with which the crop uses light to fix carbon, which depends on the proportion of incoming light intercepted by the canopy, the way it is distributed over the leaf surface and the photosynthetic potential of the leaves (Robson 1980). The importance of leaf area to pasture productivity has been reviewed extensively by Brown and Blaser (1968) and Rhodes (1973). After defoliation, when less than all the available light is intercepted crop growth rate is limited by the amount of leaf area available to intercept light As new leaf area is produced light interception increases and the growth rate of the sward increases. Growth rates begin to decline when the leaf area intercepts 90-95 % incoming light (critical LAI). At this point the lowermost leaves fall below the light compensation point and begin to lose dry matter. Yields may continue to increase beyond this point if new leaf production is greater than leaf death, but when leaf loss equals leaf gain the ceiling yield is attained (Robson 1973).

The typical pattern of dry matter accumulation for pasture grasses following defoliation has been described by Alberda and Simba (1968) and Leafe et al. (1974). After defoliation, growth rates are low but soon increase exponentially The period of exponential growth is followed by a period of nearly constant growth rate. This period of constant growth can last 6-7 weeks in spring but declines to 3-4 weeks by August. This is followed by a rapid decline in growth rate to zero and a resultant ceiling yield. The maximum growth rate for perennial ryegrass (<u>Lolium perenne</u> L.) in Europe declines as the season progresses from approximately 20 g m^{-2} d^{-1} in spring to about 10 g m^{-2} d^{-1} by September (Leafe et al. 1974). These rates for any short interval throughout the season were reported to be practically independent of soil type or year (Alberda and

Simba 1968). Lower growth rates in autumn than in spring have been attributed to the lower leaf extension rates of post flowering vegetative swards compared to that of floral stands (Parsons and Robson 1980b), and to the fact that reduced stem elongation in vegetative swards results in new leaves developing in low light and hence with low photosynthetic capacities (Parsons and Robson 1980b; Woledge and Leafe 1976; Woledge 1978).

As the season progresses in central Alberta (Lat 52 °N) daylength drops from 18 h in late June to 14 h by early September and temperatures decline. Reduced dry matter production has been observed in northern ecotypes of certain species when exposed to cool temperatures and short daylengths (Cooper 1964; Eagles 1971, Eagles and Ostgard 1971; Robson 1967). This low late season productivity has been associated with improved winter hardiness (Cooper 1964; Robson and Jewis 1968). Kelebesadal and Helm (1986) reported that in Alaska northern ecotypes of timothy (Phleum pratense) that went dormant in late season, had higher levels of root reserves and greater winter survival than mid-latitude ecotypes. The fact that in Western Canada meadow bromegrass and orchard grass can yield approximat ible that of smooth bromegrass in late season (Baron and Van Esbroeck 1986; Knowles and Sonmore 1985) indicates a differing response among commonly grown pasture grasses to the environmental conditions of late summer.

A number of possible physiological constraints to vegetative growth of pasture grasses have been previously identified. Nelson et al. (1977) described yield as a function of tiller density and weight per tiller. They concluded that following defoliation tiller density was initially the more important yield determinant but when tiller density stabilized yield per tiller was more important. The photosynthetic efficiency of the canopy and critical LAI attained is influenced by the leaf arrangement and light attenuation properties of the canopy (Rhodes 1973). Internodal elongation, will affect the light interception of a sward (Rhodes 1973), and can influence the photosynthetic potential of the leaves and critical LAI (Parsons and Robson 1980b). Reduced internodal elongation under short days is a common phenomena in grasses (Stuckey 1942, Heide et al. 1985a). Waddington and Storgaard (1971) reported internodal elongation in smooth bromegrass at Winnipeg to be limited after August 15 when daylength falls below 15.5 h.

The relationships between stem elongation and light interception, critical LAI and crop growth rates have not been determined for late season growth of commonly grown pasture grasses in central Alberta. It is therefore not known if late season dry matter production is limited by a low rate of leaf area development and light interception or if attainment of critical LAI limits yields. The objectives of this field study were to (1) determine the pattern of late season regrowth for several common pasture grasses, (2) to identify limitations to yield in these species, and (3) to identify the traits associated with differences in yield among species.

3.2 MATERIALS AND METHODS

3.2.1 Experimental design

Plots of smooth bromegrass, (Bromus inermis Leyss.) cv. Carlton, meadow bromegrass, (Bromus riparius Rhem and Schult.) cv. Regar, an interspecific cross between smooth and meadow bromegrass (S9044) (Knowles and Armstrong 1984) and meadow foxtail (Alopecurus pratensis L.), " common" were seeded in 1983 at Lacombe, Alberta on Ponoka silt loam. The experimental design was a split plot with four replicates. Species formed the main plots, each consisting of 40 rows, 0.3 m apart and 6 m long, and harvest dates the subplots. Prior to the experimental year plots were fertilized annually with 150 kg ha^{-1} N as ammonium nitrate and P_2O_5 and K_2O according to soil test recommendations. Plots were clipped in mid June, late July and late September of each year preceding the experiment which was initiated after the late July clipping in 1985. Each replicate was then divided in half, with one half used in

1985 and the other half in 1986. In each experimental year, seven weekly harvests were made starting on July 23 and 25 in 1985 and 1986, respectively, and continuing until September 12.

3.2.2 Environmental data

Data for daily soil moisture tension (15 cm depth), air temperatures and incident photosynthetlcly active photon flux density (PPFD) for the duration of the study were obtained from an automated meteorological station located 0.5 km from the plots (Devine and Vanden Born 1988).

3.2.3 Dry matter yields

The center two rows of the plots, with an area of 2.7 x 0.6 m, were harvested with a flail type mower to a height of 7.5 cm. Harvested material was dried at 65°C for three days in a forced air dryer and weighed. When fresh weight yields were high, fresh weight per plot was determined and dry matter yield was calculated from the dry weight of a 500 g sub-sample.

3.2.4 Carbohydrate analysis

A 20 x 20 cm sod was dug from the harvested portion of the plots the day following the dry matter yield harvest. Soil was removed by washing and dead tissue was separated from live material. The root and stubble material was dried at 65°C for three days in a forced air drier. Both shoot and root plus stubble material were ground in a cyclone grinder (UD Corporation, Boulder , Colorado) with a 1 mm screen. Moisture content was determined by drying samples for 4 h at 100°C. Ash content was determined by heating for 4 h at 400°C. Soluble carbohydrates were determined from a 200 mg sub-sample extracted in 0.005 N H_2S0_4 as described by Smith et al. (1964). This acid concentration is reported to completely hydrolyse fructosans and sucrose sugars (Grotelueschen and Smith 1967). Sugar concentrations were determined by a phenol sulfuric colorimetric method using a fructose standard (Meloan and Pomeranz 1978). Carbohydrate content was expressed as a percent of organic matter.

3.2.5 Sward characteristics

On each harvest date, tillers were sampled from two 182 cm^{-2} areas that were randomly selected from the center two rows of each plot. Height to the tallest leaf tip and height to the collar of the uppermost leaf was measured on 10 randomly selected tillers and the means were calculated. Tillers were counted and clipped to a height of 7.5 cm. Leaf blades were separated from stems and their area determined with a LI 3100 portable area meter (Li-Cor Ltd., Lincoln, Nebraska). Leaf and stem fractions were dried at 65°C for 3 days in a forced air drier and then weighed. Average weight per tiller (TW), tiller density (TD), average leaf area per tiller (LAT), leaf area index (LAI), specific leaf area (SLA) and percent leaves on a dry weight basis were calculated.

Light interception was determined by taking a measurement above the canopy, and perpendicular to the rows at the 2 cm level in three random locations per plot. Percent light interception was determined from the ratio of light at the base of the canopy to the light at the top of the canopy. Light measurements in the 400-700 nm range were taken with a LI 188 quantum meter (Li-Cor Ltd., Lincoln, Nebraska) with a 1.0 m line quantum sensor (10 second integration time). Measurements were taken within one hour of solar noon on cloudless days. In 1985 only one measurement was taken while weekly measurements were taken in 1986. The extinction coefficient (k) was determined from the slope of the ln (I/Io) versus LAI plot, where ln = $\log_e$, Io = the PPFD reaching the base of the canopy and I= incident PPFD.

3.2.6 Growth analysis

Curve fitting was carried out using the forward stepwi [illegible] regression procedure in the Statistical Analysis System (SAS Institute Inc. 1982). [illegible] al functions (1st and 2nd order) were fitted by replicate to the untransforme [illegible] nsformed data for LAI, and dry matter yield. In almost all cases th [illegible] mial fitted to the ln transformed data gave the best fit (ie. highest r^2). [illegible] on equations of the form ln $y= a+bx+cx^2$ were used to fit all para [illegible] ys of regrowth). Predicted values for dry matter yield and LAI were determined for each replicate at each harvest date by solving the regression equations. In 1986 dry matter accumulation abruptly stopped after 36 days of regrowth and the fitted curves deviated considerably from the actual data. Data for the final two harvests of 1986 were therefore removed and a much better fit between actual and predicted values resulted. Plots of the actual values and the antilogs of the predicted values for dry matter yield and LAI were examined to verify the accuracy of the regression equations (Appendix 3.1 and 3.2). The following growth rates were calculated according to Hunt (1982):

Where $Fw(x)$= dry matter yield and $Fl(x) = LAI$,

Relative growth rate (RGR)=$F'w(x)$,

Crop growth rate (CGR) = $F'w(x). \exp[Fw(x)]$,

Net assimilation rate (NAR) =$F'w(x). \exp[Fw(x)-Fl(x)]$,

Leaf area ratio (LAR)= $\exp[Fl(x)-Fw(x)]$.

In addition, for each species a general regression equation (combining all replicates) also of the form $\ln y= a+bx+cx^2$ was fitted to dry matter yield, LAI, and light interception data. The general equations for CGR were solved to determine the CGR at dry matter yield intervals of 20 g m^{-2}. CGR was also determined at 0.25 LAI intervals and at 10% light interception intervals. A 3rd order polynomial was used to describe the relationship of CGR with LAI and percent light interception.

3.2.7 Statistical analysis

Data for each harvest date within years were analyzed in an analysis of variance using the species x replicate interaction as the error. Mean separations (Duncan's multiple range test) were carried out when treatment effects were significant at the $P< 0.05$ level.

3.3 RESULTS

3.3.1 Environmental data

Mean monthly temperatures were near the 79 year mean for both years of the test and declined from approximately 15°C in late July to approximately 8°C by mid September (Appendix 3.3) . Daily temperatures ranged from 0-30°C throughout July and August with no killing frost occurring until the first week of September 1986 (Appendix 3.4). In 1985 rainfall was below normal in July but was above normal for August (Appendix 3.3) and soil moisture tensions were below -0.3 M Pa for the first four weeks of regrowth (Appendix 3.5). Rainfall in 1986 was above normal in July and below normal in August (Appendix 3.3) and soil moisture tension dropped below -0.3 MPa in late August (Appendix 3.5). Daylength at Lacombe (52°N) declined from 17 h in late July to 14.5 h by early September (Appendix 3.6). Daily PPFD was approximately 40 mol m^{-2} d^{-1} in late July and declined to approximately 25 mol m^{-2} d^{-1} by mid - September (Appendix 3.7).

3.3.2 Dry matter yields

All species exhibited a sigmoidal regrowth pattern (Fig 3.1). Dry matter accumulation for meadow bromegrass and S9044 was more rapid than for smooth bromegrass in both years and exhibited higher dry matter yields at all harvest dates (Fig. 3.1). Dry matter yields of meadow foxtail were higher than those of smooth bromegrass at all times except in early 1985 when high soil moisture stress was evident (Fig. 3.1, Appendix 3.5). The maximum yield observed for meadow bromegrass, S9044, and meadow foxtail ranged from 200 to 250 g m^{-2} (Fig. 3.1). Smooth bromegrass had a lower maximum of 150-200 g m^{-2} (Fig. 3.1). Maximum yields were attained after approximately 49 and 35 days of regrowth in 1985 and 1986, respectively (Fig. 3.1). In both years meadow bromegrass appeared to reach its maximum yield slightly earlier than the other species (Fig. 3.1).

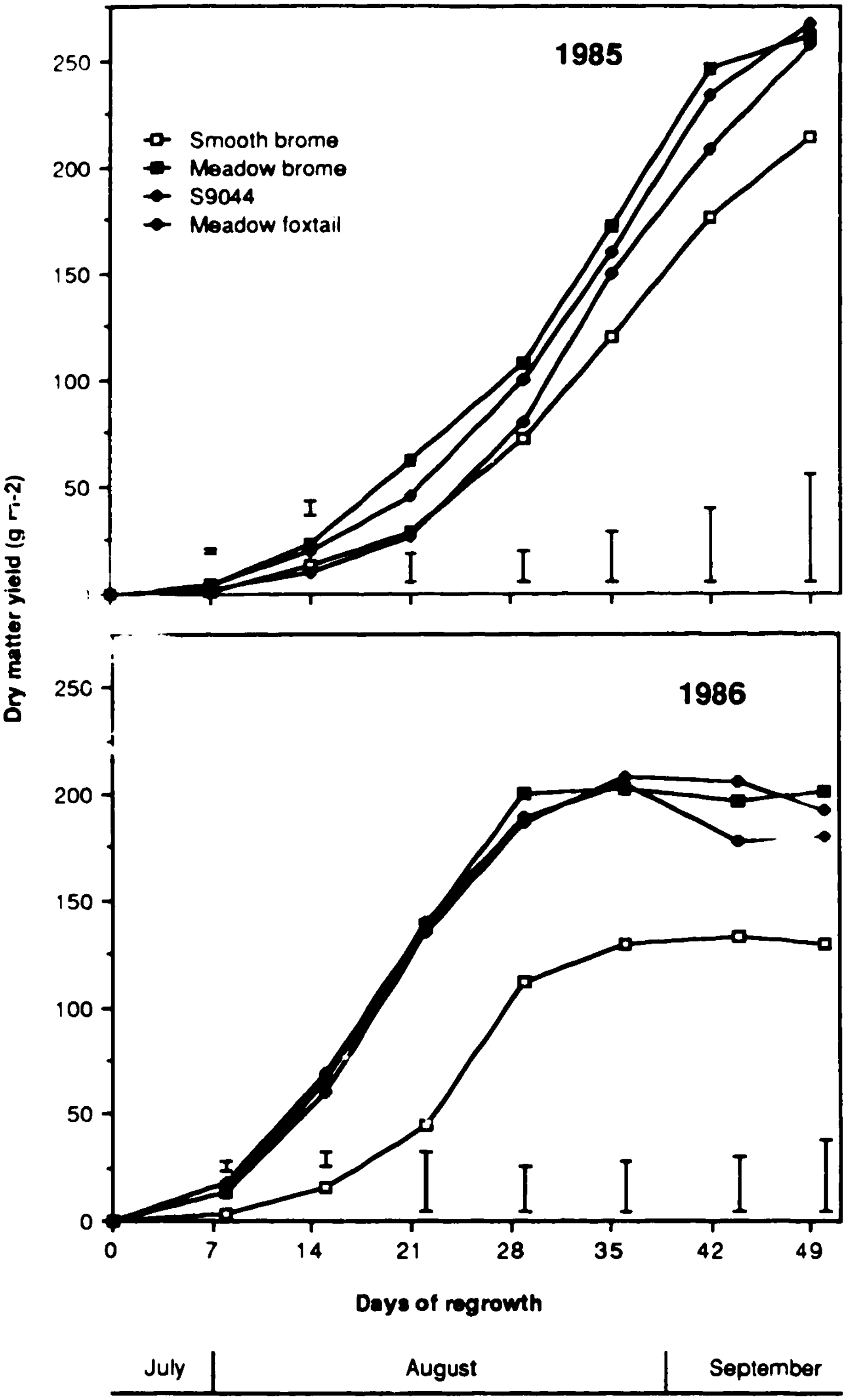

Fig. 3.1. Late season dry matter yields of four grasses during late season regrowth in 1985 and 1986 at Lacombe. Vertical bars show LSD at P=0.05.

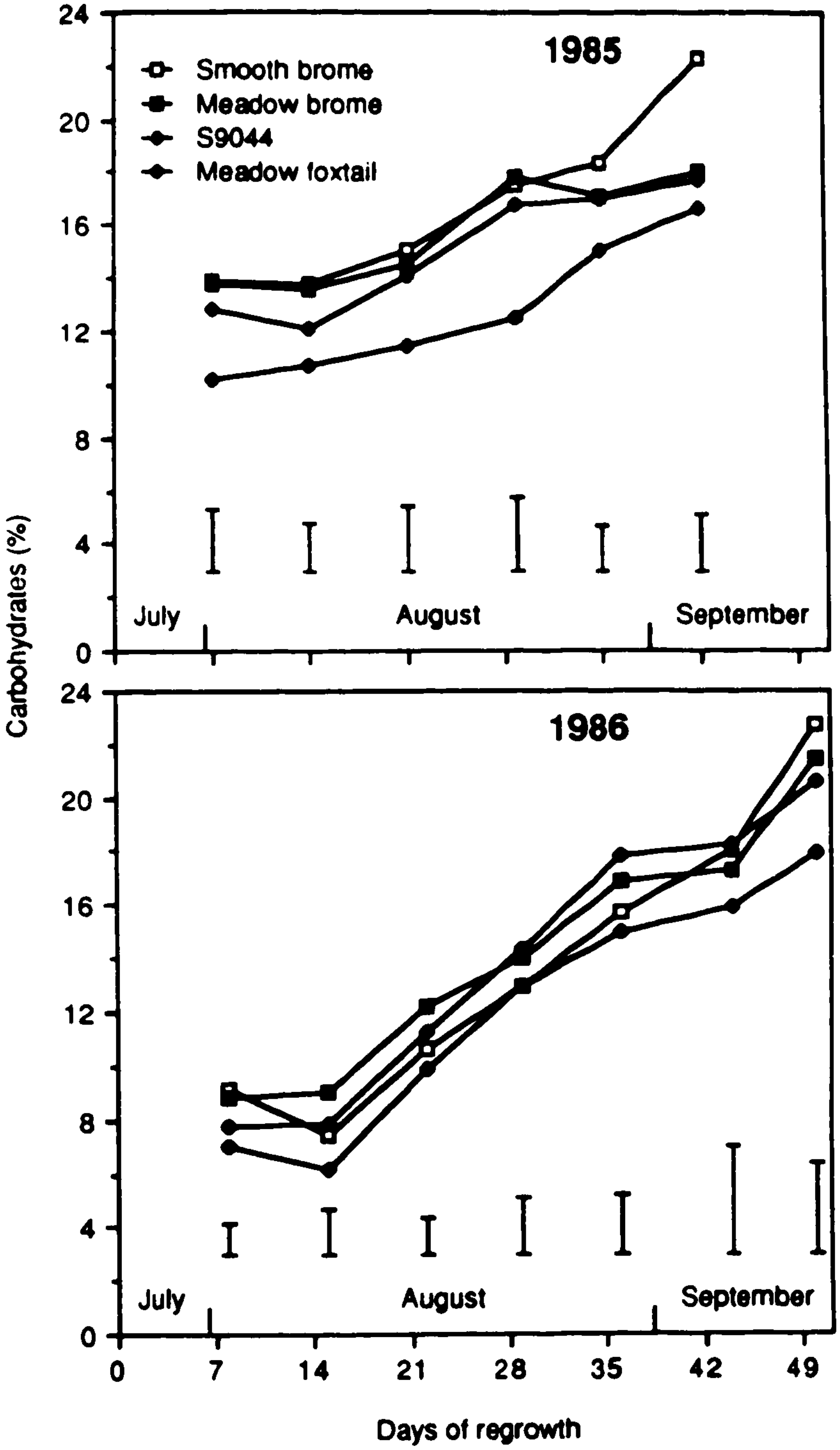

Fig. 3.2. Root carbohydrate content of four grasses during late season regrowth in 1985 and 1986 at Lacombe. Vertical bars show LSD at P=0.05.

3.3.3 Carbohydrates

Carbohydrate concentration in the roots and stubble increased with regrowth for all the grasses (Fig. 3.2). Root and stubble carbohydrate content was lower but not always significantly lower for meadow foxtail than for the other species (Fig. 3.2). Carbohydrate concentrations in the shoots were somewhat erratic but tended to increase late in the season (Fig. 3.3). Relatively high levels of shoot carbohydrates were evident in meadow foxtail early in the regrowth cycle of 1985 (Fig. 3.3).

3.3.4 Sward structure

TD was most often highest in meadow foxtail and lowest in smooth bromegrass and S9044, with meadow bromegrass intermediate (Tables 3.1a, 3.1b). In smooth bromegrass in 1986 an increase in TD of two to three-fold occurred between the day 8 and 15 harvests which indicated the removal of stem apices at the time of clipping. Although at almost all harvests the TD of S9044 and smooth bromegrass did not differ significantly ($P<0.05$), S9044 always had a numerically higher TD and did not exhibit the delay in tillering observed in smooth bromegrass in 1986 (Tables 3.1a, 3.1b). Meadow bromegrass had approximately double the TD of smooth bromegrass and S9044 (Tables 3.1a,3.1b). The TD of meadow foxtail appeared to be affected by soil moisture since a flush of tillering occurred in this species after 21 days in 1985 when soil moisture conditions improved (Table 3.1a and Appendix 3.5). The final TD of meadow foxtail was two- to three-fold greater than for smooth bromegrass and S9044.

