Physiology, Productivity and Utilisation of Warm Season (C_4) Grasses in a Short Growing Season Area

by

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A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfilment of the requirements of the degree of Doctor of Philosophy

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Dedication

To my parents, the late Noah and Tiyemuri, wife Rufaro and daughters; to whom I am eternally indebted. I love you all.

Short Title

WARM SEASON GRASS PHYSIOLOGY, PRODUCTION AND UTILISATION

"**And the earth brought forth grass..................................**

...and God saw that it was good."

Genesis 1 v. 12

"Nyika ikameresa uswa...........................Mwari akaona kuti zvakanaka."

Genesis 1 v. 12

Abstract

Ph.D. **Ignacio C. Madakadze** **Plant Science**

Warm season grasses are increasingly being cultivated in North America for summer forage, soil conservation, and biomass production. In more northern environments, temperature and length of growing season have an overriding effect on the productivity of warm season grasses. There is limited information on the adaptability and production potential of warm season grasses in these short season areas. A study was conducted in south-western Québec from 1993 to 1996 to evaluate the productivity of five species of warm season grasses. Phenological development, canopy leaf area development and architecture, radiation-use efficiency (RUE), yield and chemical composition were determined. In terms of phenology, there was a diversity of developmental patterns and the genotypes of greatest potential were characterised by early spring growth and late onset of dormancy in fall. Most of the genotypes that were early in spring growth were also early maturing and low yielding. Late maturing genotypes were generally late in spring growth, high yielding and generally of southern origin. Differences in developmental patterns were partly explained by differences in base temperatures for germination and growth, and growth rates. Seed osmoconditioning and/or matriconditioning alleviated effects of low temperatures on switchgrass seed germination and potential establishment. Maximum leaf area index ranged from 6.1 to 8 and the vertical leaf area distributions and light interception levels varied among genotypes. Average end of season biomass yields ranged from 8.5 to 14.4 Mg ha^{-1}. Swithgrass rates of DM accumulation ranged from 175 to 191 kg ha^{-1} day^{-1} and RUE 0.89 to 1.1 g MJ^{-1} of incoming solar radiation. Moderate amounts of N fertilisation increased yield and quality of switchgrass, which could be harvested in a 2-cut system. NDF and ADF ranged from 77-88 and 46-57 %, respectively, and showed a rapid increase to a mid season plateau. Nitrogen concentrations declined curvilinearly with time from 2.5 to 0.4 % and end of season ash contents averaged 4-7 %. Switchgrass energy contents averaged 17.4 MJ g^{-1} DM. Warm season grasses yielded 44-51 % kraft pulp, with short fibres ranging from 1.2 to 1.4 mm weight-weighted fibre length.

Résumé

Ph.D. **Ignacio C. Madakadze** **Phytologie**

Les espèces de graminées tropicale et sub-tropicale sont utilisées de façon croissante en Amérique du Nord comme plante fourragère annuelle, ainsi que pour la conservation des sols et la production de biomasse. Dans un environment nordique, la température et la durée de la saison de croissance ont tous deux un effet déterminant sur la production de tels graminées. Il y a présentement un manque d'information à propos de l'adaptabilité et le potentiel de production de tels espèces dans les régions possédant une courte saison de croissance. Une étude fut menée dans le sud-ouest du Québec de 1993 à 1996 afin d'évaluer la productivité de cinq espèces de graminées tropicale et sub-tropicale. Le développement phénologique, l'architecture et le développement de la superficie des feuilles, l'efficacité de l'utilisation de la radiation (EUR), le rendemment et la composition chimique furent déterminés. En terme de phénologie, une diversité parmi les types de développement fut noté; et les génotype possédant le plus grand potentiel furent caractérisés par une croissance rapide au printemps et une initiation de la période de dormance tard à l'automne. La plupart des génotypes possédant une croissance rapide au printemps furent aussi ceux démontrant une maturité rapide et ayant un faible rendement. Les génotypes possédant une maturité tardive furent généralement caractérisés par: une croissance tardive au printemps, de haut rendements et étaient originaires généralement du sud. Les différences parmi les types de développement furent explicables en partie par une différence pour la température basale de germination et de croissance, ainsi que pour les rythmes de croissance. L'osmoconditionement et/ou le matriconditionement des graines réduisirent les effets d'une basse température sur la germination et le potentiel d'établissement du panic érigé. Les valeurs maximales de l'indice de superficie des feuilles furent entre 6.1 et 8; la distribution verticale de la superficie des feuilles et le niveau de l'interception de la lumière varièrent selon les génotypes. La moyenne du rendement de biomasse à la fin de la saison fut de 8.5 à 14.4 Mg ha^{-1} . Le rythme d'accumulation de la masse de matière sèche pour le panic érigé fut de 175 à 191 kg ha^{-1} jour^{-1} et l'EUR fut de 0.89 à 1.1 g MJ^{-1} de radiation solaire. Des apports modérés d'azote augmentèrent les rendement et la qualité du panic érigé, qui peut être récolté par un système à deux coupes. Les valeurs pour l'NDF et l'ADF furent entre 77-88 et 46-57%, respectivement, et furent caractérisés par une rapide augmentation suivie par un plafonnement au milieu de la saison. Les concentrations d'azote baissèrent de façon curvilineaire avec le temps de 2.5 à 0.4% et le contenu de cendres à la fin de la saison fut de 4 à 7%. La moyenne du contenu en énergie du panic érigé fut de 17.4 MJ g^{-1} de matière sèche. Les espèces de graminées tropicale et sub-tropicale produisirent 44 à 51% de pâte kraft, avec de courtes fibres d'une longue moyenne de 1.2 à 1.4 mm lorsque pesées par poids.

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I would first of all like to thank Professor D.L. Smith who supervised me for the greater part of this study. His guidance, encouragement, enthusiasm and above all the confidence he showed in me, are very much appreciated. His review of the manuscripts was very constructive and I always learnt something from each of these reviews. I am also grateful to Drs. K. Stewart, P. Peterson and B.E. Coulman for their suggestions and assistance throughout the course of this study. These four professors were the principal supporters during my study and would like to say to them that "I came here from Zimbabwe only drought tolerant, but now I can boast of winter hardiness and quite a bit of forage plant eco-physiology and utilisation, all acquired here. Thank you." Special thanks to the following at PAPRICAN, Drs. T. Radiotis, J. Li and B. Sithole, and the personnel at the Chemical Pulping Section. I enjoyed my time at PAPRICAN.

I am also indebted to R. Samson of REAP Canada whose initial interest in warm season grasses in temperate areas was so impressive I decided to study them. Dr. A. McElroy, thank you for your assistance in the early days of the project. I would also like to acknowledge the staff at the Emile A. Lods Agronomy Research Centre, the famous "Seed Farm" , for their assistance and patience with me during field trials. Thank you to the support staff of the Department of Plant Science, in particular Rosyln James, Louise Mineau, Carolyn Bowes, Denis Nobert, Mehr Pikarnegar, Guy Rimmer, Richard Smith, and former members of staff Helen Cohen-Rimmer, Cindy Smith and May Couture. Stewart Leibovitch (when he was still a member of our lab-family) was very supportive. Thanks Stewart for all the assistance.

Hats off to the past and present members of the Crop Physiology group. *Xie-xie* Xiaomin; *amasegnalhu Ato* Sultan and *obrigado* Carlos. I also extend appreciations to fellow-graduate students and friends, Nadia (*Molto grazie*), Justin, Philippe, Tala, Suzanne, Liqun and Kayhan. Philippe Seguin merci beaucoup for the French translation of the abstract.

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List of Abbreviations

ADF	acid detergent fibre
ANOVA	analysis of variance
ATP	adenosine triphosphate
ATPase	adenosine triphosphatase
CPPA	Canadian Pulp and Paper Association
CGRI	corrected germination rate index
DM	dry matter
FAO	Food and Agriculture Organisation
GDD	growing degree-days
GRI	germination rate index
ISO	International Standards Organisation
LAI	leaf area index
LHCII	light harvesting complex II
LSD	least significant difference
Mg	mega-gram
MJ	mega-joule
NADP	nicotinamide adenine dinucleotide phosphate
NAD-ME	NAD-malic enzyme
NADP-ME	NADP-malic enzyme
NDF	neutral detergent fibre

NUE	nitrogen-use efficiency
PAPRICAN	Pulp and Paper Research Institute of Canada
PAR	photosynthetic active radiation
PEP-CK	phosphoenol pyruvate carboxykinase
RDP	rumen degradable protein
REAP	Resource Efficient Agricultural Production
RGR	relative growth rate
RUE	radiation-use efficiency
SAS	Statistical Analysis Systems
GLM	General Linear Models
NLIN	Non-Linear Models
SEM	scanning electron microscopy
TAPPI	Technical Association of Pulp and Paper Industries
T_b	base temperature
UV	ultra-violet
WUE	water-use efficiency

Contributions of Co-authors to Manuscripts for Publication

This thesis has been written in the form of manuscripts to be submitted to scientific journals. This format has been approved as outlined in the "Guidelines Concerning Thesis Preparation". The following text, from "Guidelines Concerning Thesis Preparation" by the Faculty of Graduate Studies and Research, "must be cited in full in the introductory section of any thesis to which it applies":

" ***2/Manuscript and Authorship***: *"Candidates have the option, subject to the approval of their Department, of including, as part of their thesis, copies of the text of paper(s) submitted for publication, or the clearly-duplicated text of a published paper(s), provided that theses copies are bound as an integral part of thesis. If this option is chosen, connecting texts, providing logical bridges between the different papers, are mandatory. The thesis must still conform to all other requirements of the "Guidelines Concerning Thesis Preparation" and should be in a literary form that is more than a mere collection of manuscripts published or to be published. The thesis must include, as separate chapters or sections: (1) a Table of Contents, (2) a general abstract in English and French, (3) an introduction which clearly states the rational and objectives of the study, (4) a comprehensive general review of the background literature to the subject of the thesis, when this review is appropriate, and (5) a final overall conclusion and /or summary. Additional material (procedural and design data, as well as descriptions of equipment used) must be provided where appropriate and in sufficient detail (eg. in appendices) to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis. In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis of who contributed to such work and to what extent; supervisors must attest to the accuracy of such claims at the Ph.D. Oral Defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of the different authors of co-authored papers"*.

This thesis contains eight manuscripts, Chapters 3 - 10, all of which were drawn from manuscripts for publications. The regular co-authors for the manuscripts from which Chapters 3 - 9 are based are: myself, Professor D.L. Smith, Dr. K. Stewart, Dr. P. Peterson and Dr. B.E. Coulman. Dr. B.E. Coulman was my supervisor when I started my Ph.D. studies. The inception of the overall thesis as well as the design and layout of all field experiments were done under his guidance. However, he joined Agriculture and Agri-Food Canada (Saskatchewan) after the first season, 1993. Drs. Stewart and Smith then took over supervision, as co-supervisors. Dr. Stewart became Head of Plant Science Department in January, 1994 and because of these extra duties the bulk of supervisor's responsibilities were shouldered by Dr. Smith. These responsibilities included guidance and logistical support (funding and technical assistance during field and laboratory operations). Dr. Smith offered invaluable suggestions throughout the research and writing-up phases, and he thoroughly reviewed all manuscripts. Dr. Stewart also provided financial support for the research and helped source out raw materials and equipment. She also reviewed the manuscripts. Dr. Coulman remained involved in the project mainly on an advisory basis and his suggestions from a forage perspective were very useful. Some of the chemical analyses were performed in his laboratory in Saskatchewan. He also reviewed the manuscripts for Chapters 3 - 5.

When Dr. Peterson joined the department as the Forage Professor his involvement in this study was natural. He offered many valuable field tips and suggestions especially on data collection. He also reviewed the manuscripts.

Dr. A. McLeroy of Agriculture and Agri-Food Canada (Ottawa) co-authored the manuscript on which Chapter 3 is based. He was instrumental in establishing the relevant experiment, provided some of the germplasm evaluated, and fibre analysis for this experiment was done in his laboratory in Ottawa.

Mr. R. Samson of REAP Canada co-authored manuscripts on which Chapters 4 and 5 are based. He assisted in establishment and data collection in the field experimentation on which these chapters are based.

Dr. R.M. Madakadze, University of Zimbabwe (formerly of Guelph University) co-authored the manuscript on which Chapter 7 is based. She sourced some of the raw materials and assisted in the preliminary stages of the experiment. Her assistance, as a seed physiologist, in interpretation of the data and review of the manuscript were invaluable.

The manuscript on which Chapter 10 is based was co-authored by myself, Drs Smith, T. Radiotis and J. Li, the latter two are both from the Pulp and Paper Research Institute of Canada (Paprican). These two supervised my work at PAPRICAN, provided all the funding and equipment for all the pulping work and analyses, and also reviewed the manuscript.

All manuscripts have been reformatted to be consistent throughout the thesis. Tables and Figures are at the end of each chapter and all references cited are at the end of the thesis.

Chapter 1

General Introduction

Increased interest in warm season grasses for pasture management, erosion control, range reseeding and biomass crop production has created a need for additional information on their overall performance and areas of adaptation. Widespread cultivation of perennial warm season grasses could reduce soil erosion and use of agricultural chemicals (Vaughan *et al.*, 1989; McLaughlin *et al.*, 1994). Warm season grasses are attractive as biomass crops because they have a maximum conversion efficiency of intercepted light energy into dry matter that is 40 % greater than that of cool season grasses (Long *et al.*, 1983). Herbaceous biomass is renewable and its use in energy systems would also reduce atmospheric release of CO_2 (Graham *et al.*, 1992). Higher livestock performances have been reported in summer when using warm season grasses (Anderson *et. al.*, 1985; Hafley *et al.*, 1993). However, low spring temperatures in North America restrict spring leaf development and the growth season is relatively short. The cool spring and fall temperatures are ideal for cool season grasses but have a net effect of lowering the actual performance of the warm season grasses to below theoretical potential. Since several warm season grass species are found in North America (Stubbendieck *et. al.*, 1992), it seems probable that ecotypes have evolved that are well adapted to the North American climate.

Given the broad range of edaphic and climatic conditions in North America there are variable environmental adaptations for the different strains/ecotypes of warm season grasses. Generally, a north-south climatic influence on species or ecotype performance has been reported among North American warm season grasses (Jacobson *et al.*, 1986; Olson, 1986; Hopkins *et al.*, 1995). Southern ecotypes mature later in northern latitudes, which predisposes them to winter injury. Ecotypes from the northern latitudes have shorter life cycles characterised by early growth in spring and early maturity in mid summer. However, several reports have indicated that late maturing species/ecotypes generally produced higher yields than earlier maturing ones (Jacobson *et al.*, 1986; Hopkins *et al.*, 1995; Sanderson *et al.*, 1996). Lowland ecotypes have also been reported to yield more than upland ecotypes (Sladden *et al.*, 1991; Wullschleger *et al.*, 1996).

The critical features for high biomass accumulation are early growth in spring, high leaf area development, and a reasonably long growing season. Plant biological yields increase with length of the growing season (Ludlow, 1985). Because both growth rate and length of growing season are greatly affected by temperature, efforts have been made to develop models on the quantitative effects of temperature on plant growth (Ong, 1983; Hsu *et al.*, 1985; Sanderson and Wolf, 1995b). The wide environmental variation implies different growth models for different ecotypes and regions.

This thesis is centered on the potential production of warm season grasses in a northern latitude area, largely characterised by short growing seasons. Various collections of warm season grasses were initially evaluated for winter survival and biomass productivity (Chapter 3). In Chapters 4 and 5, a select set of the initial group were further evaluated in large plots in an effort to understand some of the physiological factors underlying the differences in biomass production. This also entailed the development of temperature-based growth models. Chapter 6 further examines the differences in early season growth by determining base temperatures for germination and seedling growth. The potential use of seed treatments in alleviating low temperature effects on germination are detailed in Chapter 7. In Chapter 8, the growth efficiencies of a selected group of switchgrass cultivars was evaluated, under the limiting climatic conditions of the study area. Whether grown for forage or biomass production, cultural practices, including harvest frequency and nutrient supplementation through fertilisation are important elements in the success or failure of forage or biomass production systems. These are addressed in Chapter 9. The potential use of warm season grasses as raw materials for pulp and paper production is presented in Chapter 10.

Chapter 2

Literature Review

2.1. Productivity of warm season grasses

Grasses that are adapted to cool temperatures are termed cool season grasses. Warm season grasses are adapted to warmer, subtropic or tropic type growing conditions. These differences between cool and warm season plants are based on both biochemical and anatomical characteristics. The differences between these two groups of plants are outlined by Edwards and Walker (1983) and Hattersley and Watson (1992). In most cool season plants the primary product of carbon fixation is a three carbon compound. These cool season plants are thus known as C_3 plants. The C_3 type of carbon fixation is associated with photorespiration. During this process glycolate (from oxygenation of RuDP) is oxidised to yield hydrogen peroxide and glycoxylate. The hydrogen peroxide is decomposed by catalases while the glycoxylate is metabolised to other products such as glycine, oxalate, formate or CO_2 depending on the plant species. In other words, photorespiration results in the oxidation of a reduced form of carbon, one whose synthesis required ATP and NADPH. The rate of this process greatly increases with temperature.

Four carbon organic acids are the primary products of C_4 (warm season) plants. Carbon dioxide is first fixed as oxaloacetate in the mesophyll cells and is later converted into malate or aspartate. These products are subsequently translocated into the bundle sheath cells where the fixed CO_2 is released. In the bundle sheath the CO_2 is fixed by the C_3-cycle. The continuous release of CO_2 in the bundle sheath cells by the C_4 acids leads to an elevated intracellular CO_2 concentration. The decarboxylated products are then recycled and used again for CO_2 fixation. Energy in the form of ATP is utilised in sustaining this CO_2 pump. Based on the decarboxylation enzymes in the bundle sheath cells C_4 plants can be sub-divided into: a) NADP-malic enzyme (NADP-ME type); b) NAD-malic enzyme (NAD-ME type); c) PEP-carboxykinase (PEP-CK type). However some of the C_4 plants are intermediate in terms of their C_4 acid decarboxylase activities. Largely as a result of these anatomical and biochemical characteristics, warm season grasses have higher water-use efficiencies (WUE) and nitrogen-use efficiencies (NUE) (Stout *et al.*, 1988; Staley *et al.*, 1991)

2.1.1. Comparison of productivity of C_3 and C_4 grasses

Despite the caution that must be exercised when comparing data from different sources, C_4 grasses have been reported to have greater maximum crop growth rates than C_3 grasses (Monteith, 1978; Ludlow, 1985). Since carbohydrates are the single largest constituent of dry matter and because carbohydrates are produced by photosynthesis it is logical to study the differences in growth rate and yield of C_3 and C_4 grasses in terms of photosynthesis. Generally:

Crop growth rate (g m^{-2} day^{-1}) = intercepted solar radiation (MJ m^{-2} day^{-1}) x efficiency of conversion (g MJ^{-1}) (Monteith, 1981); or $P_c = [\alpha I_0 \tau C (1-e^{-kL}) / (\alpha I_0 + \tau C)] - R_c$ where α=light absorption efficiency of leaves; τ=leaf conductance at the top of the canopy; k = extinction coefficient for light; L = leaf area index; R_c = canopy respiration rate; I_0 = solar irradiance; and C = carbon dioxide concentration of air.

I_0 and C describe the aerial environment; the function $[1-e^{-kL}]$ accounts for the amount of I_0 intercepted by the canopy. The ability of the canopy to intercept radiation is represented by k, and is a function of leaf angle, orientation and dispersion of leaves. Leaf area is determined by the leaf area per plant and the number of plants per unit ground area. τ is proportional to the maximum leaf net photosynthetic rate, and together with α and R_c influence the efficiency with which solar radiation is converted to dry matter.

2.1.1.1. Light utilisation efficiency

Growth rates of plant stands are proportional to the amount of solar radiation intercepted by a canopy. At the photosynthesis level, the radiation quotient or quantum yield (θ, slope of the relationship between photosynthetic rate and light intensity) represents the energy conversion efficiency (Stoskopf, 1981). At low radiation levels, the highest energy conversion efficiencies are realised whilst at high intensities, enzyme activity rates restrict photosynthesis (Monteith, 1978; Russell *et al.*, 1989) resulting in lower light use efficiencies. A reduction in yield can be brought about by either low light intensity or lower quantum yield (θ). In C_3 plants, θ values decrease with rising temperatures due to photorespiration (Ehleringer and Bjorkman, 1977). In C_4 plants, Edwards *et al.* (1985) noted that the PEP-CK subgroup had uniformly high θ values, NAD-ME very low values (especially dicots) and the NADP-ME subgroup had the widest variation in θ values ($\theta = 0.045$ to 0.0645). C_4 plants have higher θ values than C_3 plants (Erhleringer and Pearcy, 1983). Ludlow and Wilson (1970) reported the highest θ value to date in a C_4 plant of 0.08 for *Sorghum almum*. Such a θ value is beyond the maximum θ value of normal C_3 plants even at low temperatures. This diversity in θ values among the C_4 types holds even at low temperatures. Absence or reduced photorespiration alone does not explain the higher θ values for C_4 plants. These values may in part explain the higher growth rates and yields of C_4 grasses.

At the level of canopy growth and crop yields, the θ values translate into radiation-use efficiencies (RUE) of biomass yield. Kiniry *et al.* (1989) reported mean RUE values of 2.2, 2.2 and 2.8 g DM MJ^{-1} of intercepted photosynthetically active radiation (IPAR) for the C_3 crops sunflower (*Helianthus annuus* L.), rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.), respectively. The means for the C_4 crops maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* (L.) Moench) were 2.8 and 3.5 g DM MJ^{-1} IPAR, respectively. The RUE estimated for tall elephant grass (*Pennisetum purpureum* Schum.) was 2.9. and 2.92 for tall energycane (*Saccharum* spp.) (Woodard *et al.*, 1993).

2.1.1.2. Radiation interception by the leaf canopy

The amount of PAR reaching the ground decreases exponentially as leaf area index increases (Muchow *et al.*, 1982; Vose *et al.*, 1995), or $I_g = I_0 e^{-kL}$; where I_0 and I_g are photosynthetic irradiance above a canopy and at ground level. The main factors affecting the value of *k* are (a) total leaf area index (LAI), (b) foliage aggregation, (c) average leaf inclination angle, (d) vertical distribution of foliage, (e) light scattering and transmission by the foliage, and (f) sun angle, row spacing and direction, and latitude (Sampson and Smith, 1993; Madonni and Otegui, 1996). In maize for example, *k* decreases from about 1.7 when the sun is only 15° above the horizon to about 0.9 at 30°; to 0.5-0.7 at sun angles above 60° (Uchijima *et al.*, 1968). Isolated plant spacing produced higher midday values of *k* (0.63) than normal 75 cm rows ($k=0.45$) in grain sorghum (Muchow *et al.*, 1982).

At solar angles above 60°, crops with planophile canopies like bermuda grass (*Cynodon dactylon* L.), pangola grass (*Digitaria decumbens* L.) and clover (*Trifolium* spp.) have *k* values of 0.7 - 1.0 (Broughman, 1960; Brown *et al.*, 1966; Ludlow *et al.*,1982). Grasses or crops with erectophile canopies have values of *k* as low as 0.3 (Ludlow *et al.* 1982; Monteith, 1981). Maize, sorghum and pearl millet are intermediate with *k* values ranging from 0.4 - 0.7 (Broughman, 1960; Begg *et al.*, 1964) because they have erect upper leaves and more planophile lower leaves.

In the planophile canopy, the upper leaves intercept most of the light and the lower leaves are largely shaded. In the erectophile canopy, light penetrates more deeply into the canopy. At high solar angles the upper leaves in the planophile canopies are more nearly perpendicular to the sun's rays than in erectophile canopies. Leaves of C_4 plants are not saturated when full sunlight falls perpendicular on the leaf (Bull, 1971), and there is sufficient curvilinearity in the C_4 photosynthetic response to irradiance to predict a slightly greater photosynthetic rate in erectophile than planophile canopies if most of the radiation is intercepted (Hesketh and Baker, 1967). There has been experimental evidence to corroborate this analysis. Mechanically manipulating a maize canopy to produce more erectophile canopies produced higher grain yields at high population densities and lower yields at low population densities than the normal canopy (Winter and Ohlrogge, 1973; Fakorede and Mock, 1978). Lambert and Johnson (1978) found similar results with isogenic hybrids differing only in leaf angle. In salt marsh grasses *Spartina patens* and *Distichlis spicata*, whether erectophile canopies were mechanically manipulated to planophile or the reverse, erectophile canopies had higher photosynthetic rates (Turitzin and Drake, 1981).

There is evidence that differences in light interception exist for the various growth stages of plant development (Gallo *et al.*, 1993; Madonni and Otegui, 1996). These differences are probably attributable to continued light interception by senesced leaves as the canopy grows, and light interception by the panicles (Rosenthal *et al.* 1985;Tetio-Kagho and Garduer, 1988). Within a species, cultivar differences in plant height (Edmeades and Lafitte, 1993), leaf number and angle, and LAI (Dwyer *et al.*, 1992) also influence radiation interception as the crop grows.

During early growth (LAI below 4-5), crop growth rate is linearly proportional to the fixation of intercepted solar radiation (Biscoe and Gallagher, 1975; Monteith, 1981). At high LAI (above 4-5), 90 -95 % of the incident PAR will be intercepted by the canopy (Ludlow, 1985). At this point, the length of the growing season determines the maximum amount of light the canopy can intercept. In conformity with this, biological yields of both C_3 and C_4 forage plants increase with the length of the growing season. The superiority of C_4 over C_3 pasture plants increases with the length of the growing season and decreases with latitude (Loomis and Gerakis, 1975, Monteith, 1978). The lower yields of C_4 plants at high latitudes is explained by the shorter growing season and the slow growth at lower temperatures. It is generally accepted that C_4 grasses are more abundant in warm climates (areas where the mean temperatures of the mid winter month exceeds 10°C). Conversely, C_3 grasses are more abundant where the mean mid-winter temperature is less than 10°C. According to Teeri and Stowe (1976), the mean minimum summer temperature at which C_3 and C_4 grasses are equally abundant is approximately 20°C. Above this temperature, C_4 grasses are relatively abundant, and below it C_3 grasses are more prevalent. However if yields from these two groups of plants are compared for the same length of growing season, or at low latitudes where temperature does not limit their growth, the C_4 plants have superior yields than C_3 plants (Ludlow, 1985) suggesting that the photosynthetic and respiratory differences work in favour of C_4 species.

2.2. Influences of temperature on growth

2.2.1. General effects of temperature

Environmental temperatures affect species distribution, photosynthesis and several other aspects of crop growth, dry matter accumulation and partitioning, expansion growth and phenological development. As already discussed, C_3 grasses are better adapted to cooler temperatures than C_4 grasses. However, there are genotypic differences across ecotypes and cultivars of C_4 grasses in their temperature responses (Sweeney and Hopkinson, 1975; Kiniry *et al.*, 1991). These differences are evident in tolerance to freezing (Hacker *et al*, 1974; Ivory and Whiteman, 1978b); chilling (Lee and Estes, 1982;

Stamp *et al.*, 1983) and high temperatures (Sweeney and Hopkinson, 1975; Ivory and Whiteman, 1978c). The differences in temperature responses in most cases reflect either the differences in the native thermal environments of the ecotypes and cultivars or areas in which they were selected.

2.2.2. Temperature effects on photosynthesis and dry matter accumulation

C_4 grasses have higher optimum temperatures for photosynthesis than C_3 grasses (Vong and Murata,1977). Ludlow and Wilson (1971a) reported that for several C_4 pasture grasses grown at 30°C, the minimum temperature for net photosynthesis is 5-10°C, the optimum temperature is 35-40°C, and the maximum temperature at which net photosynthesis is positive is 50- 60°C. Sweeney and Hopkinson (1975)'s data suggest that the optimum mean daily air temperature for C_4 grass dry matter accumulation is about 30-35°C with growth being reduced above 40°C and below 20°C (20-25°C, 30°C and 10°C are the corresponding temperatures for C_3 grasses). This differential response to temperatures explains the seasonal biomass distribution of C_3 and C_4 grasses in the North American Great Plains reported by Ode *et al.* (1980). These authors used δ^{13} to determine seasonal contribution of C_3 and C_4 grasses to total community production and their results indicated predominately C_3 production in spring and fall and predominately C_4 in the summer.

The temperature effects on photosynthesis and dry matter accumulation are similar but not identical. At suboptimal temperatures the relative photosynthetic rate is usually higher than the relative rate of DM accumulation (Miedema and Sinnaeva, 1980). As a result, plants tend to accumulate nonstructural carbohydrates in all tissue organs (leaves, stems and roots) at suboptimal temperatures. This accumulation of nonstructural carbohydrates is highest at the end of the day and lowest at the end of the night. Because low temperatures reduce dark respiration, it is argued that low temperatures decrease the magnitude of daily fluctuation in carbohydrates (Burns,1972).

In some C_4 grasses (*Cenchrus ciliaris, Chloris gayana*, and *Pennisetum clandestinum*), optimum temperature for tiller number is generally much lower than that for tiller size, but in some (*Panicum maximum* var. trichoglume and *P. coloratum*), there is little difference in the optimum temperature for tiller number and tiller size (Ivory and Whiteman, 1978b). The lower optimum temperature for tillering may reflect the higher non-structural carbohydrate in the mother tiller at lower temperatures. Supporting evidence is drawn from Downes (1968) who reported that in sorghum, auxiliary buds do not expand into tillers at mean daily temperatures above 18°C. At the four or six leaf stage, 8-16 days below 18°C was required for the plants to tiller.

Temperature is also the primary factor controlling leaf number, leaf appearance rate and leaf elongation (Kemp and Backlow, 1982; Baker *et al.*, 1986; Kiniry *et al.*, 1991). As a result, leaf appearance is often reported as the interval in accumulated thermal-time (e.g. growing degree-days, GDD) between the appearance of successive leaves, the phyllochron. The phyllochron is generally constant throughout the life of the a plant (Baker *et al.* 1986) but in some cases may increase gradually with advancing leaf number (Skinner and Nelson, 1995; Van Esbroeck *et al.*, 1997), or rapidly after floral initiation (Baker *et al.*, 1986). Considerable variation exists among species (Kiniry *et al.*, 1991) and cultivars within a species (Van Esbroeck *et al.*, 1997). Leaf elongation is a linear function of meristem temperature (Kemp and Blaclow, 1982), and rates and duration of growth are not affected equally by temperature. Monteith (1979) showed that in maize, maximum rate of leaf elongation occurs at about 30°C, but maximum final leaf length at about 20°C. This was explained by the longer duration of leaf extension at 20°C than at higher temperatures. Pollock (1990) also reported that temperature exerts a much larger effect on extension growth than it does on the chemical reactions of metabolism.

2.2.3. Temporary and diurnal thermal adaptation

Both C_3 and C_4 grasses grown at low or high temperature for certain periods become better adapted to these respective temperatures. A single day at higher or lower temperatures is sufficient for considerable photosynthetic adaptation to the new temperature regime (Bennet *et al.*, 1982; Ludlow and Wilson, 1971b). The extent and speed of adaptation varies greatly among species. Also, deacclimation is a faster process than cold acclimation and is influenced by the temperature of the "warm" regime (Chen and Li, 1980).

In their studies on C_4 forage species, Ivory and Whiteman (1978a) found that at suboptimal mean temperatures, equal day/night temperatures give the highest growth rates. At optimum or supraoptimum mean temperatures, the highest growth rates occur when day temperatures are about 10°C higher than night temperatures. Thus, at suboptimal temperatures, a reduction in night temperature causes more reduction in net photosynthesis than in dark respiration and the reverse is true for optimum and supraoptimum temperatures.

2.2.4. Freezing temperatures

Low temperature can have a fully reversible impact on yield by its influence on metabolism and the rate of enzymatic processes, or can result in lethal injury via metabolic dysfunctions or by freezing (Woodward, 1990). C_4 grasses are more susceptible to frost damage than C_3 grasses. Freezing temperatures severely damage tissues and frequently kill the entire plant in C_4 grasses. The plant's response to frosting is greatly affected by a) temperature and duration of frost period, b) relative humidity during the period, and c) temperature during hardening prior to freezing. For instance, in buffel grass (*Cenchrus ciliaris* L.), a frosting temperature of -1.75°C caused less than 50 % foliage death; at -2.5°C there was 90 % foliage death (Ivory and Whiteman, 1978b). Increasing duration of freezing from 0.5 to 4 hours increased frost damage of setaria (*Setaria anceps* L.) and green panic (*Panicum maximum* var. *trichoglume*) by 35-58 % (Ivory and Whiteman, 1978a). In the same study a decreased rate of cooling increased frost damage. At -5°C, low RH caused little frost damage to buffel grass but at high (close to 100%) RH the same temperature killed more than 90% of the tillers (Ludlow and Taylor, 1974).

It has also been demonstrated that numerous C_4 grasses undergo winter hardening in late summer. Such adaptation is associated with both structural and biochemical changes of their cells. Night temperatures of about 5-10°C for about one week provide maximum hardening to most C_4 forage grasses (Ivory and Whiteman, 1978a; Ludlow and Taylor, 1974). More frost resistant genotypes may require lower temperatures. Ivory and Whiteman (1978d) report that in non-hardened plants, cold temperatures of 1-10°C for a single night are enough to reduce the plant's stomatal conductance and net photosynthesis the next day regardless of the day temperature.

There is considerable ecotypic variation in frost tolerance among C_4 grass species, related to altitude or latitude of origin. In the south-eastern Wyoming grasslands, Boutton *et al.* (1980) reported species distribution along altitudinal transects. Many species of the *Muhlenbergia* subfamily (all members of this subfamily of Eragrostoids are of the C_4 type) have been reported to be especially tolerant to low temperatures and are found at higher altitudes and latitudes (Chazdon, 1978; Buotton *et al.*, 1980). Greater frost tolerance would be expected in ecotypes from cooler climates. Screening for frost tolerance has been achieved by measuring tissue death in controlled environments (Beard *et al.*, 1981; Ivory and Whiteman, 1978b) or by measuring the electrical conductivity of cell sap (Calder *et al.*, 1966).

2.2.5. Chilling temperatures

In C_4 grasses, chilling temperatures cause poor seed germination, retarded growth, stomatal malfunctioning, chlorosis and apparent phosphorus deficiency. In maize for example, the heterotrophic and autotrophic stages have different temperature minima. Heterotrophic growth can occur below 13°C (Eagles and Hardacre, 1979) while photosynthesis occurs slowly or not at all below 15°C. Low temperatures during the autotrophic stage result in chlorotic plants or even death. Again, there is considerable genotypic variation depending on altitude and latitude of origin.

Chilling injury can also be manifested by rapid wilting. Under chilling soil and air temperatures, stomata remain partially open despite water stress conditions caused by increased hydraulic conductivity of the root system. This results in wilting and this loss in stomatal transpirational control is thought to be a result of cold induced changes in guard cell permeability (Garber, 1977) and of the K^+ ATPase pump involved in stomatal regulation. There is also a high degree of variation in the actual level of stomatal conductance at chilling temperatures. Chilling tolerant genotypes, with lower stomatal conductance at chilling temperatures, have shown high rates of photosynthetic recovery at the onset of warmer temperatures (Murstardy *et al.*, 1982).

Chlorosis at chilling temperatures has been reported in several C_4 species (Stamp, 1981; Gallopin and Jolliffe, 1973). Some of the reasons for this chlorosis are: reduced synthesis and esterification of a precursor of protochlorophyll (McWilliam, 1978); inhibition of carotene synthesis by cold temperatures (Teeri *et al.*, 1977) which aggravates the photodestruction of existing chlorophyll. Faris bands (transverse chlorotic lesions) appear after exposure to low night temperatures. These become visible at the point of leaf emergence about 24 hours after the chilling stress (Taylor *et al.*, 1975) and high radiation. The bands are usually irreversibly chlorotic because of structural abnormalities in the mesophyll chloroplasts (perhaps due to a chilling induced failure of plastid ribosome production). Plants usually adapt to these low temperature regimes and stop producing bands. Taylor *et al.* (1975) observed that despite genotypic variation in banding, plants producing bands are not always the chilling sensitive genotypes. Critical temperatures at which chilling injury occurs is related to the lipid composition of the membrane (Hugly *et al.*, 1990; Somerville and Browse, 1991); those plants with more unsaturated, short-chain lipids being more chilling resistant.

2.2.6. Enzyme activity

Part of the decreased photosynthetic rates at low temperatures may derive from inactivation of Calvin cycle enzymes (Stamp, 1981; Sassenrata and Ort, 1990). Stamp (1981) reported a rapid decline in activity for RuBP carboxylase and NADP-malate dehydrogenase when transferred from warm to chilling temperatures. NADP-malic enzyme and in some cases PEP carboxylase activities were relatively insensitive to chilling temperatures. Loss of activity of pyruvate 1-P dikinase (PPDK) follows first order kinetics with a change in activation energy near 12 °C (Shirahashi *et al.*, 1978). This inactivation of PPDK follows changes from the tetrameric into the di- and finally monomeric forms when temperatures are lowered. Reversible transitions of the oligomeric structure and conformation of PEP carboxylase have also been reported (Kleczkowski and Edwards, 1991). Smith *et al.* (1982) detected a certain amount of pyruvate-di-kinase in *Spartina anglica* (PEP-CK plant) which is not usually found in this kind of C_4 cycle (common in NAD-ME plants). They postulated that this enzyme is used at higher rates of photosynthesis when the rate of turnover of the PEP-CK cycle is limited i.e. at low temperatures (spring and autumn) this plant would use mainly the PEP-CK cycle which is not limited by the pyruvate-di-kinase while at higher temperatures the more productive NAD-ME cycle is used. Effects of chilling temperatures are not limited to enzyme inactivation only, for instance, they also inhibit synthesis of key photosynthetic enzymes (Hahn and Walbot, 1989).

2.2.7. Chilling temperatures and photoinhibition

The effects of chilling temperatures are exacerbated if chilling occurs during exposure to high irradiance (Smillie *et al.*, 1988). Under these conditions, quantum yield and maximum light capacity can experience considerable reduction. High sun radiation leads in the first instance to the formation of zeaxanthin by oxidation of violaxanthin (Edwards and Walker, 1983). Zeaxanthin formation is increased at low carboxylase turnover, or with reduced CO_2 supply. This process results in the transformation of some light energy into heat for protection against surplus radiation (photoinhibition) and represent considerable reduction in quantum yield. As temperatures decrease, photoinhibition increases and productive capture of light via photosystems declines (Smillie *et al.*, 1988). The process can recover and is therefore reversible. Once the protection capacity is surpassed there is an inability to regulate LHCII (light harvesting complex of photosystem II) phosphorylation, which results in irreversible damage in photosystem II (Moll and Steinback, 1986). Original quantum yield and maximum light capacity cannot be recovered. Other light decay mechanisms exist in plants. For purposes of this discussion it should be realised that while these processes protect the plants against intensive radiation they are also connected with a loss of fixed carbon through additional respiration. Both appropriate leaf orientation and certain arrangements of chloroplasts can help in reducing the effects of intensive sunshine during periods of stress.

2.3. Ontogeny and biomass productivity

Crop ontogeny or phenology is the time course of crop development from the vegetative, through the reproductive to the maturation phases (Horie, 1994). Duration of each phase of development is determined by genetic and environment interactions. The ontogenetic development response to the environment determines adaptability (whether a species will survive in a region with periods of adverse conditions, e.g. cold winter), productivity and conditions under which economic yield will be produced, the effects of periodic harvests on regrowth, and the beginning and end of periods of dormancy (Hodges, 1991). Diverse ontogenetic responses to environments are recognised among species and genotypes. This is largely a reflection of the environmental conditions under which the plants evolved or to which they adapted (Roberts and Summerfield, 1987).

Duration of each phenological phase influences growth and yield. For instance, the number of leaves per tiller is related to the duration of the development interval between seedling and floral initiation, and leaf primordia initiation (Kiniry *et al.*, 1991). After final leaf number is determined, the leaves have to emerge prior to flowering. A rapid rate of leaf appearance may be associated with a short period between floral initiation and final emergence. The duration of expansion per leaf is in turn strongly related to the tiller leaf number (Arkin *et al.*, 1983; Kiniry and Bonhomme, 1991).

Most grasses are determinate in nature, usually with one flush of tillers in spring. Biomass accumulation therefore varies with floral development. Species or genotypes with long durations of vegetative growth are characterised by high biomass yields (Evans, 1993; Sanderson *et al.*, 1996). Delayed flowering results in greater leaf area (more leaves) and a prolonged period of photosynthetic activity. This has been argued as the basis for higher productivity of southerly adapted genotypes compared with northern genotypes (Hopkins *et al.*, 1995).

Temperature and daylength are the main factors that influence ontogenetic development. As a result, crop ontogenetic development models based on thermal-time accumulation (GDD) have been developed (Hodges, 1991). Initial efforts have been made to develop models for individual ontogenetic phases, for instance leaf area development (Kiniry *et al.*, 1991; Dwyer and Stewart, 1986; Van Esbroeck *et al.*, 1997), tillering (Rickman and Klepper, 1991), stem growth (Hesketh *et al.*, 1991), and flowering (Horie and Nakagawa, 1990). These have been included in models predicting yield (Kannegati and Fick, 1991; Horrie, 1994). Thermal-times vary for different species, genotypes and developmental stages. Average phyllocrons were 76 GDD per leaf for rice, 29 for sunflower, 39 for maize, 43 for pearl millet and 46 for sorghum (Kiniry *et al.*, 1991). In switchgrass, phyllocrons varied from 79 to 152 GDD per leaf for Cave-in-Rock and Alamo cultivars, respectively (Van Esbroeck *et al.*, 1997). The respective thermal-times to attain panicle emergence were 634 and 1 777 GDD.

The whole thermal-time accumulation concept relies on a reasonable estimate of base temperature, temperature below which no thermal-time accumulates (Hodges, 1991). Above this base temperature crop development rate increases with temperature to an optimum temperature, beyond which the rate of thermal-time accumulation and the accompanying crop responses decrease with further increases in temperature, until crop development ceases. Base temperatures vary among species (Jordon and Haferkamp, 1989; Probert, 1992) and on development stage (Slafer and Savin, 1991). Kiniry *et al.* (1991) reported a range of 7 to 9°C for maize, sorghum and pearl millet. Sanderson and Wolf (1995a; 1995b) and Van Esbroeck *et al.* (1997) used a base temperature of 10°C for switchgrass. In the published literature there are sometimes quite different experimental estimations of base temperatures for the same species. Because of this variation most thermal-time models are based on average base temperatures, something which has potential for introducing inaccuracies in the predictive values of these models.

2.4. Utilisation and environmental impact

2.4.1. Biomass yields

In North America, lowland ecotypes of switchgrass have yielded 20-30 Mg ha^{-1} in Alabama (Sladden *et al.*, 1991), 5.4 - 13.2 Mg ha^{-1} in Texas, and winter hardy upland ecotypes yielded 9.2 Mg ha^{-1} in North Dakota (Jacobson *et al.*,1986) and 12.5 Mg ha^{-1} in Pennsylvania (Jung *et al*, 1990). In the study by Jung *et al.* (1990), big bluestem (*Andropogon gerardii* Vitman) yields ranged from 5.0 - 9.0 Mg ha^{-1}, 6.3 - 10.8 for indiangrass (*Sorghastrum nutans* (L.) Nash), and 5.2 - 11.4 for flaccidgrass (*Pennisetum flaccidum* Griseb.). Variations in yields have been attributed largely to ecotypic differences (Jung *et al.*, 1990; Hopkins *et al.*, 1995), photosynthetic rates, and ploidy levels (Wullscheger *et al.*, 1996). Yields also varied with nitrogen fertilisation for several warm season grasses (Hall *et al.*, 1982; Jung *et al.*, 1990; Stout and Jung, 1995; Bredja *et al.*,

1996) with increased yields achieved with N inputs up to 200 kg ha^{-1}. Yields have generally declined in late summer as a result of translocation of aboveground biomass to belowground parts. Peak biomass yields were attained in late July and August (Sladden *et al.*, 1995).

2.4.2. Forage production

Warm season grasses have been traditionally used to compliment temperate grasses when they experience growth depression in mid summer (Burns and Chamble, 1979; Griffin and Jung, 1983; Anderson *et al.*, 1988). C_4 grasses have relatively lower nutritive value (crude protein content and digestibility) compared with C_3 grasses. A combination of selection (Godshalk *et al.*, 1988; Hopkins *et al.*, 1995) and well planned management strategies (George and Obermann, 1989; Mullahey *et al.*, 1991) can ensure reasonable quality of the harvested material. However, this comparison, based largely on *in-vitro* techniques, is becoming inappropriate because warm season grass tissues tend to be degraded slowly in the rumen relative to cool season grasses (Akin *et al.*, 1990). As a result, they contain on average 50 % of their N in the form of rumen non-degradable protein, most of which is available post-ruminally (Mullahey *et al.*, 1992; Hafley *et al.*, 1993).

2.4.3. Biomass feedstocks

In contrast to forage production, high lignocellulose content is the main requirement in the production of herbaceous feedstocks (Sanderson *et al.*, 1996). Generally, C_4 grasses have been observed to have higher cellulose and hemicellulose contents than C_3 grasses (Cherney *et al.*, 1988; Sanderson and Wolf, 1995b). The various end uses of herbaceous biomass include: macromolecular raw materials such as pulp and lignin (Faix *et al.*, 1989); chemicals and biofuels from biochemical and thermochemical conversions (Ortiz-Canavate, 1994); and energy from direct combustion (Trebbi, 1993). Lignocellulose, nitrogen and ash are the most crucial constituents for species/cultivars intended for biofuel or fibre production. While high lignin content is ideal for chemical production it interferes with fibre availability and properties in pulp and paper manufacture (Parham, 1983). High nitrogen and ash contents have been reported to reduce chemical output in thermochemical conversions (Agblevor *et al.*, 1992). High levels of ash are also detrimental to industrial machinery (Kurkela *et al.*, 1993).

2.4.4. Environmental Impact

Widespread cultivation of warm season grasses in temperate regions offer several solutions to modern day environmental problems. Given their high NUE and WUE (Stout *et al.*, 1988; Staley *et al.*, 1991) and deep root systems, these grasses can be grown on marginal lands and can be used in reducing erosion and runoff, which reduces loss of soil nutrients and organic matter (Vaughan *et al.*, 1989). Their cultivation implies reduced usage of fertilisers and other agro-chemicals thereby reducing pollution of streams and groundwater (McLaughlin *et al.*, 1994). Relative to the traditional row spacing cultural practices of crop production, warm season grass production could reduce erosion rates by 95 % and the use of pesticides by 90 % (Hohenstein and Wright, 1994).

If the biomass produced is used for energy production, there is an environmental benefit resulting from a reduction in the atmospheric releases of CO_2 (Graham *et al.*, 1992), a direct result from reduced usage of fossil fuels. Gebhart *et al.* (1994) also reported potential reduction in CO_2 release associated with the replacement of soil carbon depleted by long periods of row cropping if perennial forage species are grown. When the perennial grasses are used in the production of pulp and paper there is a direct benefit in terms of forestry conservation.

2.5. Hypotheses

The above discussion is based on the general comparative eco-physiology of C_3 and C_4 grasses. It can be established that C_4 plants are more productive and physiological factors strongly affect their competitiveness and distribution. Some of the most important characteristics which C_4 grasses have evolved include an efficient photosynthetic system and a more erectophile leaf arrangement, to maximise light interception. General considerations of the physiology of C_4 photosynthesis are useful, but it is now known that physiological responses are characteristics of specific C_4 plants. Over time, there have been independent environmental adaptations. Temperature and length of growing season had an overriding effect on the adaptation and distribution of C_4 plants. C_4 species decrease towards higher latitudes, both north and south, although they are not excluded in these areas. Their mere existence in northern areas highlights a potential for agricultural exploitation of these C_4 grasses. The ideal features of a successful C_4 plant in the temperate regions can be summarised as: a) an early and high rate of canopy development in spring to take advantage of the increase in availability of solar energy, faster initial growth rate at lower temperatures particularly, since increases in soil temperature lag behind solar irradiance, b) once an optimal leaf area index has been attained the ability to assimilate CO_2 rapidly, c) once the canopy is developed, a long period of photosynthetic activity (delayed senescence).

At this time, there is limited information on the eco-physiological adaptation of warm season grass species to conditions in eastern Canada. In an effort to generate information to provide guidance in identifying potential C_4 plants for widespread use in this region it was broadly hypothesised that warm season grasses have developed various adaptive mechanisms for survival in cool temperate regions and their productivity potential has not been compromised. The specific hypotheses were as follows:

1) Warm season grasses can over-winter in eastern Canada.

2) Variation exists among warm season grasses with respect to dehardening and therefore the beginning of spring growth.

3) Because of variation in chilling tolerance among warm season grasses, there are differences in base temperatures: a) among and within species b) for different growth stages.

4) Given variations in phenological development, some warm season grasses mature in the short seasons of eastern Canada.

5) Canopy development and persistence differ among North American C_4 grasses.

6) High radiation-use efficiencies and biomass yields are achieved by warm season grasses under the short seasons of eastern Canada.

7) Warm season grasses can be managed successfully in a regime where they are harvested several times during the season.

8) N fertilisation will increase yield and forage quality of warm season grasses grown in a short season area.

9) Seed conditioning treatments will alleviate effects of low temperatures on warm season grass seed germination.

10) Fibre properties of warm season grasses allow for utilisation in pulp and paper production.

2.6. Objectives

1) To assess morphological development, biomass yield, and chemical composition of warm season grasses in south-western Québec.

2) To define relationships between height, leaf number, and total LAI and growing degree-days for warm season grasses.

3) To determine canopy development and architecture of warm season grasses under short season conditions.

4) Using switchgrass a) characterise growth performance
b) estimate energy yield and radiation-use efficiency
c) determine dry matter composition at different times of the season.

5) To determine the response of switchgrass to N fertilisation and different harvest schedules.

6) To evaluate the relationship between leaf chlorophyll and tissue N concentration in switchgrass.

7) To determine the inter- and intra-specific variation in base temperatures for germination and growth among warm season grasses.

8) To evaluate the effectiveness of seed conditioning treatments in improving germination of swicthgrass.

9) To evaluate kraft pulping characteristics and pulp properties of five species of warm season grasses.

Preface to Chapter 3

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Most of the germplasm collection and evaluation has been centred in the southern states of the USA. These are generally warmer regions with fairly long growing seasons. Switchgrass is an important species there and has been evaluated ever since it was selected as a model species for the development of herbaceous energy crops. In this chapter, a collection of five species of warm season grasses are evaluated in a short growing season area. Their phenological development and yield in a space-planted nursery are evaluated.

Chapter 3

Evaluation of Selected Warm Season Grasses for Biomass Production in a Short Season Area

3.1. Abstract

Field studies were conducted in 1994 and 1995 to determine the phenology, leaf and tiller characteristics, and yield of 22 warm season grasses in south-western Québec, Canada. Cordgrass (*Spartina pectinata* L.), two cultivars of indian grass (*Sorghastrum nutans* L. (Nash)), two cultivars of big bluestem (*Andropogon gerardii* Vitman), 12 cultivars of switchgrass (*Panicum virgatum* L.) and five cultivars of prairie sandreed (*Calamovilfa longifolia* (Hook) Scibn.), were included in the study. In terms of spring regrowth, CWNC (cordgrass) and New Jersey 50 (switchgrass) were the earliest and latest respectively. Regrowth from sandreeds was predominantly from continued growth of biennial tillers, from rhizomes in cordgrass and from buds on stem bases for the other species. The earliest maturing entries were ND3743, Dakota, Ottawa3 (switchgrasses) and Bison (big bluestem). New Jersey 50 and CWNC were the latest maturing. CWNC had high tiller numbers throughout the season while the rest of the entries showed increases in tiller numbers in summer. There were significant differences among entries in height development across the season. Biomass yields ranged from 65 to 861 g per plant. Lignocellulose content was high in all entries with NDF and ADF ranging from 77-86 and 46-54 %, respectively. Nitrogen and ash content ranged from 0.4-1 and 4-7 %, respectively. The results indicate potential for some warm season grass species for biomass production in short season areas.

3.2. Introduction

Warm season grasses utilise the C_4 photosynthetic pathway and offer significant forage and biomass potential in northern latitudes. They are characterised by: (i) high optimal temperatures for photosynthesis (Edwards and Walker, 1983) which creates forage production potential during the critical months of July and August when cool season grasses exhibit low productivity, and (ii) high nitrogen and water use efficiencies for both forage and biomass production (Jung *et al.*, 1990). However, the low spring and fall temperatures of the northern latitudes tend to limit overall production of warm season grasses. A range of warm season forage grass species are found in North America (Stubbendieck *et al.*, 1992) and these have been subject to various selection pressures for adaptability to temperature and length of growing season. As a result, there are variable environmental adaptations for the different strains/ecotypes. The short life cycle of *Echinocloa crus-galli* (L.) Beav. is a likely example of an environmental adaptation to the short warm seasons in Québec (Potvin, 1986). Similar examples are reported by Jacobson *et al.* (1986) and Olson (1986) who evaluated several species in various environments and noted a north-south climatic influence on species performance. In these evaluations, southern ecotypes matured late in northern latitudes and were susceptible to winter injury. Ecotypes of northern origin generally showed early growth in spring and matured early.

With the increased interest in warm season grasses for forage, biomass production, and soil conservation, information is required on their areas of adaptation. Overall patterns of development and adaptation in northern areas, such as eastern Canada, are not currently available in the literature. It is essential to document phenology, winter injury, plant characteristics and potential yield to aid in identifying particular species/strains for specific end uses.

The various end uses of herbaceous biomass include: macromolecular raw materials such as pulp and lignin (Faix *et al.*, 1989); chemicals and biofuels from biochemical and thermochemical conversions (Ortiz-Canavate, 1994); and energy from direct combustion (Trebbi, 1993). Lignocellulose, nitrogen and ash are the most crucial constituents for species/cultivars intended for biofuel or fibre production. While high lignin content is ideal for chemical production it interferes with fibre availability and properties in pulp and paper manufacture (Parham, 1983). High nitrogen and ash contents have been reported to reduce chemical output in thermochemical conversions (Agblevor *et al.*, 1992). High levels of ash are also detrimental to industrial machinery (Kurkela *et al.*, 1993). The objective of this study was to assess the morphological development, yield and industrial biomass potential of 22 warm season grasses in south-western Québec.

3.3. Materials and Methods

The research was carried out at the Emile Lods Research Centre of McGill University, Montréal (45°28'N 73°45'W) on a free draining St Bernard loam (Hapludalf). The site has a 1 % N-S slope, and had been in fallow for the five previous years. Land was prepared by ploughing in the fall of 1992, followed by discing in the spring of 1993. Climatic data [temperature, rainfall and growing degree days (calculated with a base temperature of 5°C)] were recorded by an automatic weather station linked to Dorval International Airport, which is 15 km away from the research centre.

The cultivars/strains evaluated are detailed in Table 3.1. The entries were space planted (each in a seven-meter long row) as seedlings, 0.5 m between plants and 1 m between rows, at the end of May, 1993. The experimental design was a randomized complete block with four blocks. The nursery was hand weeded twice each year, and no fertilizer was applied. Some replacement of dead plants was required in mid-summer after a period of early summer drought.

Data collection began in spring 1994 and continued to the end of summer 1995. Data collected included morphological development, tiller number and characteristics, and biomass at the end of the growing season. Morphological development was assessed using a descriptive index developed by Simon and Park (1983). Mean stage number was assessed visually on primary tillers of each plant every week. A plot was deemed to have attained a particular stage number when approximately 10 per cent of the assessed tillers had reached that stage. Before analysis, the observation dates were converted to number of days after May 1, as a basis for standard comparison.

Tillers were counted on five plants in each row every two weeks. A secondary tiller was considered eligible for counting as soon as it emerged from the subtending leaf sheath. Tiller height was measured bi-weekly both as height to the ligule of the last fully expanded leaf and to the tip of the youngest leaf. Vernier calipers were used to measure tiller diameter. Both height and diameter measurements were made on 30 tillers (the two tallest tillers from each plant). Using the same tillers, number of green leaves per tiller, and leaf length and width of the last fully expanded leaf were also measured every two weeks.

At the end of the growing season (first week of October), eight plants were randomly selected in each row and harvested in both 1994 and 1995. The plants were cut at a height of 10 cm above the ground for biomass determination. Forty tillers were separated into leaf and stem material. These fractions as well as subsamples for dry matter determination were dried to a constant weight at 60°C. Additional subsamples were analysed for neutral detergent fibre (NDF, mainly cellulose, hemicellulose and lignin) and acid detergent fibre (ADF; mainly lignin, cellulose and insoluble ash) (on a 100°C oven dry matter basis) using an F-200 fibre unit with F-56 filter bags (Ankom Tech. Corp., Fairport, New York, USA). Kjeldahl nitrogen was analysed using the Kjeltec System 1002 Distilling Unit (Tecator, Hoganas, Sweden). Two gram samples were ignited in a muffle furnace at 525°C for 4 h to determine ash content.

All data collected were subjected to analysis of variance and if the F-test was significant ($P<0.05$) a protected Least Significant Difference (LSD) test was used to detect mean differences for each year, using the General Linear Models Procedure (SAS, 1995).

3.4. Results

3.4.1. Environment

Weather conditions for both 1994 and 1995 are presented in Table 3.2. Total rainfall for the growing season (April to September), in each year (540 and 537 mm in 1994 and 1995, respectively) was slightly above the long term average (518 mm). The 1994 growing season was characterised by a very wet spring and fairly dry summer, particularly in July. Rainfall in the 1995 season was more evenly distributed with more rain falling in summer. Accumulation of growing degree days was approximately linear in both seasons. The 1995 spring was warmer than that of 1994, resulting in an apparent earlier accumulation of growing degree days, however, the rate of accumulation between years was not significantly different ($P<0.05$).

3.4.2. *Spring regrowth*

In the warmer spring of 1995, all entries showed signs of regrowth earlier than in 1994 (Table 3.3). CWNC was the earliest in 1995 at 05 April, while NJ50 was the latest, at 01 May. In 1994 regrowth was observed to occur over a longer period. However, CWNC and NJ50 were also the earliest and latest to regrow, respectively in 1994.

Regrowth in the sandreeds was from rhizomes and, more predominantly, from continuation of vegetative growth of biennial tillers (late emerging tillers from the previous year). Sandreed rhizomes were observed as far as 50 cm from the parent plant. Regrowth in switchgrass was mostly from buds on the stem bases of the previous year's tillers. A smaller proportion of the regrowth was from rhizomes. Indian grass and big bluestem regrowth was also from buds on stem bases. Of the 60 established plants of SN31, only four survived the winter of 1993/94. No further data were recorded for this entry. For CWNC, regrowth was predominantly from rhizomes and both vertical and horizontal rhizomes supported development of new tillers. These rhizomes were very extensive, growing as far as 1 m from the original planting location. Tillers developing from terminal buds of the rhizomes were larger and more vigorous in growth than those developing from other buds along the length of the rhizome.

3.4.3. *Phenology*

Growth habit for individual entries was similar in both years, but development began earlier and was more rapid in 1995 than 1994. In mid summer, sandreeds were characterised by a secondary flush of tillers that did not flower. These tillers overwintered and continued growth the following spring. Table 3.4 shows the average number of days to a particular reproductive stage for each entry. Fig 3.1 displays the average phenological stages for all entries on July 28 for both years. Maturity differences were very distinctive with ND, DK, OTT3 and Bison being the earliest maturing. There were also notable differences in the time required for each entry to progress from one stage to another. The prairie sandreeds were generally late in maturity. Among the sandreeds, Ca44 and Ca59 were the earliest for spring growth, while PI47 was the earliest in maturity, reaching boot and hard seed stages 10-18 days earlier than the others.

Among the switchgrasses, NJ50 was the latest in maturity, reaching the hard seed stage, on average, three weeks later than the other entries. Generally, the north-western U.S.A. entries were earlier maturing than the south-eastern U.S.A. entries. There were consistent differences in phenology between Bison and NBB for the two years, the former being earlier in maturity. CWNC began growth early in the spring and matured late in the fall, that is, it was vegetatively productive for the bulk of the growing season.

3.4.4. Tiller characteristics

Tiller numbers during the two seasons are shown in Figs 3.2 and 3.3. Table 3.5 shows the seasonal maximum tiller heights and diameters for the entries. There was a general increase in these parameters as the season progressed as well as from 1994 to 1995. CWNC consistently had higher numbers of tillers and tiller diameters than the other entries.

In the spring, PI47 had the most tillers of the sandreeds, and Ca59 the least. The summer increase in tiller numbers was greatest for Ca44 which had, on average, one-and-a-half times more than the other sandreeds. There was no increase in tiller numbers during the season for ND95 (maximum of 7.5 tillers per plant). The maximum diameter measured in the sandreeds was 0.56 cm for PI47, while ND95 had the smallest average diameter at 0.4 cm.

Differences in the switchgrass entries were less distinct in 1995 than 1994. Generally, in early spring, NEB, ND, OTT4, CIR, OTT1 and OTT3 had the greatest tiller numbers, while DK, SH and PF had the least. By mid summer there were no longer any differences ($p < 0.05$) among the switchgrass entries for tiller numbers. CIR, NJ50, NEB, OTT1 and OTT2 had the thickest tillers with an average of 0.5 cm. ND, DK, SH and PF were characterised by fine tillers with small diameters.

In both seasons, Bison showed a steady increase in tiller numbers throughout the growing season, whereas NBB had a pronounced flush in mid summer. Bison also had thicker tillers than NBB. Toma had modest increases in tiller numbers in spring which was followed by a flush in mid summer. Toma had more but finer tillers than both Bison and NBB.

Height development was related to increasing temperature for all entries (Fig 3.4 and 3.5). In both years, CWNC showed steadily increasing height until mid July, followed by a period of faster increase until maximum height was attained in late August. The heights of NBB and Toma increased slowly in the spring, until mid June, followed by a period of more rapid increase, to attain maximum height in late July. Height changes for Bison occurred sooner and faster than for both NBB and Toma. All the sandreeds showed slow increases in height up to mid June, followed by faster increases until reaching maximum height in mid to late August. PI47 was distinctive in its more rapid stem elongation pattern in June, attaining 65 % of its maximum height within a two week period.

Height development for the switchgrass entries was more distinctive in 1995. Generally, the early maturing entries ND and DK attained maximum height in late June to early July. Rapid stem elongation in the other switchgrass entries was delayed until mid July. CIR, TL, OTT3 and SH were always taller than the other switchgrasses.

3.4.5. Leaf characteristics

The average leaf numbers and leaf sizes of the entries are presented in Tables 3.6 and 3.7. Leaf number and size during the season followed the maturity patterns of the entries. The big bluestems were characterised by an early flush of leaves in spring reaching an average of 7 short and narrow leaves. Bison had earlier leaf loss than NBB. The sandreeds averaged 6 to 9 long (50-70 cm) leaves that averaged 0.8-1.5 cm in width. PI47 and Ca59 had more leaves of a bigger size than the other sandreeds.

By mid summer, CWNC tillers averaged 7-9 leaves that were on average 103.6 cm long and 1.7 cm wide. These leaves were of a coarse texture and maintained their green colour well into the fall. The switchgrass entries averaged 3-6 leaves. Early maturing entries (ND and DK) attained maximum leaf numbers in late spring, compared with mid summer for the other entries. CIR had the biggest leaves, which remained green even after the hard seed stage. For the other switchgrasses, there was a decline in leaf numbers and loss of green colour after seed set.

3.4.6. Biomass potential

There was a substantial increase in biomass per plant from 1994 to 1995 (Table 3.8). The 1995 yield increases ranged from 71 to 170 %. Some of this difference was almost certainly attributable to the warmer spring in 1995 than 1994, however damage during the severe winter of 1993/94 may also have weakened stands in 1994. The entries with potential for high biomass production in south-western Québec included CWNC, CIR, NEB, OTT1, OTT2, OTT4 and TL. CWNC and the sandreeds had higher leaf proportions, compared with the other entries. Leaf to stem ratios for the switchgrass entries ranged from 21 to 36 % by weight (Table 3.8). The ranking in leaf:stem ratios by species was sandreed > cordgrass > switchgrass > big bluestem > indian grass. Generally, all entries had high proportions of NDF and ADF (Table 8). Entries with the most lignocellulose were NJ50, ND, Bison and CWNC. The species averages ranked cordgrass > big bluestem > switchgrass > sandreed > indian grass. The difference between NDF and ADF is comprised largely of hemicellulose. For all entries, hemicellulose constituted more than 25 % (Table 3.8). Generally, the sandreeds had high hemicellulose contents (averaged 32 %), while in the switchgrasses it ranged from 28 to 32 %. Nitrogen contents averaged 0.86, 0.73, 0.7, 0.25 and 0.45 % in sandreed, big bluestem, switchgrass, cordgrass and indian grass, respectively. The entries with the lowest nitrogen contents were CWNC, Toma, ND and NJ50. The average ash content was 5.22 %. Ca59, TL, Ca44 had the highest ash contents (6.88, 6.16 and 6.16 %, respectively) while Bison, OTT1 and OTT4 had the lowest ash contents with 3.92, 4.33 and 4.36 %, respectively.