In contrast to TD, which stabilized early in the regrowth cycle, TW continued to increase in all species until growth ceased late in the season (Tables 3.1a, 3.1b). Highest TW was observed in S9044 t all harvests in both years, while rankings among the other species were variable between harvests and years (Tables 3.1a, 3.1b). Meadow foxtail however usually had the lowest TW (Tables 3.1a, 3.1b).

Rankings among species for LAT were similar to their rankings for TW. In 1985 LAT was the highest for S9044 and smooth bromegrass and the lowest for meadow

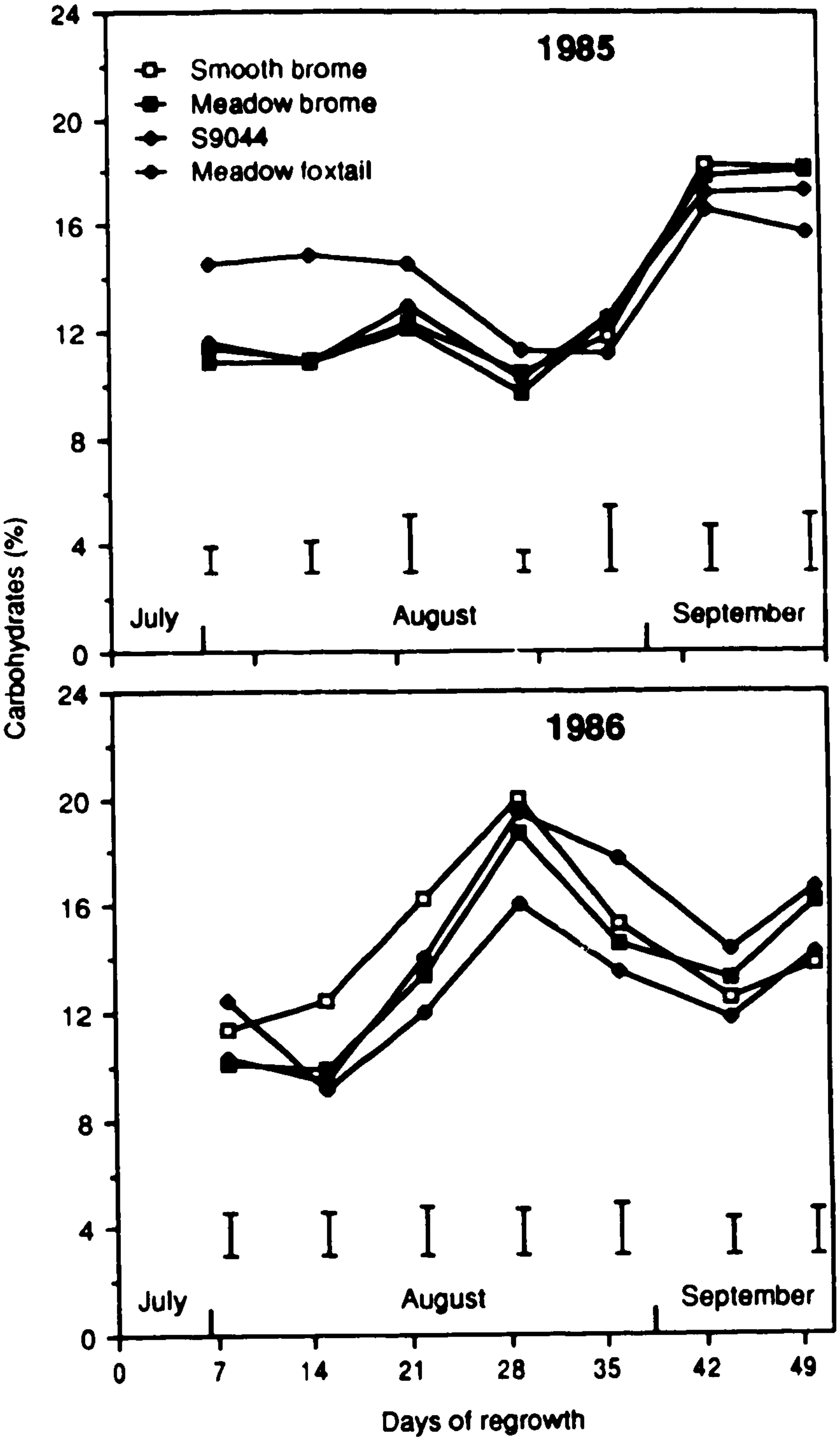

Figure 3.3. Shoot carbohydrate content of four grasses during late season regrowth in 1985 and 1986 at Lacombe. Vertical bars show LSD at P=0.05.

Table 3.1 a. Sward characteristics* of four grasses at seven intervals after clipping during 1985 at Lacombe.

Grass	TD	TW	LAT	HT	HC	%stem	SLA
				7 days			
Smooth bromegrass	6.1c**	16.5a	2.3a	14.2	-	-	15.3a
Meadow bromegrass	13.5b	12.3b	1.1b	14.2	-	-	9.2c
S9044	10.1bc	18.5a	2.5a	14.7	-	-	13.5b
Meadow foxtail	20.3a	7.5c	0.6c	14.7	-	-	9.5c
				14 days			
Smooth bromegrass	7.3b	33.0a	5.2a	18.3c	-	-	17.1a
Meadow bromegrass	18.2a	22.5b	2.6b	20.0ab	-	-	11.5c
S9044	09.6b	32.2a	4.7c	21.3a	-	-	14.8b
Meadow foxtail	18.5a	15.5b	1.5c	18.5bc	-	-	9.4d
				21 days			
Smooth bromegrass	8.3c	43.8b	8.0a	23.6b	-	-	19.0a
Meadow bromegrass	16.5ab	39.0b	4.8b	26.9a	-	-	12.6b
S9044	13.3b	53.8a	8.9a	28.0a	-	-	16.9a
Meadow foxtail	19.1a	21.0c	2.7c	22.2b	-	-	13.2b
				29 days			
Smooth bromegrass	9.9c	61.0b	12.2b	29.1b	10.2ab	9a	21.9a
Meadow bromegrass	17.9b	53.3b	8.3c	35.5a	9.1c	2b	15.7c
S9044	13.3c	81.8a	15.1a	35.7a	9.4bc	3b	19.0b
Meadow foxtail	31.0a	29.0c	4.7d	29.8b	10.4a	8a	17.4bc
				35 days			
Smooth bromegrass	11.4c	88.7ab	18.9a	32.7b	11.6ab	12a	23.7a
Meadow bromegrass	20.1b	74.7b	11.0b	41.7a	9.5b	4b	15.1c
S9044	13.6c	100.0a	18.5a	39.9a	10.8b	10ab	20.4b
Meadow foxtail	34.8a	44.3c	8.1b	38.9a	13.2a	11ab	19.5bc
				42 days			
Smooth bromegrass	12.5c	125.3ab	22.4a	38.4	13.6a	19a	21.6a
Meadow bromegrass	20.9b	90.5bc	12.9b	43.9	10.5b	7b	15.1c
S9044	13.6c	151.8a	26.6a	45.5	13.0a	16a	20.5b
Meadow foxtail	31.9a	69.0c	11.1b	43.7	12.4a	21a	19.5b
				49 days			
Smooth bromegrass	11.0c	134.3b	21.9b	39.6c	14.7a	20ab	20.2a
Meadow bromegrass	21.1b	100.0c	11.6c	47.5ab	11.7b	10b	12.7c
S9044	12.8c	188.5a	28.1a	51.5a	14.8a	21ab	18.3a
Meadow foxtail	32.0a	84.2c	10.3c	46.7b	16.2a	27a	15.7b

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* TD =tiller density (# dm $^{-2}$), TW = tiller weight (mg tiller^{-1}), LAT= leaf area per tiller (cm ^{2} tiller^{-1}), HT = height to tallest leaf tip (cm), HC = height to top collar (cm), %stem= (stem dry matter/total dry matter) x 100, SLA = specific leaf area (m^2 kg^{-1}).

** Means within columns and harvest dates followed by different letters are significantly different (Duncans multiple range test at P<0.05).

Table 3.1b. Sward characteristics* of four grasses at seven intervals after clipping during 1986 at Lacombe.

Grass	TD	TW	LAT	HT	HC	%stem	SLA	LI
	Characteristic*							
8 days								
Smooth bromegrass	2.7b	6.8c	1.2b	11.5c	-	-	16.9a	8b
Meadow bromegrass	12.1a	8.8bc	1.0b	14.5b	-	-	10.7b	27a
S9044	10.7a	13.0a	2.0a	14.3b	-	-	15.2a	35a
Meadow foxtail	13.2a	11.3ab	1.2b	17.5a	-	-	10.9b	31a
15 days								
Smooth bromegrass	9.5c	15.8c	2.6c	19.3b	-	-	15.7bc	33b
Meadow bromegrass	18.1b	32.5b	4.5b	28.3a	-	-	13.5c	65a
S9044	11.8c	47.8a	9.1a	29.8a	-	-	20.4a	69a
Meadow foxtail	25.0a	25.8b	4.6b	28.5a	-	-	18.2ab	72a
22 days								
Smooth bromegrass	11.5c	32.8b	8.3b	28.3c	8.0c	5b	26.7a	75c
Meadow bromegrass	19.6b	49.0b	6.8b	39.3a	9.4bc	4b	14.4c	85b
S9044	13.7c	73.0a	14.4a	39.8a	10.3a	6ab	20.8b	89a
Meadow foxtail	30.0a	40.5b	7.6b	33.1b	10.8a	11a	20.2b	90a
29 days								
Smooth bromegrass	14.9c	43.8c	8.6b	31.2b	8.9b	2c	19.9a	90
Meadow bromegrass	21.6b	68.0b	7.3b	44.0a	9.1b	4b	11.1b	93
S9044	15.1c	89.5a	14.6a	41.5a	10.5a	8b	17.4a	94
Meadow foxtail	30.2a	52.5bc	7.6b	40.6a	11.4a	17a	16.8a	93
36 days								
Smooth bromegrass	12.0c	49.8c	7.7b	33.8c	9.2d	6c	16.3a	92
Meadow bromegrass	19.5b	69.5b	6.2b	46.8a	10.6c	9b	9.6b	93
S9044	14.6c	106.8a	14.7a	45.4a	12.2b	13a	15.5a	95
Meadow foxtail	27.3a	62.3b	8.4b	41.7b	13.7a	19a	16.1a	92
44 days								
Smooth bromegrass	14.7b	56.8b	15.1a	34.2c	10.5b	8bc	28.1a	94
Meadow bromegrass	18.2b	61.5b	9.4b	39.3bc	9.4b	4c	15.9c	95
S9044	15.8b	84.5a	17.4a	45.9a	12.8a	14ab	23.6b	95
Meadow foxtail	26.9a	55.8b	8.3b	43.7ab	14.6a	20a	17.9c	94
49 days								
Smooth bromegrass	10.5b	68.3	11.7a	34.4b	10.1b	11b	19.2a	-
Meadow bromegrass	20.4a	71.8	6.6b	44.5a	10.3b	7b	9.7d	-
S9044	12.3b	91.0	12.2a	43.4a	11.3ab	13b	15.5b	-
Meadow foxtail	24.5a	60.3	6.5b	41.7a	12.7a	24a	13.4c	-

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* TD =tiller density (# dm $^{-2}$), TW = tiller weight (mg tiller^{-1}), LAT= leaf area per tiller (cm ^{2} tiller^{-1}), HT = height to tallest leaf tip (cm), HC = height to top collar (cm), %stem= (stem dry matter/total dry matter) x 100, SLA = specific leaf area (m^{2} kg^{-1}), LI = % light interception.

** Means within columns and harvest dates followed by different letters are significantly different (Duncans multiple range test at P<0.05).

foxtail, while in 1986 only S9044 differed from the others (Tables 3.1a, 3.1b). The height to leaf tip in both years was usually less for smooth bromegrass than for S9044 and meadow bromegrass (Tables 3.1a, 3.1b). Values for meadow foxtail were similar to S9044 and meadow bromegrass at all times except in early 1985 (Tables 3.1a, 3.1b). Little internodal elongation occurred in any of the species either year as is shown by the low height to collar values (Tables 3.1a, 3.1b). In 1985 height to collar was lowest for meadow bromegrass while in 1986 it was lowest for both smooth and meadow bromegrass (Tables 3.1a, 3.1b). Regrowth remained almost completely vegetative for smooth and meadow bromegrass, while few reproductive culms were observed in S9044 and a large number occurred in meadow foxtail. Dry matter yield therefore , consisted predominantly of leaves for all species with little stem (pseudostem) content (Tables 3.1a, 3.1b). Stem content reflected height to collar data with lowest values for meadow bromegrass in 1985 and both smooth and meadow bromegrass in 1986 (Tables 3.1a, 3.1b). Stem content for all species accounted for no more than 27% of the total dry matter.

Although SLA fluctuated from harvest to harvest, rankings among species were relatively constant. SLA was almost always highest for smooth bromegrass and S9044 (Tables 3.1a, 3.1b).

In 1985 when only one measurement of light interception was taken all species were intercepting approximately 95% of the incoming light after 35 days of regrowth. In 1986 smooth bromegrass had the lowest levels of light interception early in the regrowth cycle. Seven days after clipping smooth bromegrass intercepted only 8% of the light compared to over 27% for the other species (Table 3.1b). Light interception in smooth bromegrass remained lower than for the other species until 29 days of regrowth (Table 3.1b). Different k values among species indicated different canopy light attenuation properties (Table 3.2). The k values were highest for S9044 and meadow foxtail and lowest for smooth and meadow bromegrass

Table 3.2. Light attenuation properties of four grasses during 1986 at Lacombe. Data from 8 to 29 days of regrowth.

Grass	k*	standard error	r^2
Smooth bromegrass	1.7**	0.07	.99
Meadow bromegrass	1.3	0.11	.99
S9044	1.0	0.02	.99
Meadow foxtail	0.9	0.09	.98

* the extinction coefficient was calculated as the slope of the regression of ln (the fraction of incident light penetrating to the base of the canopy) versus leaf area index.

** treatment effect for grass species was significant at $P<0.05$

Table 3.3a. Growth analysis parameters* of four grasses at seven intervals after clipping during 1985 at Lacombe

Grass	Parameter*				
	LAI	NAR	CGR	RGR	LAR
			7 days		
Smooth bromegrass	0.14b	3.15b	0.4b	.242	75.0a
Meadow bromegrass	0.16b	6.78a	1.0a	.211	31.4b
S9044	0.23a	3.88b	0.9a	.200	51.2a
Meadow foxtail	0.11b	4.11b	0.4b	.234	56.7a
			14 days		
Smooth bromegrass	0.34b	4.85b	1.6b	.198a	40.3a
Meadow brome	0.40b	7.97a	3.1a	.172bc	21.6b
S9044	0.53a	4.91b	2.6a	.165c	33.4a
Meadow foxtail	0.29b	5.73b	1.6b	.194ab	34.1a
			21 days		
Smooth bromegrass	0.71b	6.24b	4.5b	.155a	24.7b
Meadow bromegrass	0.84ab	8.32a	6.9a	.133b	15.9a
S9044	1.06a	5.54b	5.8a	.131b	23.5b
Meadow foxtail	0.67b	6.84ab	4.5b	.155a	22.9b
			29 days		
Smooth bromegrass	1.34	6.32	8.4	.106a	16.6ab
Meadow bromegrass	1.59	7.13	11.2	.088b	12.3b
S9044	1.95	5.25	9.9	.092b	17.5a
Meadow foxtail	1.41	6.63	9.2	.110a	16.8ab
			35 days		
Smooth bromegrass	1.88b	4.90	9.1	.068ab	13.9a
Meadow bromegrass	2.14ab	5.02	10.6	.055c	10.9b
S9044	2.68a	4.15	10.7	.063bc	15.2a
Meadow foxtail	2.18ab	5.23	11.2	.077a	14.7a
			42 days		
Smooth bromegrass	2.40b	1.98	4.8	.025	12.9a
Meadow bromegrass	2.52ab	1.54	3.8	.015	10.0b
S9044	2.38a	2.03	6.6	.028	14.0a
Meadow foxtail	3.10ab	2.65	8.2	.038	14.1a
			49 days		
Smooth bromegrass	2.60b	-1.20	-2.98	-.018	13.6a
Meadow bromegrass	2.45b	-2.41	-5.78	-.024	10.0b
S9044	3.74a	-0.51	-1.27	-.006	14.0a
Meadow foxtail	3.78a	-0.08	-0.11	-.001	15.2a

* LAI = leaf area index, NAR = net assimilation rate (g m^{-2} d^{-1}), CGR = crop growth rate (g m^{-2} d^{-1}), RGR = relative growth rate (g g^{-1} d^{-1}), LAR = leaf area ratio (m^2 kg^{-1})

** Means within columns and harvest dates followed by different letters are significantly different (Duncans multiple range test at P<0.05).

Table 3.3b. Growth analysis parameters* of four grasses at five intervals after clipping during 1986 at Lacombe.

Grass	Parameter*				
	LAI	NAR	CGR	RGR	LAR
		8 days			
Smooth bromegrass	0.03c**	24.8a	0.8c	.262	10.6b
Meadow bromegrass	0.13b	27.1a	3.4b	.237	8.9b
S9044	0.23a	14.3b	3.2b	.229	16.4a
Meadow foxtail	0.19a	21.9ab	3.7a	.207	10.3b
		15 days			
Smooth bromegrass	0.24c	12.1b	2.9b	.199a	16.8a
Meadow bromegrass	0.60b	16.1a	9.6a	.165b	10.3c
S9044	0.87a	10.2b	8.9a	.162b	16[illegible]ab
Meadow foxtail	0.86a	10.9b	9.1a	.146b	13.8b
		22 days			
Smooth bromegrass	0.87c	7.8b	6.5b	.137a	18.3a
Meadow bromegrass	1.45b	9.3a	13.4a	.093b	10.1b
S9044	1.97a	6.6bc	12.8a	.095b	14.6a
Meadow foxtail	2.13a	5.6c	12.0a	.085b	15.1a
		29 days			
Smooth bromegrass	1.34b	5.7a	7.4	.075a	13.4a
Meadow bromegrass	1.77b	2.5b	4.6	.022b	8.2b
S9044	2.57a	2.2b	5.7	.028b	12.4a
Meadow foxtail	2.85a	1.7b	4.8	.024b	13.9a
		36 days			
Smooth bromegrass	0.91b	1.9a	1.7a	.012a	6.8b
Meadow bromegrass	1.14b	-10.0b	-9.5b	-0.05b	8.2b
S9044	1.96a	-4.2ab	-7.8b	-0.04b	9.8a
Meadow foxtail	2.03a	-3.7ab	-7.3b	-0.37b	10.4a

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* LAI = leaf area index , NAR = net assimilation rate (g m^{-2} d^{-1}) , CGR = crop growth rate (g m^{-2} d^{-1}), RGR = relative growth rate (g g^{-1} d^{-1}), LAR = leaf area ratio (m^2 kg^{-1})

** Means within columns and harvest dates followed by different letters are significantly different (Duncans multiple range test at P<0.05).

3.3.5 Growth analysis

Regression equations (fitted by replicates and replicates combined) for dry matter yield and LAI are given in Appendices 3.8 and 3.9, respectively. LAI values were generally the highest for S9044 and meadow foxtail (Tables 3.3a, 3.3b). In 1986 smooth bromegrass exhibited a delay in leaf area development and its LAI at day 8 was much lower than that of the other species (Tables 3.3a, 3.3b). The LAI of meadow bromegrass was equal to that of smooth bromegrass at all times except at the early stages of regrowth in 1986 (Table 3.3b).

In both years the CGR for the first 21-22 days of regrowth was higher (often double) for meadow bromegrass and S9044 than for smooth bromegrass (Tables 3.3a, 3.3b). After 21-22 days of regrowth however the CGR of smooth bromegrass was equal to or higher than the other species. In 1985 the CGR of meadow foxtail for the first 21 days of regrowth was similar to that of smooth bromegrass. After 21 days of regrowth in 1985 and in 1986 meadow foxtail's CGR was similar to that of meadow bromegrass and S9044 (Tables 3.3a, 3.3b). The maximum CGR observed for all species occurred after 31-35 days in 1985 and 21-27 days in 1986 (Tables 3.3a,3.3b). Maxima for the species ranged from 9.1 to 13.4 g m^{-2} d^{-1} and occurred near complete light interception when LAI ranged from 1.3 to 2.4 (Tables 3.3a, 3.3b).

The RGR declined in all species as the plants matured (Tables 3.2a, 3.2b). Values ranged from a high of 0.26g g^{-1} d^{-1} at the week one harvest to less than zero at the final harvests. Differences between species were slight in 1985 while in 1986 smooth bromegrass had a consistently higher RGR (Tables 3.2a, 3.2b).

The NAR values generally declined for all species as the plants matured (Tables 3.2a, 3.2b). Low NAR values for the early harvests in 1985 may be related to the high soil moisture tensions at this time (Table 3.3a, Appendix 3.5). In 1985 NAR ranged from 9.0 g m^{-2} d^{-1} to less than zero, while in 1986 values declined from a high of 28 g m^{-2} d^{-1} at week one to less than zero at the final harvest. Meadow bromegrass for the most part had a higher NAR for the first 21-22 days of regrowth, after which all species were similar (Tables 3.2a, 3.2b). Since stem content was minimal, data for LAR showed similar trends as for SLA. In almost all cases LAR was lower for meadow bromegrass than the other species (Tables 3.3a, 3.3b).