3.5. Discussion

The data confirms the existence of a great deal of diversity in development and maturity patterns among warm season grasses. Within, species there were variations in rate of growth and date of maturity. The observation that entries of mid-western U.S.A. origin flower earlier than those of south-eastern origin (Jacobson *et al.* 1986; McMillan, 1959) was demonstrated to a limited degree in the current study by switchgrass entries. ND, DK and OTT3 were relatively earlier maturing than NJ50 and CIR, which were the latest maturing entries. Except for CIR and NJ50, switchgrass entries were able to attain complete dormancy before the first killing frost or freezing of the soil. CIR retained a considerable amount of green leaf tissue even after the dry seed stage, suggesting that carbohydrates formed from these leaves were for underground storage. This is a definite advantage because rapid regrowth in spring is based largely on mobilisation of stored reserves (Schwarz and Redman, 1989). NJ50 was still growing late in the season; though this led to increased biomass yield, it might also increase susceptibility to winter injury and result in a lack of seed for stand perpetuation.

The sandreeds, big bluestem and Toma also reached dormancy before the first killing frost. The continued growth of CWNC into the fall was accompanied by high biomass yield. Growth into fall might not be a major concern for CWNC because of its numerous rhizomes, and its early spring growth which indicates a tolerance of cool temperatures.

In general, tiller numbers, height, leaf number and size increased linearly from late May to late June or late July for early or late maturing entries respectively. Beaty *et al.* (1978) also reported the regrowth of tillers from basal buds in switchgrass. The biennial nature of late emerged sandreed tillers, observed in this study, is not supported by White (1977) who reported that in Montana, sandreed tillers completed growth the year they emerged. The low general productivity of sandreeds, in terms of tiller numbers and yield, does not suggest any major economic role for this species in eastern Canada.

The high fibre content in all the entries indicates high potential for both fibre and biofuel products. The NDF values for switchgrass in the current study are within the range 71.5-83.8 % in late season (early August) cut grasses reported by Vona *et al.*

(1984). However, their ADF range of 41.7-51.5 % is lower than in our study. The nitrogen content of post head emergence herbage from NBB (0.93 %), Blackwell (OTT1, 0.8 %), Caddo (OTT2, 0.83 %) and NJ50 (0.81 %) reported by Jung *et al.* (1990) were higher than those observed by us. Our average values for big bluestem and switchgrass were also lower than those reported by Vona *et al.* (1984). Our lower values are probably due to our later harvest date (early October).

High nitrogen levels in biomass for industrial feedstock are detrimental to thermochemical reactions. Nitrogen content correlates positively with char residues: 10 and 28 % char residues at 0 and 3.5 % nitrogen (Agblevor *et al.*, 1992). The same authors reported a decrease in yield of aromatic products as the nitrogen content increased. Therefore, substantial char residues and decreased yield of aromatic products would be expected from all the entries we evaluated (range 0.43-1 % nitrogen).

The ash contents we observed in switchgrass were within the 3-7 % range reported by Wiselogel *et al.* (1994) and Agblevor *et al.* (1992). Lanning and Eleuterius (1987) reported ash contents of 1.93-5.70 and 3.55-9.48 % for different parts of big bluestem and indian grass respectively. This compares well with the respective values from our study. The ash component interferes with yield in carbohydrate pyrolysis because it also promotes char formation. In addition to formation of fusible ash at high temperatures, high ash content also damages machinery during industrial processing (Kurkela *et al.*, 1993).

Given the high lignocellulose content for all entries, the agronomic characteristics will greatly influence which entries are desirable for biomass production. The high nitrogen and ash content of the entries we evaluated limit their widespread use in industrial thermochemical conversions and processing. It would be desirable to devise a pretreatment process to reduce both nitrogen and ash content in these entries. CWNC, CIR, NEB, OTT1, OTT2, OTT4 and TL have potential for biomass production in short season areas with sufficient summer heat. The high leaf proportion of CWNC might be a limitation especially in pulping where high leaf content results in very short fibres and slow draining pulp. The early maturing cultivars might have forage potential especially in view of their fine tissue characteristics. Bison, NBB and Toma had good leaf cover early in the growing season suggesting forage potential. During this study, we did not impose any management stresses such as cutting or grazing, factors which might further define which entries would be suitable for animal production. CWNC was the only entry that was able to utilise the increases in solar radiation in early spring and still extend its growing season into the fall. This makes it an ideal biomass crop.

3.6. Conclusions

It is concluded from this study that there is potential for warm season grasses in south-western Québec. The most productive entries were CWNC (cordgrass) and several switchgrasses (CIR, NEB, OTT1, OTT2, OTT4 and TL). These entries were characterised by high numbers of tillers, large leaves, and high rates of development in the summer. The most productive switchgrasses were generally of southern origin whereas those from the mid-west tended to produce less biomass. The sandreeds showed little potential for forage or biomass production. It is desirable to impose conventional management stresses during evaluation to define which ecotypes might be suitable for particular end uses.

Table 3.1: The warm season grasses evaluated in south-western Québec

Common name	Strain/Cultivar	Abbreviation	Notes on origin
Sandreed	Pronghorn	Pron	North Dakota
(*Calamovilfa longifolia*	ND95	ND95	North Dakota
(Hook.) Scibn.)	PI477011	PI4	Rose Lake. Michigan
	9004944	Ca44	Huron Co. Michigan
	9004959	Ca59	Porter Co. Indiana
Switchgrass	Shelter	SH	W. Virginia
(*Panicum virgatum* L.)	New Jersey 50	NJ50	North Carolina
	Cave-in-Rock	CIR	S. Illinois
	Ottawa1*[1]	OTT1	selected from cv. Blackwell[3]
	Ottawa2*[1]	OTT2	" cv Caddo[3]
	Ottawa3*[2]	OTT3	open pollinated population
	Ottawa4*[1]	OTT4	selected from cv Pathfinder
	ND3743	ND	selected from Nebraska 28
	Dakota	DK	North Dakota
	Nebraska synthetic	NEB	Nebraska
	Pathfinder	PF	Nebraska
	Trailblazer	TL	Nebraska
Big Bluestem	Niagara	NBB	NW New York
(*Andropogon gerardii* Vitman)	Bison	Bison	North Dakota
Indian grass	Tomahawk	Toma	North Dakota
(*Sorghastrum nutans* L. Nash.)	315743	SN31	Michigan
Cordgrass (*Spartina pectinata* L.)	CWNC	CWNC	Waukesha Co. Wisconsin

* selection done in Ottawa, Ontario

[1] selected for winterhardiness, vigour and biomass yield

[2] open pollinated population originating from a single maternal clone from Pathfinder

[3] cultivar from Oklahoma

Table 3.2: Mean monthly temperature (° C), rainfall (mm) and growing degree days (base of 5° C) during 1994 and 1995 at Ste Anne-de-Bellevue, Québec

	Mean monthly temperature (° C)			Mean monthly rainfall (mm)			Growing degree days Base of 5° C		
	1994	1995	Normal	1994	1995	Normal	1994	1995	Normal
January	-16.6	-6.3	-10.3	20.6	61.9	20.8			
February	-11.8	-9.9	-8.8	1.2	2.6	18.8			
March	-3.0	-0.4	-2.4	17.4	20.3	34.1		5.5	
April	5.3	3.7	5.7	76.0	69.2	62.6	53.0	44.5	65.7
May	12.1	13.1	12.9	100.4	81.5	66.7	228.8	252.8	247.7
June	19.1	20.2	18.0	143.8	56.6	82.5	421.4	454.6	390.1
July	21.8	22.2	20.8	50.6	122.1	85.6	520.9	531.6	491.2
August	18.2	20.2	19.4	84.6	127.4	100.3	410.5	471.1	446.0
September	14.8	13.4	14.5	67.2	59.6	86.5	295.5	250.4	286.5
October	9.4	11.2	8.3	19.8	182.7	72.8	139.8	201.2	121.3
November	3.7	-1.0	1.6	105.7	89.1	70.4	42.0	10.4	22.4
December	-3.5	-8.6	-6.9	25.8	1.2	35.1			

Table 3.3: Dates of first spring growth of each entry

Entry	1994	1995
Switchgrass		
SH	5 May	10 April
NJ50	25 May	1 May
CIR	5 May	10 April
OTT1	5 May	10 April
OTT2	19 May	10 April
OTT3	5 May	10 April
OTT4	15 May	10 April
ND	5 May	10 April
DK	5 May	10 April
NEB	10 May	10 April
PF	15 May	10 April
TL	15 May	10 April
Prairie sandreed		
PI4	5 May	8 April
Ca44	5 May	10 April
Ca59	5 May	8 April
Pron	5 May	10 April
ND95	5 May	10 April
Others		
CWNC	31 April	5 April
Bison	15 May	10 April
NBB	15 May	10 April
Toma	1 May	10 April

Table 3.4: Mean number of days after May 1st until each entry reached a particular developmental stage during the summers of 1994 and 1995

Entry	Boot (45)[‡]		Full head exersion (58)		Full anthesis (64)		Hard seed (91)	
	1994	1995	1994	1995	1994	1995	1994	1995
Switchgrass								
SH	82.3ef[†]	68.5fgh	103.3cde	88.5cd	117.5cde	102.8fgh	138.5ef	120.5hij
NJ50	94bc	87.25a	119a	105.5a	128a	130a	167a	155ab
CIR	70.8hi	74.5cde	88.3gh	88cd	114.3def	112.5bcd	142.5cde	129.7fg
OTT1	72hi	76cd	99.3de	95.5bc	113.5ef	116.8bc	130fg	145cd
OTT2	73.5gh	68.3fgh	97.5ef	92bcd	117.3cde	109de	142cde	119.5ijk
OTT3	66.5l	67.3gh	81.25l	85.5d	104.5g	101fgh	115h	112.8kl
OTT4	67.8hi	68.3fgh	92.8fg	89cd	118.5b-e	103.3e-h	142.3cde	117.5jk
ND	53.8j	52.3j	59.5j	64.3f	72.3l	76j	103.3i	92m
DK	55.8j	50j	64.3j	62f	86.8h	76j	105hi	92m
NEB	78fg	76.5cd	99.8cde	99ab	120.3a-d	116bc	141de	126.5ghi
PF	89de	70.5efg	98.2ef	94.8bc	110fg	104.5efg	130.6fg	120.8hij
TL	83ef	79.5bc	112ab	99.3ab	126.3a	106.8def	152bc	127.3fgh
Prairie sandreed								
PI4	86.8de	64.5hi	100cde	75.5e	118.3b-e	93.5l	146.8b-e	134ef
Ca44	98.8ab	77cd	111.5ab	95.5bc	122.3abc	116.3bc	149bcd	145cd
Ca59	102.3a	83.3ab	116.8a	98ab	126.5a	112cd	149.3bcd	150bc
Pron	100.3a	75.5cde	114.3a	93bcd	125.3a	115bc	152bc	137e
ND95	93.3bc	73.3def	104.3cd	90cd	121.3abc	115bc	149.3bcd	145cd
Others								
CWNC	93.3bc	78.8bc	105.8bc	93.5bc	120a-e	116.3bc	148.3b-e	138de
Bison	70hi	61.75l	85hi	72.5e	106.5g	99ghi	127g	113.8jkl
NBB	91.5cd	76cd	117a	90.3cd	126.5a	118.3b	164a	158a
Toma	72.5gh	73.3def	97ef	89.8cd	110.3fg	97.8hi	130.3fg	110l
LSD (0.05)	5.94	5.14	6.34	7.65	6.54	5.88	10.27	7.1
CV (%)	5.24	5.24	4.56	6.26	4.03	3.98	5.22	3.98

[†] means in the same column followed by different letters differ significantly at $P < 0.05$, using a protected LSD test

[‡] numbers in brackets indicate phenological stage number (Simon and Park, 1983)

Table 3.5: Seasonal maximum height to the top ligule and to the tip of the youngest leaf, and average tiller diameter for all entries during the summers of 1994 and 1995

Entry	1994		1995		Average tiller diameter (cm)
	Height to top ligule (cm)	Height to tip of youngest leaf (cm)	Height to top ligule (cm)	Height to tip of youngest leaf (cm)	
Switchgrass					
SH	100.1e-h [†]	150.2cde	118fg	177cde	0.38ef
NJ50	105.5c-g	181.9ab	94.5i	162.5efg	0.5bcd
CIR	110b-g	145.5cde	136.8de	186.5bcd	0.47b-e
OTT1	102.3d-h	136.8d-g	122.8efg	164efcd	0.45de
OTT2	105.5c-g	141.2c-f	127.3efg	170.3def	0.5bcd
OTT3	118.3b-e	151.1cde	130.8def	168.8def	0.44de
OTT4	97.5e-i	130.2e-h	125.5efg	166.8ef	0.46cde
ND	100.3e-h	112.8f-i	98.75hi	110i	0.33f
DK	84.5hi	93.5i	96.1i	112.5i	0.22g
NEB	111.7b-f	147.9cde	131def	173.3c-f	0.47b-e
PF	78.78i	101.7hi	112.3gh	144gh	0.41def
TL	104.3c-h	140.5c-g	126.8efg	170.8def	0.45de
Prairie sandreed					
PI4	130.3b	181ab	137.5de	191bc	0.56b
Ca44	122bcd	166.3bc	163.3b	222.5a	0.44de
Ca59	91.1f-i	125.3e-h	144.3cd	198.3b	0.47b-e
Pron	112.5b-e	145.1cde	124.5efg	160efg	0.46cde
ND95	90.8ghi	111.6ghi	89.4i	108.6i	0.4def
Others					
CWNC	161.1a*	208.6a*	181.5a*	235a*	0.77a
Bison	160.9a	164.6bcd	156bc	159.8efg	0.55bc
NBB	124bc	136.7d-g	143.5cd	158fge	0.47b-e
Toma	118b-e	144.1cde	113gh	135.5h	0.34f
LSD (0.05)	20.88	29.12	16	18.95	0.10
CV (%)	13.5	14.6	8.91	8.17	22.2

[†] means in the same column followed by different letters differ significantly ($P < 0.05$) using a protected LSD test

Table 3.6 : Mean leaf number, length (cm) and width (cm) of all entries in spring and summer of 1994

Entry	Spring			Summer		
	leaf number	leaf length	leaf width	leaf number	leaf length	leaf width
Switchgrass						
SH	4.6fg [†]	32.9c-f	0.98b-e	5.5de	42.5f-i	1.18c-g
NJ50	3.1h	38.1cde	0.93b-f	5.6de	57.8bcd	1.4abc
CIR	5fg	41.6bc	1.28a	6.3d	53.0b-f	1.55a
OTT1	4.1g	35.9cde	1.08ab	4.5ef	55.1b-f	1.33a-d
OTT2	4.8fg	38.3cde	0.93b-f	4.5ef	58.3bcd	1.42abc
OTT3	4.6fg	35.6cde	1.0bcd	4.3f	40.6ghi	1.23c-f
OTT4	4.8fg	28.2efg	0.92b-f	4.9ef	49.4d-g	1.2c-g
ND	5.6def	29.6d-g	0.8c-g	4.3f	30.1ijk	0.95g-i
DK	4.6fg	21.5gh	0.7fgh	4.3f	34.8jk	0.75j
NEB	4.9fg	40.9bc	1.05abc	4.4ef	51.9c-g	1.28bcd
PF	4.3g	34.4cde	0.8c-g	4.8ef	34.6hij	1.1d-h
TL	4.8fg	32.3c-f	0.93b-f	4.8ef	55.4b-e	1.25cde
Prairie sandreed						
PI4	4.3ab	68.3a	0.9b-g	9.5a	63.1bc	1.25cde
Ca44	6.6bcd	50.8b	0.75d-h	9.6a	65.0b	1.0e-j
Ca59	6.1cde	49.9b	0.73e-h	8.0b	64.5bc	1.0e-j
Pron	6.1cde	41.6bc	0.65gh	8.6ab	54.2b-f	0.95g-i
ND95	5.0fg	40.2bcd	0.5h	8.8ab	44.0e-g	0.85hij
Others						
CWNC	6.8bc	65.1a	1.28a	8.8ab	94.1a	1.53ab
Bison	8.1a	29.0efg	0.83b-g	6.5cd	30.1ijk	1.20e-i
NBB	5.4ef	15.4h	0.68fgh	7.6bc	18.9k	0.79ij
Toma	4.3g	23.3fgh	0.83b-g	4.4ef	30.3ijk	0.98f-i
LSD (0.05)	1.1	10.7	0.26	1.2	12.8	0.25
CV (%)	14.6	20.0	21.05	14.0	18.6	15.78

[†] means in the same column followed by different letters differ significantly ($P < 0.05$) using a protected LSD test

Table 3.7 : Mean leaf number, length (cm) and width (cm) of all entries in spring and summer of 1995

Entry	Spring			Summer		
	Leaf number	Leaf length	Leaf width	Leaf number	Leaf length	Leaf width
Switchgrass						
SH	4.1gh [†]	39.5c-g	1.17d-g	5.3fgh	51.0hi	1.41c-f
NJ50	3.1i	46.1cde	1.74a	5.0fgh	71.9c-e	1.76ab
CIR	3.6hi	49.9bc	1.53abc	7.0de	63.5d-h	1.86a
OTT1	3.9hi	48.1cd	1.29cde	5.5fgh	66.1c-f	1.59abc
OTT2	3.4hi	41.0c-f	1.36bcd	5.8efg	69.9b-e	1.68abc
OTT3	3.9hi	43.0c-f	1.2c-f	5.5fgh	48.7ji	1.47cde
OTT4	3.8hi	36.3d-h	1.27cde	5.3fgh	56.8f-i	1.59abc
ND	4.1gh	35.5e-h	0.96e-i	4.3h	36.2jkl	1.14f-i
DK	4.3fgh	27.0hi	0.84ghi	4.8fgh	31.2kl	0.9i
NEB	3.5hi	49.4bc	1.26acde	5.8efg	62.3e-h	1.57bc
PF	3.9hi	41.3c-f	0.96e-i	5.5fgh	48.3ji	1.46cde
TL	3.6hi	38.7fgh	1.11d-h	5.8efg	71.5b-e	1.55cd
Prairie sandreed						
PI4	6.4a	81.9a	1.08d-h	9.0bc	75.8bcd	1.5bcd
Ca44	6.1ab	61.0b	0.93f-i	9.3b	77.9bc	1.2e-h
Ca59	5.8a-e	61.0b	0.90f-i	11.5a	82.9b	1.2e-h
Pron	5.4b-e	49.9bc	0.78hi	5.3bcd	65.0c-g	1.14f-i
ND95	5.1def	49.0c	0.65i	7.0de	52.8ghi	1.12ghi
Others						
CWNC	5.3cde	78.1a	1.66ab	9.0bc	113.0a	1.87a
Bison	5.9a-d	35.1e-h	1.04d-h	7.8cd	37.6jk	1.26d-g
NBB	5.0efg	18.5i	0.89f-i	8.1bcd	24.2l	0.95hi
Toma	3.4hi	27.9ghi	0.99e-h	4.5gh	36.3jkl	1.20e-h
LSD (0.05)	0.9	12.0	0.33	1.5	13.1	0.28
CV (%)	14.4	18.6	20.84	16.0	15.7	14.14

[†] means in the same column followed by different letters differ significantly ($P < 0.05$) using a protected LSD test

Table 3.8: The seasonal yields (g/plant), mean leaf:stem ratios (wt %), and mean chemical composition (wt %) of all entries

Entry	1994	1995	Leaf:Stem ratio	Nitrogen	NDF	ADF	Hemicellulose[•]	Ash
Switchgrass								
SH	204.1c[†]	385.2fg	30.95de	0.63ij	83.11b	50.77fg	32.34	4.96i
NJ50	190.7cd	293.3ghi	21.11h	0.43l	85.27a	55.85a	29.42	4.97i
CIR	405.3ab	860.6a	28.21efg	0.69gh	82.06de	52.07d	29.99	4.83j
OTT1	491.8a[•]	659.5cdg	31.11de	0.73efg	77.37k	45.48l	31.89	4.33l
OTT2	360.7b	671.6bc	22.5gh	0.92b	81.41fg	50.3ghi	31.11	5.09h
OTT3	207.5c	551de	21.11h	0.75e	80.68hi	51.24ef	29.44	5.34fg
OTT4	413.6ab	699.8bc	30.30def	0.66hi	---------[#]	--------[#]	------	4.36l
ND	191cd	261.6hij	29.17def	0.45l	82.53a	54.4b	28.13	4.65k
DK	82.6ef	213.2ij	29.17def	0.74ef	82.49bcd	50.13hi	32.36	5.43fg
NEB	429.3ab	778.5ab	22.5gh	0.71fg	82.92bc	53.34c	29.58	4.60k
PF	216.9c	455.2ef	24.29fgh	0.75e	81.85ef	51.86de	29.99	5.33g
TL	421.4ab	634.9cd	34.85d	0.93b	78.26j	50.15ghi	28.11	6.67b
Prairie sandreed								
PI4	161.8cde	332gh	52.27b	0.83cd	81.78gh	48.15j	33.63	5.41fg
Ca44	86.1ef	238.8hij	42.86c	1.01a	80.65hi	48.67j	31.98	6.17c
Ca59	28.3g	187.4ij	66.67a	0.81d	80.22i	47.37k	32.85	6.88a
Pron	66.9ef	187.3ij	52.25b	0.90b	82.30cde	50.08i	32.22	5.86d
ND95	29.45g	64.8k	43.73c	0.75e	82.15de	51.14f	31.01	5.56e
Others								
CWNC	452.3ab	850.3a	50b	0.52k	85.24a	53.27c	28.97	5.18h
Bison	119.7c-f	198.5ij	22.5gh	0.61j	85.4a	54.70b	30.7	3.92m
NBB	68.8ef	191.3ij	29.17def	0.85c	80.92gh	50.73fgh	30.19	5.44f
Toma	99.6def	170.7jk	19.0i	0.45l	80.99gh	50.64fghi	30.35	4.65k
LSD (0.05)	100.5	113.2	6.11	0.041	0.63	0.63		0.10
CV %	23	19.5	13.06	3.47	0.67	1.08		1.20

[†] means in the same column followed by different letters differ significantly ($P < 0.05$) using a protected LSD test;
[#] not analysed [•] estimated from the difference between NDF and ADF

Fig. 3.1: Average phenological stage of all entries on 28 July of 1994 and 1995: stage 45 = boot; stage 62 = anthesis; stage 87 = hard dough; stage 91 = endosperm hard (according to Simon and Park, 1983). T-bars Extending beyond bar graphs denote SE.

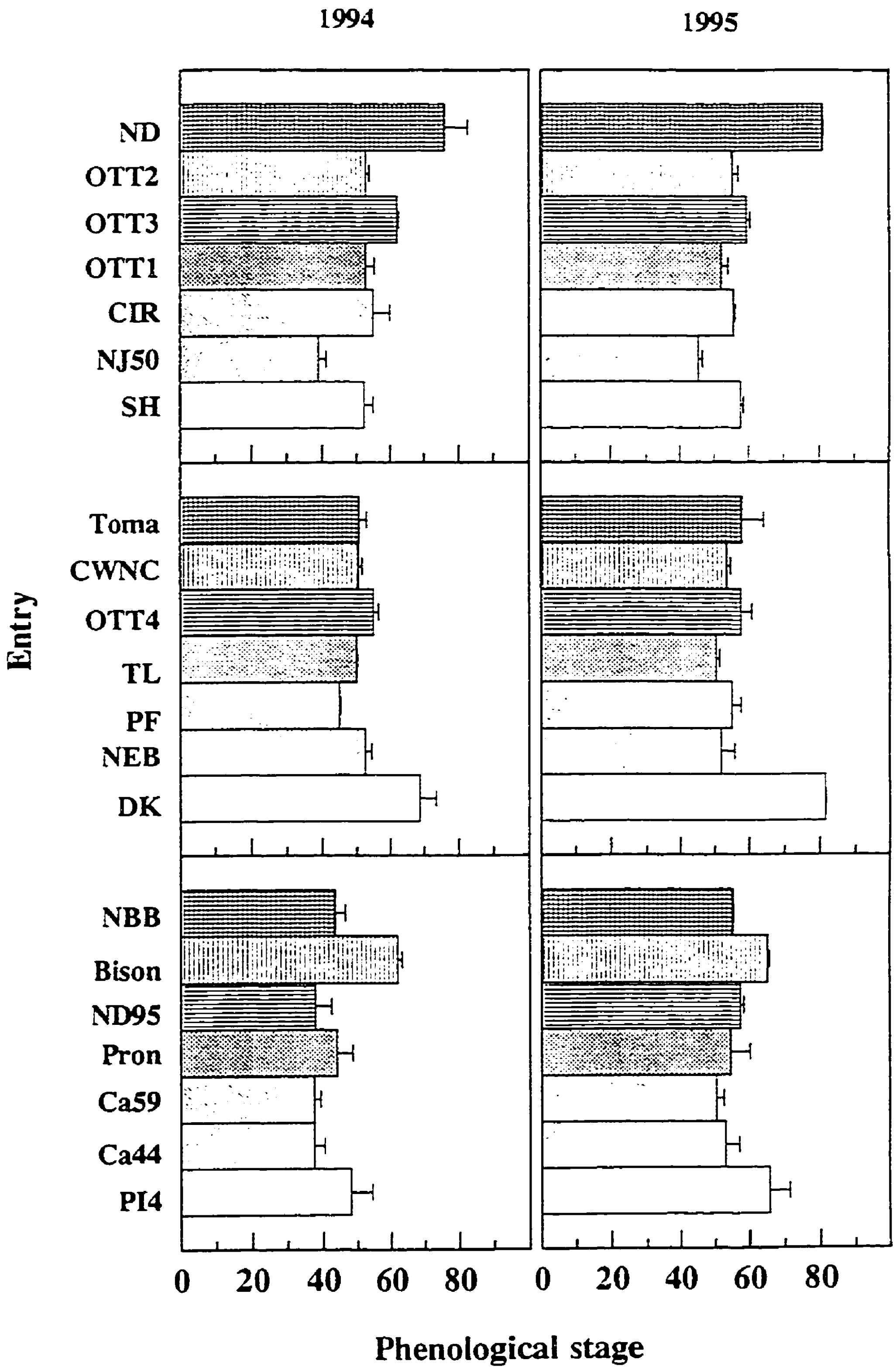

1994
1995
ND
OTT2
OTT3
OTT1
CIR
NJ50
SH
Toma
CWNC
OTT4
TL
PF
NEB
DK
NBB
Bison
ND95
Pron
Ca59
Ca44
PI4
Entry
0
20
40
60
80
0
20
40
60
80
Phenological stage

Fig. 3.2: The average number of tillers of CWNC, Toma, sandreed and big bluestem over the 1994 and 1995 seasons. T-bars extending beyond bar graphs denote SE.

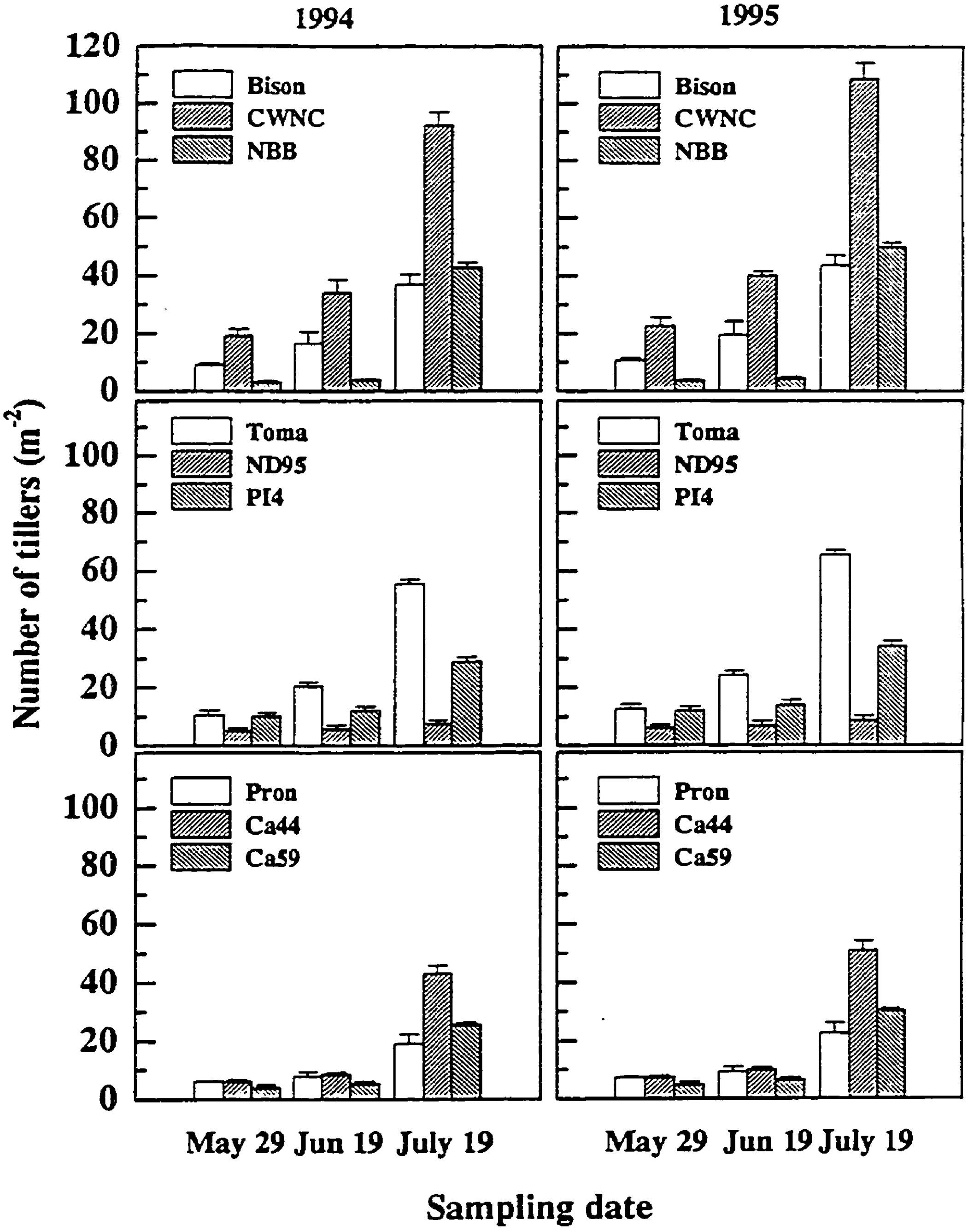

1994
1995
Bison
CWNC
NBB
Toma
ND95
PI4
Pron
Ca44
Ca59
120
100
80
60
40
20
0
Number of tillers (m^{-2})
May 29
Jun 19
July 19
Sampling date

Fig. 3.3: The average number of tillers of switchgrass entries during the 1994 and 1995 growing seasons. T-bars extending beyond bar graphs denote SE.