When the CGR of the grasses was plotted versus dry matter, several trends became evident(Fig. 3.4). At low dry matter yields (below 100 and 50 g m^{-2} in 1985 and 1986, respectively), all grasses had similar growth rates. After this point however smooth bromegrass exhibited a lower CGR per unit of dry matter than the other species (Fig. 3.4).

The graphs of CGR versus LAI showed a relatively linear increase in CGR with LAI up to a certain point (Fig 3.5). In both years the CGR of smooth and meadow bromegrass declined at an approximate LAI of 1.5 while the CGR of S9044 and meadow foxtail declined at an LAI of 2-2.5. At low LAI levels the CGR per unit of LAI was generally higher for meadow bromegrass than the other species (Fig. 3.5). In 1986 the CGR per unit of intercepted light was lower for smooth bromegrass than for the other species (Fig. 3.6).

3.4 DISCUSSION

3.4.1 General limitations to regrowth in central Alberta

The relatively linear relationship between CGR and LAI prior to canopy closure indicated a strong dependance of CGR on leaf area development (Fig 3.5). Complete light interception was achieved after 21-35 days of regrowth in all species, when CGR was at its maximum (Tables 3.1b, 3.3a, 3.3b). It was thus concluded that for three to five weeks after a severe defoliation the CGR of all species was limited by the light interception of the canopy. Rhodes (1973) previously concluded that prior to canopy closure leaf area is the primary determinant of CGR. Nelson et al. (1982) suggested that in situations where light interception is not complete, strategies should be developed to improve the light

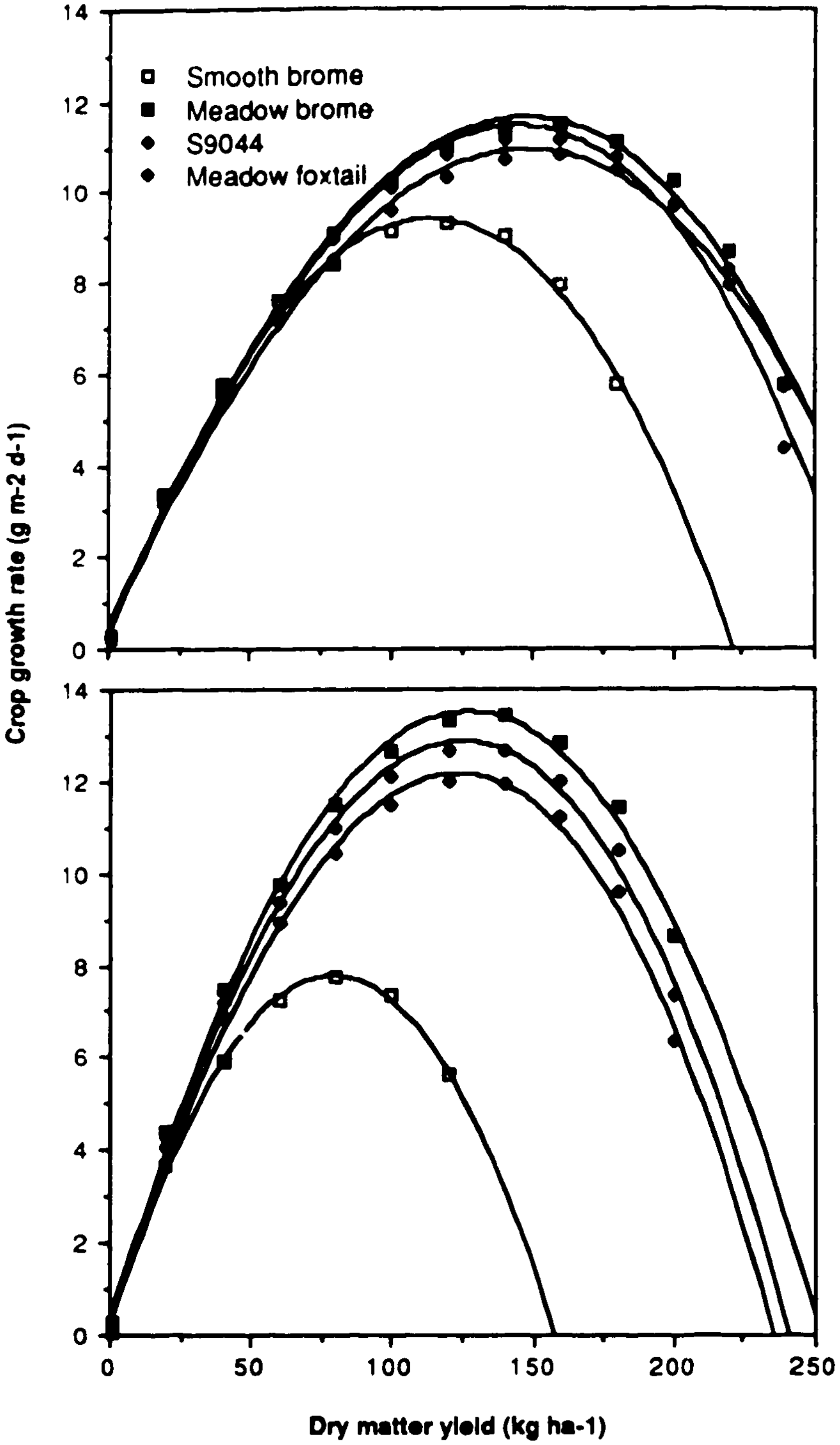

Fig. 3.4. Crop growth rate versus dry matter yield of four grasses during late season regrowth in 1985 and 1986 at Lacombe. Regression equations are given in Appendix 3.11.

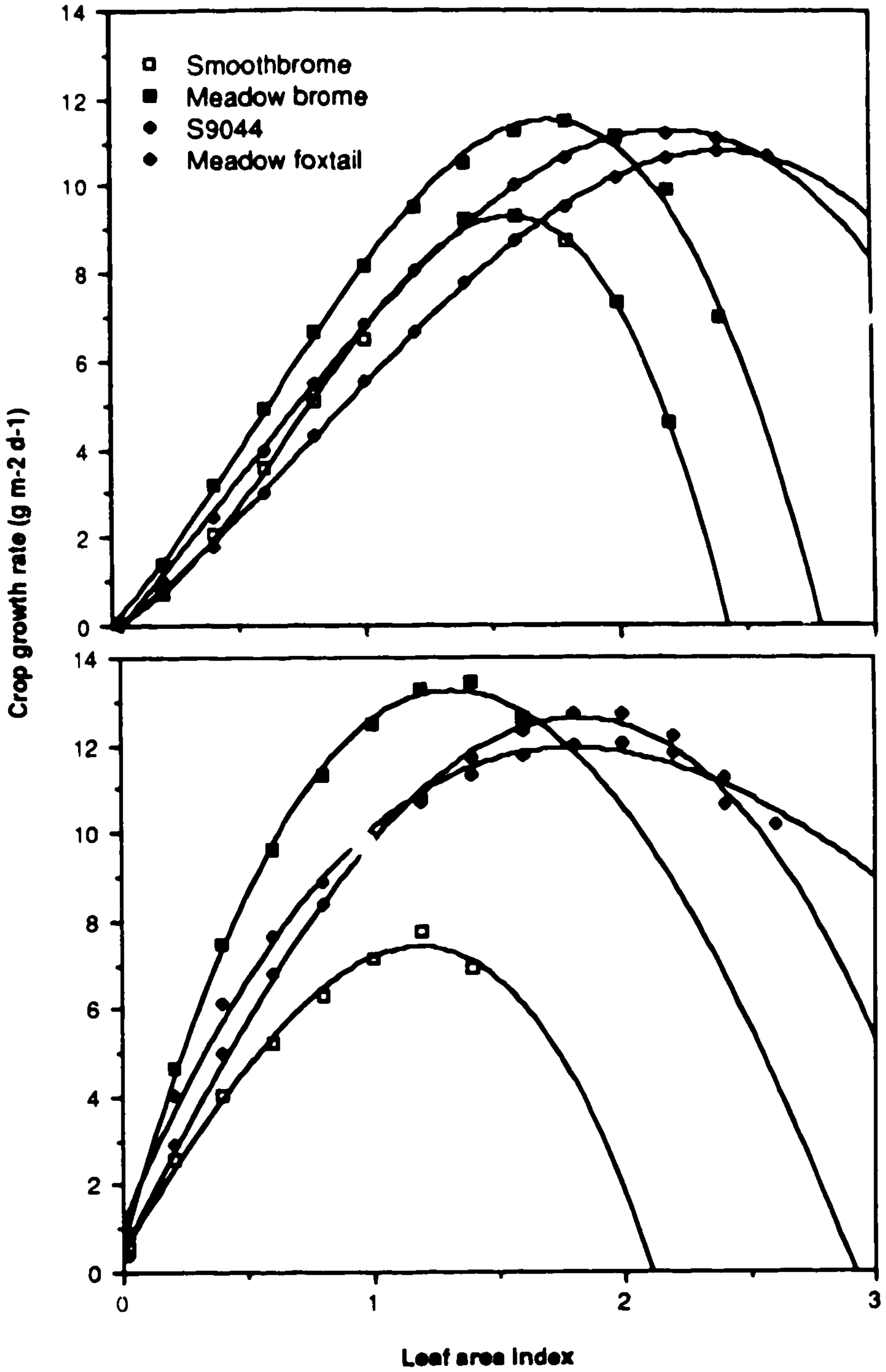

Fig. 3.5. Crop growth rate versus leaf area index of four grasses during late season regrowth in 1985 and 1986 at Lacombe. Regression equations are given in Appendix 3.12.

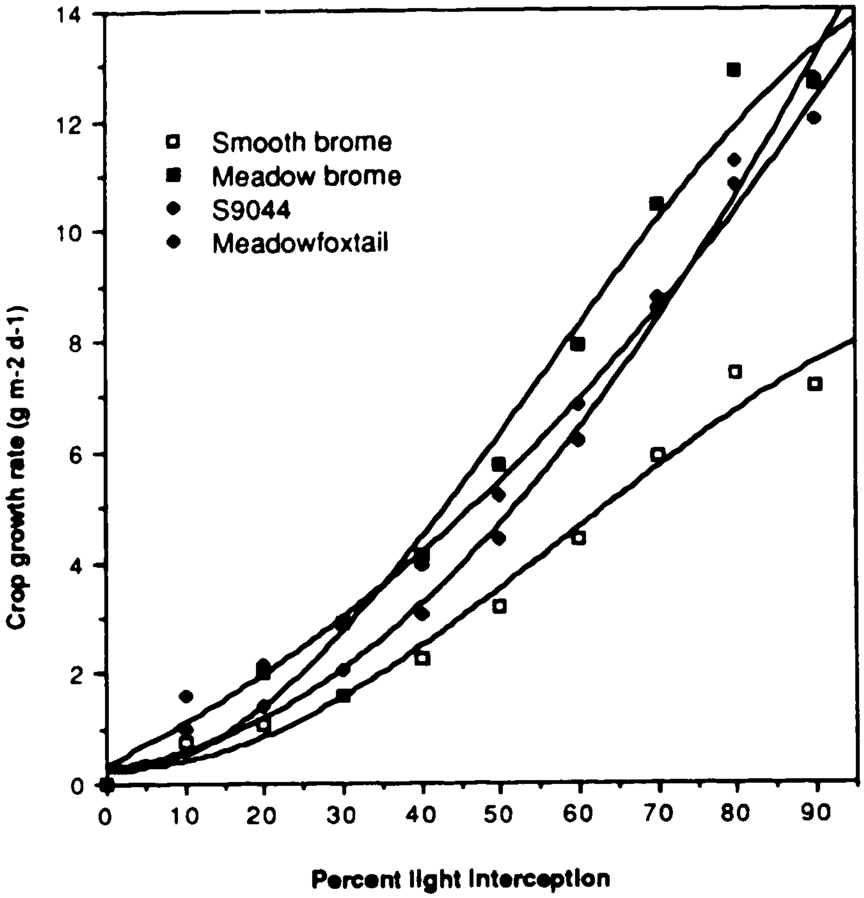

Fig. 3.6. Crop growth rate versus percent light interception of four grasses during late season regrowth in 1986 at Lacombe. Regression equations are given in Appendix 3.13.

interception by the canopy. Slow rates of leaf area development in late season have been attributed to the fact that post flowering vegetative stands have lower leaf extension rates than the floral stands of spring (Parsons and Robson 1980b). Low temperatures have been cited as possible factors contributing to a slow rate of leaf area development (Nelson et al. 1978), but in this study day time maximum temperatures in August (15-20^{o}C) were close to the optimum range for leaf area expansion (20-25^{o}C) (Kemp 1985).

The maximum CGR observed for all species, ranged from 9.1-13.4 g m^{-2} d^{-1} (Table 3.3a, 3.3b). These maximum growth rates were approximately half that frequently observed spring growth rates (20 g m^{-2} d^{-1}) for a number of grass species in Europe (Leafe et al. 1974). The peak CGR attained of 9.1-13.4 g m^{-2} d^{-1} was surprisingly similar to the late August growth rate of 11.6 g m^{-2} d^{-1} obtained for ryegrass swards in Wageningen, Netherlands (52^{o}N), (Alberda 1968). Using an average energy input of 35 mol m^{2} d^{-1} (Appendix 3.7) the maximum CGR obtained at Lacombe corresponded to a 2-3% conversion of solar energy into harvestable dry matter (calculated as in Gardner 1985). These conversion efficiencies are typical for mid summer pasture growth in England (Cooper 1970). The NAR at this time ranged from 4.0 to 9.9 g m^{2} d^{-1} (Table 3.6). These values were also typical of those observed for closed ryegrass swards in summer in England (MacColl and Cooper 1966). The RGR at Lacombe declined for all species from over 0.2 g g^{-1} d^{-1} for young tissue to near 0.1 g g^{-1} d^{-1} at canopy closure, again typical for late summer pastures elsewhere (Hunt and Cooper 1967). Since CGR, NAR, RGR, and solar efficiencies at canopy closure were similar or higher than those reported for other areas of similar climate and latitude, it appeared that the maximum growth rates observed in this study were close to potential.

Once the peak growth rates were attained they rapidly declined to near zero, resulting in ceiling yields ranging from 130 to 270 g m^{-2}. These yields were about one third of the first cut hay yields reported by Baron and Van Esbroeck (1986) and Knowles and Sonmore (1985). In contrast to Lacombe, the peak CGR in August in Wageningen and England was maintained for three to four weeks until yields of 500 g m^{-2} were attained (Alberda and Simba 1968; Leafe et al. 1974). Engel et al. (1986) in Nebraska found maxima fall yields of smooth bromegrass of 280 g m^{-2} to be a half to a quarter of spring maxima. Similar results were also reported for tall fescue with fall maxima of 400 g m^{-2}, half to a third of the spring maxima (Wolf 1979). The decline in ceiling yield from spring to summer at Lacombe was comparable to that in other areas of the world. However, the ceiling yields observed (130-270 g m^{-2}) were lower than for areas of similar latitude in Europe and for other areas in North America.

Ceiling yields at Lacombe appeared to be limited by factors related to the decline in CGR once a maximum had been attained. The clearly defined maximum in CGR was perhaps in part an artifact related to the fact that a 2nd order polynomial was used to fit dry matter yield data. The CGR calculated from such a curve by nature always produces a CGR that peaks (Hunt 1982). An examination of the actual dry matter yield data, however, revealed that, at most, CGR was at its maximum for only two weeks (Fig. 3.1).

The CGR declined at generally similar LAI levels for each species in both years and when 85-95% of the incident light was intercepted. In 1985 the drop in CGR occurred in late August when moisture and temperature appeared adequate. In 1986 the decline in CGR occurred about a week earlier and was much more abrupt but this may reflect the declining soil moisture at the time. The relationship between CGR and light interception suggested that the drop in CGR was probably not due to the changing late summer environmental conditions but rather to factors relating to critical LAI.

The k values for most grasses range from 0.4 to 0.7 (Rhodes 1973) which means that a LAI of 7.5 to 4.3 can be attained at 95% light interception. In this study the k values obtained, ranged from 0.9 to 1.7 and maximum LAI ranged from 3.8 to 2.6 (Tables 3.2, 3.3). These values were considerably lower than reported for late summer growth elsewhere. Maximum LAI values in England and the Netherlands for August growth were reported to range from 5 to 8 (Alberda and Simba 1968; Hunt and Cooper 1967).

Nelson et al. (1982) reported a LAI value of 6.0 for tall fescue in Missouri. Engel et al (1986) found values ranging from 2.9 to 5.2 for smooth bromegrass in Nebraska.

3.4.2 Comparisons among species

3.4.2.1 Dry matter yields

The results of this experiment clearly indicated that meadow bromegrass and S9044 were superior to smooth bromegrass for late season regrowth regardless of the length of regrowth period. These results are in agreement with previous reports showing higher late season yields for meadow than smooth bromegrass (Baron and Van Esbroeck 1986, Knowles and Sonmore 1985). The species studied showed considerable differences not only in yield but in the mechanisms by which yield was achieved. The yield advantage of the other species over smooth bromegrass could not be attributed to a single factor but resulted from a range of traits that often varied in importance among species and harvest times.

3.4.2.2 Importance of tiller density and tiller weight

Nelson et al. (1977) expressed the yield of tall fescue as a product of TW and TD. They considered TD important early in regrowth but after a stable TD was attained TW was considered the major yield determinant.

Since the TD of all the species stabilized after three to four weeks it appeared that tillering had a major influence on the CGR early in the regrowth cycle but TW probably limited ceiling yields. Meadow bromegrass usually had about twice the TD of smooth bromegrass but its TW was lower or similar to that of smooth bromegrass. Its yield advantage thus can be attributed to its higher TD which more than compensated for its lower TW. This was particularly evident 8 days after clipping in 1986 when the TD of meadow bromegrass exceeded that of smooth bromegrass by 300% (Tables 3.1a, 3.1b).

The S9044 cross showed improved regrowth ability compared to smooth bromegrass in that its TD after 8 days of regrowth was 50% higher than for smooth bromegrass (Tables 3.1a, 3.1b). However in subsequent harvests TD was generally similar between species and S9044's yield advantage must have resulted chiefly from its larger TW.

Since meadow foxtail had the lowest TW, yet often had the highest yields it relied on a high TD to achieve these high yields. Tillering in meadow foxtail and hence yields appeared to be very dependent on good soil moisture conditions. Meadow foxtail exhibited a low rate of tiller development early in 1985 when soil moisture tensions were below -0.3 MPa for the first 14 days of regrowth. When moisture conditions improved after 21 days, tillering increased rapidly

3.4.2.3 Traits associated with crop growth rate

The contribution of the various yield components and growth analysis parameters to CGR varied among species and harvest times. The relatively linear relationship between CGR and LAI indicated the importance of leaf area development to achieving high yields early in the regrowth cycle (Fig 3.5). In 1985 a higher TD in meadow than smooth bromegrass compensated for its lower LAT, and LAI values were similar for both these species at all harvests (Tables 3.1a, 3.3a). Since CGR=NAR x LAI (Hunt 1982), the higher CGR in meadow bromegrass for the first 21 days of regrowth in 1985 must have resulted from its higher NAR (Table 3.3a). In 1986 the higher CGR for meadow bromegrass for the first 22 days of regrowth was the result of a higher LAI and often a higher NAR,. The higher LAI was achieved by both a higher TD and LAT (Table 3.1b).

Despite its higher CGR and NAR in the first 21-22 days of regrowth, meadow bromegrass was not able to maintain its advantage and after this point the CGR and NAR values of smooth and meadow bromegrass were usually similar. Since the LAI for both these species remained similar after 21-22 days of regrowth, the relatively lower CGR of meadow bromegrass at the later stages of regrowth was attributed to a rapid decline in its NAR. The NAR of all species however declined as the plants matured which made comparisons between species difficult to interpret as plants were perhaps at different physiological ages (Hunt 1978). A lower NAR for meadow bromegrass than smooth bromegrass in later harvests may have been due to the fact that the leaves of meadow bromegrass were older as they had developed earlier.

Further evidence showing the importance of a high NAR to CGR in meadow bromegrass is shown in Fig. 3.5. When smooth and meadow bromegrass were compared at a similar LAI, meadow bromegrass had a consistently higher CGR and hence a higher NAR (Fig. 3.5). A greater CGR per unit of intercepted light for meadow compared to smooth bromegrass substantiated this (Fig. 3.6). Since these species distributed a given amount of light over relatively similar leaf areas differences in light attenuation properties did not appear to account for differences in NAR.

Several factors may account for the apparently higher photosynthetic efficiency of meadow bromegrass leaves. The NAR values were determined from above ground dry matter and thus may only reflect differences in partitioning between the shoot and root. Since NAR= RGR/LAR (Hunt 1982) variation in RGR or LAR contributes to the variation in NAR. Differences were observed in both these parameters, however, the difference in LAR was of a greater magnitude (Table 3.3a,3.3b). Differences in SLA appear to explain differences in NAR. This is substantiated by Fig. 3.4 which showed that early in regrowth the CGR of the two species at similar dry matter levels (essentially leaf dry matter) was similar.

A higher NAR due to a lower SLA has been reported to explain differences in productivity between species, with the greater NAR attributed to a larger amount of photosynthetic apparatus per unit leaf area (Hunt and Cooper 1967). Attempts to select for low SLA within a species have however not been successful (Carlson et al. 1981), and within species variation in canopy architecture is usually considered to play a more important role in productivity than variation in NAR (Rhodes 1973; Sugimana et al 1985).