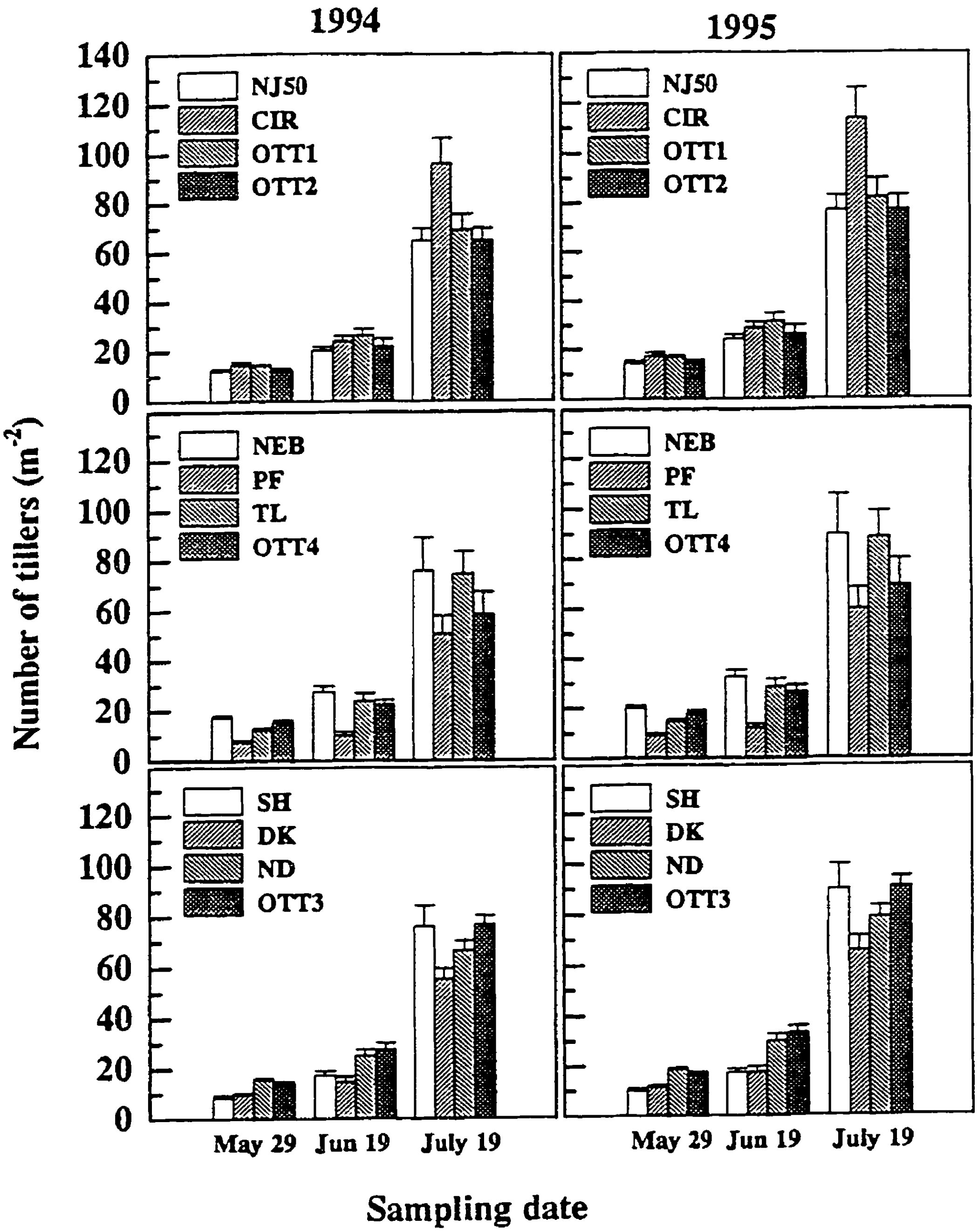

1994
1995
140
120
100
80
60
40
20
0
NJ50
CIR
OTT1
OTT2
NEB
PF
TL
OTT4
SH
DK
ND
OTT3
Number of tillers (m^{-2})
May 29
Jun 19
July 19
Sampling date

Fig. 3.4: Timing of stem elongation in switchgrass entries during the 1994 and 1995 growing seasons. Vertical lines in each graph denote least significant difference ($p<0.05$) for each sampling time.

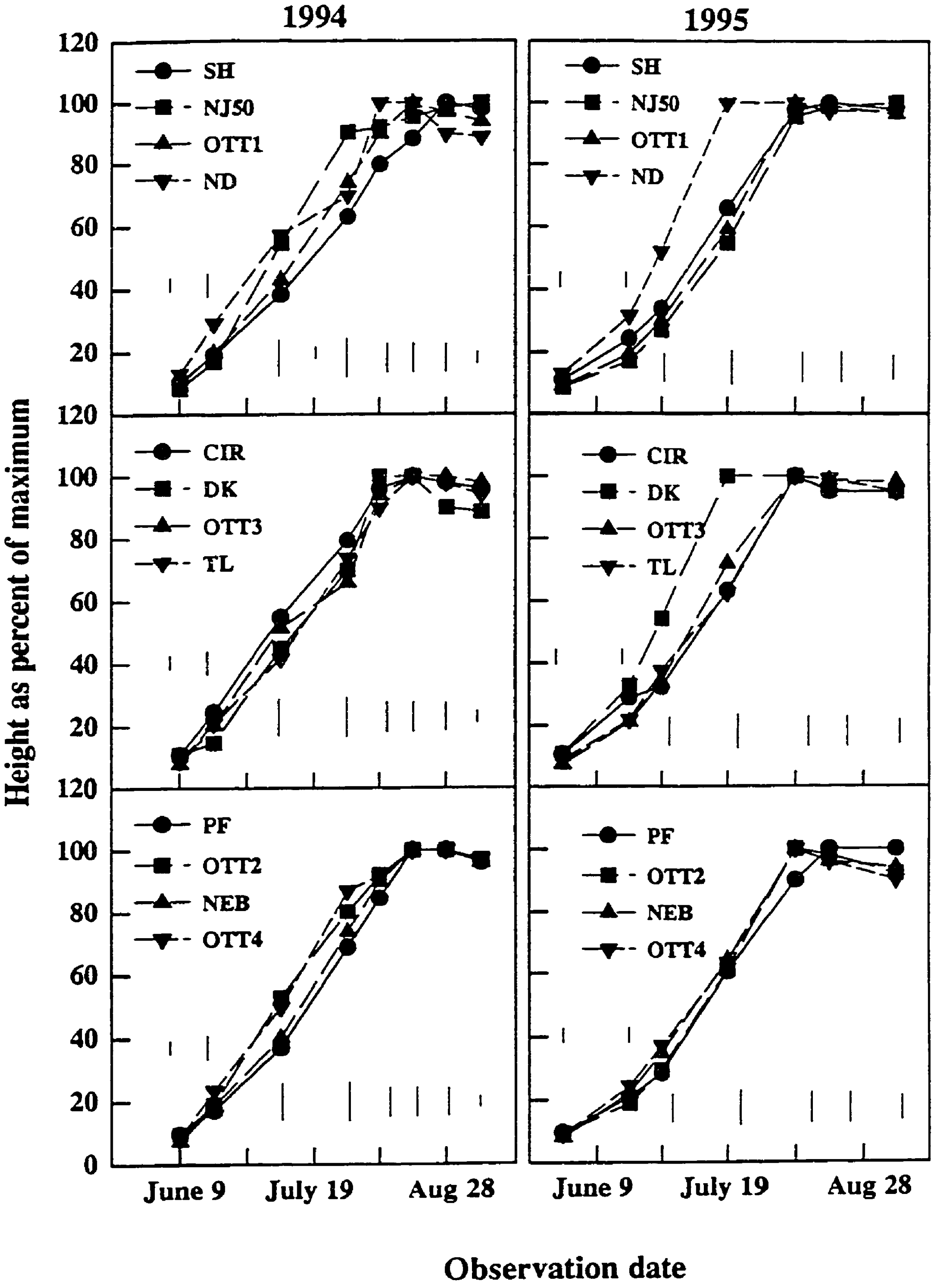
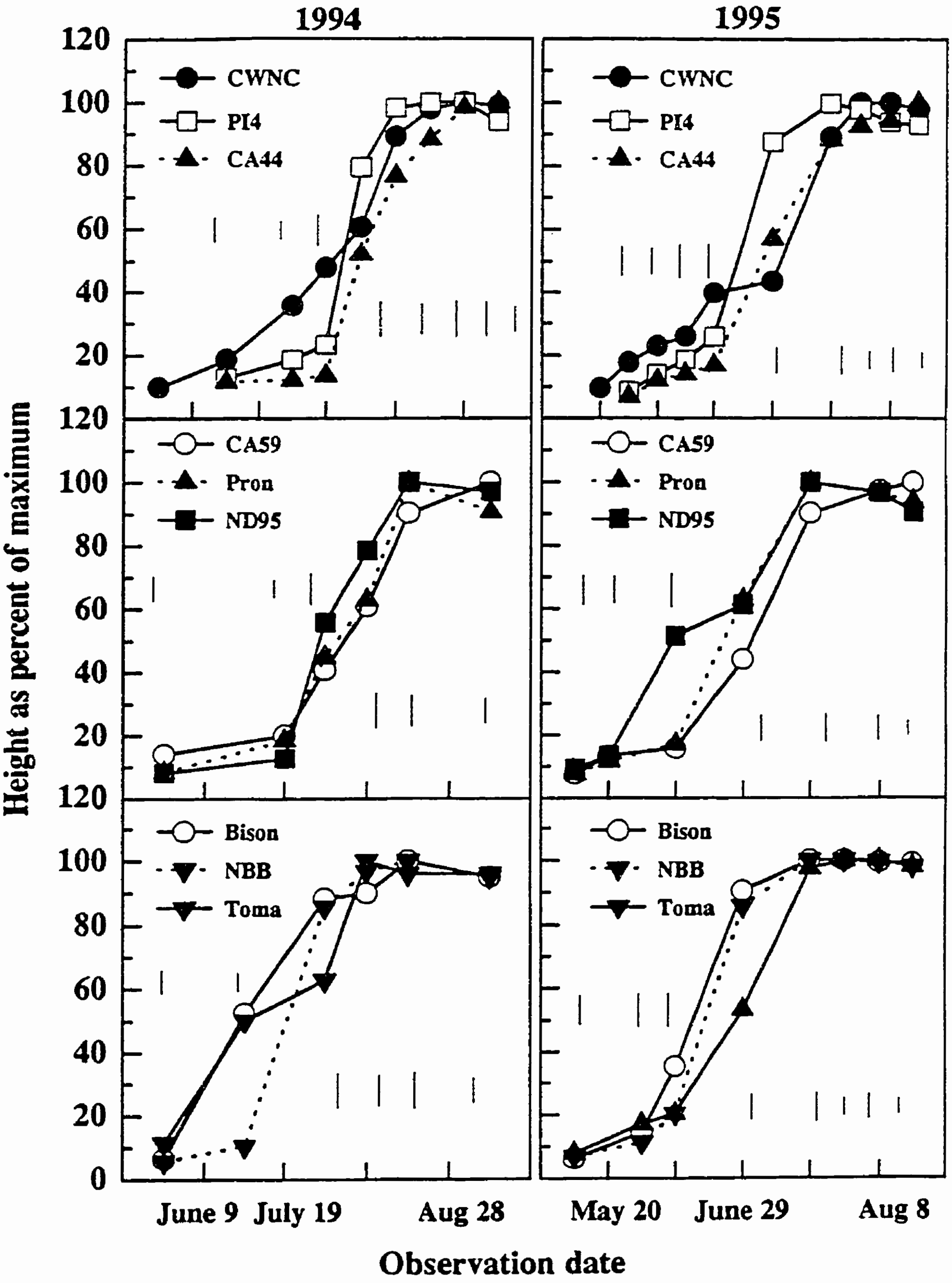

1994
1995
Height as percent of maximum
120
100
80
60
40
20
0
SH
NJ50
OTT1
ND
CIR
DK
OTT3
TL
PF
OTT2
NEB
OTT4
June 9
July 19
Aug 28
Observation date

Fig. 3.5: Timing of stem elongation in CWNC, Toma, sandreed and big bluestem during the 1994 and 1995 growing seasons. Vertical lines in each graph show least significant difference ($p < 0.05$) for each sampling time.


1994
1995
120
100
80
60
40
20
0
CWNC
PI4
CA44
CA59
Pron
ND95
Bison
NBB
Toma
Height as percent of maximum
June 9
July 19
Aug 28
May 20
June 29
Aug 8
Observation date

Preface to Chapter 4

Chapter 4 is based on a manuscript submitted for publication to the *Agronomy Journal* in 1997.

A great diversity of developmental patterns were demonstrated in Chapter 3. Several of the warm season grasses tested can mature in the short seasons of eastern Canada. Chapter 4 examines the more successful entries from Chapter 3 under solid sward conditions where leaf and tiller characteristics can be substantially modified. The choice of entries used in this study were partly dictated by seed availability; switchgrass seed was readily available. Efforts were also made to develop thermal-time based developmental models of the entries used.

Chapter 4

The Phenology and Tiller Characteristics of Big Bluestem (*Andropogon gerardii*) and Selected Cultivars of Switchgrass (*Panicum virgatum*) in a Short Growing Season Area.

4.1. Abstract

Warm season grasses are increasingly being cultivated in North America for summer forage and biomass production. In more northern environments, temperature and length of growing season are major factors in the success of warm season grass production. This research assessed the morphological development and relationship of growing degree-days to plant morphology and tiller characteristics in nine cultivars of switchgrass (*Panicum virgatum* L.; Blackwell, Cave-in-Rock, Dakota, Forestburg, Pathfinder, Shelter, Sunburst, ND3743 and New Jersey 50) and Niagara big bluestem (*Andropogon gerardii* Vitman). The study was conducted for three years on a St. Bernard loam in south-western Québec, Canada. Stand cover, plant morphology, tiller number, height and diameter, and leaf number per tiller were all assessed during the season. All entries persisted through the three years of the study and showed increases in tiller numbers from one year to the next. Dakota, Cave-in-Rock and Shelter switchgrasses had the best stand ratings after three years. The cultivars Dakota, ND3743 and Forestburg were early maturing while New Jersey 50 was the latest in maturity. Niagara big bluestem had the tallest tillers and highest rates of increase in height followed by Cave-in-Rock and Blackwell. Dakota and ND3743 had the shortest tillers. Changes in leaf number per tillers were best described by quadratic regression models (r^2 values ranged from 80-97 %). These models were stable over two years.

4.2. Introduction

Recent years have seen an increased interest in warm season grasses both for summer forage and biomass production. In summer, high temperatures and, in some cases low soil moisture, limit forage production by cool season grasses (Matches and Burns, 1985). However, warm season grasses are characterised by high optimal temperatures for photosynthesis (Edwards and Walker, 1983), creating forage potential during the critical months of July and August. Difficult stand establishment in spring and limited overall production because of low spring and fall temperatures are the main disadvantages of warm season grasses in areas like Québec, Canada. The ideal warm season grass species would be characterised by an early high rate of canopy development in spring. Tiller number, leaf number, rate of leaf appearance and rate of leaf extension collectively determine the rate at which the canopy develops.

The nutritive value (digestibility and intake) of warm season grasses has been reported to decrease from spring to summer (Jung and Vogel, 1992; MacAdam et al.. 1996) largely due to increased cell wall and lignin constituents. Minson and Laredo (1972) reported intake increases with increasing leafiness in warm season grasses. The decline in nutritive value closely follows the morphological development of the plant. The rate of morphological development in these grasses is determined largely by air temperature (or accumulated growing degree-days) (George *et al.*, 1988; Frank and Ries, 1990; Gillen and Ewing 1992). This has resulted in the development of temperature-plant phenology relationships in studying the physiological and ecological status of the plant. Knowledge of rate of morphological development is also important in scheduling defoliation. Timing of initial cut/grazing greatly influences dry matter yield, tiller and bud numbers and persistence (Mullahey *et al.*, 1990, 1991). Currently, there is no information on adaptability and morphological development to guide adoption of warm season grasses in short season areas such as eastern Canada.

The objectives of this study were to a) assess the morphological development of warm season grasses in south-western Québec, and b) to define relationships between height, leaf development and growing degree-days for these warm season grasses in this short growing season area.

4.3. Materials and Methods

This field study was conducted from 1993 to 1995 at the Emile A. Lods Research Centre of McGill University, Montréal (45° 28'N 73° 45'W) on a free draining St. Bernard loam (Hapludolf). In June of 1992, Niagara big bluestem (NBB, *Andropogon gerardii* Vitman, originally from north-western New York), and nine switchgrass cultivars (*Panicum virgatum* L.), Blackwell (BL, from northern Oklahoma), Cave-in-Rock (CIR, from southern Illinois), Dakota (DK) and ND3743 (ND)(both from North Dakota), Forestburg (FB) and Sunburst (SB)(both from south-eastern South Dakota), Pathfinder (PF, from south-eastern Nebraska), Shelter (SH, originally from West Virginia) and New Jersey 50 (NJ50, from North Carolina) were broadcast in 8 m x 5 m plots as solid stands, at a seed rate of 12 g per plot. The plots were arranged in a randomised complete block design with four blocks. Fifty kg N ha^{-1} were applied at planting and in spring of each of the successive years. The stands were allowed to develop without harvest through the 1992 growing season. In early spring of each year, plant residues from the previous growing season were removed by mowing.

Climatic data [rainfall, temperature and growing degree-days (calculated with a base of 5°C)] were recorded by an on-site automated weather station. This weather station was linked to Dorval International Airport (15 km east of the site) from which processed records were obtained.

Data collection on the plots began in spring 1993. Morphological development was assessed using the Simon and Park (1983) descriptive index. The plots were assessed visually on a weekly basis and each plot was deemed to have attained a stage number when approximately 10 per cent of the primary tillers had reached that stage. These assessments were referenced to days after May 1st, as a basis for standard comparison. Morphological assessment was conducted in each of the three years. In 1994 and 1995, tiller number, height and diameter; tiller leaf number, length and width were also recorded.

Tiller numbers were counted on two randomly selected 0.5 m^2 quadrats in each plot in mid July. Tiller height was measured bi-weekly as the average height to the ligule of the last fully expanded leaf of 10 tillers from each plot. These height measurements were discontinued in late August when inflorescences were fully emerged on more than 50 per cent of the tillers for all entries. Tiller diameters were measured on the same 10 tillers using Vernier calipers, in mid June and mid July. Average leaf numbers per tiller were determined every two weeks until late August by averaging leaf numbers on 10 tillers in each plot.

4.3.1. Statistical Analysis

All the data collected were subjected to an analysis of variance. When the F-test was significant ($p<0.05$) a protected Least Significant Difference (LSD) test was used to detect mean differences. Linear functions were fitted on the linear phase of height development. These were of the form

$$Y = b_o + b_1X$$

where Y was the height and X represented either days since May 1st or accumulated growing degree-days since the beginning of the season, b_o and b_1 being regression coefficients. Changes in leaf number (Y) were fitted quadratic functions of the form

$$Y = b_o + b_1X + b_2X^2$$

In all cases, plot means per sampling date were used as observations. All statistical analyses were conducted using Statistical Analysis System procedures (SAS, 1995).

4.4. Results and Discussion

4.4.1. Environment

Average air temperatures above zero were recorded between April and November in 1993 and 1994 and end of October in 1995 (Fig. 4.1). Growing degree-days (calculated with a base temperature of 5°C) were higher ($p<0.05$) in 1995 than in either 1993 or 1994. The rates of accumulation of growing degree-days were 365, 366 and 389 growing degree-days per month for 1993, 1994 and 1995, respectively. Total rainfall during the growing seasons (547, 540 and 537 for 1993, 1994 and 1995, respectively) was above the long term average of 518 mm for each of the three years (Fig. 4.1). In 1993, rainfall was generally evenly distributed except for a relatively drier August; in 1994 it was drier in July while in 1995, rainfall was relatively evenly distributed.

4.4.2. Stand persistence

Visual stand assessments (% ground cover) in spring of 1993 suggested some winter damage in most plots, especially for NJ50 and NBB. The entries from northern areas had higher ground cover ratings than those from more southernly regions (Table 4.1). Improvements in stand ratings were evident through 1994 and 1995. CIR, SH and NBB showed the greatest improvement. The increases in stand ratings may be attributed to the warmer spring of 1995 and increased tiller numbers per m^{-2}. Unlike this study, NJ50 and NBB had outstanding persistence in a Pennsylvania study (Jung *et al.*, 1990), probably due to the somewhat warmer conditions in Pennsylvania than Québec.

4.4.3. Phenology

There were entry differences for all phenological stages compared. In 1994 and 1995, all entries reached the various phenological stages about a week earlier than in 1993, largely due to a cooler spring period in the latter. A comparison of the various phenological stages (averaged over years) is presented in Table 4.2. The northern most entries DK and ND were the earliest to commence growth and most vigorous in spring. These cultivars were also the earliest maturing. On the other hand, NJ50 was the latest to commence growth in spring and also late maturing in the fall, and reached the end of anthesis about 50 days later than the early maturing ND and DK. Although CIR showed earlier growth in spring than BL, these two cultivars had similar phenology. PF was on average three days later than CIR and BL, otherwise it had a similar phenology. SH was comparable to CIR and BL up to the boot stage after which it went through anthesis and seed set considerably faster, reaching the soft dough stage a week earlier. SB and FB had similar developmental patterns up to the boot stage after which FB matured more rapidly. End of anthesis and soft dough stages were attained about 10 days earlier in FB than SB. NBB matured later than ND, DK and FB but earlier than the rest of the entries.

Diversity in rates of development and maturity patterns has been reported in similar warm season grasses (Olson, 1986; Jung *et. al.*, 1990). In the study by Olson (1986), there were no differences in maturity patterns of FB and SB while in our study differences were apparent after booting. However, Olson (1986) also observed similar developmental patterns for BL, CIR and PF. The maturity patterns of switchgrass cultivars followed a north-south pattern of origin. MacMillan (1959) reported that ecotypes from northern and western areas flowered earlier than those from more southern and eastern areas. Late maturity in environments like south-western Québec poses the danger of limited production of viable seed and low levels of root reserves for winter survival. This is reinforced by the relatively low stand ratings for NJ50.

4.4.4. Tiller characteristics

4.4.4.1. Tiller numbers

The average number of tillers per m^2 was 573 in 1994 and increased to 683 in 1995 (average increase of 19 per cent). Individual increases varied giving rise to a year x entry interaction ($p<0.001$, Fig. 4.2). In general, PF had the highest number of tillers, followed by SB, CIR, and FB. There was no difference among the rest of the switchgrass cultivars. NBB had an intermediate number of tillers, an average of 588 m^{-2}.

4.4.4.2. Height

All cultivars showed a height increase with increasing degree-day accumulation. Average tiller height increased from 1994 to 1995 and this could be attributable to the warmer 1995 season. NBB had the tallest tillers in both years averaging 15 to 36 cm taller than the next tallest entry in 1994 and 1995, respectively (Table 4.3). Among the switchgrass cultivars, CIR and BL had the tallest tillers followed by SB, PF, FB, NJ50 and SH. ND and DK had the shortest tillers in both years.

Following a slow height increase in spring, NBB was characterised by increased stem elongation in early summer to reach a maximum in mid August (Fig 4.3). In 1994, CIR and PF showed similar increased stem elongation starting in mid and late July, respectively. This pattern was not obvious in 1995 for these two entries, perhaps because of the warmer season. The other entries showed a steady increase in height until attainment of a maximum value. ND and DK both had completed most of their stem elongation by mid July. The slopes (b_1) of the linear functions fitted on the linear phase of height increase against days from May 1st are presented in Table 4.4. There was an average increase of 18 per cent in the slopes (height increase per day) from

1994 to 1995. In both years, NBB had the highest height increase per day (average of 2.8 cm per day). CIR and BL had the highest among switchgrass entries. Except for ND and DK, pooling the data over the two years did not reduce the coefficients of determination (r^2, Table 4.4). The relatively lower r^2 values from pooled data for ND and DK could be explained by the different timing of height increases between 1994 and 1995. Similar r^2 values before and after pooling data were obtained when using accumulated growing degree-days.

Rapid stem elongation was accompanied by a decrease in tiller diameter for CIR, PF and NBB (Table 4.3). The other entries showed an increase in tiller diameter from spring to mid summer. In both spring and summer, ND and DK had the finest tillers (averaging 0.21 and 0.31, cm respectively). The short and fine tillers from these two entries suggest better grazing potential.

4.4.4.3. Leaf number

The rate of leaf development was closely related to growing degree-day accumulation (or days from May 1st)(Figs. 4.4 and 4.5). More leaves per tiller were generally observed in 1995 than in 1994. There were year x entry x time of assessment interactions for leaf length and width (Table 4.5) demonstrated by changes in the ranking for these leaf parameters as the season advanced. On average, CIR, BL, SB, SH and NJ50 all had long and wide leaves in mid summer. In both spring and summer, ND and DK had short and narrow leaves. NBB leaves, though many, were relatively short and narrow in summer. Earlier maturing entries ND, DK, FB and SB, showed earlier declines in leaf numbers.

The fitted quadratic equations were good descriptors of the changes in leaf numbers per tiller for both years. When based on accumulated growing degree-days the models accounted for 88 to 97 % of the variation in leaf number (Table 4.6)(90 to 98% when based on days from May 1st, data not presented). When the data were pooled for the two years, the r^2 values were 80 to 94 % and 79 to 94 % when based on growing degree-days and days since May 1st, respectively.

These data suggest both days since May 1st and accumulated growing degree-days can be used as indices of leaf development and height changes. Similar relationships have been reported for other grasses (George et al., 1988; Cao and Moss, 1991; Gillen and Ewing 1992). The use of growing degree-days is reinforced by the observation that plants develop primarily in response to air temperatures (Frank and Ries, 1990). However, George *et al.* (1988) suggest a close relationship between regression coefficients of fitted functions and site productivity (for example soil moisture status and fertility). Site and stand differences might explain the relatively higher leaf numbers per tiller and lower r^2 values reported by Gillen and Ewing (1992) when data were pooled over years.

4.5. Conclusions

The data show differences in maturity patterns of warm season grasses. All entries had consolidated stands in the fourth year suggesting there is potential for warm season grass production in south-western Québec, Canada. Height changes and leaf development could be described in terms of accumulated growing degree-days or days since the beginning of the season, the latter being easier to compute. The strong relationships between developmental pattern and growing degree-days (or days of the season) can be used to guide management strategies. Forage yield and quality could be approximated from these basic relations.

Table 4.1: Ground cover ratings (%) of the warm season grass stands in spring of 1993 and 1995 at Montréal, QC

Entry	% ground cover rating	
	1993	1995
Dakota	66a[†]	85a
Cave-in-Rock	30c	85a
Shelter	31c	84a
Sunburst	51b	79ab
Pathfinder	48b	73abc
Forestburg	46b	69bc
ND3743	63	68bc
Blackwell	34c	68bc
New Jersey 50	19d	63c
Niagara Big Bluestem	11e	43d
LSD (0.05)	5.7	14.3
CV	9.8	13.8

[†] means in the same column followed by different letters are significantly different ($p<0.05$) using a protected LSD test.

Table 4.2: Mean number of days after May 1st taken to attain a particular phenological stage by the warm season grasses at Montréal, QC

Entry	Phenological stage number[1]					
	22	37	45	58	68	85
New Jersey 50	46.8a[2]	86.9a	97.3a	115.5a	129.4a	153.9a
Blackwell	44.9ab	66.5cd	78.5c	97.9b	108.8bc	129.3c
Pathfinder	44.9ab	72.8b	82.8b	99.7b	109.8b	137.3b
Sunburst	44.9ab	63.9cde	66.7d	89.8d	102.3d	117.4de
Shelter	43.2b	67.1c	75.9c	93.6cd	105.3cd	122.5d
Cave-in-Rock	43.4b	64.3cde	75.8c	97.7b	107.1bc	129c
Forestburg	44.4b	61.1e	68d	83.8e	92.7e	102.9f
Dakota	40.8c	50.7f	56.5e	66.8f	78.4f	93.5g
ND3743	40.3c	49.9f	56.7e	67.5f	78.6f	93.2g
Niagara B/B	45ab	63de	76.2c	89.5d	96.5e	113.8e
LSD (0.05)	2.1	3.9	3.7	4.2	4.3	5.49
CV	5.89	7.29	6.19	5.67	5.24	5.67

[1] stage 22 - two elongated sheaths; stage 37- flag leaf just visible; stage 45 - boot swollen

stage 58 - base of inflorescence just visible; stage 68 - end of anthesis;

stage 85 - endosperm soft doughy according to Simon and Park (1983)

[2] means in the same column followed by different letters differ significantly ($p<0.05$) using a protected LSD test

Table 4.3: Mean maximum height and diameter of warm season grasses in 1994 and 1995 at the Emile A. Lods Research Centre, Montréal, QC

Entry	1994			1995		
	Maximum height (cm)	Tiller diameter (cm)		Maximum height (cm)	Tiller diameter (cm)	
		Spring	Summer		Spring	Summer
Niagara B/B	183.5a[†]	0.52a	0.47ab	182.5a	0.57a	0.55a
Blackwell	136.5bc	0.39bc	0.39de	157b	0.44bcd	0.43bc
Cave-in-Rock	147.4b	0.48ab	0.35cde	152.8bc	0.53ab	0.42bcd
Sunburst	126.3c	0.39bc	0.5a	144cd	0.43bc	0.55a
New Jersey 50	128c	0.28de	0.41bc	136de	0.33de	0.41bcd
Forestburg	128.3c	0.29cde	0.39de	135de	0.36cd	0.44bc
Pathfinder	125c	0.38bcd	0.35cde	135de	0.42bcd	0.4bcd
Shelter	125.3c	0.33cde	0.47ab	129.5ef	0.39cd	0.49ab
ND3743	109.1d	0.28de	0.28e	127ef	0.33cde	0.32d
Dakota	102.8d	0.23e	0.32de	120f	0.23e	0.37cd
LSD (0.05)	12.6	0.10	0.08	9.9	0.12	0.10
CV (%)	6.63	20.11	13.62	4.83	19.87	15.58

[†] means in the same column followed by different letters differ significantly ($p<0.05$) using a protected LSD test

Table 4.4: The slopes (b_1) of linear functions fitted to the linear phase of height increase against the number of days since May 1st for the warm season grasses , Montréal, QC

Entry	1994		1995		Pooled data	
	b_1	r^2	b_1	r^2	b_1	r^2
	n = 20		n = 20		n = 40	
Dakota	1.24 ± 0.17[*]	0.95	1.82 ± 0.06[*]	0.94	1.43 ± 0.21[']	0.85
Pathfinder	1.32 ± 0.17	0.97	2.0 ± 0.10	0.99	1.56 ± 0.19	0.90
ND3743	1.38 ± 0.23	0.93	1.93 ± 0.22	0.96	1.55 ± 0.20	0.88
Sunburst	1.55 ± 0.17	0.97	2.01 ± 0.06	0.92	1.72 ± 0.13	0.95
New Jersey 50	1.59 ± 0.09	0.99	1.75 ± 0.12	0.98	1.63 ± 0.10	0.97
Forestburg	1.65 ± 0.17	0.97	1.89 ± 0.11	0.99	1.73 ± 0.10	0.97
Shelter	1.67 ± 0.18	0.97	1.94 ± 0.07	0.99	1.74 ± 0.12	0.96
Blackwell	1.73 ± 0.15	0.98	1.96 ± 0.07	0.99	1.77 ± 0.12	0.97
Cave-in-Rock	1.91 ± 0.17	0.98	2.09 ± 0.46	0.99	1.96 ± 0.10	0.98
Niagara B/B	2.88 ± 0.27	0.97	2.68 ± 0.25	0.97	2.75 ± 0.16	0.97
Mean	1.69		2.01		1.78	

['] all b_1 values significant ($p<0.05$)

[*] standard error (SE) of coefficient

Table 4.5: The leaf lengths and widths of warm season grasses during spring and summer of 1994 and 1995, Montréal, QC.

Entry	1994				1995			
	spring		summer		spring		summer	
	length (cm)	width (cm)	length (cm)	width (cm)	length (cm)	width (cm)	length (cm)	width (cm)
Blackwell	55a[†]	1.18ab	62.7ab	1.33a	58.1a	2.03ab	65.6ab	2.21a
Pathfinder	50.6ab	0.98bcd	52.3b	1.08bc	53.7ab	1.83bcd	60.1ab	1.96bc
Forestburg	42.2c	0.9cd	54.6b	1.1bc	45.3c	1.75cd	57.5b	1.98bc
Cave-in-Rock	54.6a	1.18ab	68.3a	1.4a	57.7a	2.03ab	71.1a	2.28a
ND3743	33.4d	0.9cd	23.4d	0.93c	36.5d	1.75cd	26.2d	1.81c
New Jersey 50	38.9cd	1.03cd	62.6ab	1.35a	42.0cd	1.88a-d	65.5ab	2.23a
Shelter	46.1bc	1.25a	60.3ab	1.43a	49.2bc	2.1a	63.1ab	2.31a
Dakota	33.8d	0.78d	36.2c	0.97c	36.9d	1.63d	39.5c	1.86c
Sunburst	53.6ab	1.13abc	64ab	1.28ab	56.7ab	1.98abc	66.9ab	2.16ab
Niagara B/B	41.8cd	1.22ab	30.8c	1.1bc	44.9cd	2.08ab	33.6cd	1.98bc
LSD (0.05)	8.4	0.3	10.7	0.2	8.4	0.3	10.7	0.2
CV(%)	12.9	17.1	14.2	12.1	12.0	9.4	13.4	7.0

[†] means in the same column followed by different letters differ significantly ($p<0.05$) using a protected LSD

Table 4.6: Regression statistics of quadratic functions fitted to the relation between tiller leaf number and accumulated growing degree-days at the Emile A. Lods Research Centre, Montréal, QC

Entry	r^2	b_0[1]	b_1 ($\times 10^{-3}$)	b_2 ($\times 10^{-6}$)	rMSE
1994 (n=28)					
BL	0.96	1.68	7.27	-3.19	0.236
CIR	0.94	1.89	9.45	-4.81	0.275
DK	0.96	2.46	7.24	-4.24	0.167
FB	0.93	2.38	7.03	-3.94	0.199
ND	0.88	2.1	7.12	-4.03	0.28
NJ50	0.95	1.44^{ns}	5.89	-2.1	0.316
PF	0.97	1.91	7.4	-3.46	0.189
SB	0.89	1.8	8.1	-4.24	0.32
SH	0.90	1.68	8.68	-4.72	0.331
NBB	0.96	1.54^{ns}	14.17	-7.33	0.347
1995 (n=28)					
BL	0.95	0.79^{ns}	8.98	-3.36	0.483
CIR	0.94	0.64^{ns}	10.44	-4.71	0.437
DK	0.90	1.87	8.23	-4.58	0.359
FB	0.91	1.67	7.90	-4.08	0.339
ND	0.90	1.81	7.42	-4.06	0.325
NJ50	0.98	-0.54^{ns}	10.69	-4.59	0.246
PF	0.92	1.52	7.21	-2.89	0.438
SB	0.97	0.36^{ns}	10.27	-4.61	0.299
SH	0.95	1.3	7.89	-3.16	0.38
NBB	0.96	1.92	12.12	-5.46	0.412
Pooled data (n=56)					
BL	0.88	1.30	7.68	-2.92	0.533
CIR	0.88	1.07	10.29	-4.87	0.475
DK	0.91	2.08	7.91	-4.49	0.275
FB	0.88	1.93	7.61	-4.05	0.3
ND	0.89	1.91	7.37	-4.09	0.275
NJ50	0.94	0.10^{ns}	9.18	-3.84	0.364
PF	0.92	1.70	7.26	-3.13	0.317
SB	0.93	1.12^{ns}	8.61	-3.92	0.527
SH	0.80	1.62	7.68	-3.40	0.555
NBB	0.90	1.98	12.21	-5.76	0.511

^{ns} regression coefficient not significant at $p = 0.05$

[1] all regression coefficients are significant except when followed by ns

[2] root of mean square error of regression model

Fig. 4.1: Mean temperature (°C), rainfall (mm) and accumulated growing degree-days (base of 5°C) during the 1993, 1994 and 1995 growing seasons, Montréal, Québec.

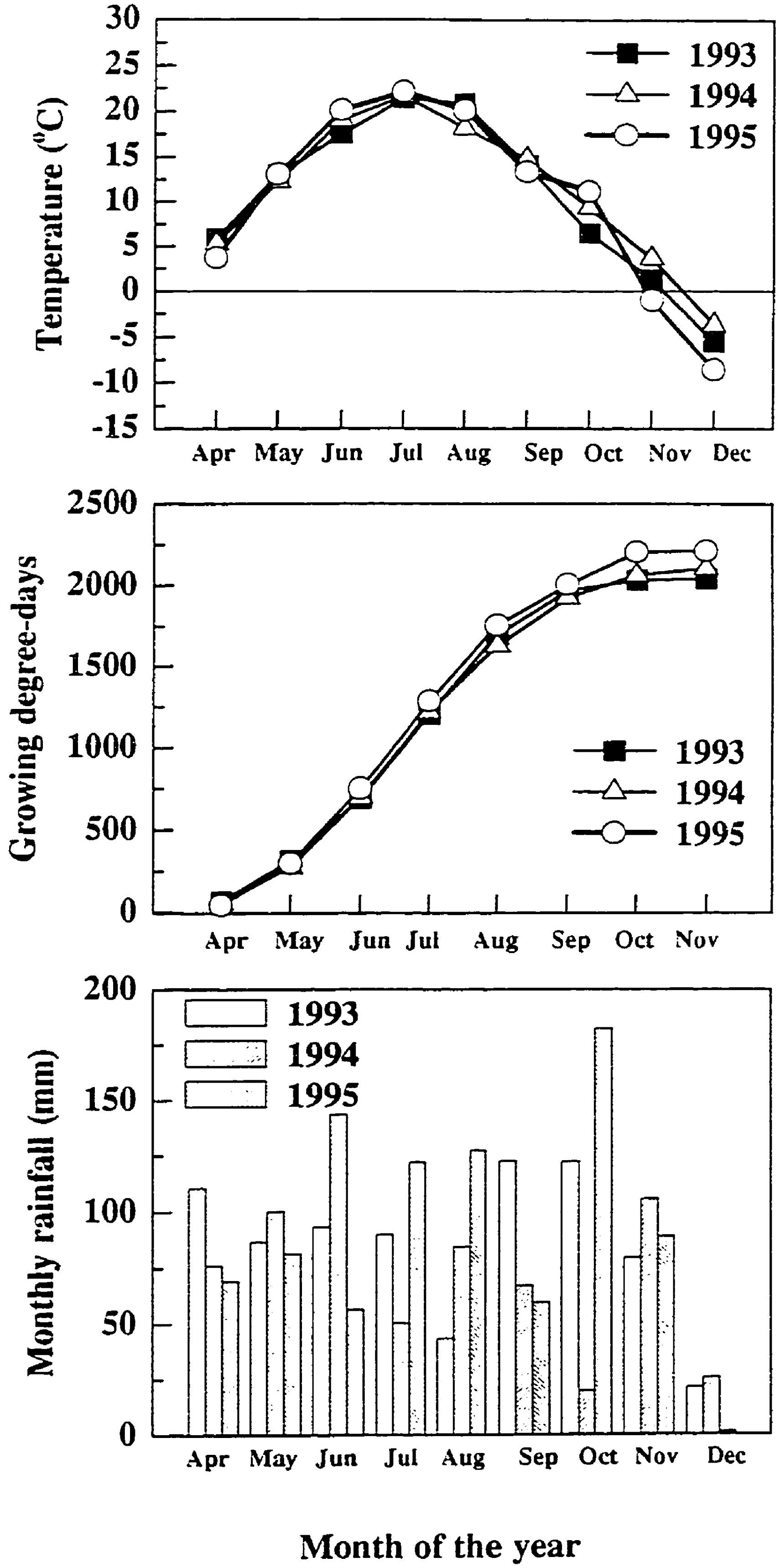

Temperature (°C)
30
25
20
15
10
5
0
-5
-10
-15
1993
1994
1995
Apr May Jun Jul Aug Sep Oct Nov Dec
Growing degree-days
2500
2000
1500
1000
500
0
1993
1994
1995
Apr May Jun Jul Aug Sep Oct Nov
Monthly rainfall (mm)
200
150
100
50
0
1993
1994
1995
Apr May Jun Jul Aug Sep Oct Nov Dec
Month of the year

Fig. 4.2: The average number of tillers m^{-2} of big bluestem and switchgrass cultivars in summer of 1994 and 1995, Montréal, Québec. T-bars extending beyond each bar graph denote SE.

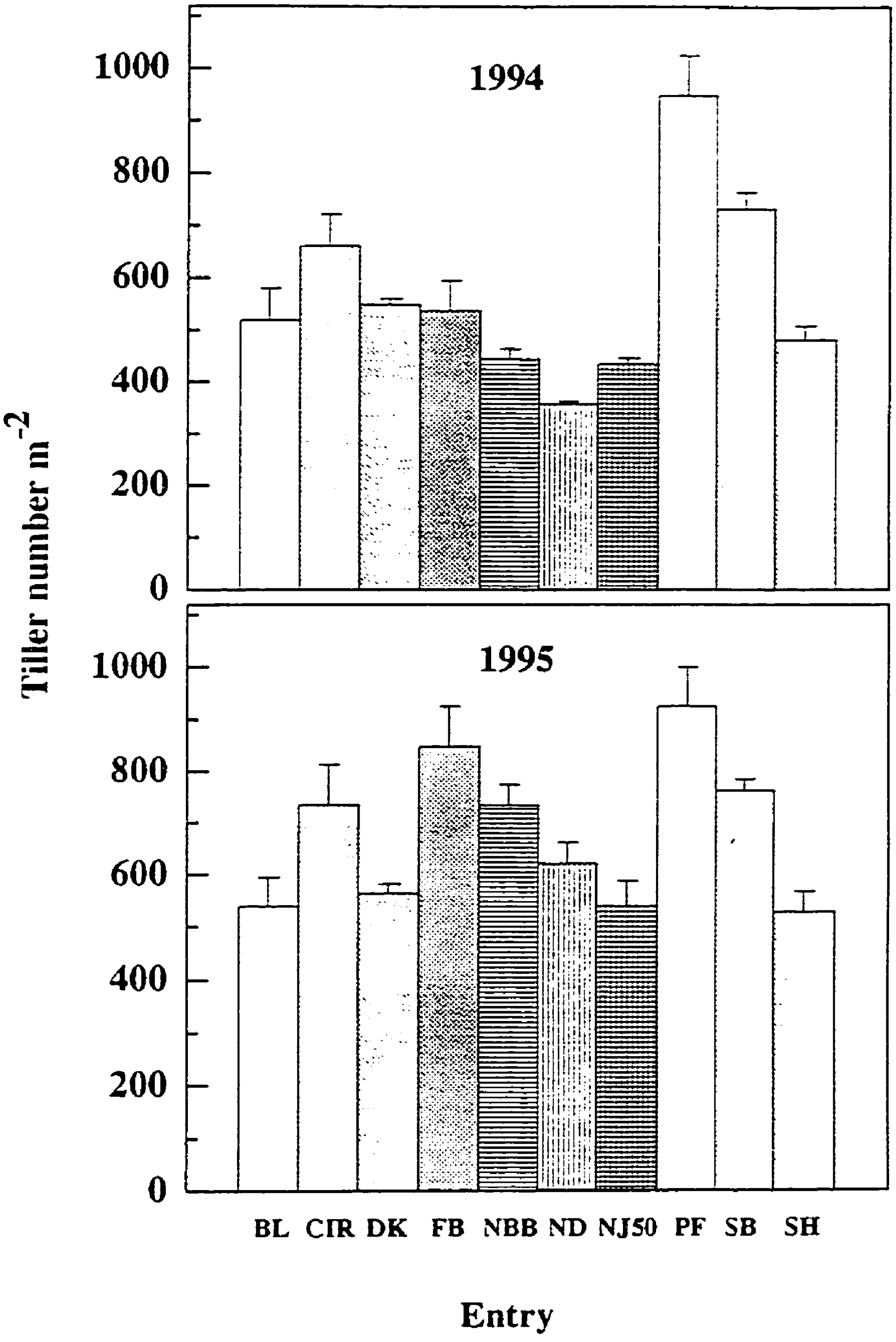

1994
1995
Tiller number m^{-2}
0
200
400
600
800
1000
BL
CIR
DK
FB
NBB
ND
NJ50
PF
SB
SH
Entry

Fig. 4.3: Changes in height for big bluestem and switchgrass cultivars during 1994 and 1995, Montréal, Québec. Parameters of equations fitted to the near-linear phases of height increase are presented in Table 4.4. Bars extending beyond each point denote SE.

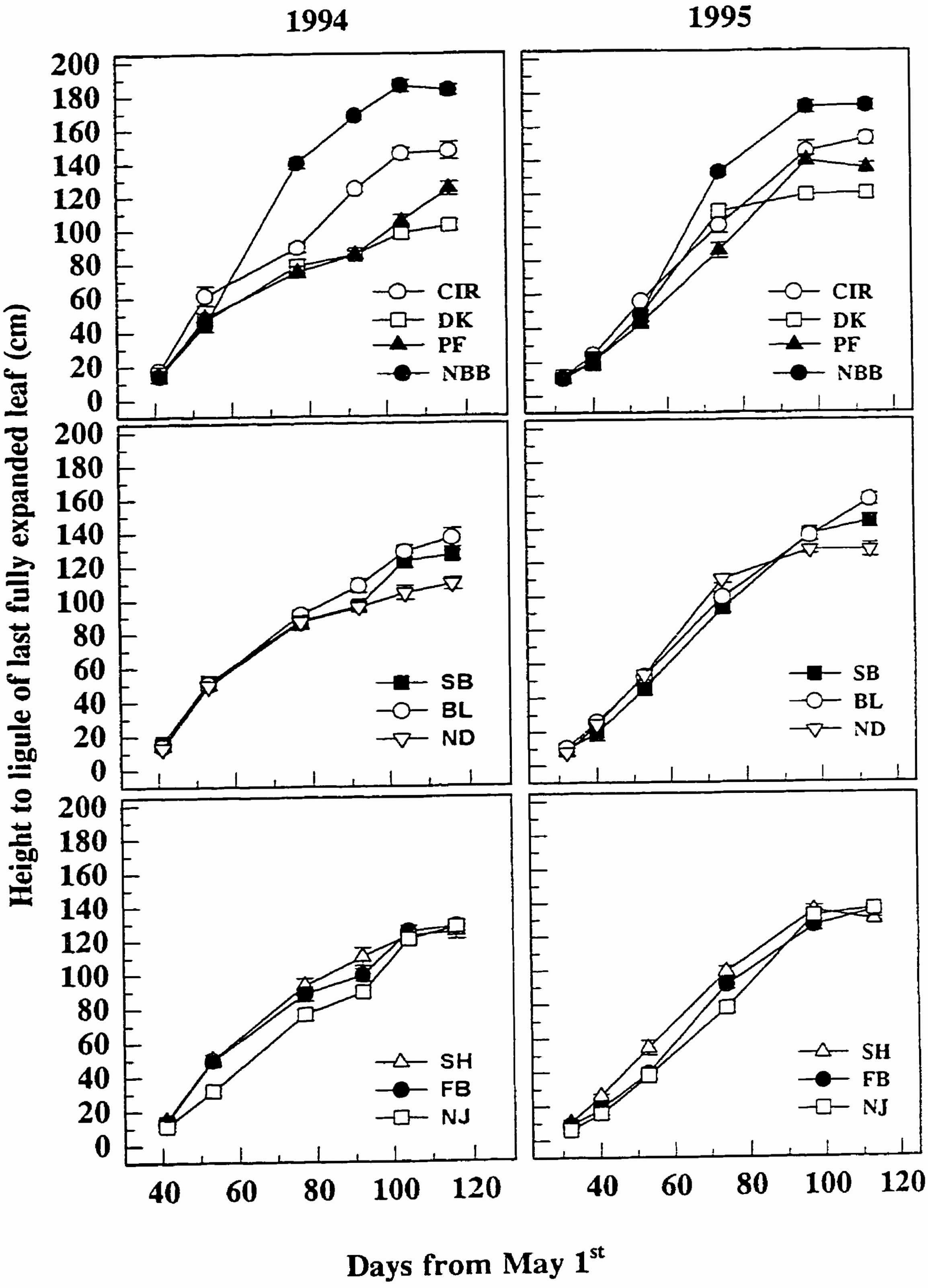

1994
1995
Height to ligule of last fully expanded leaf (cm)
200
180
160
140
120
100
80
60
40
20
0
CIR
DK
PF
NBB
SB
BL
ND
SH
FB
NJ
40
60
80
100
120
Days from May 1st

Fig. 4.4: Changes in tiller leaf numbers for switchgrass cultivars during 1994 and 1995, Montréal, Québec. Regression equations fitted to the relationships are presented in Table 4.6. Bars extending beyond each point denote SE.

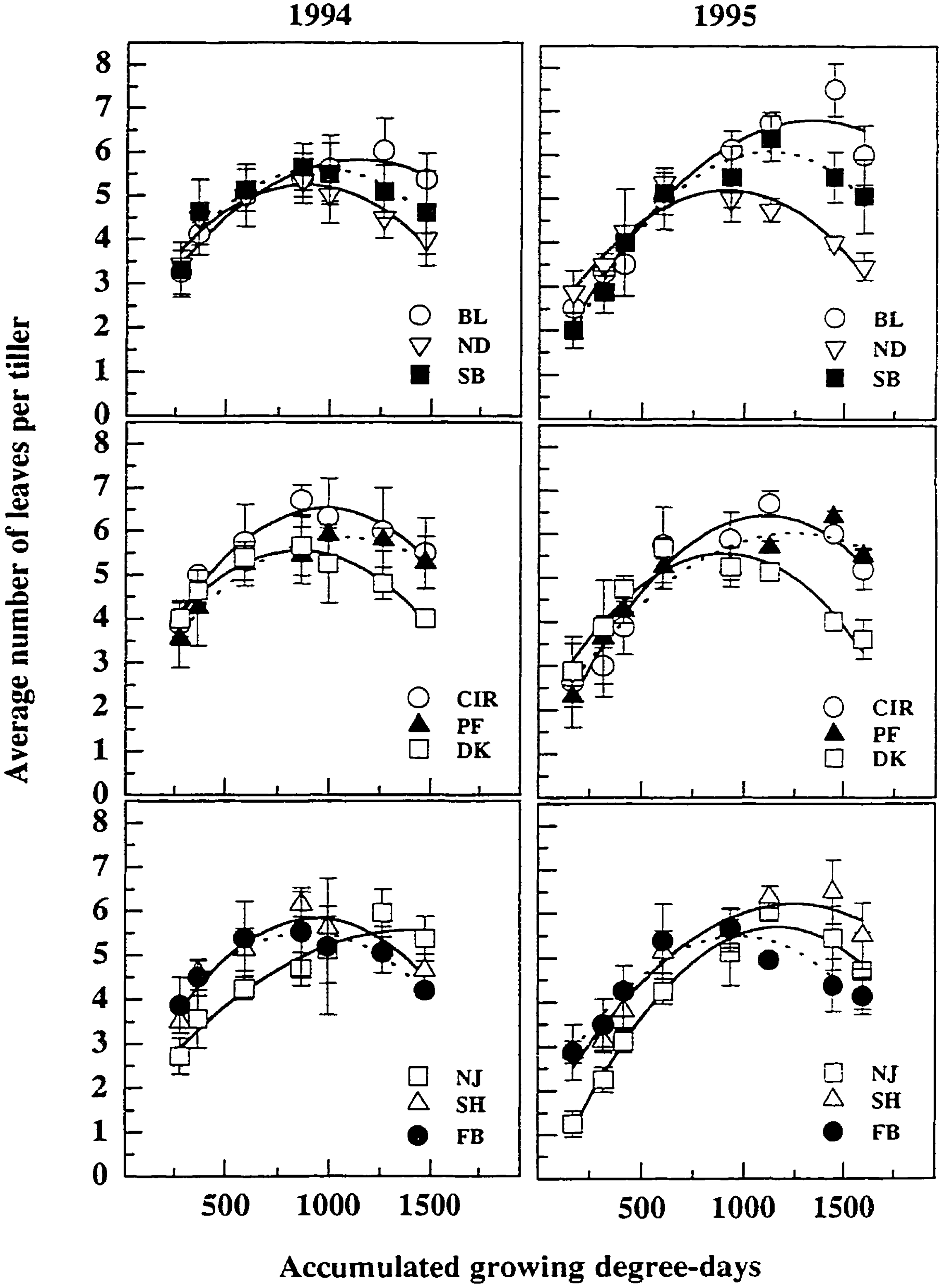
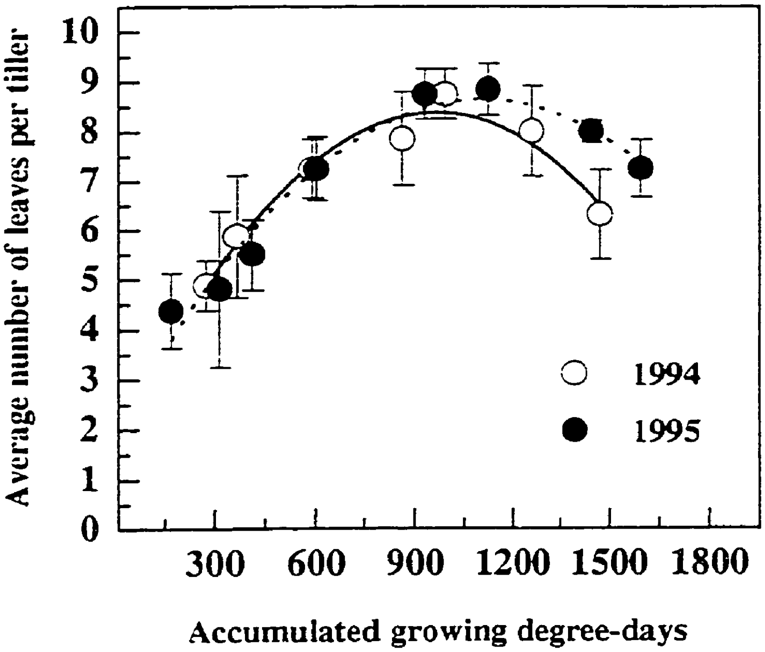

1994
1995
Average number of leaves per tiller
0
1
2
3
4
5
6
7
8
BL
ND
SB
CIR
PF
DK
NJ
SH
FB
500
1000
1500
Accumulated growing degree-days

Fig. 4.5: Changes in tiller leaf number for big bluestem during 1994 and 1995, Montréal, Québec. Regression equations fitted to the relationships are presented in Table 4.6. Bars extending beyond each point denote SE.


Average number of leaves per tiller
10
9
8
7
6
5
4
3
2
1
0
300
600
900
1200
1500
1800
Accumulated growing degree-days
○ 1994
● 1995

Preface to Chapter 5

Chapter 5 is based on a manuscript submitted for publication to the journal *Crop Science* in 1997.

This is an extension of the work presented in Chapter 4. Canopy developmental changes were monitored and canopy architecture of the ten entries characterised. Changes in leaf area indices were related to thermal-time. The biomass yield and its chemical composition for the evaluated entries are presented.

Chapter 5

Leaf Area Development, Light Interception and Yield of Big Bluestem (*Andropogon gerardii* Vitman) and Switchgrass (*Panicum virgatum* L.) in a Short Growing Season Area

5.1. Abstract

Cool temperatures in spring and early summer have limited the adoption of warm season grass production in northern environments like eastern Canada. This study was carried out to evaluate the potential of warm season grass production in south-western Québec. Niagara (NBB) big bluestem (*Andropogon gerardii* Vitman) and nine switchgrass (*Panicum virgatum* L.) cultivars (Blackwell, BL; Cave-in-Rock, CIR; Dakota, DK; Forestburg, FB; ND3743, ND; New Jersey 50, NJ; Pathfinder, PF; Sunburst, SB and Shelter, SH) were evaluated for three years on a St. Bernard loam in Montréal. Leaf area index (LAI), light interception and end of season biomass yield were the main parameters evaluated. Leaf area development patterns during the season fitted second degree polynomial models. Maximum LAI ranged from 6.1-8 and CIR, NJ and NBB had the highest LAI. The entries had different vertical leaf area distributions. In BL, CIR and SH more than 50% of the leaf area was in the top third of the canopy. NJ and PF had uniform leaf area distribution down the canopy. Light extinction coefficients (*k*) ranged from 0.57-0.72. Average end of season biomass yields were 8477, 9943 and 10869 ton/ha for 1993, 1994 and 1995, respectively. End of season yield was positively correlated to leaf area duration (r=0.78). CIR, NJ and BL were the highest yielders. All entries had high NDF and ADF levels (81-87 and 51-57%, respectively). Nitrogen and ash contents ranged from 0.32 to 0.82 and 4.7 to 6.6%, respectively.

5.2. Introduction

In recent years there has been an increased interest in warm season grasses for forage and biomass production. In central and southern USA, warm season grasses are widely grown for summer grazing and conservation (Hall *et al.*, 1982; Jacobson *et al.*, 1986; Jung *et al.*, 1990). However these grasses have been adopted to a limited scale in more northern areas like Canada. Much of Canada is characterised by cool temperatures in spring and early summer as well as in fall, resulting in a short growing season. For example, in eastern Canada, maize (*Zea mays* L.) can only be sown in late May (MAPAQ, 1984).

Ideal warm season grass species for short season areas should have faster initial leaf area development for high light interception, and therefore plant growth and yield (Coombs, 1984; Muchow *et al.*, 1990). As the canopy develops spatial distribution and subsequent variations in light interception become important (Russell *et al.*,1989; Barnes *et al.*, 1990; Ober-Blom and Kellomaki, 1982). These aspects have both been reported to vary among and within species (Hart, 1988; Kiniry *et al.*, 1989).

In a preliminary evaluation, switchgrass (*Panicum virgatum* L.) and big bluestem (*Andropogon gerardii* Vitman) showed potential in south-western Québec (Madakadze *et al.*, 1996a). However, currently there is no information to guide the adoption of these grasses into either herbage-livestock systems or biomass production. Understanding canopy development would be important in identifying ideal cultivars as well as establishing management schedules. Because cool temperatures are the most limiting it would be ideal to describe leaf area development as a function of temperature, as has been done in maize (Dale *et al.*,1980, Dwyer *et al.*, 1992).

With regards to biomass production, the extra determinants of ideal species/cultivar include yield and chemical composition. Lignocellulose, nitrogen and ash are the most important constituents in biofuel or fibre sources. While high levels of lignocellulose are desirable for chemical and biofuel production (Trebbi, 1993), high levels of nitrogen and/or ash reduce chemical output in thermochemical conversions (Agblevor *et al.*,1992). High levels of ash levels increase wear and tear on industrial machinery and can also be fusible at high temperatures (Kurkela *et al.*,1993)

The objectives of this study were to determine a) canopy development and architecture b) biomass yield and chemical compositional differences of nine cultivars of switchgrass and one of big bluestem.

5.3. Materials and Methods

5.3.1. Site

Ten cultivars of warm season grasses, nine switchgrasses and one big bluestem, were seeded in 8 x 5 m plots as solid swards in June of 1992. The ten cultivars were Niagara big bluestem (NBB) and Blackwell (BL), Cave-in-Rock (CIR), Dakota (DK), Forestburg (FB), ND3743 (ND), New Jersey 50 (NJ), Pathfinder (PF), Sunburst (SB) and Shelter (SH) switchgrasses. The free draining sandy clay loam (St. Bernard, Typic Hapludalf) soil site was located at the Emile A. Lods Research Centre of McGill University, Montréal, Québec (45° 28'N 73° 45'W). The plots were arranged in a four block randomised complete block design. Fifty kg of N ha^{-1} (as ammonium nitrate) were applied at seeding and in spring of each of the three successive years. Rainfall, air temperature and growing degree days (calculated with a base of 5°C) were measured with an on-site automatic weather station. This weather station is linked to Dorval International Airport (15 km east of research centre) from which processed records were obtained.

5.3.2. Leaf area index and light transmission

The swards were allowed to develop undisturbed through the 1992 and 1993 growing seasons. In mid July of 1994 and 1995, tillers were counted on two 0.5 m^{-2} quadrats in each plot. During the 1994 and 1995 seasons, leaf area index (LAI) was measured in each plot at two weekly intervals using a Li-Cor 2000 Plant Canopy Analyser (Li-Cor Inc., Lincoln, Nebraska, USA). These measurements began when the canopy height was at least 20 cm and discontinued either when by visual assessment about 50 % of the of the leaves were undergoing senescence or during the first week of September. As the canopy height increased, measurements were made at 25 cm strata. In both 1994 and 1995 seasons, interception of photosynthetic active radiation (PAR) was measured above the canopy (incoming PAR, I_o) and if possible at 25 cm strata (I_i). PAR measurements were also made every two weeks using a LI-191SA line quantum sensor connected to an LI-1000 Data Logger (Li-Cor Inc., Lincoln, Nebraska, USA).

Measurements were made between 1100 and 1500 hours (near solar noon) on days with slightly hazy to clear sky conditions. This follows the observation that observations around solar noon can be representative of daily radiation (Tollenaar and Bruulsema, 1988). The actual measurements were made on four positions in each plot and an inverted quantum sensor estimated reflected PAR.

5.3.3. Extinction coefficients

Linear regression models (no intercept) were used to calculate canopy extinction coefficients (k) using the Beer-Lambert equation; $\ln(I_i/I_o) = k(LAI_i)$ (Saeki, 1960) and this equation assumes random distribution of foliage in a horizontally homogeneous canopy. Despite the fact that this equation is insensitive to violations of this assumption, it has been successfully used in several crops including groundnuts (Marshall *et al.*, 1992), sorghum (Rosenthal *et al.*, 1993), and maize (Maddonni and Ottegui, 1996).

5.3.4. Biomass yield

Biomass yield estimates were made early October in 1993, 1994 and 1995. During harvests, two 1 m^2 quadrats per plot were cut leaving a stubble 10 cm in height. Samples from the quadrats were weighed separately and a 500 g sub-sample taken for moisture determination. These sub-samples were dried to constant weight at 60°C in a forced draught oven. Sub-samples were also analysed for neutral detergent fibre (NDF) and acid detergent fibre (ADF), using an F-200 Fibre Unit with F-56 filter bags (Ankom Tech Corp., Fairport, New York, USA). Nitrogen was determined using the Kjelteck System 1002 Distilling Unit (Tecantor, Hoganas, Sweden). Ash content was determined by igniting 2 g samples in a muffle furnace at 525°C for 4 hours.

5.3.5. Statistical Analysis

All data collected were analysed using SAS procedures (SAS, 1995). Where F tests were significant ($p<0.05$) in analysis of variance, a protected Least Significance Difference (LSD) test was used to detect mean differences (Steel and Torrie, 1980). Quadratic regression models were fitted to the changes in LAI against accumulated growing degree days or days since the beginning of the growing season.

5.4. Results and Discussion

5.4.1. Weather

A summary of the weather at Emile A. Lods Research Centre from 1993 to 1995 is presented in Fig. 5.1. Between April and October, it was generally warmer in 1995 than either 1993 or 1994. Total growing degree-days were higher ($p < 0.05$) in 1995 than in both 1993 and 1994 (2206, 2032 and 2070 growing degree-days, respectively). The respective rates of accumulation of the growing degree-days were 389, 365 and 366 growing degree-days per month. For all three seasons, total rainfall exceeded the long term average of 518 mm (545, 540 and 537 mm for 1993, 1994 and 1995, respectively).

5.4.2. Leaf Area Index

LAI development patterns during the growing season were different for the different cultivars (Fig 5.2 and 5.3). Cultivars could be grouped into either those that attained maximum LAI in early summer (FB, DK, NBB, and ND) or mid to late summer (BL, CIR, NJ, PF, SB and SH). Seasonal maximum LAI ranged from 6.1 to 8 in both 1994 and 1995. The highest LAI were from CIR, NBB and NJ. Using repeated measures of analysis, the time x entry effects were significant and the developmental patterns fitted a second order polynomial (Fig 5.2 and 5.3). The coefficients of determination (r^2) of the fitted quadratic regression models ranged from 0.81 to 0.97 and 0.85 to 0.96 in 1994 and 1995, respectively. Since the patterns for each cultivar were similar in both years, quadratic regressions were fitted on the pooled data (Table 5.1). The r^2 on the pooled data ranged from 0.81 to 0.94 when regressions were based on accumulated growing degree-days, and 0.81 to 0.89 when based on days since the beginning of the season. On average, models based on accumulated growing degree-days had better fits than those based on days of the season. These LAI development patterns are similar to those reported for several grass species by Hazlett (1992).

5.4.3. Vertical distribution of LAI

Throughout the growing season there were variations in the vertical distribution of LAI among the entries. In both seasons, time x entry x height interactions were significant. Cumulative LAI between 0 - 100 cm was linear for all entries (Fig. 5.4a). NJ, NBB, PF and SB had near perfect linear cumulative LAI down the canopy. Except for SB which had an increasingly planophile canopy with increasing height (Fig. 5.4b), all switchgrass entries had erect canopies, about 40° to the horizontal. The mean tilt angle for NBB differed with canopy height. The vertical LAI distribution of the cultivars averaged over the period mid-July to end of August is presented in Fig. 5.5. During this period, BL, CIR and SH had 51-57 % of LAI in the top third of the canopy; DK, FB and ND had 20-26% in the same layer. NBB, NJ, PF and SB were in between these two groups with 34-47% of their LAI in the top third of the canopy. NJ and PF had near uniform distribution between 0 and 100 cm (Fig. 5.5) which when coupled with the erect canopies would allow more light penetration in the canopy. ND was also characterised by even LAI distribution between 0-50 cm. For BL and CIR, the proportion of total LAI increased with increasing canopy height up to 100 cm.

These differences in canopy architecture reflect the evolutionary history of the cultivar, whether acquired naturally or through deliberate breeding and selection programmes. It is argued that maximum rates of photosynthesis are usually found in the top part of the canopy (Woodman, 1971), therefore making it an advantage to have high leaf area proportions in the top portion of the canopy. However the overall effect of these canopy architectures on growth and yield will also be modified by the overall canopy height, leaf shapes and sizes (Taylor, 1975).