Despite a higher CGR for meadow than smooth bromegrass early in regrowth the RGR of smooth bromegrass was higher. Since CGR= dry matter x RGR (Hunt 1982) , the greater existing dry matter for meadow bromegrass compensated for its lower RGR. Since RGR declines with maturity the lower RGR in meadow bromegrass may reflect its more rapid regrowth and hence its more mature herbage. When these species were examined at similar dry matter yield after having achieved 50-100 g m^{-2}, meadow bromegrass grass clearly had a higher CGR (Fig 3.4). This showed that the inability of smooth bromegrass to maintain its photosynthetic efficiency to a high dry matter yield was involved in its lower yields late in the regrowth cycle.

The plot of CGR versus LAI may explain the reason why smooth bromegrass' RGR declined at a lower dry matter yield compared to meadow bromegrass. Fig 3.5 showed that CGR of both these species declined at a relatively similar LAI of 1.25 in both years (Fig 3.5). However, at this time, meadow bromegrass with its lower SLA, had accumulated a dry matter yield of approximately 150 g m^{-2} in comparison to 100 g m^{-2} for smooth bromegrass. This clearly indicated meadow bromegrass' reliance on a low SLA to achieve high yields despite its low critical LAI.

S9044, like meadow bromegrass had a higher CGR than smooth bromegrass for the first 21-22 days of regrowth. Although S9044 had at times a lower NAR than smooth bromegrass, its larger LAI appeared responsible for its higher CGR (Tables 3.3a, 3.3b). Since TD was generally similar between these species S9044's higher LAI must have resulted from its higher LAT. The yield advantage of S9044 over smooth bromegrass early in regrowth thus appeared to be the result of a larger leaf area per tiller expansion rate. After 29 days of regrowth a slightly lower NAR in S9044 compared to smooth bromegrass offset the advantage of its high LAI and the CGR of these species was similar. The RGR of S9044 was lower than smooth bromegrass but when compared at similar dry matter levels the CGR of S9044 was equal to or higher than for smooth bromegrass (Fig 3.4). In S9044 the CGR was maintained over a wider range of LAI than in smooth bromegrass and S9044 attained a higher maximum LAI (Fig 3.5). In addition data for 1986 showed that at similar light interception levels S9044 was more efficient in using light to produce dry matter (Fig 3.6). Unlike meadow bromegrass, S9044 has a generally similar SLA to smooth bromegrass and its more efficient use of light must have resulted from other factors. This phenomena may be in part related to S9044's pattern of light interception. S9044 had a lower k value, and thus was able to spread incoming light over a larger leaf area than smooth bromegrass (Table 3.2). The basis for S9044's improved performance over smooth bromegrass appeared to have been its more rapid leaf area development early in regrowth due primarily to larger LAT and to an improved canopy architecture (i.e. lower k values). The increased light penetration into the canopy may have also contributed to it maintaining its CGR over a large yield and LAI range. Previously CGR was found to be highly correlated with k values (Sheehy and Cooper 1973) and genotypes with highest critical LAI were most productive under infrequent clipping (Rhodes 1971).

Since meadow foxtail had similar or lower NAR than smooth bromegrass its higher CGR in late 1985 and in 1986 resulted from its larger LAI (Tables 3.3a, 3.3b). Its rapid rate of leaf area development appeared to have been the result of its high TD since it had low LAT. The relationships of CGR to dry matter, LAI, and light interception for meadow foxtail were also similar to S9044. It had a generally similar SLA to smooth bromegrass and hence this could not explain the higher CGR per unit of intercepted light. Like S9044 meadow foxtail had a lower k value than smooth bromegrass indicating an improved canopy architecture (Table 3.2). Meadow foxtail's yield advantage over smooth bromegrass thus appeared to result from its more rapid leaf area development early in regrowth, and subsequently to its improved canopy architecture. Data for 1986 showed that S9044 and meadow foxtail which had the highest k values also had highest stem content. Although other factors such as leaf length and leaf angle affect k, it appeared stem height had a positive influence on light attenuation.

3.4.2.4 Role of carbohydrate partitioning

Sheard (1973) postulated that the need to store carbohydrates may limit the regrowth potential of grasses in northern climates In this study all species exhibited generally similar levels of carbohydrate reserves and accumulated them at similar rates indicating that differing regrowth patterns were probably not related to carbohydrate partitioning. The relatively similar carbohydrate levels between species lends support to the view that carbohydrate partitioning plays no important role in late season productivity (Parsons and Robson (1980c)

3.4.4 Conclusions

Yields of S9044 and meadow bromegrass were higher than for smooth bromegrass at all harvest dates. Meadow foxtail outyielded smooth bromegrass at all times except when soil moisture was low. The growth of all species was limited by light interception for the first three to five weeks of regrowth for1985 and 1986, respectively. At this time leaf area development appeared to be the major limitation to the CGR of all species. The CGR peaked and then rapidly declined when light interception was complete and LAI ranged from 1.3 to 2.4. At this point the light attenuation properties of the canopy appeared to limit the productivity of all species. A comparison of yield components and growth analysis parameters showed large differences in how these species achieved their yields. The fact that similarly high yields were attained by species relying on either a high TD or TW suggests that no one strategy is superior. The superiority of meadow bromegrass over smooth bromegrass was associated with a higher NAR for the initial three weeks of regrowth. A generally higher CGR for meadow foxtail and S9044 than for smooth bromegrass early in regrowth was associated with a higher LAI. Selection for traits resulting in a more rapid leaf area accumulation offers the potential to increase yields for short duration grazing. To increase ceiling yields improvements in light attenuation properties appear to be warranted.

4. EFFECTS OF TEMPERATURE AND PHOTOPERIOD ON YIELD AND YIELD COMPONENTS OF SIX TEMPERATE GRASSES

4.1 INTRODUCTION

Recent studies have shown that late season growth rates and pasture yields were lower for smooth bromegrass than for a number of other commonly grown species (Knowles and Sonmore 1985). Important influences on late season growth in northern latitudes are lower temperatures and shorter photoperiods. In central Alberta (52°N) daylength declines from 18 h in June to 14 h by September while mean temperature declines from 14°C to 7°C.

The influence of temperature and photoperiod on forage productivity has been reviewed by Kemp (1984) and Tainton and Cooper (1968). Differences among species or ecotypes in their response to both temperature and daylength extremes have been attributed to an adaptation to the climatic conditions at the species origin (Eagles 1971, Heide et al. 1985a). Short photoperiods and low temperatures were reported to cause dormancy in grasses originating in high latitudes (Cooper 1964; Ostgard and Eagles 1971) and were associated with increased levels of winter hardiness (Cooper 1964; Klebesadel 1970, 1971; Robson and Jewis 1968). In addition long photoperiods increased the growth of a number of species, but effects were most pronounced in high latitude ecotypes, and may explain why dry matter production of northern ecotypes is skewed to the early part of the season (Hay and Heide 1983; Hay 1985).

Greater productivity of southern versus northern ecotypes of orchard grass (Dactylis glomerata L.) was attributed to greater partitioning into leaves and leaf area (Eagles and Ostgard 1971). Yield enhancements of up to 195% due to daylength extension were observed in high latitude ecotypes of timothy (Phleum pratense L.) (Hay and Heide 1983). Smaller yield enhancements under long days were observed in orchard grass (Eagles and Ostgard 1971), Kentucky bluegrass (Poa pratensis L.) (Hay and Heide 1983), and smooth bromegrass (Heide et al. 1985a) with effects most pronounced at low to moderate temperatures. Night break experiments have resulted in similar effects and confirmed the photoperiodic nature of the response (Heide et al. 1985b).

Dry matter yield increases with daylength extension were associated with a more erect growth habit, increased shoot/root ratios and increased leaf area production (Bowman and Law 1963; Hay and Heide 1983; Heide et al. 1985a; Stukey 1949; Templeton et al. 1961). Higher yields observed under extended photoperiods in orchard grass, timothy, smooth bromegrass and Kentucky bluegrass were associated with higher relative growth rates. They were attributed to higher leaf area ratios resulting from increases in shoot:root ratios and specific leaf area (Eagles 1971; Heide et al. 1985b).

No data is available that relates vegetative regrowth of commonly grown grasses to the seasonal change in temperature and daylength typical to central Alberta. The objectives of this study were to assess the influence of temperature and photoperiod typical to central Alberta on vegetative yield and yield components of several temperate grasses.

4.2 MATERIALS AND METHODS

The species studied were: smooth bromegrass (*Bromus inermis* L.) cv. Carlton, meadow bromegrass, (*Bromus riparius* Rhem and Schult.) cv. Regar, an interspecific cross between smooth and meadow bromegrass (S9044) (Knowles and Armstrong 1984) and meadow foxtail (*Alopecurus pratensis* L.), " common", orchard grass (*Dactylis glomerata* L.) cv. Kay and tall fescue (*Festuca arundinacea* Schreb.) cv. Alta. The locations where the cultivars were developed and their parental origin is given in Table 4.1.

For each ge[illegible]pe three tillers were planted into each of 72, 15 cm pots containing a mixture [illegible] peat and soil (1:1:1) and grown for twelve weeks in a greenhouse at 18°C w[illegible] h photoperiod. Plants were fertilized weekly with a liquid

Table 4.1 Origin of cultivars studied

Species	Cultivar	Location released	Original population
Smooth bromegrass	Carlton	Saskatoon(52°N)	Northern Germany (52°N)
Meadow bromegrass	Regar	Idaho (45°N)	Turkey (40°N)
Meadow foxtail	"common"		Europe and Asia (45-55°N)
Orchard grass	Kay	Ottawa (45°N)	Moscow (56°N)
Tall fescue	Alta	Oregon (45°N)	Germany (50°N)

fertilizer and clipped to 2.5 cm after six and twelve weeks. The purpose of the clippings was to remove floral tillers and to ensure vegetative regrowth for the duration of the experiment.

After the clipping at the twelfth week plants were transferred to one of four controlled growth environments which consisted of a combination of two temperature regimes (15/5 and 25/15^{o}C; day/night) and two photoperiods (14 h and 18 h). Lighting was supplied by a mixture of 60 watt incandescent bulbs and cool-white fluorescent bulbs. The height of the lamps was adjusted weekly to maintain a PPFD of 400-450 µmol m^{2} s^{-1} at the top of the canopy. The 18 h photoperiod was attained by extending the normal 14 h day with a single 40 watt incandescent bulb for two hours in the morning and evening.

A total of 18 pots per species were placed into each of the growth cabinets. Plants were rearranged within the cabinets each week to prevent any possible effects of uneven environmental conditions. The relative humidity in the cabinets was maintained at 50%. After two, four and six weeks of regrowth in the cabinets six pots per species were harvested. Tillers were counted, plants clipped to a height of 2.5 cm and separated into leaf lamina, stems (stem plus leaf sheath) and stubble (material below the 2.5 cm cutting height and above the soil). Roots to a depth of 7.5 cm were collected and washed to remove soil. Fresh weight of the leaf lamina was recorded and lamina area determined with a Li-Cor LI 3100 leaf area meter (Li-Cor Ltd., Lincoln, Nebraska). All material was dried at 70^{o}C for three days in a forced air oven and weighed. Harvestable dry matter yield per pot was determined as the leaf blades plus stem material. The pot totals for leaf lamina area, leaf weight, stem weight and dry matter were divided by the tiller number (TN) per pot to give leaf area per tiller (LAT), leaf yield per tiller (LYT), stem yield per tiller(SYT), and tiller weight (TW), respectively. Specific leaf area was determined as (leaf area/leaf dry weight) and shoot:root ratio was calculated as [(leaves + stem + stubble wt.)/root weight]. Leaf area ratio (LAR) was determined as [leaf area /(leaf + stem + stubble + root wt.)].

The complete experiment was carried out in 1986 and again in 1987 (trials). The data were analyzed as a three factor factorial with temperature, photoperiod and trial considered fixed effects. An analysis of variance was carried out for each species at each harvest using the combined pots within treatments and trial interactions as the error term. Effects with a $P<0.05$ were considered significantly different.

4.3 RESULTS

4.3.1 Temperature effects

No temperature by photoperiod interactions occurred for harvestable dry matter yield. Increasing the temperature increased the harvestable dry matter yields of all species at almost all harvests (Table 4.2). Only in meadow bromegrass at week four and in meadow foxtail and smooth bromegrass at week six were the temperature effects not significant. The largest harvestable dry matter yield enhancement with temperature occurred at the week two harvest, with the average yield increased 110%. The response temperature at week two was largest for smooth bromegrass which showed an increase of 214%. In subsequent harvests the harvestable yield increase due to temperature was less pronounced and by the final harvest the yields at the high temperature were only 24% higher than yields at the low temperature.

Temperature significantly increased whole plant weight (root plus shoot) at week two in smooth bromegrass, meadow bromegrass, and tall fescue (Table 4.3a). The higher whole plant weights at the week two harvest were primarily the result of higher shoot weights as root weights were unaffected (Table 4.3a). As regrowth progressed root weights declined somewhat with increasing temperature while increases in shoot weight became less pronounced. At week four in smooth bromegrass and S9044 the increase in shoot weight due to temperature was comparatively greater than the decline

Table 4.2. Effects of **temperature** in controlled conditions on the harvestable dry matter yield (g pot^{-1}) of six grasses after two, four, and six weeks of regrowth.

Temperature	Grass					
	Smooth bromegrass	Meadow bromegrass	S9044	Meadow foxtail	Orchard grass	Tall fescue
			two weeks			
15/5 °C	0.50	0.96	0.57	1.03	1.45	1.05
25/15 °C	1.57	1.73	1.20	1.95	2.49	2.04
F test	*	*	*	*	*	*
			four weeks			
15/5 °C	3.08	3.68	2.33	4.17	4.88	3.59
25/15 °C	5.26	4.60	4.46	5.92	6.68	5.62
F test	*	-	*	*	*	*
			six weeks			
15/5 °C	11.37	8.11	7.22	10.29	12.51	7.71
25/15 °C	13.19	10.39	9.15	11.39	14.48	11.42
F test	-	*	*	-	*	*

* significant at $P< 0.05$

\- not significant at $P< 0.05$

Table 4.3a. Effects of **temperature** in controlled conditions on the shoot weight, root weight, whole plant weight, shoot:root ratio, leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA) of six grasses after **two weeks** of regrowth.

Temperature	shoot weight (g pot^{-1})	root weight (g pot^{-1})	whole plant weight (g pot^{-1})	shoot: root ratio (g g^{-1})	LAR (m^2 kg^{-1})	LWR (g g^{-1})	SLA (m^{2}kg^{-1})
			Smooth bromegrass				
15/5 °C	0.78	3.07	3.84	0.28	3.93	0.11	33.4
25/15 °C	1.88	3.57	5.46	0.51	9.21	0.24	38.9
F test	*	-	*	*	*	*	*
			Meadow bromegrass				
15/5 °C	1.44	3.86	5.30	0.40	4.13	0.16	25.3
25/15 °C	2.15	4.20	6.35	0.58	5.63	0.25	22.3
F test	*	-	*	*	*	*	*
			S9044				
15/5 °C	0.94	3.39	4.33	0.28	3.51	0.12	30.4
25/15 °C	1.55	3.29	[illegible].84	0.50	6.80	0.22	31.5
F test	*	-		*	*	*	-
			Meadow foxtail				
15/5 °C	1.88	4.09	5.98	0.49	4.48	0.15	30.9
25/15 °C	2.93	4.40	7.32	0.71	6.99	0.23	30.4
F test	*	-	-	*	*	*	-
			Orchard grass				
15/5 °C	2.52	4.46	6.98	0.62	6.42	0.19	34.3
25/15 °C	3.52	3.83	7.36	1.02	10.07	0.30	33.5
F test	*	-	-	*	*	*	-
			Tall fescue				
15/5 °C	1.90	2.56	4.46	0.79	4.68	0.22	20.8
25/15 °C	3.01	2.77	5.77	1.16	6.85	0.32	20.8
F test	*	-	*	*	*	*	-

* significant at $p<0.05$

\- not significant at $p<0.05$

in root weight, resulting in an increase in whole plant weight (Table 4.3b). No significant temperature effects on whole plant weight were observed in the other species at week four and in any species at week six because gains in shoot weight were more closely matched with declines in root weight (Tables 4.3b, 4.3c).

Increasing the temperature increased the shoot:root ratio in all species at all harvests (Tables 4.3a, 4.3b, 4.3c). This occurred as enhanced shoot weights were combined with similar or lower root weights. In all cases the higher shoot:root ratios at the high temperature were associated with a higher LWR and LAR (Tables 4.3a, 4.3b, 4.3c). In some instances SLA increased with increasing temperature, however increases were small and not consistent from harvest to harvest (Tables 4.3a, 4.3b, 4.3c).

Temperature, for the most part had no affect on TN but almost always affected TW (Tables 4.4a,4.4b,4.4c). Exceptions occurred in smooth bromegrass and S9044 at the week two harvest where TN was increased by temperature (Table 4.4a). Also at the week six harvest increasing temperature reduced TN in meadow foxtail and tall fescue but the reduction was small (less than 15%) in comparison to corresponding TW increase (32-73%) (Table 4.4c).

In all species the higher TW with the high temperature was associated with a higher LAT, LYT and SYT (Tables 4.4a,4.4b,4.4c). In all species the LYT and SYT were increased to a similar extent by temperature (Tables 4.4a,4.4b,4.4c).

4.3.2 Photoperiod effects

Photoperiod effects on harvestable dry matter yield were significant only in smooth bromegrass at the week four and six harvest and in S9044 at the week six harvest (Table 4.5). The yield increase in smooth bromegrass with photoperiod extension, amounted to 39 and 22 % for the week four and six harvest, respectively. A 24% yield increase was shown in S9044 at week six (Table 4.5).

Whole plant yield however was only enhanced in smooth bromegrass at week four (Table 4.6b). This resulted from an increase in shoot weight combined with a

Table 4.3b. Effects of **temperature** in controlled conditions on the shoot weight, root weight, whole plant weight, shoot:root ratio, leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA) of six grasses after **<u>four weeks</u>** of regrowth.

Temperature	shoot weight (g pot^{-1})	root weight (g pot^{-1})	whole plant weight (g pot^{-1})	shoot: root ratio (g g^{-1})	LAR (m^2 kg^{-1})	LWR (g g^{-1})	SLA (m^{2}kg^{-1})
Smooth bromegrass							
15/5 °C	3.53	4.40	7.93	0.78	9.8¶	0.31§	33.8
25/15 °C	5.78	4.22	10.00	1.52	14.7	0.44	32.9
F test	*	-	*	*	*	*	-
Meadow bromegrass							
15/5 °C	4.30	5.25	9.55	0.83	6.6	0.33	19.9
25/15 °C	5.17	4.21	9.38	1.34	10.3	0.43	23.7
F test	-	*	-	*	*	*	*
S9044							
15/5 °C	2.87	4.28	7.14	0.68	7.3	0.28	25.8
25/15 °C	5.02	3.93	8.95	1.28	12.8	0.43	29.3
F test	*	-	*	*	*	*	*
Meadow foxtail							
15/5 °C	5.16	5.64	10.80	0.99	10.1	0.32	[illegible]
25/15 °C	6.97	5.30	12.28	1.41	12.4	0.40	29.5
F test	*	-	-	*	*	*	
Orchard grass							
15/5 °C	6.54	5.53	12.07	1.30	9.6	0.33	29.0
25/15 °C	8.15	5.34	13.48	1.75	13.0	0.43	29.6
F test	*	-	-	*	*	*	-
Tall fescue							
15/5 °C	5.16	4.54	9.70	1.13	5.9	0.33	18.1
25/15 °C	6.95	3.67	10.62	1.95	10.3	0.47	20.7
F test	*	*	-	*	*	*	*

* significant at P<0.05

\- not significant at P<0.05

¶ Temperature x photoperiod interaction was significant. Values were 9.6 and 11.0 for the low temperature and 16.0 and 13.5 for the high temperature for the 14 and 18 h photoperiod respectively.

§ Temperature x photoperiod interaction was significant. Values were .29 and .33 for the low temperature and .45 and .43 for the high temperature for the 14 and 18 h photoperiod respectively.

Table 4.3c. Effect of **temperature** in controlled conditions on the shoot weight, root weight, whole plant weight, shoot:root ratio, leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA) of six grasses after **six weeks** of growth.

Temperature	shoot weight (g pot^{-1})	root weight (g pot^{-1})	whole plant weight (g pot^{-1})	shoot: root ratio (g g^{-1})	LAR (m^{2} kg^{-1})	LWR (g g^{-1})	SLA (m^{2}kg^{-1})
Smooth bromegrass							
15/5 ^{o}C	12.73	7.52	20.25	1.69	11.3	0.43	25.6
25/15 ^{o}C	14.37	7.21	21.58	2.13	15.3	0.48	30.7
F test	-	-	-	*	*	*	*
Meadow bromegrass							
15/5 ^{o}C	9.51	9.06	18.58	1.07	7.1	0.39	18.3
25/15 ^{o}C	11.59	7.33	18.92	1.67	10.9	0.47	22.0
F test	*	*	-	*	*	*	*
S9044							
15/5 ^{o}C	8.59	7.24	15.83	1.18	9.6	0.39	24.1
25/15 ^{o}C	10.23	6.19	16.42	1.69	13.9	0.49	27.6
F test	*	-	-	*	*	*	*
Meadow foxtail							
15/5 ^{o}C	12.28	9.97	22.25	1.28	11.4	0.38	29.4
25/15 ^{o}C	13.19	8.13	21.32	1.62	12.4	0.44	27.7
F test	-	*	-	*	*	*	-
Orchard grass							
15/5 ^{o}C	15.42	11.04	26.46	1.45	9.7	0.38	25.3
25/15 ^{o}C	17.04	9.77	26.82	1.83	13.3	0.45	29.0
F test	-	-	-	*	*	*	*
Tall fescue							
15/5 ^{o}C	10.50	7.23	17.72	1.48	6.9	0.39	17.6
25/15 ^{o}C	13.64	5.77	19.41	2.39	9.6	0.50	17.6
F test	*	*	-	*	*	*	-

* significant at P<0.05

\- not significant at P<0.05

Table 4.4a Effect of **temperature** in controlled conditions on the tiller number (TN), leaf area per tiller (LAT), leaf yield per tiller (LYT), pseudostem yield per tiller (SYT), and total tiller weight (TW) of six grasses after **two weeks** of regrowth.