5.4.4. Canopy light transmission and k

By the end of June, PAR interception was above 85 % for all cultivars and increased to seasonal highs between 96 -99 % of incoming PAR. In early season, the increases in light interception closely followed increases in LAI. The plot of canopy light transmittance (averaged over the period mid July to end of August) against cumulative LAI is presented in Fig 5.6. Canopy light transmittance plots show reasonable fit to the Beer-Lambert model. The negligible transmittance in the 0-25 cm stratum suggest potential violations of the model at this level. Linear regression models relating transmittance and cumulative LAI were all significant ($p<0.05$) and the average *k* values are presented in Table 5.2. The *k* values ranged from 0.57-0.72 and there was a tendency of early maturing cultivars (DK, ND and SB but not FB) to have lower *k* values, partly because of early leaf senescence. For each unit LAI, a canopy/cultivar with a higher *k* , for example BL, will intercept more light (Oker-Blom and Kellomaki, 1983). Exclusion of the 0-25 cm stratum did not improve the regression fit and resulted in *k* values that were, on average, up to 15% lower (data not presented). Extinction coefficients computed by simple substitution in the equation $k=(\ln I_i/I_o)/LAI$ ranged from 0.62-0.81 (Table 5.2) and were, on average, 11% higher than those obtained by linear regression. The high k value for NJ despite lower tiller numbers per m^2 can be attributed to the more uniform leaf area distribution and erect canopy (Fig 5.4 and 5.5). Good architecture can also be argued for the high *k* in BL while poor architecture against SB which had a relatively more planophile canopy structure (Fig 5.4).

In addition to canopy architecture, differences in *k* values are also attributable to other factors including differences in overall plant height (Edmeades and Laffitee. 1993), leaf number (Dwyer *et al.*, 1992) and plant population (Giauffreit *et al.*, 1991). Several authors including Clegg *et al.* (1974) and Muchow *et al.*(1982) have reported non-linear attenuations of PAR down crop canopies. Contrary to our findings, these studies reported better linear relationships when the 0-25 cm layer was excluded.

5.4.5. Biomass yield

There was a linear increase in average yield over the three seasons (8477, 9943 and 10869 kg ha^{-1} for 1993, 1994 and 1995 seasons, respectively). This was partly due to stand consolidation and to increasingly warmer seasons. Entry x year interactions were significant. Switchgrass cultivars BL, CIR and NJ were consistently the highest yielders (Fig. 5.7). The early maturing cultivars DK and ND were the lowest yielders. BL and PF had high steady increases of about 2 ton DM ha^{-1} yr^{-1}. Despite increases in yield from 1993-1994 DK, NBB and ND showed slightly decreased yields in 1995. There is no apparent explanation for this decline.

Biomass yields were positively correlated with leaf area duration (r=0.78, Fig 5.8). Leaf area duration was calculated as area under curves in Fig. 5.2 and 5.3 (Beadle, 1985) based on accumulated growing degree-days or days since the beginning of the season. Higher yields were realised from cultivars which maintained high LAI values late into the growing season. The high yields for NJ also reflect its good canopy architecture. Although the results suggest longer leaf duration to be desirable, growth into fall increases susceptibility to winter injury. Our average yields for DK, FB, NBB and SB are comparable to those reported by Jacobson *et al.* (1986) and Jung *et al.*(1990). However, yield for BL, CIR, NJ and PF in our study were higher than those from either of these two studies. As in this study, Jung *et al.* (1990) reported higher yield performances from NJ compared with other switchgrasses.

At the end of the season, all entries had high levels of NDF (range 81-87%) and ADF (range 51-57 %) (Table 5.3) and, at least for the group of cultivars evaluated, fibre offers limited potential as a selection criterion. However, when yield is considered, BL, CIR and NJ have potential as biomass crops. The nitrogen contents ranged from 0.32 to 0.85 % and cultivars BL, SB, CIR, ND and NJ had levels below 0.5 %. According to Agblevor *et al.* (1992), these levels of nitrogen would generate about 10 % char residues in thermochemical reactions. The ash contents ranged from 4.7 to 6.6 % and are comparable to those reported by Wiselogel *et al.* (1994) and Agblevor *et al.* (1992). It might be desirable to devise pretreatment processes to reduce residual nitrogen and ash content.

5.5. Conclusions

This study showed that warm season grasses can successfully be grown in south-western Québec. Biomass yields were highest with New Jersey 50, Cave-in-Rock and Blackwell switchgrasses. Differences in leaf area development and architecture were also shown. No management strategies were imposed on the grass stands, these might influence which cultivars might be ideal for specific forage management strategies.

Table 5.1: The pooled regression parameters when leaf area index was regressed against time for ten warm season grass cultivars, Montréal, Québec.

Growing degree-days

Entry	Regression parameters				
	a[1]	b_1	b_2 (x 10^{-6})	r^2	rMSE[2]
BL	-1.28	0.0148	-7.31	0.94	0.335
CIR	-2.15	0.0179	-8.30	0.93	0.488
DK	-1.14^{ns}	0.0173	-10.1	0.81	0.617
FB	-1.74	0.0171	-9.34	0.91	0.405
NBB	0.17^{ns}	0.0142	-7.43	0.90	0.412
ND	-2.36	0.0197	-10.86	0.90	0.485
NJ	-1.74	0.0149	-6.71	0.93	0.403
PF	-0.64^{ns}	0.0133	-6.24	0.90	0.442
SB	-2.14	0.0180	-9.02	0.91	0.489
SH	-0.93^{ns}	0.0146	-6.99	0.92	0.417

Days since May 1st

Entry	Regression parameter				
	a	b_1	b_2 (x 10^{-3})	r^2	rMSE
BL	-3.74	0.243	-1.48	0.89	0.471
CIR	-5.42	0.301	-7.13	0.84	0.728
DK	-5.07	0.329	-1.79	0.81	0.608
FB	-5.34	0.311	-2.40	0.87	0.484
NBB	-2.84	0.258	-2.14	0.88	0.469
ND	-6.59	0.361	-1.71	0.87	0.546
NJ	-4.44	0.249	-2.52	0.84	0.606
PF	-3.07	0.225	-1.44	0.81	0.594
SB	-5.94	0.323	-1.35	0.88	0.568
SH	-3.69	0.250	-1.53	0.85	0.577

[1] all regression coefficients are significantly different from zero except when followed by ns

[2] square root of Mean Square Error

Table 5.2: The mean (± SE) number of tillers and extinction coefficients (*k*) of switchgrass and big bluestem, Montréal, Québec.

Entry	Tiller numbers m^{-2}	*k* regression	*k* simple substitution
Blackwell	527.8 ± 19.7	0.72 ± 0.04	0.74 ± 0.04
Cave-in-Rock	697.8 ± 26.8	0.67 ± 0.05	0.72 ± 0.03
Dakota	555.3 ± 5.7	0.57 ± 0.04	0.68 ± 0.03
Forestburg	692.3 ± 62.8	0.68 ± 0.05	0.81 ± 0.05
Niagara	588.0 ± 54.0	0.66 ± 0.04	0.76 ± 0.03
ND3743	488.3 ± 50.9	0.58 ± 0.03	0.72 ± 0.07
New Jersey 50	485.5 ± 22.9	0.69 ± 0.03	0.72 ± 0.04
Pathfinder	956.3 ± 19.5	0.70 ± 0.04	0.71 ± 0.04
Sunburst	747.0 ± 11.0	0.60 ± 0.03	0.62 ± 0.03
Shelter	504.0 ± 14.1	0.63 ± 0.04	0.70 ± 0.03

Table 5.3: The average chemical composition (%) of biomass harvested at the end of the growing season, Montréal, Québec

Entry	Nitrogen	NDF	ADF	Ash
Blackwell	0.32f[†]	86.42a	57.17a	4.47f
Cave-in-Rock	0.43de	85.11b	56.50b	5.71b
Dakota	0.74b	82.27c	50.37g	5.43c
Forestburg	0.73b	82.41c	54.49d	6.61a
Niagara	0.85a	81.25d	50.87fg	5.44c
ND3743	0.44d	85.58b	54.50d	4.65ef
New Jersey 50	0.43de	85.40b	55.65c	4.97d
Pathfinder	0.75b	82.27c	52.03e	5.33c
Sunburst	0.39e	86.50a	57.14a	4.72e
Shelter	0.63c	82.96c	51.03f	4.96d
LSD	0.043	0.804	0.601	0.183
CV	4.38	0.817	0.952	2.03

[†] means in the same column followed by different letters are significantly different by an ANOVA protected LSD test ($p < 0.05$)

Fig. 5.1: Mean temperature (°C), rainfall (mm) and accumulated growing degree-days (calculated with a base temperature of 5°C) during 1993, 1994 and 1995 growing seasons, Montréal, QC.

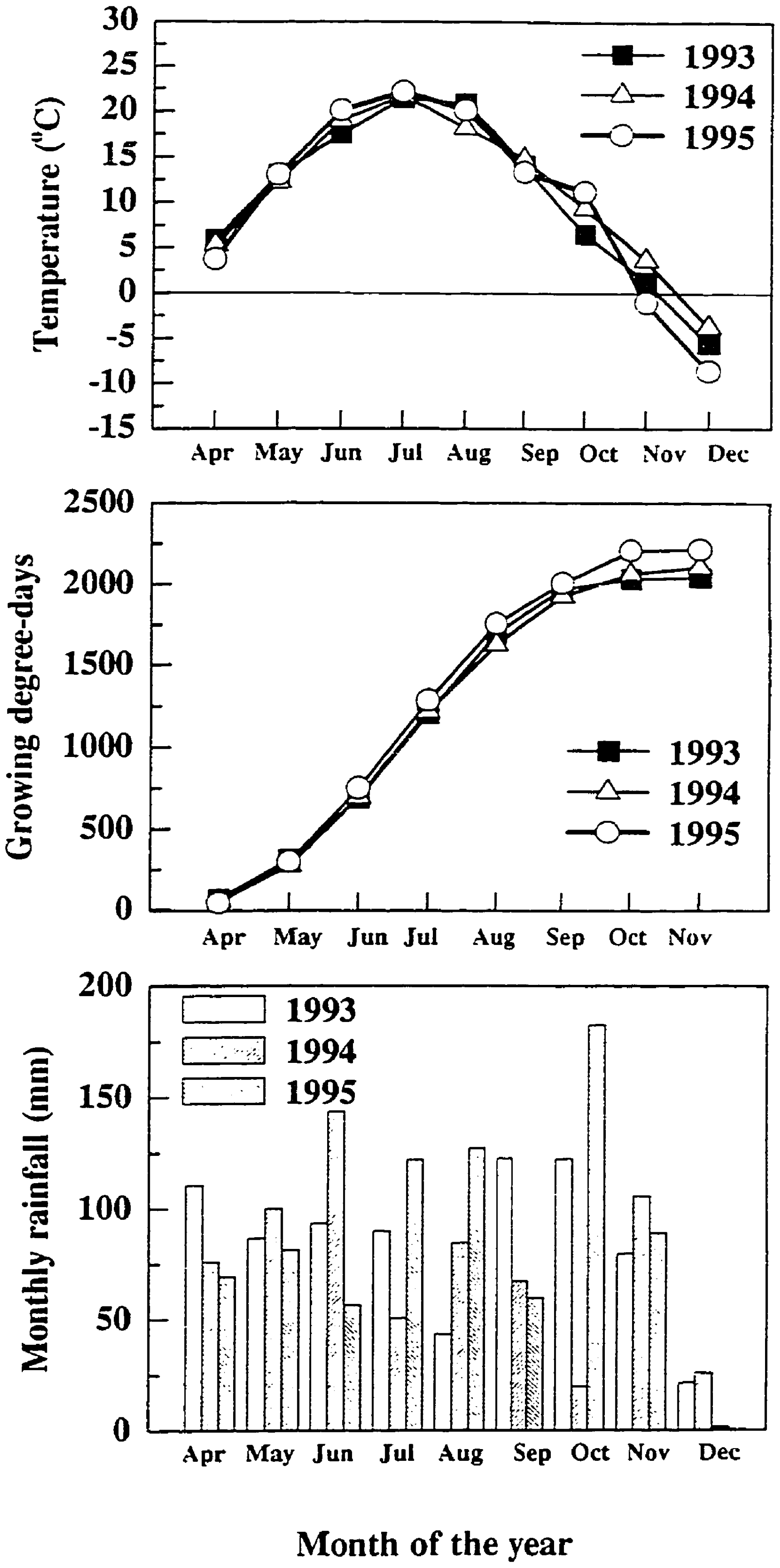

Temperature (°C)
30
25
20
15
10
5
0
-5
-10
-15
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
1993
1994
1995
Growing degree-days
2500
2000
1500
1000
500
0
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
1993
1994
1995
Monthly rainfall (mm)
200
150
100
50
0
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
1993
1994
1995
Month of the year

Fig. 5.2: Seasonal leaf area development patterns of switchgrass cultivars during 1994 and 1995, Montréal, QC. Regression equations fitted to the relationships between LAI and time are presented in Table 5.1. Bars extending beyond each point denote SE.

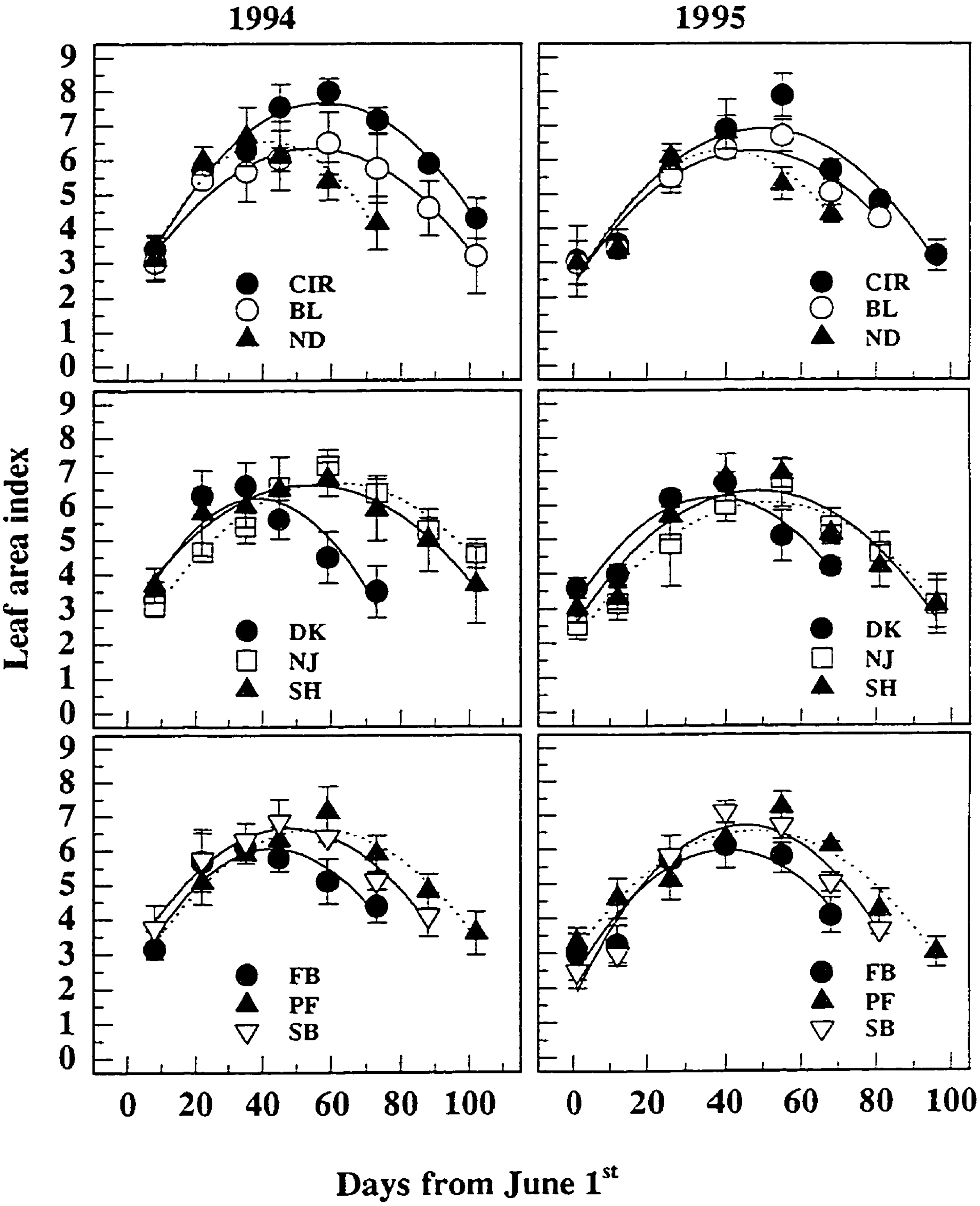

1994
1995
Leaf area index
0
1
2
3
4
5
6
7
8
9
CIR
BL
ND
DK
NJ
SH
FB
PF
SB
0
20
40
60
80
100
Days from June 1st

Fig. 5.3: Seasonal leaf area development patterns of Niagara big bluestem during 1994 and 1995, Montréal, QC. Regression equations fitted to the relationships between LAI and time are presented in Table 5.1. Bars extending beyond each point denote SE.

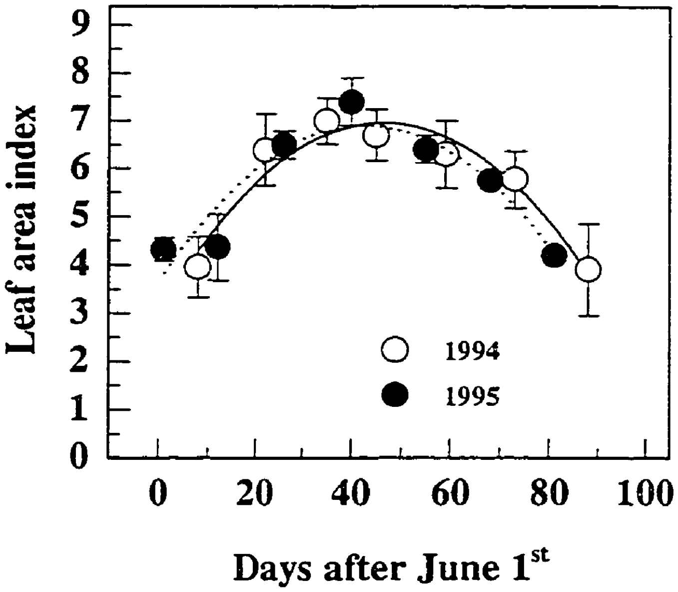

Leaf area index
0
1
2
3
4
5
6
7
8
9
0
20
40
60
80
100
Days after June 1st
○ 1994
● 1995

Fig. 5.4: Average downward cumulative leaf area index and mean tilt angles of warm season grasses during summer of 1994 and 1995, Montréal, QC. Bars extending beyond each point denote SE.

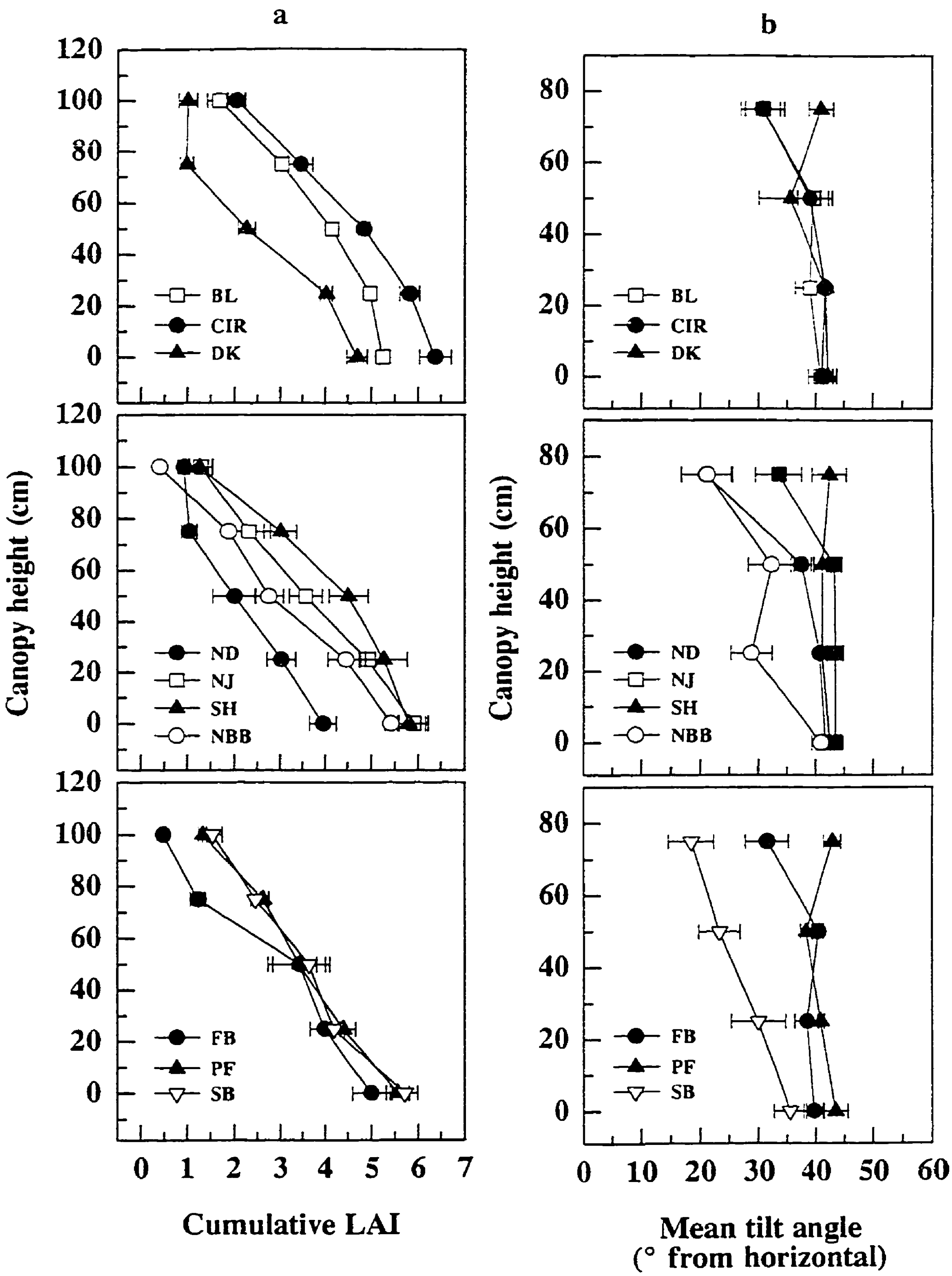

a
b
Canopy height (cm)
Canopy height (cm)
BL
CIR
DK
ND
NJ
SH
NBB
FB
PF
SB
120
100
80
60
40
20
0
0
1
2
3
4
5
6
7
Cumulative LAI
0
10
20
30
40
50
60
Mean tilt angle
(° from horizontal)

Fig. 5.5: Mean vertical distribution of total leaf area of warm season grasses in summer during 1994 and 1995. Values were obtained by difference between successive height strata within the canopy. Bars extending beyond each point denote SE.

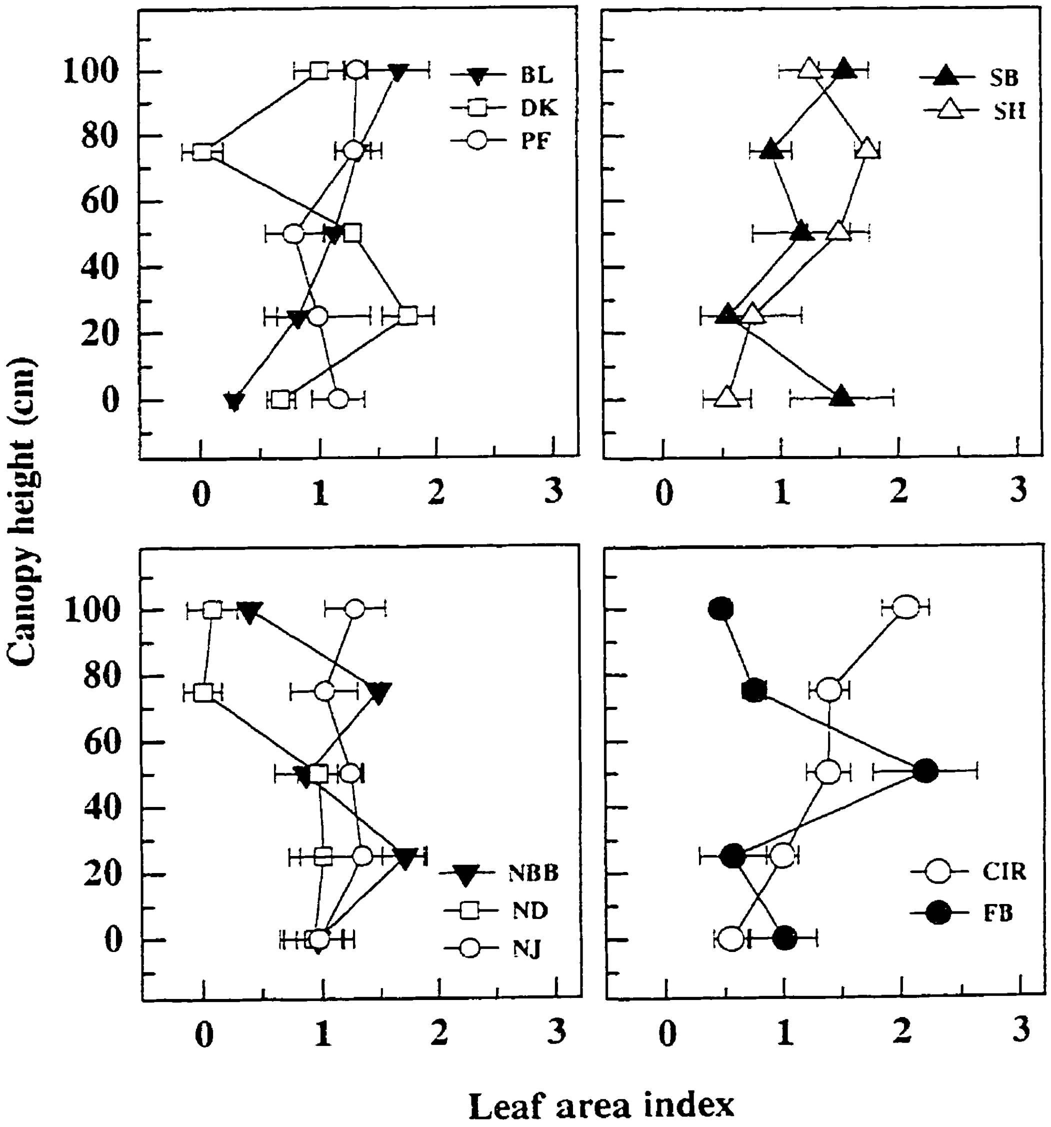
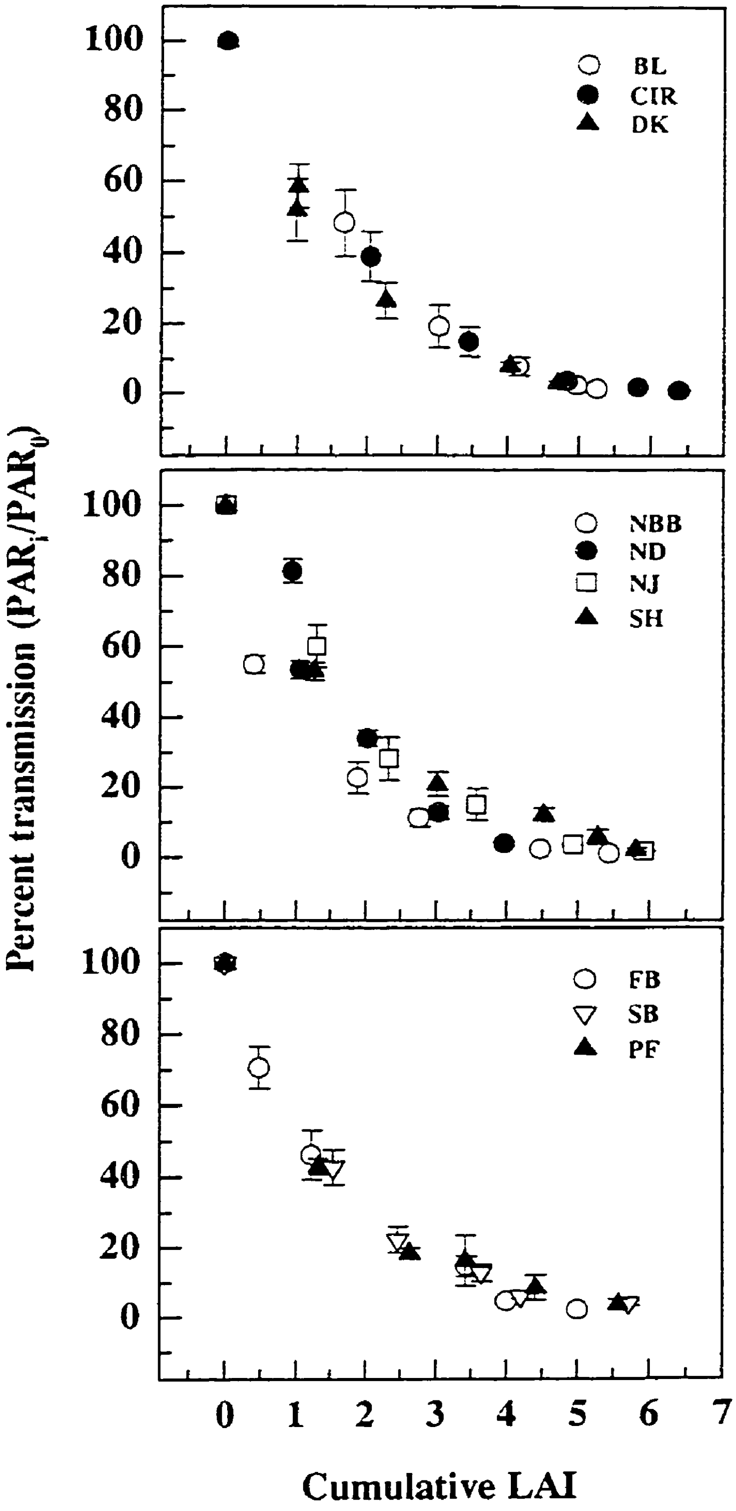

BL
DK
PF
SB
SH
NBB
ND
NJ
CIR
FB
Canopy height (cm)
100
80
60
40
20
0
0
1
2
3
Leaf area index

Fig. 5.6: Canopy light transmittance plotted against cumulative leaf area index for warm season grasses, Montréal, QC. Data are averaged for the period mid July to end of August over 1994 and 1995. Bars extending beyond each point denote SE.



Percent transmission (PAR$_i$/PAR$_0$)
Cumulative LAI
BL
CIR
DK
NBB
ND
NJ
SH
FB
SB
PF
100
80
60
40
20
0
0
1
2
3
4
5
6
7

Fig. 5.7: Annual dry matter yield (Mg ha^{-1}) of warm season grasses, 1993 through 1995, Montréal, QC. T-bars extending beyond each bar graph denote SE.

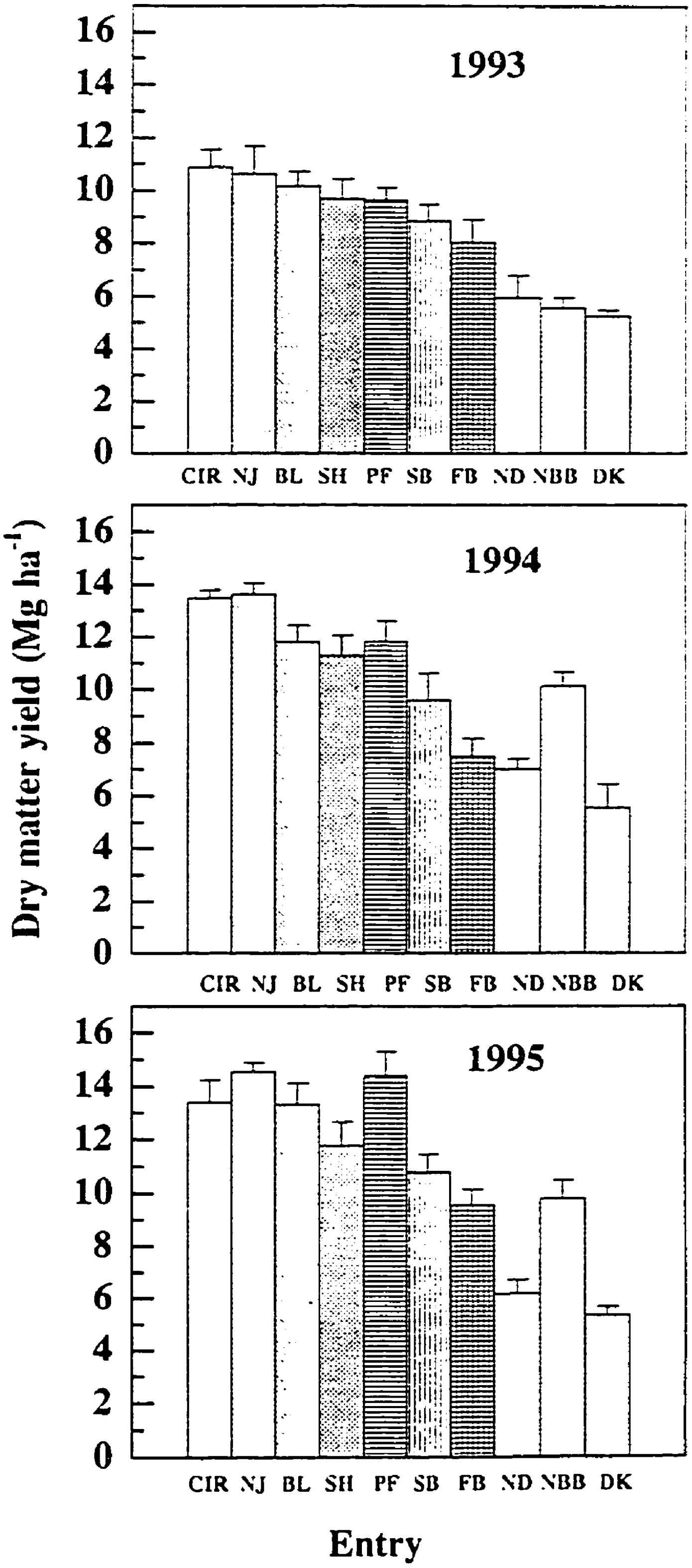
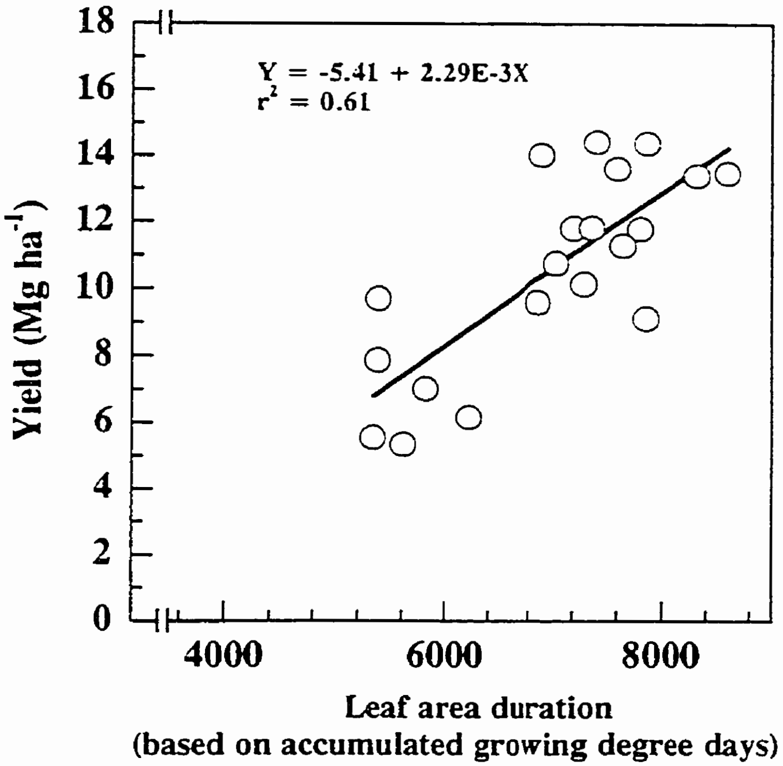
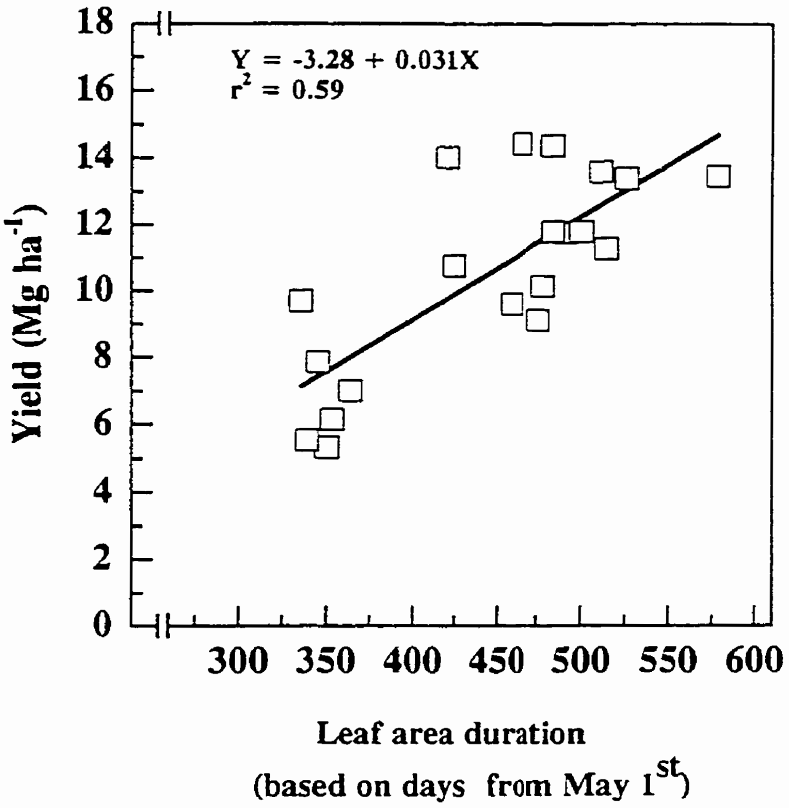

1993
1994
1995
Dry matter yield (Mg ha^{-1})
16
14
12
10
8
6
4
2
0
CIR NJ BL SH PF SB FB ND NBB DK
Entry

Fig. 5.8: The relationship of annual dry matter yield (Mg ha^{-1}) to leaf area duration. Data were combined for the years 1994 and 1995


Y = -5.41 + 2.29E-3X
r² = 0.61
Yield (Mg ha⁻¹)
0
2
4
6
8
10
12
14
16
18
4000
6000
8000
Leaf area duration
(based on accumulated growing degree days)


Y = -3.28 + 0.031X
r² = 0.59
Yield (Mg ha⁻¹)
0
2
4
6
8
10
12
14
16
18
300
350
400
450
500
550
600
Leaf area duration
(based on days from May 1st)

Preface to Chapter 6

Chapter 6 is based on a manuscript submitted for publication to the *Journal of Range Management* in 1997.

The differences in early season growth among entries presented in Chapters 3, 4 and 5 imply differences in low temperature tolerance. Although entries like Cave-in-Rock and New Jersey 50 were relatively late in early season growth, they showed high growth rates when temperatures increased. Thus, the different entries appeared to have different base temperatures and growth rates. This is addressed in Chapter 6, in which variations in base temperatures for germination and growth were determined.

Chapter 6

Variation in Base Temperatures for Germination and Seedling Growth in Warm Season Grasses

6.1. Abstract

Recently, efforts have been made to develop heat unit based growth models for warm season grass production in cool season environments. These models require the accurate determination of base temperatures. Variations in base temperatures for germination and seedling growth were determined in four switchgrasses (*Panicum virgatum* L.), three big bluestem grasses (*Andropogon gerardii* Vitman), two indian grasses (*Sorghastrum nutans* L. Nash) and two prairie sandreeds (*Calamovilfa longifolia* (Hook) Scribn.). During the germination study, seeds were allowed to germinate in petri dishes at 4, 8, 12, 16 and 20°C. In the seedling growth study, seedlings initially at the two leaf stage were grown at 4, 8, 12, 16 and 24°C for four weeks with representative harvests every week. The germination and relative growth rates were used in estimating base temperatures using regression techniques. There were variations, among and within species, in both germination and growth kinetics. Estimates of base temperature for germination were 5.5 to 10.9, 7.3 to 8.7, 7.5 to 9.6 and 4.5 to 7.9 for switchgrass, big bluestem, indian grass and prairie sandreed. Absolute values in each case depended on whether linear or non-linear techniques were used. The results also indicated differences between base temperature estimates for germination and for seedling growth. Differences in base temperatures for some of the cultivars corroborated field observations.

6.2. Introduction

Warm season grasses are increasingly being tested in cool season climates as alternative sources of forage in summer (Jung *et al.*, 1990) and industrial raw materials (Sanderson and Wolf, 1995a). The widespread adoption of these grasses in cool seasons is largely limited by temperature. In addition to its effect on the length of the growing season, temperature affects germination through removal of seed dormancy (Benech-Arnold *et al.*, 1988; Probert, 1992) and by determining rate of germination of non-dormant seeds (Hsu *et al.*,1985; Jordon and Haferkemp, 1989; Roundry and Biendenbender, 1996; Orozco-Segovia *et al.*, 1996). This has led to the development of heat unit based models of the quantitative effects of temperature on germination and/or stand establishment. Determination of the minimum or base temperature (T_b) is a critical aspect of these models. This determination has largely been based on linear regression (for example Garcia-Huidoboro *et al.*, 1982; Jordon and Haferkemp, 1989; Lawlor *et al.*, 1990) of the relationships between temperature and germination rates (reciprocal of time to germination) of different percentile subpopulations. Over a wide range of temperatures, germination rates of a particular subpopulation can be normally distributed (Orozco-Segovia *et al.*, 1996). Therefore, linear model analysis breaks the distribution into suboptimal and supraoptimal phases, neglecting the optimum plateau. Also when the germination rates are observed at temperatures far from the base, small changes in the slopes of the fitted lines greatly affect the estimated T_b (Gbur *et al.*, 1979). These workers suggested the use of a temperature range which includes the T_b. This leads to the use of non-linear regression models.

Reported values of T_b for germination vary between species (Angus *et al.*,1981; Covel *et al.*, 1986; Jordon and Haferkemp, 1989), with intraspecific variation as in sorghum (Harris *et al.*, 1987; Lawlor *et al.*, 1990) or without as in chickpea (Ellis *et al.*, 1986). Probert (1992) reviewed several studies that link intraspecific differences in germination to geographical and ecological areas of distribution/origin.

Post emergence slow stand establishment may be due to slow seedling growth and late development of the root system. These processes are also affected by temperature. As with germination, several thermal unit based models have been used to predict the growth and development of crops. In warm season grasses, relationships between growing degree days and rate of morphological development can be important in scheduling defoliation/grazing management (Mullahey *et al.*, 1990; 1991; Sanderson and Wolf, 1995a). Sanderson and Wolf (1995b) also used growing degree days to study seasonal changes in the chemical composition of switchgrass. These models are still dependent upon the accurate determination of T_b. For pearl millet (Ong, 1983) and groundnut (Leong and Ong, 1983), there were only small variations in base temperatures for different growth and developmental phases. However, for wheat, values of T_b have been reported to vary depending on plant age (Angus *et al.*, 1981) and phenological stage (Slafer and Savin, 1991).

The objectives of this study were to determine the base temperatures for germination and growth of different genotypes of switchgrass, big bluestem, indian grass and prairie sandreed; and to determine if there is intraspecific variation in these base temperatures.

6.3. Materials and Methods

6.3.1. Germination

Constant temperature germination was conducted on seeds of switchgrass (*Panicum virgatum* L.) cv. Cave-in-Rock (CIR, originally from southern Illinois), Dakota (North Dakota), Pathfinder (Nebraska) and New Jersey 50 (North Carolina); big bluestem (*Andropogon gerardii* Vitman) cv. Bison (Nebraska), Niagara (NW New York) and Rountree (Iowa); indian grass (*Sorghastrum nutans* L. Nash) cv. Holt (Nebraska) and Tomahawk (composite from North and South Dakota) and prairie sandreed (*Calamovilfa longifolia* (Hook) Scribn.) cv. ND95 (North Dakota) and Pronghorn (southern Nebraska).

Seeds were dusted with the fungicide Captan [N-(Trichloromethythio)-4-cyclohexene-1,2-dicarboximide] before imbibition and placed on two layers of Whatman no. 2 filter paper in 9 cm petri dishes. The filter papers were moistened with distilled water. The petri dishes, each with 100 seeds, were placed in growth chambers (Conviron ModE15, Controlled Environments Ltd., Winnipeg, Manitoba, Canada) maintained at constant temperatures of 4, 8, 12, 16 and 20°C. Light intensity was maintained at 100 μmol m^{-2} s^{-1} for 14 hours a day. The filter papers were kept moist by addition of distilled water at appropriate times. Four replicate petri dishes for each cultivar were completely randomised in each growth chamber. The whole experiment was conducted twice.

Seeds were considered germinated when the radicle/plumule was at least 2 mm in length. Germinated seeds were counted and removed initially twice a day and later once a day until there was no germination for at least three consecutive days. Germination rate index (GRI) was computed as the total of the daily germination percent divided by the respective accumulated number of days since placement on the temperature treatment. The obtained GRI values were corrected for final germination (corrected germination rate index, CGRI) (Hsu *et al.*, 1985) by dividing them by the respective final germination and multiplying by 100.

The reciprocal of the time taken for a percentile of germination (based on 100 germinable seeds) was defined as its rate of germination. Both linear and non-linear regression analyses were conducted on the relationship between the rate of germination (Y) of 50, 60, 70 and 80 % subpopulations and temperature (X). With linear regression, the T_b of germination was estimated when Y = 0 and solving for X. Non-linear regressions were conducted using the equation

$$^{1}/_{t} = k(T-T_b) \quad .... \quad 1$$

where $^{1}/_{t}$ represents the rate of germination; T, germination temperature and T_b is the base temperature at which $^{1}/_{t}$ equals zero; k is a constant (Garcia-Huidoboro *et al.*, 1982). The first temperature showing no germination was included in the analysis to ensure inclusion of the base temperature. The condition that $T > T_b$ otherwise $^{1}/_{t} = 0$, was also mandated in the analysis.

The linear regression analysis and ANOVA on final germination and CGRI were carried out using SAS Proc GLM (SAS Institute, 1995), while SAS Proc NLIN was used for the segmented regression analysis. The final germination percentages were arcsin transformed (Steel and Torrie, 1980) before statistical analysis.

6.3.2. Seedling growth

Ten to 15 seeds of each cultivar (except Rountree because of a seed shortage) were initially sown in 12.7 cm pots containing 2:1:1 (v/v/v) promix (Premier

Horticulture Inc., Rivière-du-Loup, Québec), vermiculite (Vil Vermiculite Inc., Montrél, Québec) and soil. The seeds were allowed to germinate in a greenhouse maintained at 24°C and under natural light conditions with supplementary automatic lighting to maintain a 14 h day length and at least 400 μmol m^{-2} s^{-1} PAR. The seedlings were watered as frequently as was necessary and fertilised with 20-20-20 mix (Plant Products Co. Ltd., Brampton, Ontario, Canada) at the recommended concentration, once a week. At the two leaf stage, all pots were thinned (for each cultivar) to five fairly uniform plants per pot. Based on preliminary trials, the different cultivars were germinated at different times to synchronise the beginning of the experiment. The pots were then transferred to growth chambers maintained at 4, 8, 12, 16 and 24°C. In each chamber, there were four randomly placed pots per cultivar. At the end of each of four consecutive weeks, one pot per cultivar was removed (harvested) and the plants washed free of the potting mixture, dried for 48 hours at 80°C, and weighed for total biomass. This experiment was conducted three times. Representative plants from the thinning exercise were used to estimate total biomass at the beginning of each run.

Biomass changes over the four harvests were subjected to linear regression analysis and the slope of each of the fitted lines gave the mean relative growth rate (RGR) over the four weeks. The changes in RGR with temperature for each cultivar were subjected to non-linear regression analysis using either equation 1 (where $^{1}/_{t}$ represented RGR) or an exponential relationship of the form

$$RGR = e^{k}(T-T_{b})-1 \qquad ....2$$

where k is a growth rate constant (Unruh *et al.*, 1996).

6.4. Results and Discussion

6.4.1. Germination

On average, final germination increased with increasing temperature (Table 6.1). Between 12 and 20°C, the increases in final germination percent were not different among ND95, Pronghorn, Bison and Rountree. There were also no differences between final germination percent at 12 and 16°C among cultivars Pathfinder, Tomahawk and Dakota. At 8°C, the highest final germination percent was recorded for ND95 followed by Pathfinder, Dakota and Pronghorn. There was little germination in Toma, Holt, Niagara, Rountree and NJ50 and none in CIR at 8°C. Between 12 and 20°C, Pathfinder had the highest final germination percent followed by Dakota and CIR. The big bluestems as a group had relatively low final germination percentages between 12 and 20° C. Among the switchgrasses, NJ50 was notable for its relatively low final germination percentages at all temperatures.

The CGRI also increased for all cultivars with increasing temperature (Table 6.2), the highest in all cases being at 20°C. Unlike the final germination percentages, the CGRI increases were different for all entries at each temperature increase, that is in spite of small increases in the final germination, germination was hastened by increasing temperatures. From 12 to 20°C, the highest CGRI were recorded for Pathfinder, ND95 and Dakota. NJ50 and the big bluestems had relatively low CGRI values. Change in ranking was most noticeable for CIR which was among the lowest at 12°C, but the fourth highest at 20°C. The low final germination and CGRI in NJ50 were also found in a different seed lot even at 24°C (data not shown). This suggests, relative to the other switchgrasses, the existence of other factors affecting germination in this cultivar. Except for Holt and Tomahawk, differences in final germination and CGRI all indicate different germination kinetics.

For all entries linearity of the relationship between rate of germination and temperature was high enough ($r^2 = 0.80$ to 0.93, Table 6.3) to proceed with estimation of T_b. Absolute values of T_b depended on the subpopulation used. The estimates of T_b from linear regressions ranged from 5.5 to 9.0, 7.3 to 8.2, 7.5 to 8.5, and 4.5 to 6.1 for switchgrass, big bluestem, indian grass and sandreed, respectively. Since single seed lots were used for each cultivar, the different subpopulations are presumed to estimate the same T_b and linear relationships from these subpopulations should converge on one point (Fig. 6.1). Base temperature was also estimated from this point of convergence (Table 6.3). In all cases, this value was higher than the individual estimations from different subpopulations. Our observation that higher percentile subpopulations required more thermal time is consistent with results reported by Garcia-

Huidoboro *et al.* (1983), Washitami (1985) and Orozco-Segovia *et al.* (1996).

In big bluestem, estimations of T_b and thermal times from linear regression analysis were similar to those from non-linear analysis. On average, non-linear estimations of T_b were 23 and 30% higher than those from linear estimation in Pronghorn and ND95, respectively. Corresponding comparisons in switchgrass ranged from 14-29% higher. In indian grass, differences were, on average, less than 10% higher. Because non-linear analysis allows us to use the information derived from the highest temperature where germination did not occur, without introducing any bias (as this temperature is probably below the actual T_b), and linear analysis does not allow this, all further discussions will focus on results from non-linear analyses.

Dakota and Pathfinder had similar T_b values which were significantly lower than those for NJ50 and CIR. The latter two cultivars had similar T_b values. These intraspecific differences could be due to different areas of origin as was suggested for other warm season grass characteristics (Jacobson *et al.*, 1986). Dakota and Pathfinder are from more north-western regions compared with CIR (southern) and NJ50 (eastern). The three cultivars of big bluestem evaluated had similar T_b values for germination, as did the two indian grass cultivars. In the sandreeds, Pronghorn had a lower value than ND95. Our results are in general agreement with those reported by Hsu *et al.* (1985) and Jordon and Haferkemp (1989). Intraspecific differences have also been reported in sorghum (Lawlor *et al.*, 1990), and in cool season grasses (Probert, 1985). The results in Table 6.3 also demonstrate variations due to different methods for estimating T_b. These variations, though small, are likely to have practical implications, for example, as demonstrated by Jordon and Haferkemp (1989), small differences in base temperature may mean large differences in germination time.

6.4.2. Seedling growth

As temperature increased, total dry matter increased for all cultivars (examples in Fig. 6.2). In most of the cultivars studied, the increase in biomass with time at 24°C followed an exponential trend. These dry matter increases were similar to those reported by Hsu *et al.* (1985). RGR values were obtained by linear regression using ln transformed dry matter weights. The cultivar x temperature interaction was significant ($p<0.05$) over the temperature range studied. The increases in RGR with temperature were linear in Bison, Dakota, ND95 and Pronghorn and exponential for the rest of the cultivars studied (Fig. 6.3). Estimations of T_b and growth constants were made using non-linear regression using either equation 1 or 2, depending on the relationship in Fig. 6.3.

The highest T_b was estimated for CIR, followed by NJ50 and Niagara (Table 6.4) and the lowest was for Bison. Among the switchgrasses the ranking in T_b for growth was, in increasing order, Dakota, Pathfinder, NJ50 and CIR. Niagara big bluestem had a higher T_b value than Bison. There was no difference between the two indian grasses or between the two sandreeds. The growth rate constants did not follow the same ranking as the T_b values. CIR had a higher growth rate constant than all the other cultivars tested. Differences in growth rate constants might have been compromised by the use of total dry weight. Hsu *et al.* (1985) reported higher growth rates for above ground tissues than roots.

The T_b values for growth seem to confirm the low spring growth observed in the field for CIR and NJ50, and the early spring growth by Dakota, Pathfinder and the sandreeds (Madakadze *et al.*, 1996a). Given differences in places of origin, at least for the switchgrasses and big bluestems tested, differences in T_b for growth might also be due to differences in evolution patterns of these cultivars or at least the parent populations. As was noted for common centepedegrass (*Eremochloa ophiuroides* (Munro) Hackel) (Unruh *et al.*, 1996), the slow spring growths of CIR and NJ50 were followed by rapid growth as temperature increased. In a field evaluation (Madakadze *et al.*, 1996a), these two cultivars were the highest yielders. However, only moderate yields were recorded for Pathfinder which in this study had a combination of a relatively low T_b for growth and high rate constant.

The differences in T_b estimated for germination and seedling growth for each cultivar might be evidence that neither is an indication of the other. This is at variance with Ong (1983) and in agreement with the suggestion by Lawlor *et al.* (1990). Slafer and Savin (1991) reported different T_b values for different developmental stages in wheat.

6.5. Conclusions

Intraspecific variations exist in base temperatures for germination and growth in warm season grasses. This variation probably reflects different places of origin or, at least, adaptation to specific environmental pressures. The choice of methodology influences the absolute value of base temperature estimated. Differences in base temperature for germination and growth suggests differences in base temperature for different phases of development.

Table 6.1: Effect of temperature on the final germination (%) of warm season grass seeds

Entry	Temperature (°C)				
	8	12	16	20	LSD (0.05)
Cave-in-Rock	0dF	54.33cC	66.84bC	80.57aC[†]	0.62
Dakota	15.91cBC	79.37bB	84.43abB	92.16aB	2.24
New Jersey 50	0.18cEF	14.84bE	35.78aFG	39.42aE	1.65
Pathfinder	17.29cB	93.05bA	96.00bA	99.87aA	1.76
Bison	9.32bC	43.16aD	45.35aEF	46.68aE	0.77
Niagara	2.04cDE	16.48bE	34.99aG	38.22aE	0.81
Rountree	3.80bD	15.24aE	18.09aH	18.21aF	0.37
Holt	1.94cDE	48.97bCD	56.16aD	57.02aD	0.37
Tomahawk	0.56cEF	50.37bCD	51.64bDE	57.52aD	0.24
ND95	27.02bA	49.60aCD	51.28aDE	53.01aDE	0.88
Pronghorn	14.67bBC	49.08aCD	49.34aDE	55.08aDE	1.03
Mean	5.85d[‡]	46.78c	54.83b	60.87a	0.08
LSD (0.05)	1.12	0.82	1.04	1.78	

[†] means in the same row followed by different lower case letters and within same column followed by different upper case letters are significantly different ($p<0.05$) using a protected LSD test

[‡] temperature means followed by different letters are significantly different ($p<0.05$) using a protected LSD test

Table 6.2: Effect of temperature on the corrected germination rate index of warm season grass seeds

Entry	Temperature (°C)				
	8	12	16	20	LSD (0.05)
Cave-in-Rock	0dF	4.44cEF	9.41bBC	16.87aBC[†]	0.952
Dakota	1.59dDE	3.96cB	11.96bA	22.94aA	1.789
New Jersey 50	1.48dE	4.01cFG	7.91bDE	12.40aD	1.689
Pathfinder	1.86dCDE	6.51cA	13.18bA	25.22aA	1.428
Bison	3.37cA	4.66cDE	8.08bD	10.99aD	1.453
Niagara	2.50dBC	3.95cG	6.69bE	10.80aD	0.827
Rountree	2.50dBC	4.74cDE	7.53bDE	9.97aD	1.209
Holt	2.50dBC	4.90cD	8.74bCD	15.97aC	1.126
Tomahawk	1.78dCDE	5.36cC	9.56bBC	15.55aC	1.457
ND95	3.28dAB	6.14cAB	10.50bB	19.25aB	0.935
Pronghorn	2.39dCD	4.81cDE	7.74bDE	11.74aD	0.756
Mean	0.33d[‡]	2.52c	5.34b	10.46a	0.347
LSD (0.05)	0.85	0.44	1.26	2.96	

[†] Means in the same row followed by different lower case letters and within same column followed by different upper case letters are significantly different ($P<0.05$)

[‡] Temperature means followed by different letters are significantly different ($p<0.05$)

Table 6.3: Estimates of base temperature and thermal time of germination of warm season grass seeds using linear and non-linear regression of germination rates on temperature

Entry	Sub population (% germination)	Linear regression				Non-linear regression	
		Base temperature (°C)	Thermal time (°C day)	r^2	Convergence point[†]	Base temperature (°C)	Thermal time (°C day)
Cave-in-Rock	50	9.02	52.63	84	10.40	10.86	40.00
	60	8.82	64.10	89		10.41	50.76
	70	8.87	69.93	90		10.30	55.87
	80	8.40	90.91	93		9.33	80.65
Dakota	50	5.62	83.33	94	7.00	7.18	71.43
	60	6.10	75.76	91		7.95	62.50
	70	6.02	84.03	92		7.82	69.44
	80	5.90	97.09	93	9.40	7.64	80.65
New Jersey50	50	8.75	67.61	87		10.25	54.47
	60	8.62	76.63	90		9.93	63.86
	70	8.52	85.54	91		9.66	73.21
	80	8.34	100.00	92		9.15	89.85
Pathfinder	50	5.86	63.29	91	7.20	7.57	52.91
	60	6.00	66.22	91		7.80	54.85
	70	5.76	76.10	92		7.42	64.31
	80	5.52	91.35	93		7.01	78.93
Bison	50	7.96	90.91	85	8.20	7.96	90.96
	60	7.58	112.36	89		7.58	112.36
	70	7.33	131.58	87		7.33	131.58
	80	7.42	144.93	91		7.42	144.93
Niagara	50	8.19	93.90	85	9.20	8.67	88.50
	60	8.07	106.25	86		8.24	104.06
	70	7.76	125.88	87		7.76	125.94
	80	7.60	140.79	88		7.60	140.79
Rountree	50	8.05	73.77	87	9.00	8.19	72.46
	60	7.90	90.09	90		7.89	90.09
	70	7.68	108.11	93		7.68	108.11
	80	7.37	132.71	91		7.37	132.71
Holt	50	8.49	62.89	86	9.20	9.57	54.35
	60	8.31	74.07	86		9.05	67.34
	70	8.08	88.50	86		8.29	86.66
	80	7.95	106.61	80		7.95	106.61
Tomahawk	50	8.34	59.52	86	9.60	9.14	53.76
	60	8.17	72.94	84		8.60	69.20
	70	8.32	75.02	87		9.09	67.98
	80	7.47	113.79	80		7.47	113.79
ND95	50	6.09	61.96	82	7.30	7.94	51.02
	60	5.88	72.99	85		7.61	61.27
	70	5.45	95.57	89		6.89	83.06
	80	5.34	106.95	89		6.69	93.94
Pronghorn	50	5.04	108.70	88	6.00	6.41	93.72
	60	4.99	123.05	85		6.31	106.84
	70	4.67	147.08	89		5.63	132.45
	80	4.46	172.41	90		5.16	161.03

[†] estimated as the abscissa of the point fitted lines of all sub-populations intersected

Table 6.4: Estimations of the base temperatures (T_b) and growth constants (k) for seedling growth of warm season grasses

Entry	Base temperature (°C)		Growth rate constant (k x10^{-3}) (°C^{-1})
Cave-in-Rock	7.26a[†]	(2)[‡]	5.61a[†]
Dakota	2.79 cd	(1)	1.95b
New Jersey 50	5.80 ab	(2)	2.47b
Pathfinder	4.49 bcd	(2)	2.45b
Bison	2.59d	(1)	2.22b
Niagara	5.03b	(2)	1.86b
Holt	4.45bcd	(2)	1.44b
Tomahawk	2.82cd	(2)	1.52b
ND95	3.81bcd	(2)	0.87b
Pronghorn	4.80bc	(1)	0.55b

[†] mean estimations in the same column followed by different letters are significantly different after Tukey's test ($p < 0.05$)

[‡] number in brackets indicates the equation that was fitted to the relationship between relative growth rate and temperature

Fig. 6.1: Relationships between rates of germination and temperature of different percentile subpopulations in selected cultivars of warm season grasses

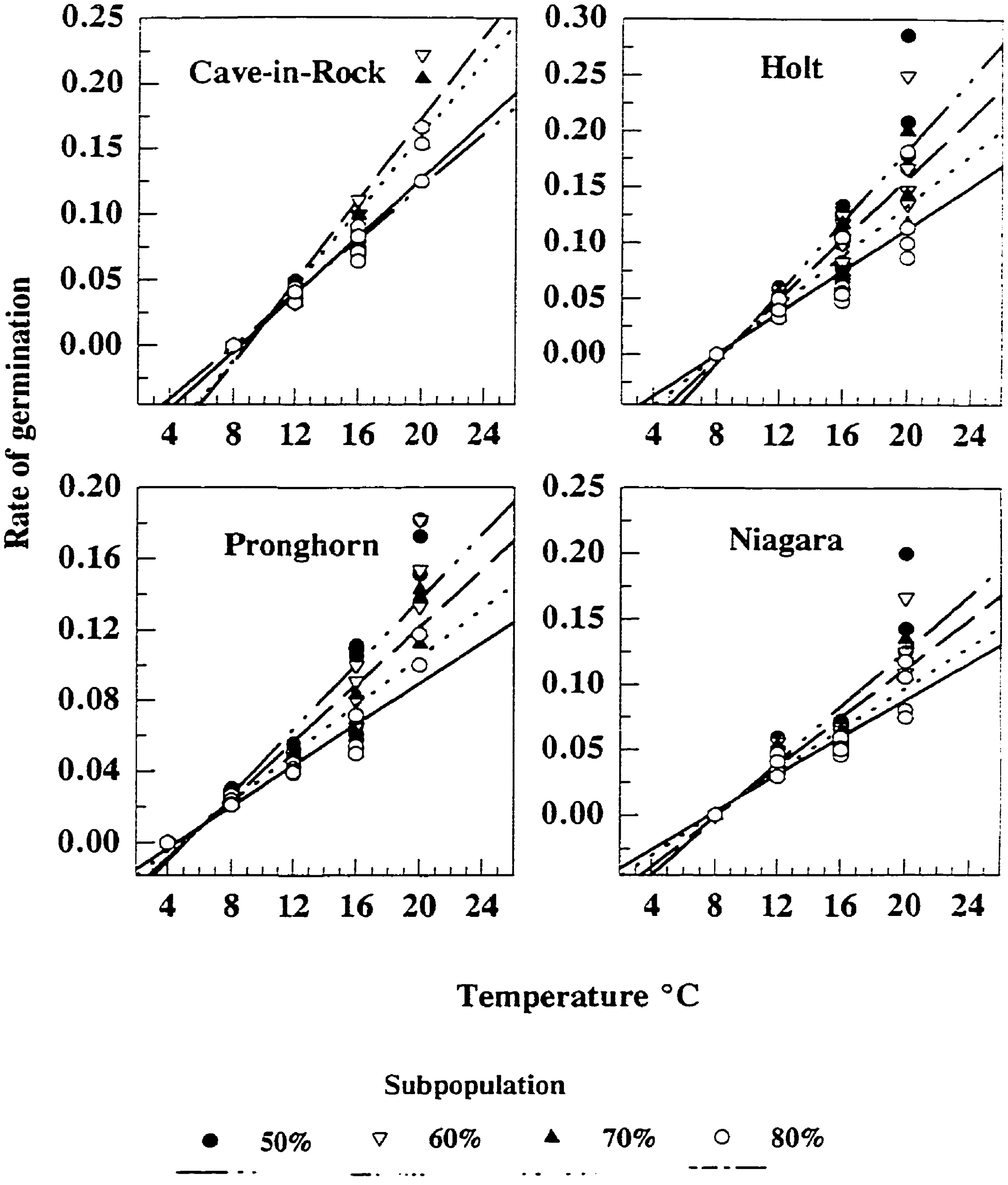

Rate of germination
Cave-in-Rock
0.25
0.20
0.15
0.10
0.05
0.00
Holt
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Pronghorn
0.20
0.16
0.12
0.08
0.04
0.00
Niagara
0.25
0.20
0.15
0.10
0.05
0.00
4
8
12
16
20
24
Temperature °C
Subpopulation
● 50%
▽ 60%
▲ 70%
○ 80%

Fig. 6.2: Total dry weight changes with time for Cave-in-Rock, Holt, Pronghorn and Niagara seedlings under different temperatures regimes. Different scales on the Y-axis also indicate the relative sizes of the seedlings from the different species. Bars extending beyond each point denote SE.