Temperature	TN (no.)	LAT (cm^2 $tiller^{-1}$)	LYT (mg $tiller^{-1}$)	SYT (mg $tiller^{-1}$)	TW (mg $tiller^{-1}$)
Smooth bromegrass					
15/5 °C	18.0	7.6	21.7	2.6	24.3
25/15°C	24.8	20.8	53.6	8.2	61.9
F test	*	*	*	*	*
Meadow bromegrass					
15/5 °C	30.3	8.0	31.5	3.8	35.4
25/15°C	31.4	11.7	52.2	5.8	58.0
F test	-	*	*	*	*
S9044					
15/5 °C	19.8	7.9	26.0	1.7	27.7
25/15°C	25.3	13.5	43.4	4.1	47.6
F test	*	*	*	*	*
Meadow foxtail					
15/5 °C	54.8	4.9	15.4	2.7	18.2
25/15°C	62.6	8.4	27.2	5.1	32.3
F test	-	*	*	*	*
Orchard grass					
15/5 °C	31.2	14.6	42.6	6.5	49.0
25/15°C	31.4	23.2	69.5	10.7	80.0
F test	-	*	*	*	*
Tall fescue					
15/5 °C	31.6	6.5	31.3	2.0	33.3
25/15°C	33.1	11.9	57.3	4.9	62.2
F test	-	*	*	*	*

* significant at $P<0.05$

\- not significant at $P<0.05$

Table 4.4b Effects of **temperature** in controlled conditions on the tiller number (TN), leaf area per tiller (LAT), leaf yield per tiller (LYT), psudostem yield per tiller (SYT), and total tiller weight (TW) of six grasses after **four weeks** of regrowth.

Temperature	TN (no.)	LAT (cm^2 $tiller^{-1}$)	LYT (mg $tiller^{-1}$)	SYT (mg $tiller^{-1}$)	TW (mg $tiller^{-1}$)
Smooth bromegrass					
15/5 °C	36.3	21.4	68.4	12.7	81.1
25/15°C	36.2	41.5	125.2	24.8	150.0
F test	-	*	*	*	*
Meadow bromegrasss					
15/5 °C	37.3	17.6	87.7	11.6	99.3
25/15°C	38.8	24.4	103.5	14.1	117.6
F test		*	*	*	*
S9044					
15/5 °C	36.8	14.5	56.5	6.9	63.4
25/15°C	37.9	30.3	103.6	12.4	116.0
F test	-	*	*	*	*
Meadow foxtail					
15/5 °C	112.7	9.5	30.6	6.3	36.9
25/15°C	121.0	13.1	45.1	9.7	54.8
F test	-	*	*	*	*
Orchard grass					
15/5 °C	41.9	27.3	94.6	22.1	116.7
25/15°C	42.9	39.1	131.4	25.3	156.7
F test	-	*	*	-	*
Tall fescue					
15/5 °C	37.5	15.4	85.3	8.7	94.0
25/15°C	38.4	28.4	132.8	14.7	147.4
F test	-	*	*	*	*

* significant at $P<0.05$

\- not significant at $P<0.05$

Table 4.4c Effects of **temperature** in controlled conditions on the tiller number (TN), leaf area per tiller (LAT), leaf yield per tiller (LYT), pseudostem yield per tiller (SYT), and total tiller weight (TW) of six grasses after **six weeks** of regrowth.

Temperature	TN (no.)	LAT (cm^2 $tiller^{-1}$)	LYT (mg $tiller^{-1}$)	SYT (mg $tiller^{-1}$)	TW (mg $tiller^{-1}$)
Smooth bromegrass					
15/5 °C	54.7	42.4	165.3	46.1	211.5
25/15°C	58.3	58.8	184.2	50.0	234.3
F test	-	*	-	-	-
Meadow bromegrass					
15/5 °C	55.6	24.0	131.3	15.3¶	146.6
25/15°C	56.5	36.4	161.3	22.7	184.1
F test	-	*	*	*	*
S9044					
15/5 °C	57.8	27.8	112.6	16.2	128.8
25/15°C	57.4	40.7	147.1	19.1	166.2
F test	-	*	*	-	*
Meadow foxtail					
15/5 °C	172.3	15.3	51.8	10.8	62.6
25/15°C	150.8	18.7	68.0	14.6	82.7
F test	*	*	*	*	*
Orchard grass					
15/5 °C	61.9	41.4	162.6	42.2	204.8
25/15°C	59.3	59.5	205.4	42.2	247.6
F test	-	*	*	-	*
Tall fescue					
15/5 °C	72.9	17.2	96.8	13.3	110.1
25/15°C	62.0	30.2	163.8	27.4	191.2
F test	*	*	*	*	*

* significant according at $P<0.05$

\- not significant according at $P<0.05$

¶ temperature x photoperiod interaction was significant. Values were 14.5 and 16.1 for the low temperature and 18.9 and 26.6 for the high temperature for the 14 and 18 h photoperiod respectively.

Table 4.5 Effects of **photoperiod** in controlled conditions on the harvestable dry matter yield (g pot^{-1}) of six grasses after two, four, and six weeks of regrowth.

Photoperiod	Grass					
	Smooth bromegrass	Meadow bromegrass	S9044	Meadow foxtail	Orchard grass	Tall fescue
			two weeks			
14 h	1.04	1.29	0.83	1.35	1.87	1.65
18 h	1.04	1.39	0.94	1.63	2.07	1.44
F test	-	-	-	-	-	-
			four weeks			
14 h	3.52	4.02	3.27	4.82	5.61	4.51
18 h	4.91	4.26	3.52	5.27	5.95	4.71
F test	*	-	-	-	-	-
			six weeks			
14 h	11.04	9.19	7.31	10.84	12.76	9.26
18 h	13.51	9.32	9.06	10.84	14.22	9.88
F te	*	-	*	-	-	-

* significant at $P < 0.05$

\- not significant at $P < 0.05$

similar root weight and also resulted in an increase in shoot:root ratio (Table 4.6b). By the week six harvest however only the shoot weight remained enhanced (Table 4.6c). For S9044 the higher harvestable dry matter at week six was positively associated with shoot weight and shoot:root ratio (Table 4.6c).

Both LWR and LAR at the week four harvest in smooth bromegrass were affected by a temperature by photoperiod interaction. At the low temperature both LWR and LAR were increased by photoperiod extension but at the high temperature these parameters declined with photoperiod (Tables 4.6b). Since SLA was unaffected, the varying LAR response to photoperiod must be related to varying partitioning into the stem. In the other species significant photoperiod effects on partitioning were occasionally observed but they were small and not consistent from harvest to harvest.

At the week four and six harvest photoperiodic enhancement of harvestable yield in smooth bromegrass was associated with an increase in TW. The TN was unaffected at week four but was reduced by 10% at the week six harvest(Tables 4.7b, 4.7c). This was more than compensated for by a 47% increase in TW (Tables 4.7c). At the week four and six harvest all the components of TW in smooth bromegrass (LAT, LYT and SYT) were increased by daylength extension. The stem fraction was increased proportionately more than the leaf fraction. At week four photoperiod extension increased the SYT by 176 % while LA and LYT were increased by only 18-28% (Tables 4.7b,4.7c).

In S9044 the photoperiodic yield enhancement observed at week six was associated with an increase in SYT. Photoperiod extension had few effects on the tiller characteristics of the other species.

Table 4.6a. Effect of **photoperiod** in controlled conditions on the shoot weight, root weight, whole plant weight, shoot:root ratio, leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA) of six grasses after **two weeks** of regrowth.

Photoperiod	shoot weight (g pot^{-1})	root weight (g pot^{-1})	whole plant weight (g pot^{-1})	shoot: root ratio (g g^{-1})	LAR (m^2 kg^{-1})	LWR (g g^{-1})	SLA (m^{2}kg^{-1})
Smooth bromegrasss							
14h	1.31	3.09	4.40	0.40	6.59	0.18	34.2
18h	1.35	3.55	4.90	0.39	6.55	0.17	37.9
F test	-	-	-	-	-	-	*
Meadow bromegrass							
14h	1.74	3.91	5.65	0.50	4.92	0.21	24.0
18h	1.85	4.15	6.00	0.48	4.84	0.21	23.5
F test	-	-	-	-	-	-	-
S9044							
14h	1.20	3.23	4.43	0.39	5.10	0.17	31.2
18h	1.29	3.46	4.75	0.39	5.22	0.17	30.7
F test	-	-	-	-	-	-	-
Meadow foxtail							
14h	2.26	4.41	6.67	0.55	5.23	0.18	30.2
18h	2.55	4.08	6.63	0.65	6.25	0.20	31.2
F test	-	-	-	*	*	*	-
Orchard grass							
14h	2.88	4.22	7.10	0.81	8.25	0.24	34.4
18h	3.17	4.07	7.24	0.83	8.24	0.25	33.5
F test	-	-	-	-	-	-	-
Tall fescue							
14h	2.58	2.82	5.41	0.97	5.74	0.27	20.5
18h	2.32	2.50	4.82	0.98	5.79	0.27	21.1
F test	-	-	-	-	-	-	-

* significant at $p<0.05$

\- not significant at $p<0.05$

Table 4.6b. Effects of **photoperiod** in controlled conditions on the shoot weight, root weight, whole plant weight, shoot:root ratio, leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA) of six grasses after **four weeks** of regrowth.

Photoperioiod	shoot weight (g pot^{-1})	root weight (g pot^{-1})	total weight (g pot^{-1})	shoot: root ratio (g g^{-1})	LAR (m^2 kg^{-1})	LWR (g g^{-1})	SLA (m^{2}kg^{-1})
Smooth bromegrass							
14 h	3.97	3.93	7.90	1.01	12.6¶	0.37§	34.2
18 h	5.45	4.68	10.12	1.30	11.9	0.38	32.5
F test	*	-	*	*	*		-
Meadow bromegrass							
14 h	4.64	4.18	8.81	1.16	8.9	0.39	22.5
18 h	4.83	5.28	10.12	1.01	7.9	0.37	21.1
F test	-	*	-	*	*	-	*
S9044							
14 h	3.78	4.22	8.00	0.92	9.7	0.35	29.3
18 h	4.11	3.99	8.10	1.04	10.4	0.37	31.5
F test	-	-	-	*	-	-	-
Meadow foxtail							
14 h	5.81	5.45	11.26	1.15	10.9	0.36	31.4
18 h	6.32	5.50	11.82	1.25	11.7	0.37	29.2
F test	-	-	-	-	-	-	-
Orchard grass							
14 h	7.17	5.59	12.76	1.51	11.4	0.38	28.9
18 h	7.51	5.28	12.79	1.54	11.2	0.37	29.6
F test	-	-	-	-	-	-	-
Tall fescue							
14 h	5.94	4.06	10.00	1.54	8.0	0.40	19.0
18 h	6.17	4.15	10.32	1.53	8.2	0.40	19.7
F test	-	-	-	-	-	-	-

* significant at $p<0.05$

\- not significant at $p<0.05$

¶ Temperature x photoperiod interaction was significant. Values were 8.5 and 11.1 for the low temperature and 16.7 and 12.7 for the high temperature for the 14 and 18 h photoperiod respectively

§ Temperature x photoperiod interaction was significant. Values were .29 and .33 for the low temperature and .45 and .43 for the high temperature for the 14 and 18 h photoperiod respectively.

Table 4.6c. Effect of **photoperiod** in controlled conditions on the shoot weight, root weight, whole plant weight, shoot:root ratio, leaf area ratio (LAR), leaf weight ratio (LWR), and specific leaf area (SLA) of six grasses after **six weeks** of regrowth.

Photoperiodic	shoot weight (g pot^{-1})	root weight (g pot^{-1})	whole plant weight (g pot^{-1})	shoot: root ratio (g g^{-1})	LAR (m^2 kg^{-1})	LWR (g g^{-1})	SLA (m^{2}kg^{-1})
			Smooth bromegrass				
14 h	12.30	7.04	19.34	1.87	14.2	0.47	28.5
18 h	14.7[illegible]	7.67	22.46	1.96	12.4	0.43	27.4
F test	*	-	-	-	*	*	-
			Meadow bromegrass				
14 h	10.45	8.47	18.97	1.30	9.0	0.42	20.2
18 h	10.61	7.91	18.52	1.44	9.0	0.44	19.8
F test	-	-	-	-	-	-	-
			S9044				
14 h	8.48	6.56	15.04	1.31	11.7	0.43	26.3
18 h	10.34	6.86	17.21	1.56	11.8	0.45	25.2
F test	*	-	-	*	-	*	-
			Meadow foxtail				
14 h	12.81	9.14	21.95	1.43	11.5	0.41	27.9
18 h	12.66	8.96	21.62	1.47	12.3	0.42	29.2
F test	-	-	-	-	-	-	-
			Orchard grass				
14 h	15.51	10.51	26.02	1.54	11.6	0.41	27.6
18 h	16.96	10.31	27.26	1.73	11.4	0.42	26.4
F test	-	-	-	-	-	-	-
			Tall fescue				
14 h	11.71	6.44	18.14	1.92	8.6	0.45	18.1
18 h	12.43	6.56	18.99	1.95	7.9	0.44	17.2
F test	-	-	-	-	-	-	-

* significant at $P<0.05$

\- not significant at $P<0.05$

Table 4.7a. Effects of **photoperiod** in controlled conditions on the tiller number (TN), leaf area per tiller (LAT), leaf yield per tiller (LYT), psudostem yield per tiller (SYT), and total tiller weight (TW) of six grasses after **<u>two weeks</u>** of regrowth.

Temperature	TN (no.)	LAT (cm^2 tiller^{-1})	LYT (mg tiller^{-1})	SYT (mg tiller^{-1})	TW (mg tiller^{-1})
Smooth bromegrass					
14 h	20.6	14.2	38.8	4.7	43.5
18 h	22.2	14.2	36.5	6.2	42.7
F test	-	-	-	-	-
Meadow bromegrass					
14 h	30.1	9.8	40.9	4.7	45.6
18 h	31.6	10.0	42.9	5.0	47.8
F test	-	-	-	-	-
S9044					
14 h	23.6	9.9	31.9	2.1	34.0
18 h	21.5	11.5	37.6	3.7	41.2
F test	-	-	-	-	-
Meadow foxtail					
14 h	57.9	6.2	20.3	3.6	23.8
18 h	59.4	7.1	22.4	4.2	26.6
F test	-	-	-	-	-
Orchard grass					
14 h	31.5	18.3	53.4	7.6	61.0
18 h	31.1	19.4	58.6	9.6	68.2
F test	-	-	-	-	-
Tall fescue					
14 h	33.2	9.4	45.9	3.5	49.4
18 h	31.5	9.0	42.7	3.4	46.1
F test	-	-	-	-	-

* significant according at $P<0.05$

- not significant according at $P<0.05$

Table 4.7b. Effects of **photoperiod** in controlled conditions on the tiller number (TN), and leaf area per tiller (LAT), leaf yield per tiller (LYT), pseudostem yield per tiller (SYT), and total tiller weight (TW) of six grasses after **four weeks** of regrowth.

Photoperiod	TN (no.)	LAT (cm^2 $tiller^{-1}$)	LYT (mg $tiller^{-1}$)	SYT (mg $tiller^{-1}$)	TW (mg $tiller^{-1}$)
Smooth bromegrass					
14 h	36.0	28.8	86.2	10.1	96.3
18 h	36.5	34.1	109.9	27.9	137.8
F test	-	*	*	*	*
Meadow bromegrass					
14 h	38.3	20.0	88.7	11.9	100.6
18 h	37.9	22.0	102.5	13.9	116.3
F test	-	-	*	-	*
S9044					
14 h	36.8	21.9	79.7	7.9	87.6
18 h	37.9	22.9	80.5	11.4	91.8
F test	-	-	-	*	-
Meadow foxtail					
14 h	112.2	11.0	38.4	7.7	46.1
18 h	121.5	11.6	37.4	8.3	45.6
F test	-	-	-	-	-
Orchard grass					
14 h	43.0	32.5	112.2	21.2	133.4
18 h	41.8	33.9	113.8	26.2	140.1
F test	-	-	-	-	-
Tall fescue					
14 h	35.4	22.7	114.4	10.9	125.3
18 h	40.6	21.1	103.6	12.5	116.1
F test	*	-	-	-	-

* significant at $P<0.05$

\- not significant at $P<0.05$

Table 4.7c. Effects of **photoperiod** in controlled conditions on the tiller number (TN), and leaf area per tiller (LAT), leaf yield per tiller (LYT), psudostem yield per tiller (SYT), and total tiller weight (TW) of six grasses after **six weeks** of regrowth.

Photoperiod	TN (no.)	LAT (cm^2 $tiller^{-1}$)	LYT (mg $tiller^{-1}$)	SYT (mg $tiller^{-1}$)	TW (mg $tiller^{-1}$)
Smooth bromegrass					
14 h	62.5	45.3	153.0	27.1	180.1
18 h	50.8	56.1	196.1	68.3	264.4
F test	*	*	*	*	*
Meadow bromegrass					
14 h	56.7	29.6	142.1	16.7¶	158.8
18 h	55.4	30.8	150.6	21.4	171.9
F test	-	-	-	*	-
S9044					
14 h	55.3	33.1	124.6	13.5	138.1
18 h	59.9	35.5	135.1	21.9	157.0
F test	-	-	-	*	-
Meadow foxtail					
14 h	168.6	16.0	58.1	11.8	70.0
18 h	154.4	17.9	61.7	13.6	75.3
F test	-	*	-	-	-
Orchard grass					
14 h	60.3	50.3	179.8	36.3	216.1
18 h	60.9	50.7	188.2	48.1	236.3
F test	-	-	-	*	-
Tall fescue					
14 h	68.4	23.9	127.9	17.0	144.8
18 h	66.6	23.5	132.8	23.7	156.5
F test	-	-	-	*	-

* significant according at $P<0.05$

\- not significant according at $P<0.05$

¶ temperature x photoperiod interaction was significant. Values were 14.5 and 16.1 for the low temperature and 18.9 and 26.6 for the high temperature for the 14 and 18 h photoperiod respectively.

4.4 DISCUSSION

4.4.1 Temperature

Significant temperature effects on dry matter yield were observed in all species. However, effects were large only early in regrowth and tended to be largest in smooth bromegrass, S9044 and tall fescue. Regrowth response to temperature has been related to latitude of origin with more northerly species often expressing dormancy at low temperatures (Ostgard and Eagles 1971). The absence of large differences among species in response to temperature in this study may be due to the fact that the temperatures used were too high to initiate dormancy. Dormancy has been reported only below a constant 5^{o}C in tall fescue (Cooper 1964) and below 8^{o}C in orchard grass (Ostgard and Eagles 1971; Ryle 1966a). Yield enhancement due to temperature diminished as the plants matured. This is probably because respiration increases in relation to photosynthesis as plants mature and subsequently the optimum temperature for dry matter accumulation shifts downward as plants mature (Kemp 1986).

Associated with dry matter yield increases in all species were higher shoot:root ratios. This was the result of an increase in shoot weight combined with a constant or lower root weight, and is in agreement with earlier reports for a number of grasses (Cooper and Tainton 1968). In addition to partitioning more into shoots at the high temperature all species partitioned more of their dry matter into leaf area. This can be attributed to higher shoot:root ratios associated with greater partitioning into leaf weight and at times a higher SLA. Higher growth rates in smooth bromegrass, due to temperature were previously attributed mainly to greater partitioning into leaf area as a result of a higher SLA and LWR with variation in NAR of lesser importance (Tan et al. 1978).

Dry matter yield can be expressed as the product of tiller number and tiller weight (Nelson et al. 1977). Temperature effects on harvestable dry matter yield resulted mainly from a higher TW as TN was unaffected or affected only slightly. An exception to this was at week two where TN in smooth bromegrass was increased. Harvestable dry matter yield in this species was perhaps somewhat more responsive to temperature than the other species at this harvest because of the enhancement of both yield components. Cooper and Tainton (1968) reviewed effects of temperature on tillering and concluded tillering has a lower optimum temperature than tiller weight.

4.4.2 Photoperiod

Significant enhancement of harvestable dry matter yield ranging from 22 to 39% as a result of photoperiod extension was observed only in smooth bromegrass and S9044, and was independent of temperature. Heide et al. (1985a) found a similar dry matter yield increase of 33% in smooth bromegrass cv. Manchar when daylength was extended from 8h to 24h at a constant temperature of 15°C, but a decline at constant 21°C. Our results did not show a temperature by photoperiod interaction but this may be due to our use of an alternating temperature. Opposite effects of photoperiod for a constant versus alternating temperature have been reported by Templeton et al. (1961). Another possibility is that Carlton smooth bromegrass is very well adapted to the high summer temperatures of western Canada.

Response to photoperiod has been attributed to an adaptation of species to the climatic conditions at the species origin (Eagles 1971, Heide et al 1985a, Klebesadel and Helm 1986). Yield enhancement under long days was reported to be larger in more northerly species (Hay and Pedersen 1985) with greatest enhancement at low to moderate temperatures (Eagles and Ostgard 1971, Hay and Heide 1983, Heide et al. 1985). This response would enable northern species to regrow rapidly in the long cool days of spring in northern latitudes (Heide et al. 1985a). Smooth bromegrass exhibited the largest yield response to daylength (Table 4.5). The photoperiod response was absent in the species with the lowest latitude of origin (meadow bromegrass) but not necessarily present in the higher latitude cultivars (Table 4.5).

Lack of response to photoperiod does not appear related to winter hardiness. Meadow foxtail and meadow bromegrass are very winter hardy in central Alberta and exhibited no photoperiod response, while orchard grass which showed a slight photoperiod response is less winter hardy (Anonymous 1984).

Plant partitioning data showed that higher dry matter yields for smooth bromegrass under long days were due mainly to an enhancement of top growth with root growth unaffected and thus yield enhancements were not simply the result of alterations in partitioning. A similar conclusion was made by Heide et al. (1983, 1985a) for timothy, bluegrass and smooth bromegrass. The larger photoperiodic increase in shoot than root growth accounts for the increased shoot:root ratios observed in smooth bromegrass and S9044. These findings are consistent with the previous work by Heide et al. (1985). In contrast to the work by Eagles (1971), Ryle (1966a) and Tempelton (1968), no photoperiod effect on shoot:root ratio in orchard grass was observed. This may be due to the fact that only a 4 h photoperiod extension was used in this study as compared to an 8-10 h difference in the previous studies.

The parameters associated with photoperiodic yield enhancements in smooth bromegrass and S9044 varied with maturity and temperature. It appeared that early in the life of the tiller (for example week four at the low temperature) yield enhancements were the result of a greater partitioning into leaves. However as the tillers matured and stem content of the tiller increased (week four at the high temperature and week six at both temperatures) yield enhancements occurred despite a reduced partitioning into leaf weight and area (Tables 4.6b, 4.6c).

Previously Hay and Heide (1985a) and Heide et al. (1987) concluded that yield enhancement at extended photoperiods in timothy occurred as a result of a higher LAR. Since in their case the proportion of leaves was unaffected (LWR), they attributed the increase in LAR at extended photoperiods to a higher shoot:root ratio and a higher SLA. Robson and Jewis (1968) also concluded that a higher RGR in a North African tall fescue ecotype, than in a British type in winter resulted from higher LAR. In this study, however, changes in LAR early in the life of the tiller appeared to account for the higher LWR.

The lower LAR at extended photoperiods for smooth bromegrass in this study at week four and six at the high temperature are in contrast with previous findings by Heide et al. (1985a,1985b). The lower LAR observed under long days was to a great extent a result of a reduced proportion of leaves (larger portion of stem), as SLA was relatively unaffected. The question arises as to how smooth bromegrass achieved a higher yield under an extended daylength when it had a lower LAR. Since RGR= NAR x LAR, by deduction one might conclude a higher NAR was involved. Although Heide et al. (1985b) observed a short term increase in NAR at 9^{O}C in bluegrass when daylength was extended from 8 to 24h, they concluded that growth stimulation occurred mainly as the result of an increased LAR.

These conflicting findings between species and researchers suggest that the mechanisms of photoperiodic yield enhancement vary with maturity and among species. In light of the large role of stem production in smooth bromegrass, mechanisms may also vary between induced and non-induced plants.

Photoperiodic dry matter yield enhancement in smooth bromegrass resulted al exclusively from larger tillers as TN remained largely unaffected. An exception was the week six harvest where a 19% reduction in TN was observed under extended daylength but this was slight in comparison to the 47% increase in TW (Table 4.7c). Reductions in tillering in smooth bromegrass at extended photoperiods have previously been reported by Gall (1947).

An examination of the photoperiod effect on tiller characteristics for smooth bromegrass at week four showed that the increased LYT was the result of a higher LAT since SLA was unaffected. The increased leaf area and weight at an extended photoperiod was in agreement with earlier reports (Bowman and Law 1963, Heide et al

1985a). Photoperiod effects on TW in smooth bromegrass were much more pronounced on stem than leaf growth. At week four SYT was increased by 176% in comparison to the 27% increase for LYT. This resulted in the stem fraction almost doubling to account for 10 and 20% of the total TW at the low and high photoperiod, respectively. Meanwhile leaf content of the tiller dropped from 90 to 80% as photoperiod was extended. In S9044 photoperiodic yield enhancement observed at week six was associated with increases only in SYT.

4.4.3 Conclusions

Photoperiod and temperature effects on harvestable dry matter yield were independent. Yield enhancements due to temperature ranged from 110 % at week two to 24% by week six averaged over all species. In general temperature affected only TW and not TN. Temperature effects on harvestable dry matter yield were largest in smooth bromegrass at week two where both TN and TW were increased. Photoperiod extension from 14 to 18 h with low levels of incandescent light increased the yields of smooth bromegrass and S9044 by 22-39%. Photoperiodic yield enhancement occurred as a result of a stimulation of top growth and was associated primarily with a larger TW as TN was relatively unaffected. The stem fraction of smooth bromegrass was increased proportionally more than leaves. Despite higher yields at an extended photoperiod for smooth bromegrass at the week six harvest LAR was reduced but may have reflected a period of rapid stem accumulation.

5. EFFECTS OF TEMPERATURE AND PHOTOPERIOD ON THE EXTENSION GROWTH OF LEAVES AND STEMS OF SIX TEMPERATE GRASSES

5.1 INTRODUCTION

A linear relationship between canopy photosynthesis and light interception has led to the conclusion that crop growth rate (CGR) is primarily dependent on the leaf area index (LAI) (Beadle et al. 1986). Lower late season pasture yield of smooth bromegrass in comparison with meadow foxtail and S9044 was attributed to a lower rate of leaf area production (Chapter 3). In controlled conditions, lower yields at reduced temperatures in a range of grass species were associated primarily with reductions in individual tiller leaf area and stem dry matter (Chapter 4). Shortening the photoperiod however reduced yields of only smooth bromegrass and was also associated with reductions in individual tiller leaf area and stem production (Chapter 4). In grasses high leaf area extension rates were suggested as a mechanism for rapidly achieving a high LAI and high growth rates following defoliation (Edwards 1967; Nelson et al. 1978). The final size of leaves and the rate of leaf appearance are considered the two principal components of leaf area production in grasses (Edwards 1967). Final size of leaves is largely determined by the final length, which is the product of leaf elongation rate and duration of extension (Ong and Baker 1985). Horst et al. (1978) concluded leaf extension rate to be 1.7 times as important as leaf width in determining leaf area expansion rate, and observed a positive relationship between leaf elongation rate and herbage yield. In field experiments with wheat, Gallagher (1978) showed that leaf extension rate was directly related to leaf area expansion rate. Norris (1985) concluded leaf extension rate to be the major contributor to yield of ryegrass in the field in summer.

In grasses when one leaf ceases to elongate a new leaf begins to elongate and therefore the rate of new leaf appearance is directly related to the duration of extension (Edwards 1967). The duration of extension and final leaf length are also directly related (Copper and Edwards 1961; Edwards 1967; Nelson et al. 1978) and thus, selection for increased leaf size or rate of appearance (reduced duration) would likely result in a reduction in the other character. Selection for increased leaf length has however resulted in a yield increase in ryegrass (Rhodes and Mee 1984). Zarrough et al. (1978) reported that in tall fescue selection for high yielding tillers, increased leaf extension rate to a larger degree than it reduced duration of extension.

Steady rates of leaf elongation with constant temperature have been reported for monocotyledonous plants (Gallagher 1978; Robson 1972; Wilson 1970). Constant rates of leaf appearance at constant temperature were also shown in wheat (Triticum aestivum L.) (Friend et al. 1962; Gallagher 1978), pearl millet (Pennisetum typhoides S & H.) (Ong 1983) and ryegrass (Salisbury 1970). Considerable variation however, was shown to exist between and within species for both rate of extension and rate of initiation or duration of extension in response to temperature and photoperiod (Cooper 1964, Hede et al. 1985; Nelson et al. 1978; Ryle 1966a). Differing species or ecotype responses were most evident at temperature and photoperiod extremes (Cooper 1964; Eagles 1971; Nelson et al. 1978). Although temperature, daylength and ontogenetic position can affect leaf expansion, the number of leaves elongating on a tiller remains virtually constant (Robson 1967, 1972).

Stem extension in non-initiated tillers of certain species can also be influenced by daylength (Milthorpe and Moorby 1979). Rapid stem extension under long days may act as a strong sink to stimulate photosynthetic rates (Deinum 1976) or to elevate developing leaves to higher light levels which have been associated with high leaf photosynthetic rates (Parsons and Robson 1980; Woledge 1978). Ryle (1966b) attributed higher net assimilation rates under long days in orchard grass to changes in the light attenuation properties of the canopy caused by culm elongation.

Temperature and photoperiod decline as autumn approaches in central Alberta. The mechanisms by which temperature and photoperiod affect leaf area expansion or stem extension of commonly grown species in central Alberta have not been well defined. These environmental parameters could influence the growth of leaves and stems directly and may have indirect effects on canopy photosynthesis by altering the light attenuation properties of the canopy. The objective of this study was to assess the influence of temperature and photoperiod on the extension growth of leaves and stems in six temperate grasses.

5.2 MATERIALS AND METHODS

Leaf and stem growth of individual tillers was studied on the plants from Chapter 4 that were harvested on week six. Grass species, plant preparation and treatments were thus identi[illegible] Chapter 4. A single tiller per pot was marked one week after the experiment was in[illegible] length of each leaf lamina from its tip to its collar [illegible]ed on the selected tillers once a week. If a collar had not yet formed, [illegible] rement was taken from the leaf tip to the uppermost collar on the tiller. Th[illegible] of all exposed lamina lengths on the tiller was then termed "accumulated leaf lamina length per tiller". Once a leaf had been measured its length was included in subsequent weeks even though it may have senesced. The following measurements were also taken on the selected tillers: the number of leaves, the culm height (height from the [illegible]rface to the uppermost collar), and the length of the most recently collared leaf lamina. The number of elongating leaves per tiller was determined as the number of visible leaves that had not formed a collar. Liner regression of leaf number per tiller and accumulated leaf lamina length per tiller versus time (weeks) was used to determine the leaf appearance rate and lamina extension rate per tiller (LER), respectively. Data were analyzed in an analysis of variance as indicated in Chapter 4.

5.3 RESULTS

5.3.1 Temperature

Accumulated leaf lamina length per tiller showed a linear relationship with time (the mean r^2 was .98), and thus within each species and growing environment leaf lamina length accumulated at a constant rate. There were no temperature by photoperiod interactions for LER. Increasing the temperature increased the LER rate in all species with meadow foxtail least responsive (+37%) and tall fescue most responsive (+72%) (Table 5.1). Thus, the Q_{10} value for leaf extension between 15/5 and 25/15°C ranged from 1.37 to 1.72.

Within each species and treatment the number of leaves per tiller increased linearly with time (the mean r^2 was .93) which indicated a constant leaf appearance rate. A temperature by photoperiod interaction occurred for leaf appearance rate in smooth bromegrass with the increase in leaf appearance rate due to daylength extension 15 and 41% at the low and high temperature, respectively (Table 5.2). No temperature by photoperiod interaction occurred for leaf appearance rate in the other species and temperature effects were evident in meadow bromegrass, meadow foxtail and orchard grass (Table 5.2).

No temperature by photoperiod interactions were evident for leaf length. The temperature increase resulted in an increase in final lamina length of all species ranging from 8 to 53% (Table 5.3). The number of visibly extending leaves, although significant in two cases, was almost identical for the two temperature treatments. Values however varied somewhat between species (Table 5.4).

Stem extension in most instances did not increase in a linear fashion (Fig. 5.1). Temperature increased stem height in all cases but effects for the most part were less than on leaf extension. Data for final stem heights (week six) showed temperature effects in smooth bromegrass, meadow bromegrass orchard grass and tall fescue (Table 5.5).

Table 5 Effect of temperature and photoperiod in controlled conditions on the leaf lamina tiller extension rate per tiller (cm lamina week^{-1} tiller^{-1}) of six grasses

Treatment	Species					
	Smooth bromegrass	Meadow bromegrass	S9044	Meadow foxtail	Orchard grass	Tall fescue
Temperature						
15/5 °C	26.4	21.9	22.4	13.4	21.7	11.5
25/15 °C	38.8	3[illegible]	31.2	18.3	33.8	[illegible]
F	*	*	*	*	*	*
% change	[illegible]7	+49	+39	+37	+56	+72
Photoperiod						
14 h	28.6	26.3	2[illegible]4	15.1	26.1	15.2
18 h	36.7	28.3	29.2	16.6	29.4	16.1
F	*	-	*	-	*	-
% change	+28	+8	+20	+10	+13	+6

* significant at $p < 0.05$.
\- not significant at $p < 0.05$.

Table 5.2 Effect of temperature and photoperiod in controlled conditions on the leaf appearance rate (leaves week^{-1}) of six grasses

Treatment	Grass					
	Smooth ¶ bromegrass	Meadow bromegrass	S9044	Meadow foxtail	Orchard grass	Tall fescue
Temperature						
[illegible]	1.03	0.80	0.84	0.59	0.81	0.50
[illegible]	1.25	0.61	0.91	0.77	0.95	0.56
F test	*	*		*	*	-
% change	+21	+24	+8	+31	+17	+12
Photoperiod						
14 h	1.00	0.69	0.85	.066	0.87	0.50
18 h	1.28	0.71	0.89	0.70	0.89	0.56
F test	*	-	-		-	-
% change	+29	+3	+5	+6	+3	+12

* significant at $p < 0.05$

\- not significant at $p < 0.05$

¶ the temperature x photoperiod interaction was significant. Values were 0.96 and 1.10 for the low temperature and 1.04 and 1.47 for the high temperature for the 14 and 18 h photoperiod respectively.

Table 5.3 Effect of temperature and photoperiod in controlled conditions on the lamina leng (cm) of the most recently collard leaf of six grasses. Values are from four to six weeks of regrowth.

Treatment	Grass					
	Smooth bromegrass	Meadow bromegrass	S9044	Meadow foxtail	Orchard grass	Tall fescue
Temperature						
15/5 °C	27.2	36.0	29.7	24.0	30.0	23.2
25/15 °C	31.4	45.1	37.3	25.9	39.0	35.4
F test	*	*	*	*	*	*
% change	+15	+25	+26	+8	+30	+53
Photoperiod						
14 h	29.7	39.5	30.8	24.3	33.3	29.2
18 h	28.9	41.6	36.2	25.7	35.7	29.4
F test	-	-	*	-	-	-
% change	-3	+5	+18	+6	+7	+1

* significant at $P < 0.05$

- not significant at $P < 0.05$

Table 5.4 Effect of temperature and photoperiod in controlled conditions on the number of visibly extending leaves per [illegible] six grasses.

Treatment	Grass					
	Smooth bromegrass	Meadow bromegrass	S9044	Meadow foxtail	Orchard grass	Tall fescue
Temperature						
15/5 °C	1.80	1.70	1.69	1.06	1.68	1.12
25/15 °C	1.58	1.84	1.70	1.05	1.69	1.17
F test	*	*	-	-	-	-
Photoperiod						
14 h	1.69	1.81	1.63	1.06	1.66	1.14
18 h	1.69	1.73	1.76	1.05	1.71	[illegible]
F test	-		*	-	-	-

* significant at $P < 0.05$

\- not significant at $P < 0.05$

5.3.2 Photoperiod

Photoperiod extension increased the LER only in smooth bromegrass, S9044 and orchard grass with increases of 28% and 20% and 13%, respectively (Table 5.1). The effect of photoperiod extension on leaf appearance rate varied with temperature (Table 5.2). At the high temperature photoperiod extension increased leaf appearance rate (+41%) more than at the low temperature (+15%) (Table 5.2). Photoperiod extension affected lamina length only in S9044 where the increase was 18% (Table 5.3).

Stem height was increased by photoperiod in smooth bromegrass (+94%) and in orchard grass (11%). Data from the third to sixth week for smooth bromegrass revealed an average stem extension of 1.1 cm week $^{-1}$ at the short photoperiod in comparison to 3.1 cm week $^{-1}$ at the long photoperiod. In contrast, temperature increased the stem extension rate from 1.9 to 2.3 cm week $^{-1}$ (Fig 5.1).

5.4 Discussion

The constant rates of lamina accumulation observed under constant environment were consistent with earlier findings (Ong and Baker 1985; Robson 1972). A constant rate of laminar increase would imply that when tiller number is stable and leaf width constant leaf area expansion should be linear. This has been confirmed in pearl millet where Squire et al. (1984) found LAI linearly related to temperature

The responsiveness of leaf lamina extension to temperature (Q_{10} values ranged from 1.37 to 1.72) was similar to that observed by other researchers. Kemp (1986) reported a value of 1.5 at 15°C for ryegrass in the autumn. Data from Nelson (1978) indicated a Q_{10} of 2.8 and 1.4 between temperature ranges of 10-20 and 15-25°C, respectively, for a range of vegetative tall fescue ecotypes. Robson (1972) concluded that day temperature had a greater effect on leaf growth than night temperature and this may explain why the Q_{10} value from this study was closer to the 1[illegible]

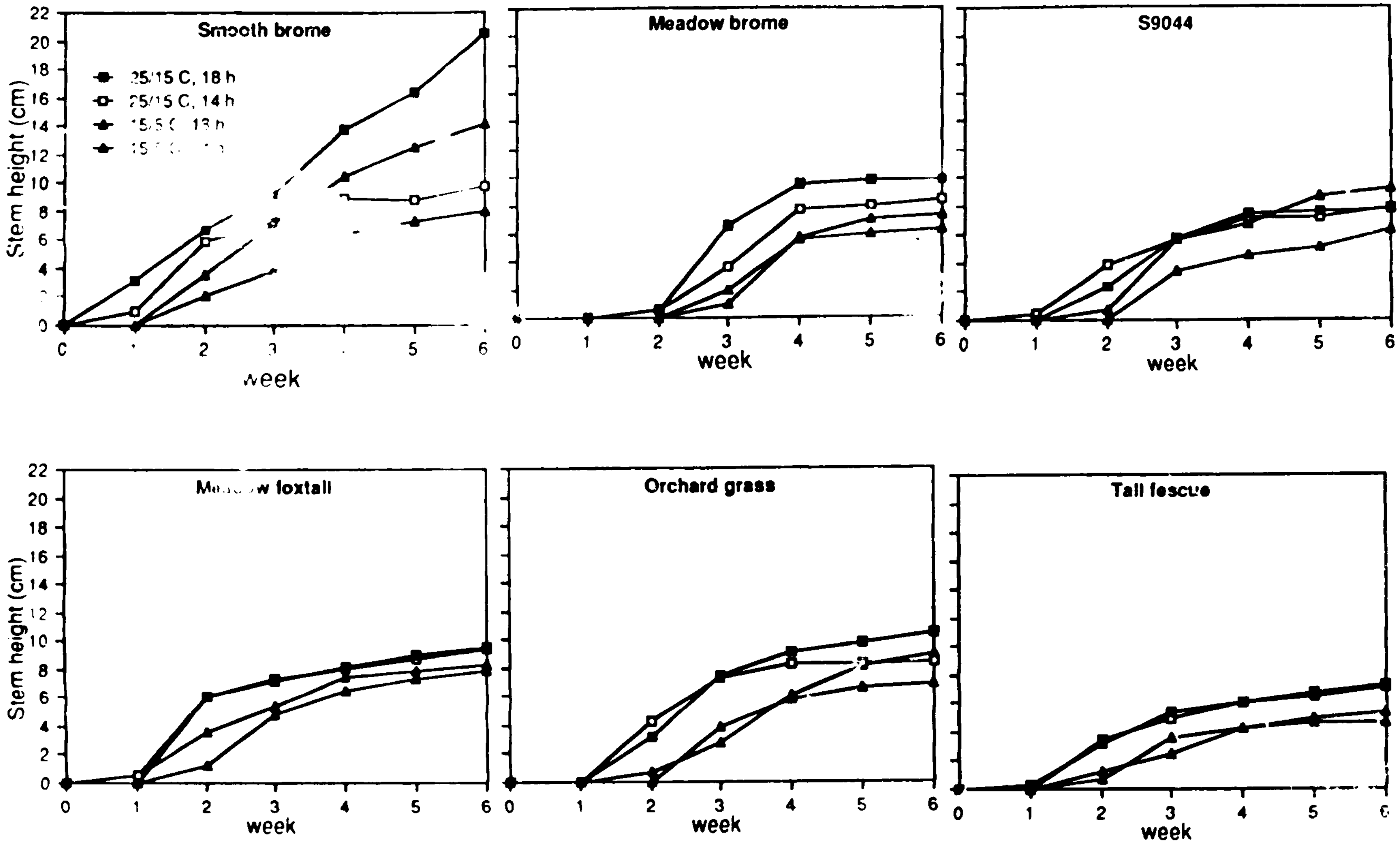

Fig. 5.1 Effect of temperature and photoperiod treatments in controlled conditions on the stem height (cm) of six grasses.

Table 5.5. Effect of temperature and photoperiod in controlled conditions on the pseudostem height (cm) of six grasses after six weeks of regrowth.

Treatment	Grass					
	Smooth bromegrass	Meadow¶ bromegrass	S9044	Meadow foxtail	Orchard grass	Tall fescue
Temperature						
15/5 °C	11.1	6.8	7.7	8.1	7.9	5.0
25/15 °C	15.2	9.0	7.8	9.4	9.4	7.2
F test	*	*	-	-	*	*
Photoperiod						
14 h	8.9	7.8	7.1	8.6	7.7	6.0
18 h	17.4	8.1	8.4	8.9	9.7	6.3
F test	*	-	-	-	*	-

* significant at $p< 0.05$

\- not significant at $p< 0.05$

¶ the temperature x photoperiod interaction was significant. Values were 7.2 and 6.3 for the low temperature and 8.3 and 9.8 for the high temperature for the 14 and 18 h photoperiod respectively.

Nelson (1978). Nelson (1978) found few differences between tall fescue ecotypes for leaf growth until temperature declined to 8^{o}C, and Eagles (1971) showed effects on leaf growth in orchard grass ecotypes only at temperature extremes, below 5^{o}C and above 30^{o}C under short photoperiods. The lack of large differences among species to temperature in this study may reflect the moderate temperatures used.

The fact that the number of extending leaves remained constant is in agreement with Langer (1954) and Robson (1967, 1972) who also found a nearly constant number of leaves extending in tall fescue and timothy. Since in all instances the number of extending leaves remained relatively unaffected by treatment, increases in LER were the result of increases in individual leaf extension rates. The treatment effects on leaf length reflected the balance between effects on rate of extension and rate of new leaf appearance. In general the temperature increase resulted in a larger increase in lamina extension rate than leaf appearance rate and final lamina length increased. A similar result showing temperature to have a greater effect on leaf extension rate than on leaf appearance rate was obtained for ryegrass (Peacock 1975) and tall fescue (Robson 1972). This direct relationship between rate of extension and rate of appearance has been previously noted (Dale 1982, Zarrough et al. 1984). A direct relationship between rate of appearance and final length was also apparent (Tables 5.2, and 5.3), as was previously found in tall fescue by Nelson et al. (1978) and Robson (1972).

In smooth bromegrass the photoperiodic increase in lamina extension and stem extension rate, 28 and 94% respectively, was consistent with Heide et al. (1987) who reported increased tiller extension growth, measured as plant height. It was, however, not possible to discern from their study if this was the result of leaf extension growth or sheath and culm extension. Higher rates of leaf extension under long days have been attributed to higher rates of cell division and extension which result in broader and longer epidermal cells (Hay and Heide 1983, Stuckey 1942).

In smooth bromegrass the photoperiodic increase in lamina extension rate was matched with a similar increase in leaf appearance rate, and final lamina length remained unaffected (Tables 5.1, 5.2 and 5.3). In S9044 photoperiod extension enhanced leaf extension rate to a greater extent than leaf appearance rate, and resulted in longer leaves (Tables 5.1, 5.2 and 5.3). Previously Heide et al. (1985a) reported a 60% increase in the leaf appearance rate in smooth bromegrass when photoperiod was extended from 8 to 24 h. Ryle (1966a) observed no effect of photoperiod on leaf appearance rate in tall fescue and ryegrass but recorded a reduction in the leaf appearance rates of orchard grass when daylength was increased from 8 to 16 h. Templeton (1961) found the opposite effect in orchard grass, a decrease in leaf appearance rate with photoperiod extension. In this experiment increasing the photoperiod by 4 h did not produce an affect on leaf appearance rate in orchard grass. Differences between experiments may be due to genotype or possibly to varying temperature regimes or light levels used. Templeton et al. (1961) observed different effects of photoperiod on leaf appearance rate at a constant versus alternating temperature. Leaf emergence in several species was delayed at low levels of light (Dale 1982, Peacock 1975). Weak tungsten illumination, used in daylength extension experiments, was shown to restrict the rate at which primordia were initiated (Baker and Gallagher 1983).

The absence of a photoperiodic effect on lamina length in smooth bromegrass is in contrast with Heide et al. (1984) who reported a large increase in leaf length in smooth bromegrass and Stuckey (1942) and Ryle (1966a) who observed longer leaf lengths in orchard grass with daylength extension. Although the increase in leaf production under long days was consistent among researchers the mechanisms appear to be different and may reflect influence of the growing environment on leaf morphology.

Although temperature effects on lamina extension were evident in smooth bromegrass they were not large in comparison to the effect of photoperiod on stem extension. Stem elongation did not cease at the 14 h photoperiod in smooth bromegrass as had been noted in the field by Waddington and Storgaard (1971) but continued at a slow rate. Large photoperiodic effects on culm elongation were previously observed in smooth bromegrass (Gall 1947, Heide et al. 1984).

Both leaf length and stem height can influence the light attenuation properties of canopies (Rhodes 1973). Shorter leaves at lower temperatures were common for all species, but marked effects on stem elongation were observed only in smooth bromegrass. The effect of reduced stem height on the light attenuation properties in this species needs further study. If stem extension under short days could improve late season growth rates without affecting winter survival then selection for photo insensitive stem extension may be warranted.

In conclusion, a temperature increase from 15/5 to 25/15°C; day/ night increased lamina accumulation rate in all species by a factor of 1.5. Extending the photoperiod from 14 to 18 h increased the LER of smooth bromegrass, S9044, and orchard grass by 28 , 20 and 13%, respectively, and had no effect on meadow bromegrass, meadow foxtail and tall fescue. Temperature and photoperiodic induced changes in final lamina length reflected interrelationships between leaf extension rate and duration of extension. Photoperiod extension in smooth bromegrass and S9044 effected leaf extension to a lesser extent than a 10°C temperature increase. The 10°C Temperature increase resulted in a 47 and 39 % increase in LER for smooth bromegrass and S9044, respectively. In comparison the 4 h photoperiod extension increased LER by only 20-28%.

6. GENERAL DISCUSSION

The pattern of late season dry matter accumulation observed in the field at Lacombe was similar to the general pattern of late season regrowth described by Alberda and Simba (1968) and Leafe et al. (1974). The steady increase in CGR as LAI and light interception increased prior to canopy closure, confirmed the view that under frequently clipped systems light interception is the most important limitation to the growth of the crop. Thus, to improve forage production during the first month of regrowth when light interception is incomplete breeding or management strategies should be developed to increase the light interception of the canopy (Nelson 1982).

During this first month of regrowth, yields of meadow bromegrass, meadow foxtail and S9044 were often double that of smooth bromegrass (Fig 3.1). Traits associated with a higher yield and CGR in these species were a high TN, LAI and a high NAR (Chapter 3). Traits previously associated with rapid light interception and high yields in frequently clipped stands include a large number of tillers, a large residual leaf area and a high leaf area expansion rate (Rhodes 1973). Wilhelm and Nelson (1982) suggested selection for a rapid rate of leaf area expansion in order to achieve greater utilization of incident light energy early in regrowth.

The low yield of smooth bromegrass early in regrowth may have in part been due to the removal of stem apices. In greenhouse experiments despite smooth bromegrass' slower initial regrowth it attained higher growth rates than meadow bromegrass, and yields of the two species were equal after five weeks (Baron and Knowles 1984). In the field experiment, despite a seven week regrowth period, smooth bromegrass did not attain the yields of meadow bromegrass (Fig 3.1). This poor performance of smooth bromegrass in comparison to the other species suggested a different species response to the environmental conditions of late season. However, temperatures at Lacombe declined only slightly from late July to early September, while photoperiod declined by about 4 h (Appendices 3.3, 3.4).

In controlled conditions, yields of all species were affected by temperature while photoperiodic effects on harvestable dry matter yield were observed only in smooth bromegrass and S9044 (Chapters 4). These results implicated smooth bromegrass' response to shortened day as a factor involved in its poor late season yield. S9044 yielded well in the field yet showed a photoperiod response. It however took longer to respond to daylength than did smooth bromegrass and was affected to a lesser extent. The delay in regrowth of smooth bromegrass in the field (Fig 3.1) may have contributed to its poor performance by pushing its growth into a period of lower temperatures and shorter days.

The experiments in controlled conditions showed how environment affected some of the yield influencing factors. In the field, a lower CGR of smooth bromegrass compared to meadow bromegrass was attributed to its lower NAR in 1985 and and in 1986 to both a lower LAI and NAR (Chapter 3). A higher CGR for S9044 and meadow foxtail than smooth bromegrass was attributed mainly to larger LAI (Chapter 3). When CGR in the field was compared at a given LAI or level of light interception, smooth bromegrass had a lower CGR than meadow bromegrass, meadow foxtail, and S9044 (Fig 3.5, 3.6). Thus, both a lower rate of leaf area development and a possible lower efficiency in converting light energy into harvestable dry matter (i.e. NAR) were involved in smooth bromegrass' poor performance in relation to the other species.

In controlled conditions, shoot:root ratios of smooth bromegrass were lower at short versus long photoperiods (Table 4.1). This implied that smooth bromegrass would partition a greater percentage of its assimilate into roots in late season than in ..spring, and may in part explain its apparently lower photosynthetic efficiency in the field. In controlled conditions when photoperiod declined LWR and LAR of smooth bromegrass increased yet whole plant yield declined (Tables 4.6b,4.6c, 4.5). This suggested that photoperiod exerts an influence on the NAR of smooth bromegrass.

Results from the experiment in controlled conditions of smooth bromegrass showed generally similar TD but a reduced TW at short compared to long photoperiods (Table 4.7a, 4.7b, 4.7c). The reduction in tiller weight was associated with a lower leaf area, leaf weight, and stem dry matter (Table 4.2). Stem weight was however the most responsive trait with a 4 h photoperiod reduction reducing the stem content by half.

Little stem extension occurred during vegetative growth of all the species studied in the field, or under short photoperiods in the cabinets. Only in smooth bromegrass under long days was there a considerable stem extension response to daylength. Walton and Murchison (1979) found second cut hay yields in smooth bromegrass to be highly correlated to stem length and the ratio of elongated to non elongated tillers. It is interesting to note that high yields of the other species were attained with little stem production but with smooth bromegrass reduced stem production was associated with low yields at short days. Further study is needed in smooth bromegrass to elucidate the role of stem elongation to the canopy light attenuation, yield and photosynthetic rates.

Although late season dormancy is often associated with winter hardiness, both smooth and meadow bromegrass which had contrasting late season growth habits, accumulated carbohydrates in a similar manner and had good winter survival in the field. The relationship between fall growth pattern and winterkill in these species thus needs further study.

Since CGR declined at a critical LAI of 1.3 to 2.4 in all species, a second limitation to yield was the low critical LAI. Nelson(1980) suggests that when critical LAI is low strategies should be developed to increase the leaf area illuminated by improving light attenuation properties of the canopy. Critical LAI is related to leaf length, leaf angle and erectness of the canopy. Selection for morphological characters such as long rigid leaves has resulted in a higher critical LAI and higher yields in ryegrass (Wilson et al. 1980). The low critical LAI may in part be due to lack of stem elongation which can result in poor light attenuation properties (Rhodes 1973). Lack of stem elongation may also influence the photosynthetic capacity of leaves, as young leaves on non elongated tillers develop low in the canopy under low light, which results in reduced photosynthetic capacity (Woledge 1978).

The higher ceiling yields of S9044 and meadow foxtail compared to smooth bromegrass were associated with improved light attenuation properties. Meadow bromegrass had a relatively similar critical LAI to smooth bromegrass but was able to compensate with a low SLA. In regard to smooth bromegrass, an early August clipping of an elongated stand could delay tiller regeneration and push the regrowth into a period of short daylengths, which then would reduce leaf extension rates, and culm elongation. This could affect light attenuation into the canopy, lower critical LAI and lower ceiling yields.

The peak growth rates observed, with the exception of smooth bromegrass, in this field experiment, were close to those observed for late season growth in Europe at a similar latitude, and therefore were probably close to potential. If ceiling yields of swards are to be increased, then CGR will need to be maintained over a longer period. Since frost can occur in early September in central Alberta there is limited time in which to extend the growing season. However, if peak growth rates were to be maintained even for a short period of time large yield increases could result. In meadow bromegrass for example, the peak CGR was about 13 g m^{-2} d^{-1}. Maintaining this for one week would result in an increase in yield of 91 g m^{-2}, and would represent a yield increase of 30-40%. In smooth bromegrass peak CGR was 9.3 g m^{-2} d^{-1} and an additional week would increase yields by 40%.

Lower late season productivity of smooth bromegrass in comparison to the other species studied appears related to its response to a declining photoperiod. In controlled conditions photoperiodic influences in smooth bromegrass were confined to the above ground portion of the plant with lower yields under shortened photoperiods associated with reduced lamina and stem extension rates. This study indicated the importance of using pasture species insensitive to daylength change for maximizing late season pasture productivity.

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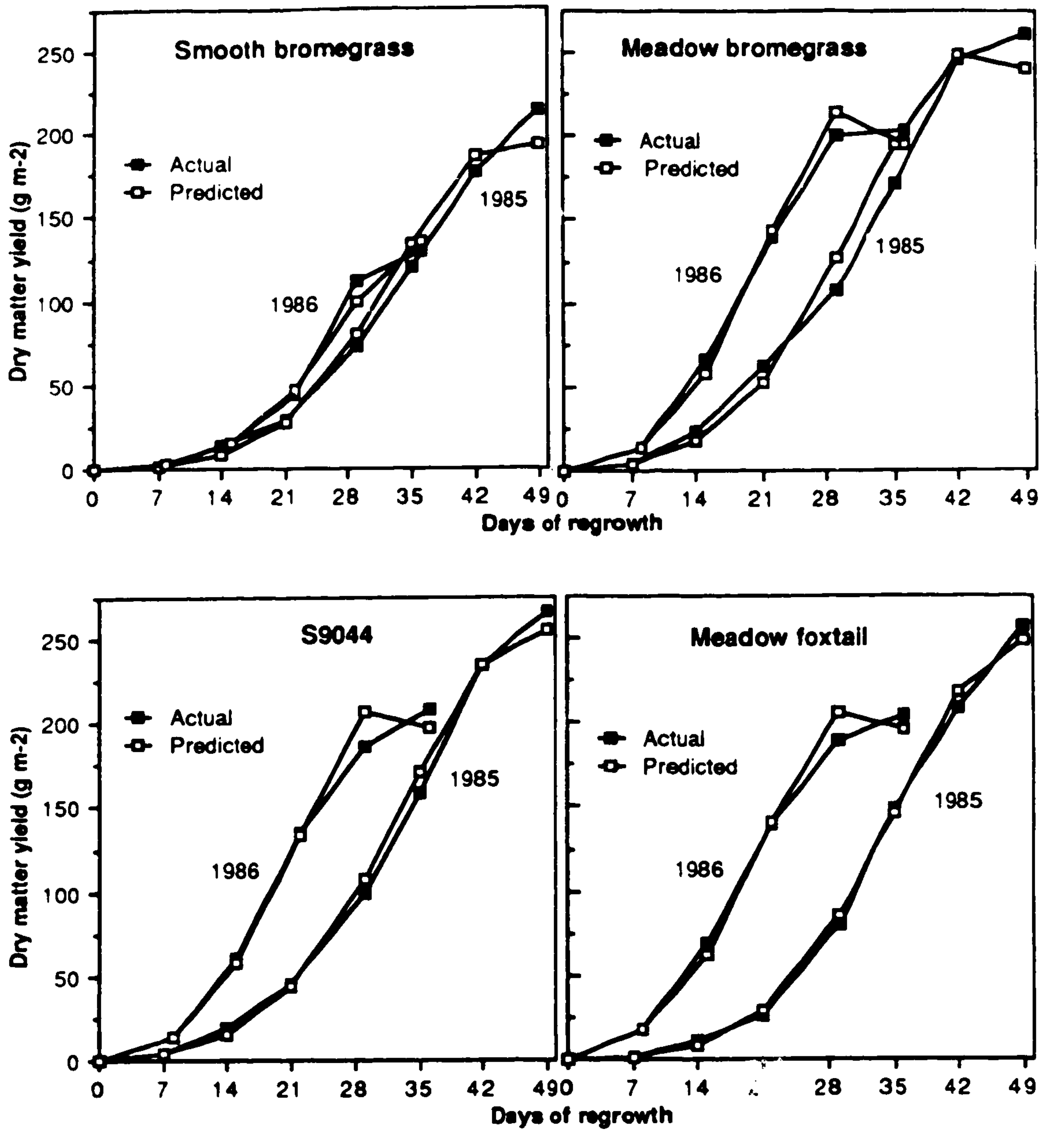
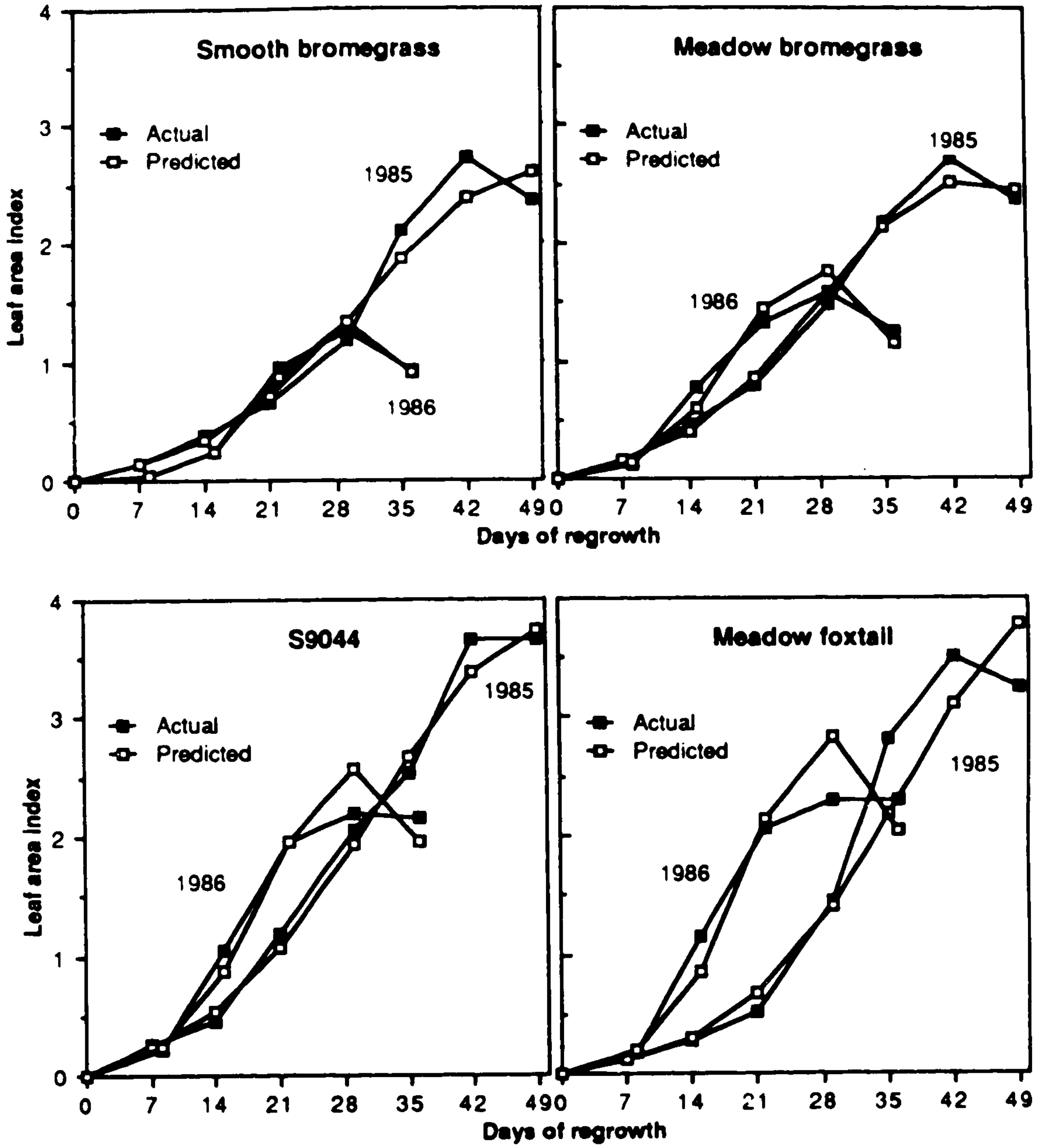


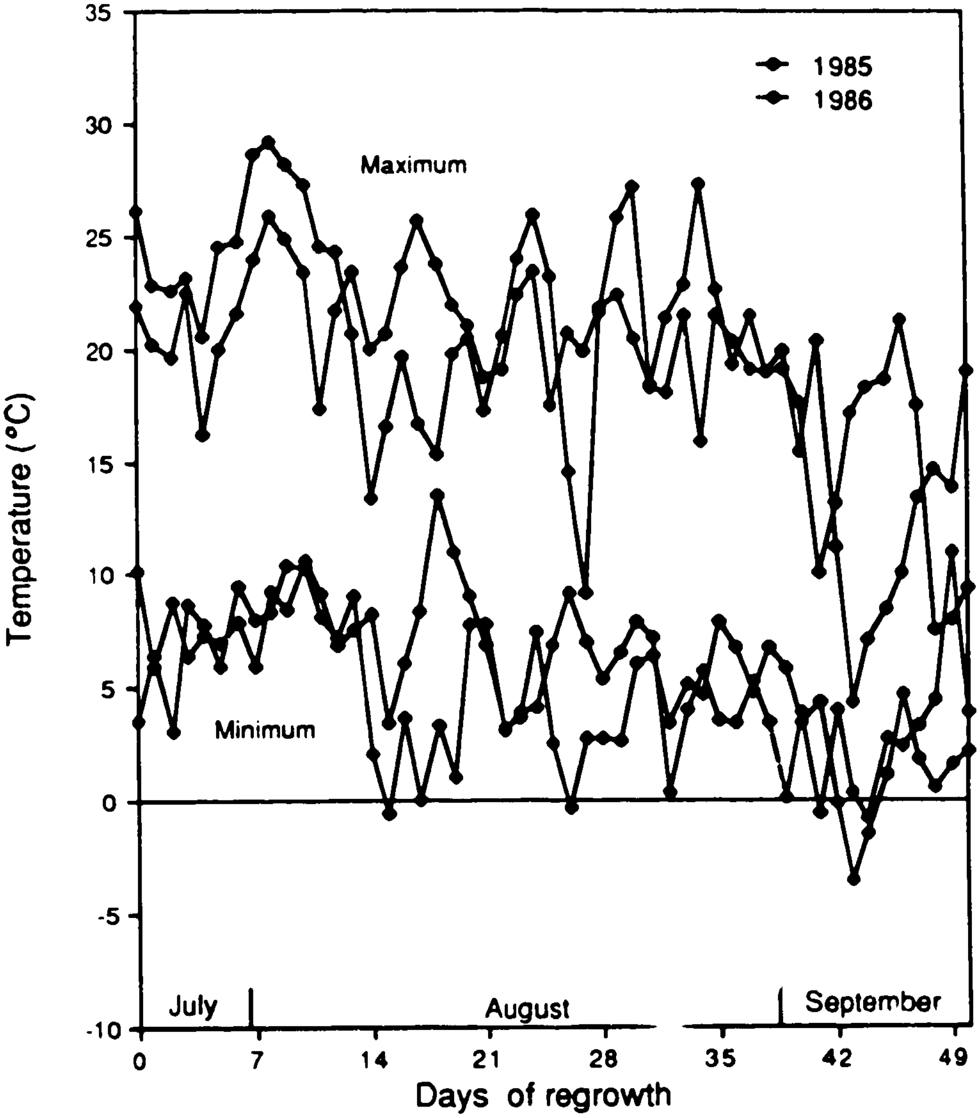
Appendix 3.1. Actual and predicted means for late season dry matter yield of four grasses in 1985 and 1986 at Lacombe. Predicted values are antilogs of the regression equations given in Appendix 3.8.



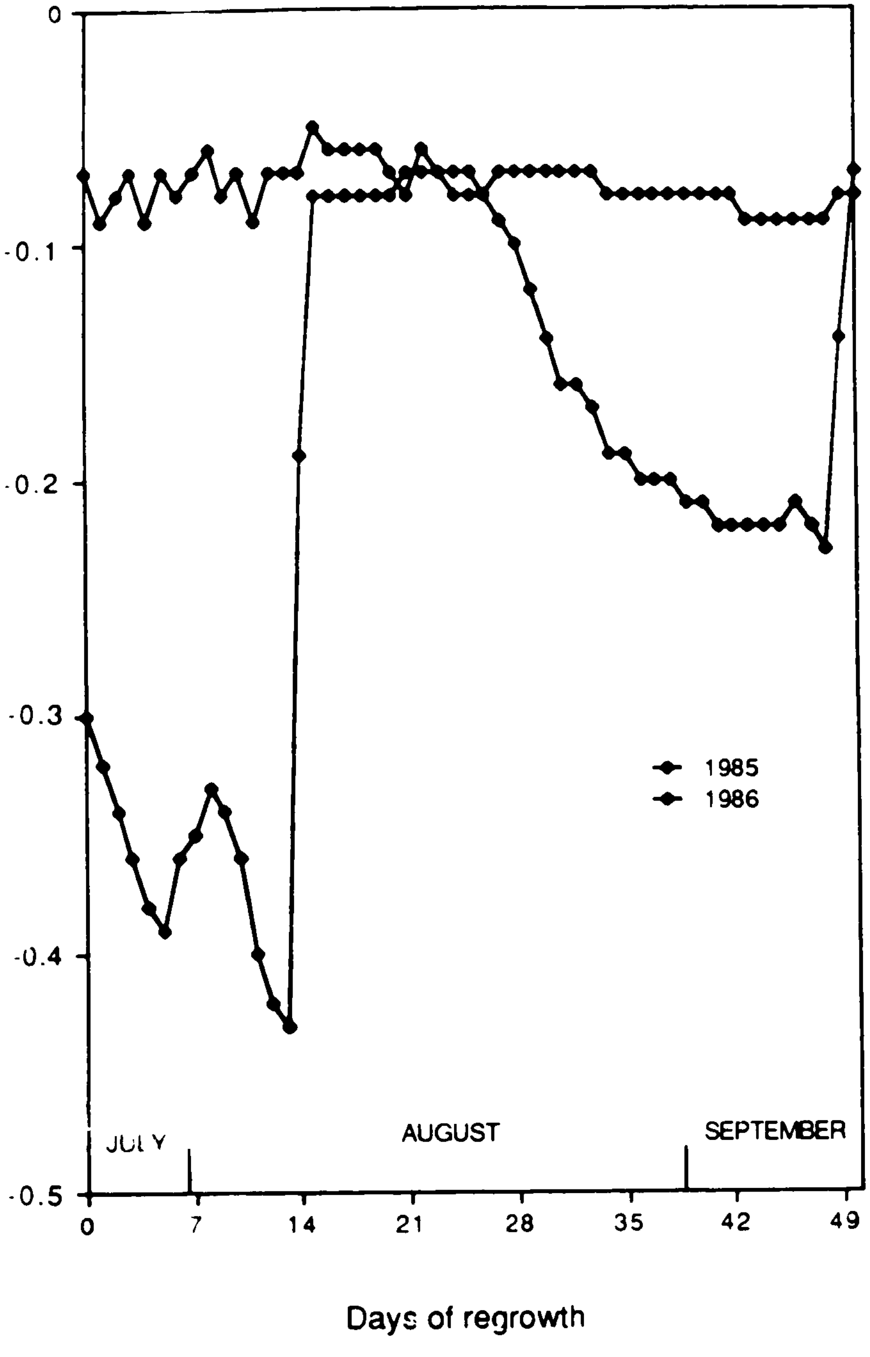
Appendix 3.2. Actual and predicted means for late season leaf area index of four grasses in 1985 and 1986 at Lacombe. Predicted values are antilogs of the regression equations given in Appendix 3.9.

Appendix 3.3. Mean monthly precipitation and temperature for 1985 and 1985 and 79 year mean for Lacombe Alberta.

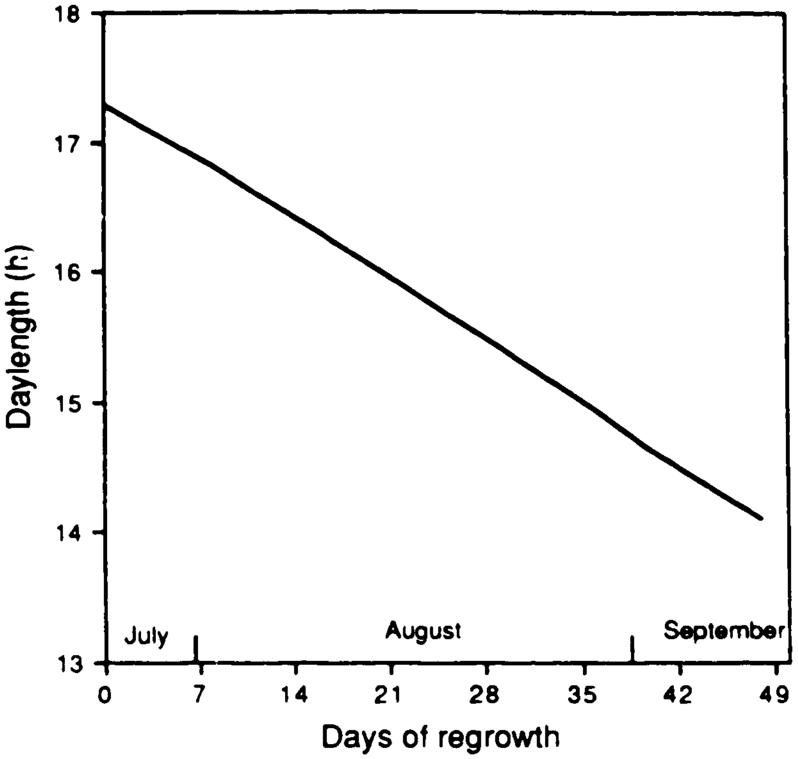
Month	1985	1986	79 year mean
------------------------------------- precipitation (mm)-------------------------------------			
July	62.1	143.7	76.5
August	133.3	26.0	63.5
September	74.4	84.7	42.1
------------------------------------mean tempertaure (^{o}C) ------------------------------------			
July	16.6	14.0	16.5
August	12.3	15.0	15.4
September	7.0	7.7	9.9



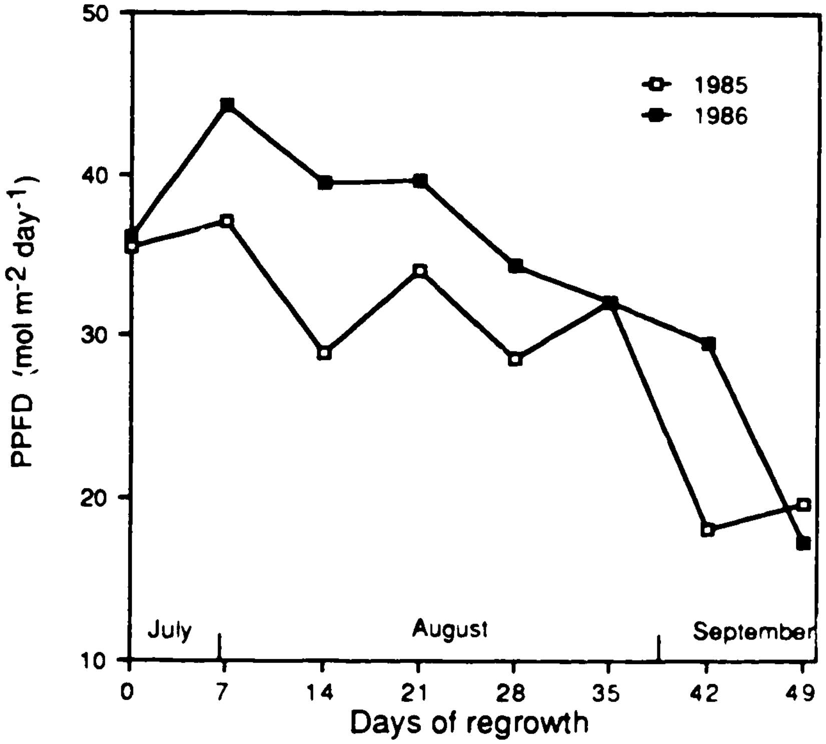
Appendix 3.4. Daily maximum and minimum temperatures during the late season regrowth study in 1985 and 1986 at Lacombe.



Appendix 3.5. Soil moisture tension for the late season regrowth study in 1985 and 1986 at Lacombe.



Appendix 3.6. Late season daylength (civil twilight to civil twilight) for Lacombe (52°N). (U. S. Naval Observatory 1987).



Appendix 3.7. Photosynthetic photon flux density (PPFD) averaged over seven day periods during the late season regrowth study in 1985 and 1986 at Lacombe.

Appendix 3.8. Regression coefficients, root error mean square (REMS), and coefficient of determination (r^2), for dry matter yield fitted to $\ln y = a+bx+cx^2$, where y=dry matter yield (g m^{-2}) and x= days of regrowth.

Grass	Replicate	Coefficient			REMS	r^2	n
		a	b	c			
			1985				
Smooth bromegrass	1	-1.417	0.287060	-0.00312	0.4679	.96	7
	2	-1.320	0.30664	-0.00361	0.2521	.99	7
	3	-1.747	0.29574	-0.00309	0.1235	.99	7
	4	-0.668	0.25044	-0.00256	0.3158	.98	7
	1-4	-1.288	0.28497	-0.00309	0.3128	.97	28
Meadow bromegrass	1	-0.008	0.24577	-0.00274	0.2455	.98	7
	2	-0.320	0.27250	-0.00313	0.3689	.97	7
	3	-0.241	0.25599	-0.00281	0.0975	.99	7
	4	0.276	0.22821	-0.00253	0.1691	.99	7
	1-4	-0.073	0.25062	-0.00280	0.2118	.98	28
S9044	1	0.087	0.21652	-0.00215	0.1127	.99	7
	2	-0.400	0.24354	-0.00253	0.1416	.99	7
	3	0.465	0.21107	-0.00211	0.1296	.99	7
	4	-0.375	0.26645	-0.00303	0.2507	98	7
	1-4	-0.056	0.23440	-0.00246	0.2107	.98	28
Meadow foxtail	1	-1.008	0.27016	-0.00286	0.1082	.99	7
	2	-1.240	0.27767	-0.00284	0.2366	.99	7
	3	-0.697	0.23354	-0.00214	0.1784	.99	7
	4	-1.603	0.30937	-0.00334	0.2280	.99	7
	1-4	-1.137	0.27268	-0.00280	0.1884	.99	28
			1986				
Smooth bromegrass	1	-1.539	0.35327	-0.00487	0.4168	.97	5
	2	-1.950	0.37446	-0.00507	0..0699	.99	5
	3	-0.767	0.29673	-0.00384	0.9752	.98	5
	4	-0.997	0.30747	-0.00403	0.2767	.98	5
	1-4	-1.313	0.33298	-0.00445	0.2456	.98	20
Meadow bromegrass	1	0.825	0.27052	-0.00404	0.1748	.99	5
	2	0.376	0.32281	-0.00513	0.0376	.99	5
	3	0.161	0.34807	-0.00578	0.1601	.99	5
	4	0.377	0.33273	-0.00553	0.1257	.99	5
	1-4	0.435	0.31853	-0.00512	0.1175	.99	20
S9044	1	0.441	0.31391	-0.00491	0.1126	.99	5
	2	0.750	0.28826	-0.00457	0.0990	.99	5
	3	0.480	0.30055	-0.00464	0.2086	.98	5
	4	0.302	0.32103	-0.00508	0.1466	.99	5
	1-4	0.493	0.30593	-0.00480	0.1257	.98	20
Meadow foxtail	1	0.686	0.29442	-0.00464	0.0445	.99	5
	2	0.519	0.31420	-0.00502	0.1520	.99	5
	3	0.985	0.28814	-0.00214	0.1657	.99	5
	4	1.653	0.21278	-0.00309	0.0658	.99	5
	1-4	0.961	0.27738	-0.00438	0.1358	.98	20

Appendix 3.9. Regression coefficients, root error mean square (REMS) and coefficient of determination (r^2), for leaf area index fitted to the equation $\ln y = a+bx+cx^2$ where y=leaf area index and x= days of regrowth.

Grass	Replicate	Coefficient			REMS	r^2	n
		a	b	c			
1985							
Smooth bromegrass	1	-0.617	0.08868	-0.00055	0.2825	.94	7
	2	-2.569	0.14324	-0.00147	0.3093	.94	7
	3	-3.401	0.17345	-0.00168	0.2205	.98	7
	4	-3.091	0.15449	-0.00144	0.2505	.97	7
	1-4	-3.050	0.1633	-0.00166	0.2344	.96	28
Meadow bromegrass	1	-3.137	0.18202	-0.00267	0.1115	.99	7
	2	-3.635	0.23039	-0.00280	0.2600	.97	7
	3	-3.526	0.20069	-0.0022[illegible]	0.0990	.99	7
	4	-2.505	0.12860	-0.00117	0.0632	.99	7
	1-4	-3.053	0.17921	-0.00202	0.2258	.96	28
S9044	1	-2.258	0.11849	-0.001[illegible]	0.2238	.96	7
	2	-2.163	0.1[illegible]	-0.001[illegible]	0.2070	.97	7
	3	-2.338	0.14578	-0.00128	0.383	.93	7
	4	-3.086	0.21672	-0.00272	0.1321	.99	7
	1-4	-2.461	0.15137	-0.00153	0.2954	.93	28
Meadow foxtail	1	-3.292	0.18290	-0.00182	0.2940	.97	7
	2	-3.164	0.15826	-0.00139	0.3723	.94	7
	3	-3.258	0.16716	-0.00146	0.3571	.95	7
	4	-3.784	0.19127	-0.00178	0.1328	.99	7
	1-4	-3.374	0.17490	-0.00161	0.2692	.96	28
1986							
Smooth bromegrass	1	-6.810	0.47832	-0.00810	0.2131	.99	5
	2	-8.056	0.61263	-0.01081	0.3049	.99	5
	3	-6.202	0.43927	-0.00756	0.1524	.99	5
	4	-6.254	0.40691	-0.00655	0.4269	.96	5
	1-4	-6.830	0.48428	-0.00826	0.2881	.96	20
Meadow bromegrass	1	-4.226	0.32095	-0.00538	0.4275	.93	5
	2	-5.130	0.41797	-0.00741	0.3790	.95	5
	3	-5.322	0.46591	-0.00920	0.2488	.97	5
	4	-4.100	0.32542	-0.00577	0.1606	.99	5
	1-4	-4.695	0.38257	-0.00694	0.2968	.92	20
S9044	1	-4.241	0.37504	-0.00652	0.1447	.99	5
	2	-3.805	0.34775	-0.00651	0.0849	.99	5
	3	-3.675	0.30706	-0.00502	0.4312	.90	5
	4	-3.101	0.25611	-0.00423	0.0389	.99	5
	1-4	-3.705	0.32149	-0.00557	0.2487	.94	20
Meadow foxtail	1	-5.395	0.45179	-0.00792	0.3092	.97	5
	2	-4.251	0.37623	-0.00652	0.2371	.98	5
	3	-3.554	0.32889	-0.00598	0.3615	.93	5
	4	-3.897	0.32485	-0.00538	0.3425	.95	5
	1-4	-4.274	0.37044	-0.00645	0.3005	.93	20

Appendix 3.10 Regression coefficients, root error mean square (REMS), and coefficient of determination (r^2), for percent light interception fitted to the equation $y = a+bx+cx^2$, where y= percent light interception and x= da [illegible] rowth. Data for four grasses grown at Lacombe Alberta during1986.

Grass	Replicate	Coefficient			REMS	r^2	n
		a	b	c			
Smooth bromegrass	1-4	-46.279	7.90836	-0.11167	6.5445	.97	20
Meadow bromegrass	1-4	-18.095	7.51616	-0.12427	5.0610	.97	20
S9044	1-4	-6.212	6.83999	-0.11261	2.6510	.99	20
Meadow foxtail	1 4	-15.936	7.92992	-0.13861	4.9292	.96	20

Appendix 3.11. Regression coefficients, root error mean square (REMS), and coefficient of determination (r^2), for the relationship between crop growth rate (y) and Idry matter yield (x) where $y = a+bx+cx2+ cx3$. Data for four grasses grown in 1985 and 1986 at Lacombe Alberta.

Grass	Coefficient				REMS	r^2
	a	b	c	d		
1985						
Smooth bromegrass	.283	.1543	-0.000599	-0.0000005	0.208	.99
Meadow bromegrass	.453	.1406	-0.000364	-0.0000005	0.299	.99
S9044	.413	.1327	-0.000354	-0.0000004	0.267	.99
Meadow foxtail	.515	.1341	-0.000286	-0.0000008	0.378	.99
1986						
Smooth bromegrass	.173	.1924	-0.001205	-0.0000001	0.151	.99
Meadow bromegrass	.411	.2001	-0.000717	-0.0000004	0.299	.99
S9044	.426	.1894	-0.000567	-0.0000006	0.267	.99
Meadow foxtail	.428	.1778	-0.000567	-0.0000008	0.314	.99

Appendix 3.12. Regression coefficients, root error mean square (REMS), and coefficient of determination (r^2), for the relationship between crop growth rate (y) and leaf area index (x) where $y = a+bx+cx^2+ dx^3$ Data for four grasses grown in 1985 and 1986 at Lacombe Alberta.

Grass	Coefficient				REMS	r^2
	a	b	c	d		
1985						
Smooth bromegrass	0.307	0.603	9.301	-3.756	0.628	.98
Meadow bromegrass	0.034	6.254	4.253	-2.332	0.207	.99
S9044	-0.035	3.794	2.599	-0.952	0.165	.99
Meadow foxtail	-0.222	6.817	0.829	-0.698	0.173	.99
1986						
Smooth bromegrass	0.392	11.685	-6.935	1.934	0.093	.99
Meadow bromegrass	0.675	20.312	-9.114	0.711	0.236	.99
S9044	0.452	11.660	-1.783	-0.523	0.231	.99
Meadow foxtail	1.382	11.809	-3.053	-0.101	0.480	.98

Appendix 3.13. Regression coefficients, root error mean square (REMS), and coefficient of determination (r^2), for the relationship between crop growth rate (y) and percent light interception(x) where $y = a+bx+cx^2+ dx^3$. Data for four grasses grown in 1986 at Lacombe Alberta.

Grass	Coefficient				REMS	r^2
	a	b	c	d		
Smooth bromegrass	1.680	-0.1138	.004229	-.000025	0.355	.99
Meadow bromegrass	2.855	-0.1830	.007091	-.000042	0.548	.99
S9044	1.656	-0.0898	.003703	-.000015	0.323	.99
Meadow foxtail	1.950	-0.0527	.003130	-.000014	0.224	.99