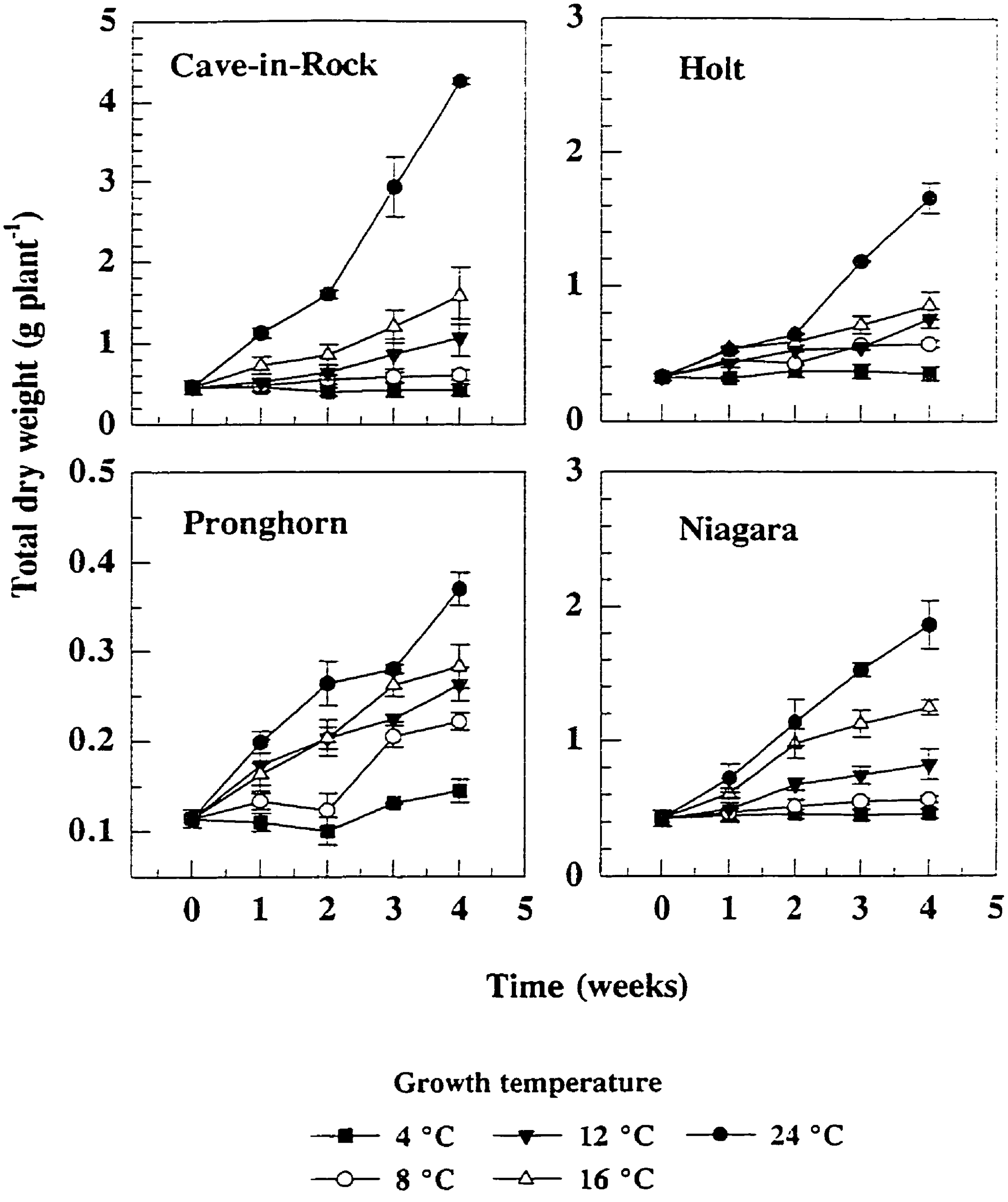
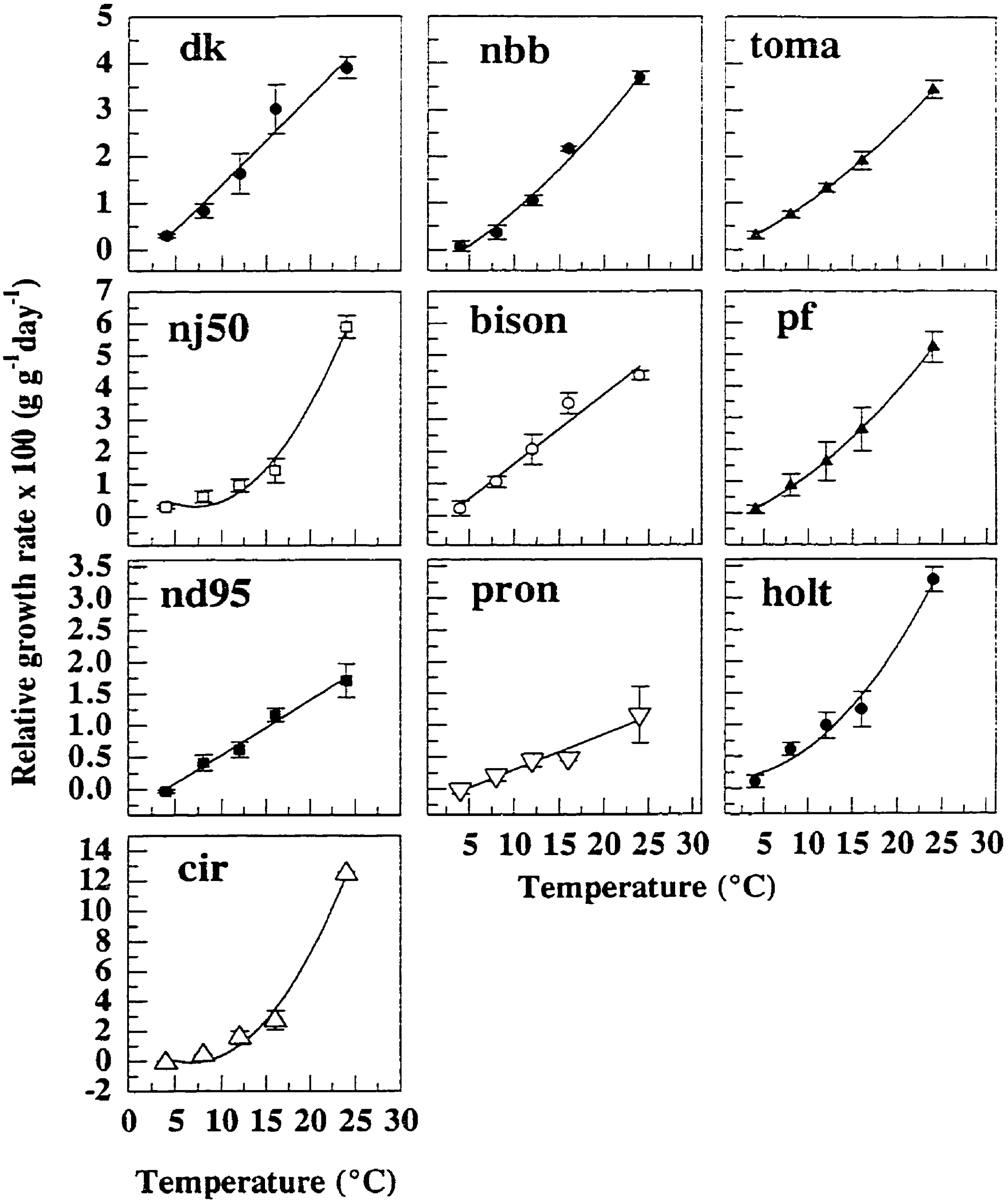

Cave-in-Rock
Holt
Pronghorn
Niagara
Total dry weight (g plant^{-1})
Time (weeks)
0
1
2
3
4
5
0.1
0.2
0.3
0.4
0.5
Growth temperature
4 °C
12 °C
24 °C
8 °C
16 °C

Fig. 6.3: The effect of temperature on the relative growth rates of warm season grass seedlings. Bars extending beyond each point denote SE.


dk
nbb
toma
nj50
bison
pf
nd95
pron
holt
cir
Relative growth rate x 100 (g g^{-1}day^{-1})
5
4
3
2
1
0
7
6
5
4
3
2
1
0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
14
12
10
8
6
4
2
0
-2
0 5 10 15 20 25 30
5 10 15 20 25 30
5 10 15 20 25 30
Temperature (°C)
Temperature (°C)

Preface to Chapter 7

Chapter 7 is based on a manuscript submitted for publication to the journal *Seed Science and Technology* in 1997.

Entries that showed late spring growth, e.g. Cave-in-Rock and New Jersey 50, had higher base temperatures for germination than entries such as Dakota and Pathfinder (which were relatively earlier in spring growth). However, Cave-in-Rock and New Jersey 50 had higher growth rate constants and yields. If these entries are chosen for production, delayed or poor establishment in spring reduces economic viability. In this chapter, various pre-germination seed treatments were evaluated for enhancement of germination under cold temperatures.

Chapter 7

Effect of Preplant Seed Conditioning Treatment on the Germination of Switchgrass Seeds.

7.1. Abstract

Switchgrass (*Panicum virgatum* L.) is being developed and evaluated for summer forage and biomass production. Uneven germination and slow seedling growth in spring are some of the factors limiting widespread cultivation. In this study, efforts were made to reduce seed dormancy and to improve germination at suboptimal temperatures in switchgrass cvs. Cave-in-Rock (CIR), Dakota (DK) and New Jersey 50 (NJ). Seed from these cultivars was osmoconditioned with 0.2% potassium nitrate (KNO_3) alone, polyethylene glycol 8000 (PEG) solution with or without 0.2% KNO_3 or 1 mM gibberellic acid (GA_3); or matriconditioned with Micro-Cel E (MC) with either water, 0.2% KNO_3 or 1 mM GA_3. The seeds were conditioned at 8 or 16°C for 4 days and then germinated at 8, 16 or 24°C. Cultivar, conditioning treatment, and both conditioning and germination temperatures influenced seed germination and were often involved in interactions. For CIR seeds germinated at 8°C, conditioning with PEG at 8°C increased germination from 0 (control) to 22%. When germinated at 16°C, conditioning at 8°C was better than at 16°C. All conditioned treatments germinated earlier and the proportion of seeds that eventually germinated was higher than for the unconditioned control. At 24 °C, osmoconditioning with PEG decreased final germination (65 compared with 78% for control). For NJ, conditioning at 16°C with water or 1 mM GA_3 increased germination to 12 and 17% respectively (0 for the control) when seeds were germinated at 8°C. When germinated at 16°C treatments containing 1 mM GA_3 germinated earlier; PEG with 1 mM GA_3 had the highest final germination at 56% (37% for control). At 24°C, rate and final germination were similar for all MC mixtures and conditioning with PEG at 16°C resulted in the highest final germination of 70 % (40% for control). For DK, only seeds soaked in 1 mM GA_3 at 8°C increased final germination (47 relative to 33% for control) when germinated at

8°C, the other treatments having no effects or negative effects. At 16°C, final germination was inhibited most by treatments with 1 mM GA_3, 0.2% KNO_3 or simply wetting at 16°C with subsequent germination at the same temperature (51, 48 and 21% respectively versus 85% for control). MC and PEG mixtures neither increased nor decreased germination at 24°C. Overall, both osmoconditioning and matriconditioning improved earliness of germination in all cultivars, and total germination in CIR and NJ.

7.2. Introduction

Switchgrass is being developed and evaluated for both summer forage and as a biomass crop (Jung *et al.*, 1990; Tischler *et al.*, 1994; Sanderson *et al.*, 1996). However, uneven germination and slow seedling growth in spring results in both poor stand establishment and weed competition from cool season weeds. This has been attributed primarily to seed dormancy (Wolf *et al.*, 1989). As in many other warm season grasses switchgrass seed remains dormant for considerable periods of time following harvest (Zarnstoff *et al.*, 1994; Voigt and Tischler, 1997; Sanderson *et al.*, 1996) and this dormancy declines naturally with storage.

In warm season grasses, imbibitional chilling injury can also be a factor in poor stand establishment in spring (Khan, 1992). In addition, switchgrass seed is small and should therefore be planted at shallow depths, which predisposes the seed to drying along with the top soil. Successful establishment would therefore depend on rapid germination and root extension to tap moisture from deeper soil levels.

Stratification (moist-chilling at 4-10°C for various periods) is widely used to break dormancy (Khan, 1992; Sanderson *et al.*, 1996). Special equipment and long time requirements are disadvantages associated with stratification. Other procedures that have been developed include osmoconditioning and matriconditioning (Mueller, 1996; Khan *et al.*, 1995), and scarification with or without the prechilling (Zarnstoff *et al.*, 1994). Imbibitional chilling injury can be alleviated by using osmoconditioners (PEG, organic and/or inorganic acids or salts) or matriconditioners (Micro-Cel E or vermiculite)(Khan *et al.*, 1992). In addition to controlling hydration, these conditioners allow enhancement of physiological and biochemical events of germination.

Germination time was reduced in wildrye (*Psathyrostachys juncea* (Fisher) Nevski) and western wheatgrass (*Pascopyrum smithii* (Rydb.)) following osmoconditioning (Mueller, 1996) while seed matrix priming with or without wet-chilling improved germination and adventitious root development in switchgrass and emergence only in big bluestem (*Andropogon gerardii* Vitman)(Beckman *et al.*, 1993).

In a recent evaluation of warm season grasses (Madakadze *et al.*, 1996a), differences were noted in both stand establishment and persistence among switchgrass populations. Following preliminary germination tests, we hypothesised that poor stand establishment was due to seed dormancy and low germination at low spring temperatures. The objective of this study was to evaluate the ability of various seed conditioning treatments to improve germination in switchgrass.

7.3. Materials and Methods

7.3.1. Seed material

Switchgrass cultivars CIR, DK and NJ were chosen for this study based on their germination kinetics in preliminary tests. DK seeds were characterised by high levels of germination at 24°C (at least 80%) and reasonable germination under suboptimal temperatures, 16 and 79% at 8 and 12 °C respectively. NJ had relatively low seed gemination values at all temperatures tested, 0, 15 and 40 % at 8, 12 and 24°C respectively. CIR was intermediate between these two populations with germination percentages of 0, 54 and 80% at 8, 12 and 24°C respectively. All the seeds used in this study were produced the previous year at the Emile A. Lods Research Centre in experimental plots.

7.3.2. Seed conditioning

For purposes of this study, the following terms are defined after Khan (1992): 1) conditioning is the enhancement of physiological and biochemical events in seeds during controlled hydration and suspension of germination by low water potential of the imbibing medium, 2) matriconditioning is defined as conditioning in a moist solid, characterised by low matric potential and negligible osmotic potential, 3) osmoconditioning is conditioning in a liquid medium, characterised by low osmotic potential and negligible matric potential, 4) permeation with hormones involves soaking of seeds in hormone solutions, the response to permeation being elicited during subsequent hydration, and, 5) moist-chilling (or stratification) is the dormancy breaking of seed by hydration with water at 1-10 °C.

Seeds were conditioned by placing them in 9 cm petri plates on two layers of Whatman No. 2 filter paper. The filter paper was moistened with either

(a) 8 mL of 1 mM GA_3 (GA); 0.2%KNO_3 (nitrate) or distilled water, or

(b) 8 mL of -1.5 MPa polyethylene glycol 8000 (PEG) with or without GA or nitrate.

In a third set of treatments, the seed was mixed with Micro-Cel E (a synthetic, hydrous calcium silicate, Celite Corporation, Lompoc, California, USA) in a 1:0.3:1.5 seed:carrier:water mixture. Solutions of GA or nitrate replaced the water in some treatments. All treatments were supplemented with captan (N-tri-chloromethylthio-4-cyclohexane-1,2-dicarboximide). The treated seeds were conditioned at 8 or 16°C for 4 days under a 14 hour light (100 μmol m^{-2} s^{-1}) regime. At the end of the conditioning exercise, the seeds were washed in running water and dried by forced air for 2 hours at 24 °C.

7.3.3. Germination tests

Conditioned and nonconditioned seeds were placed in 9 cm petri plates (50 seeds per plate). Each plate was lined with two layers of Whatman No.2 filter paper and kept moist with distilled water. Three replicate petri plates for each conditioned and nonconditioned treatment, for each cultivar, were completely randomised in growth chambers (Conviron ModE15, Controlled Environment Ltd., Winnipeg, Manitoba, Canada) maintained at constant temperatures of 8, 16 and 24 °C. Light intensity was maintained at 100 μmol m^{-2} s^{-1} for 14 hours a day. For each cultivar, the overall arrangement was a 2 x 10 x 3 factorial design (conditioning temperature, conditioning mixture and germination temperature, respectively). The whole experiment was conducted twice.

Germinated seed was counted and removed initially three times a day and later once a day until there was no new germination for at least three consecutive days. Seeds were considered germinated when the radicle was at least 2 mm in length. Time required for germination of 50% of germinable seeds was computed as T_{50}.

The germination results were analysed by ANOVA using SAS procedures (SAS, 1995). The final germination percentages were arcsin transformed (Steel and Torrie, 1980) before analysis.

7.4. Results and Discussion

Interaction components were significant for all cultivars and the results will be presented for each cultivar, mainly by germination temperature.

7.4.1. Cave-in-Rock

Germination was generally low at 8°C with the highest value of 22% being recorded following osmoconditioning with PEG alone at 8°C (Table 7.1). A proportion of this increase in germination was due to moist-chilling. Even the highest value of 22% would still be low for good stand establishment. When germinated at 16°C, the effects of conditioning differed depending on both the conditioning mixture and the conditioning temperature. When water, GA or nitrate were used alone or in a matriconditioning mixture (Fig. 7.1 A and B) conditioning at 8°C resulted in higher final gemination percentages than at 16°C. Such enhanced improvements due to integrating moist-chilling and conditioning treatments have been reported by Khan and Karssen (1981). While moist-chilling breaks seed dormancy, conditioning reduces germination time and invigorates the seed (Khan, 1992). Seed treatments with nitrate or GA at 8°C resulted in faster germination and higher final germination values than wetting with water at the same temperature. However, moist-chilling (water alone at 8°C) resulted in equal or better germination kinetics to these treatments when the seed was treated at 16°C. For the matriconditioning mixtures, MC alone or with nitrate resulted in the best improvements in germination (Fig. 7.1B). MC-GA3 treatments resulted in smaller improvements than MC or GA alone. This might, as suggested by Madakadze *et al.* (1993), be due to either reduced uptake of GA in a matriconditioning mixture at 16°C and/or the pH of Micro-Cel E (pH 8.4). In PEG osmoconditioning mixtures, the highest final germination was recorded from seed conditioned with PEG alone at 16°C. This final germination was similar to those obtained following permeation with GA or osmoconditioning with nitrate alone at 8°C. Although germination occurred earlier in seed osmoconditioned with PEG at 8°C and PEG-nitrate at 16°C (Fig. 7.1C, Table 7.2), these treatments decreased final germination levels. Overall increases in final germination were not always accompanied by decreases in T_{50} (Table 7.2) and in the case of osmoconditioning with PEG at 8°C the lower T_{50} was accompanied by reduced final germination (Fig. 7.1C). For germination at 16°C, the best treatments were permeation with GA, matriconditioning with MC alone at 8°C or with nitrate at either 8 or 16 °C, and osmoconditioning with nitrate alone at 8°C or with PEG alone at 16°C.

No interaction occurred at 24 °C. Conditioning at a temperature of 8 °C generally improved germination (Fig. 7.2). Osmoconditioning with PEG alone decreased final germination. The fact that most of the conditioned seeds had higher total germination values than the control nonconditioned seeds at 24°C confirms that low stand establishment might be due to both dormancy and low germination at suboptimal temperatures.

7.4.2. New Jersey 50

On average, seed conditioning at 8°C did not improve cold temperature germination (Table 7.1). Wetting with water or permeation with GA at 16°C increased germination to 12 and 17% respectively. This would also be a low germination level for a good stand. For seeds germinated at 16°C, nitrate and water alone were effective in increasing total germination (Fig 7.3A). Although germination started earlier following GA permeation than in the control nonconditioned seeds, these two treatments had similar final germination percentages. In combination with MC or PEG, GA treatments germinated earlier and in the case of PEG-GA resulted in the highest final germination value (about 15 percentage units higher than control seeds, Fig. 7.3 B and C). These differences illustrate two points about conditioning. First, the importance of controlled imbibition and second, the fact that two physiological treatments can be synergistic in improving germination. Osmoconditioning with PEG plus nitrate at 16°C actually increased T_{50} compared with the control.

At 24 °C, there was an interaction between conditioning mixture and temperature during conditioning. All conditioning treatments resulted in earlier germination (started 2 days into the germination test), (Fig.7.4). However, final germination percentages (at day 12) following conditioning with GA and water alone at 16°C were similar to those of the control nonconditioned seeds (Fig. 7.4A). Rate and final germination were similar for all MC conditioning mixtures, 54-60% final germination (Fig. 7.4B). In PEG osmoconditioning mixtures, seeds conditioned with PEG alone or with nitrate (and not with GA) at 16°C had higher germination percentages than those from the respective treatments conditioned at 8°C. The highest final germination was recorded for seeds osmoconditioned with PEG at 16°C (70 compared with 40% for the control seeds). Together, the effects of osmoconditioning with PEG alone at 16°C for CIR and NJ suggest that this treatment can overcome switchgrass dormancy mechanisms and/or other physiological factors slowing germination.

7.4.3. Dakota

Germination percentages for DK were generally higher at all germination temperatures. Germination of the nonconconditioned seed was 33, 85 and 93% at 8, 16 and 24°C, respectively. The corresponding values were 0, 35, 40 and 0, 60 and 77% for NJ and CIR, respectively. For Dakota, except for seeds permeated with GA at 8°C, conditioning treatments resulted in either the same or lower final germination when germinated at 8°C (Fig. 7.5). For this germination temperature, responses from conditioning at 16°C were better than at 8°C.

When germinated at 16°C, seed conditioning resulted in equal or lower seed germination than nonconditioning. Seed treatments with GA, nitrate or water (alone) at 16°C had the most detrimental effects on final germination when germinated at 16°C (GA and water when germinated at 24°C) (Fig. 7.5-A2). The decreases in final germination were lower in conditioning mixtures with MC and PEG than without them. However, GA, nitrate and water treatments (all alone) following conditioning at 8°C performed better than the respective treatments conditioned at 16°C. This negates increased imbibition as a possible explanation for the lower performance of the MC and PEG treatments. Responses following matriconditioning were slightly better than after osmoconditioning with PEG. Taken together, this indicates that adverse changes occur in DK seeds during conditioning at 16°C and are expressed during subsequent germination at 16°C. It is conceivable that the promotive effects of GA, nitrate or water alone may be blocked by inhibitory factors in the seed following conditioning at 16°C. These inhibitors may have properties permitting them to be selectively exchanged with the Micro-Cel E, which adsorbs various types of organic and inorganic chemicals. Matriconditioning or PEG osmoconditioning mixtures, while not necessarily increasing, did not reduce final germination at 24°C (Fig. 7.5). Despite this, background germination was, on average, initiated 1 and 2 days earlier in conditioned seeds germinated at 16 and 24 °C, respectively (data not presented).

In general, these results are consistent with previous studies with grasses and warm season plants (Beckman *et al.*, 1993; Hardegree, 1994; Khan *et al.*, 1995; Mueller, 1996) that have shown increased germination rates and totals for conditioned seeds. Faster germination would improve the ability of seedlings to escape insects and pathogens. Some germination at 8°C for CIR and NJ following seed conditioning supports the suggestion that conditioning does not lower base temperature for germination (Dahal *et al.*, 1990). Instead, the thermal time requirement is reduced, that is, conditioning increases rate at which seeds progress towards germination. A proportion of the benefits from matric and osmotic conditioning are due to alleviation of imbibitional chilling injury by reducing electrolyte leakage (Weges and Karssen, 1990; Khan *et al.*, 1995). Also consistent with our results, Beckman *et al.* (1993) and Zarnstorff *et al.* (1994) reported cultivar variation in responses to pregermination seed treatments. Despite potential variation due to environmental differences during seed production this cultivar variation suggests an underlying genetic difference in both seed dormancy and germination kinetics. This might be similar to the genetic variations in seed dormancy that have been reported in another member of the Panicum species, kleingrass *(Panicum coloratum* L.)(Tischler and Young, 1987).

7.5. Conclusions

Matriconditioning and osmoconditioning improved germination time and total germination for CIR and NJ. These improvements were achieved by both breaking dormancy and increasing low temperature germination. Moist-chilling could achieve a substantial proportion of this improvement. Improvements in T_{50} and final germination levels following conditioning were not necessarily linked. Different cultivars responded differently to various conditioning treatments. Our results provide an indication of the responses of a number of cultivars . However, this work was conducted under constant temperature, laboratory conditions and must be confirmed under field conditions.

Table 7.1: The effect of pregermination seed condition on the final germination of CIR and NJ50 seeds germinated at 8°C

Treatment	Cave-in-Rock		New Jersey 50	
Conditioning temperature	8°C	16°C	8°C	16°C
Control	0d[†]	0c	0.00	0.00c
GA_3	11.20ab	15.15a	3.33	16.67a
KNO_3	8.30abc	5.89ab	2.00	0.67c
Water	8.73abc	3.83abc	1.33	12.00b
MC-GA_3	4.06bcd	0.68bc	1.33	1.33c
MC-KNO_3	1.30cd	0.00c	0.00	0.67c
MC	0.45d	3.83abc	0.67	0.67c
PEG-GA_3	0.45d	1.68bc	1.33	2.00c
PEG-KNO_3	0.68cd	5.55ab	0.00	2.67c
PEG	21.65a	0.91bc	1.33	1.33c
LSD	4.70	4.40	2.40	2.10

[†] means within a column followed by a different letter are significantly different ($p < 0.05$) using a protected LSD test

Table 7.2: The effect of seed conditioning on the time (days) taken to 50% of final germination in switchgrass

Cultivar	Cave-in-Rock		Dakota		New Jersey 50	
Conditioning temperature	8 °C	16 °C	8 °C	16 °C	8 °C	16 °C
Treatment						
Control	9.1a[†]	9.1a	6.2	6.2	10.7	7.2cd
Water	7.0abc	9.2a	5.7	8.4	10.7	9.4abc
GA_3	6.7bcd	5.4c	7.9	9.3	9.5	8.2cd
KNO_3	5.9cd	9.9a	7.0	5.9	9.5	10.8ab
MC	7.1abc	7.7abc	6.6	6.2	7.7	8.9bcd
MC-GA_3	8.8ab	8.6ab	7.5	7.2	11.5	6.8d
MC-KNO_3	7.2abc	7.83abc	5.9	8.1	11.5	11.3a
PEG	4.5d	6.4bc	6.0	9.4	8.0	9.5abc
PEG-GA_3	9.2a	8.3ab	8.2	7.7	9.7	7.2cd
PEG-KNO_3	7.8abc	7.8abc	7.2	7.3	8.0	9.5abc
LSD(0.05)	2.32	2.43	2.13	2.10	3.69	2.38

[†] means within a column followed by different letters are significantly different ($p<0.05$) using a protected LSD test

Fig. 7.1: The effect of pregermination seed conditioning at 8° or 16°C on time and final germination of Cave-in-Rock seeds germinated at 16°C. Bars extending beyond the symbols denote standard error (SE).

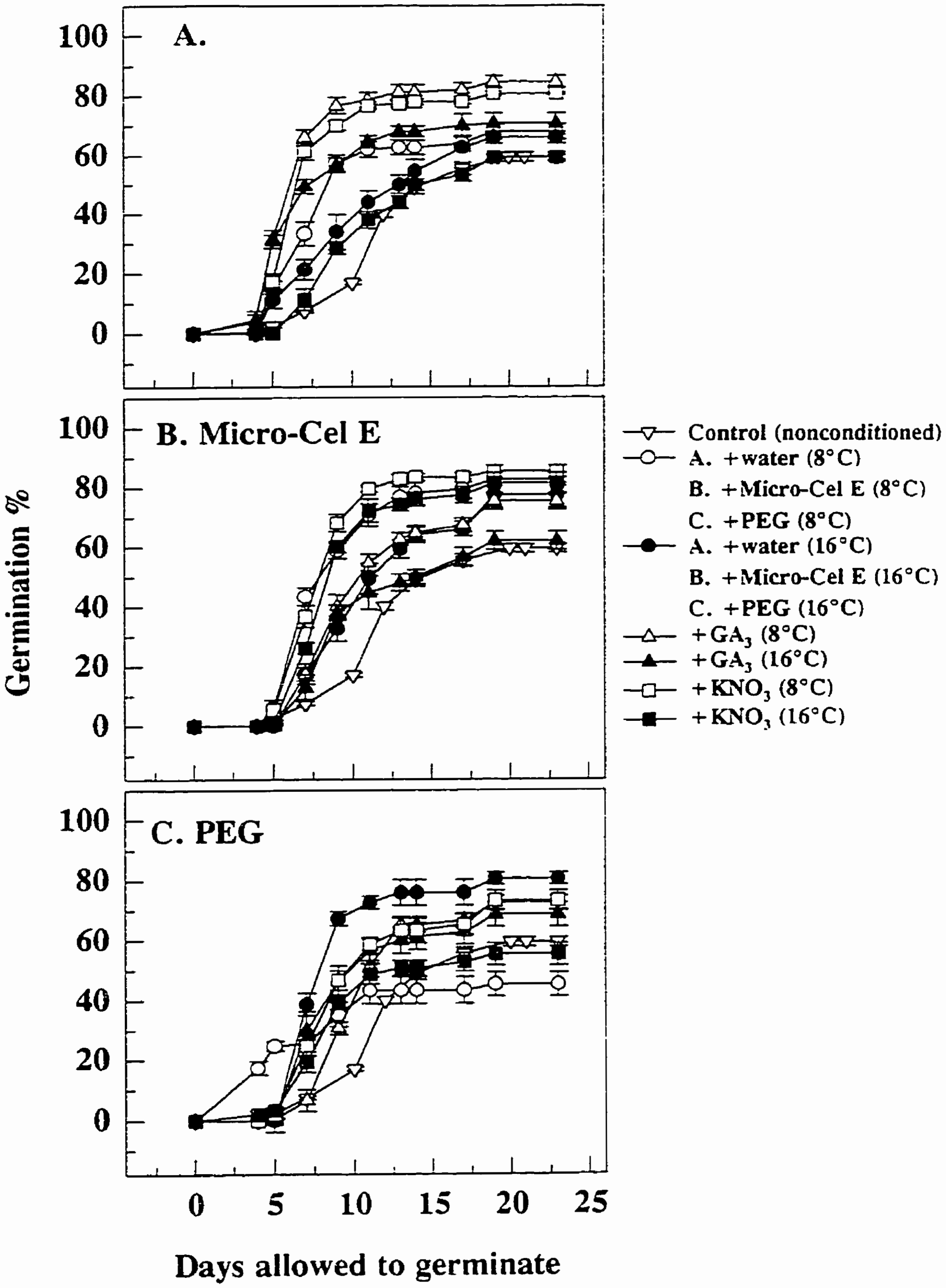

A.
B. Micro-Cel E
C. PEG
Germination %
100
80
60
40
20
0
0
5
10
15
20
25
Days allowed to germinate
Control (nonconditioned)
A. +water (8°C)
B. +Micro-Cel E (8°C)
C. +PEG (8°C)
A. +water (16°C)
B. +Micro-Cel E (16°C)
C. +PEG (16°C)
+GA$_3$ (8°C)
+GA$_3$ (16°C)
+KNO$_3$ (8°C)
+KNO$_3$ (16°C)

Fig. 7.2: Final germination percentage of preconditioned seeds of Cave-in-Rock germinated at 24°C. T-bars extending beyond the bar graphs denote SE.

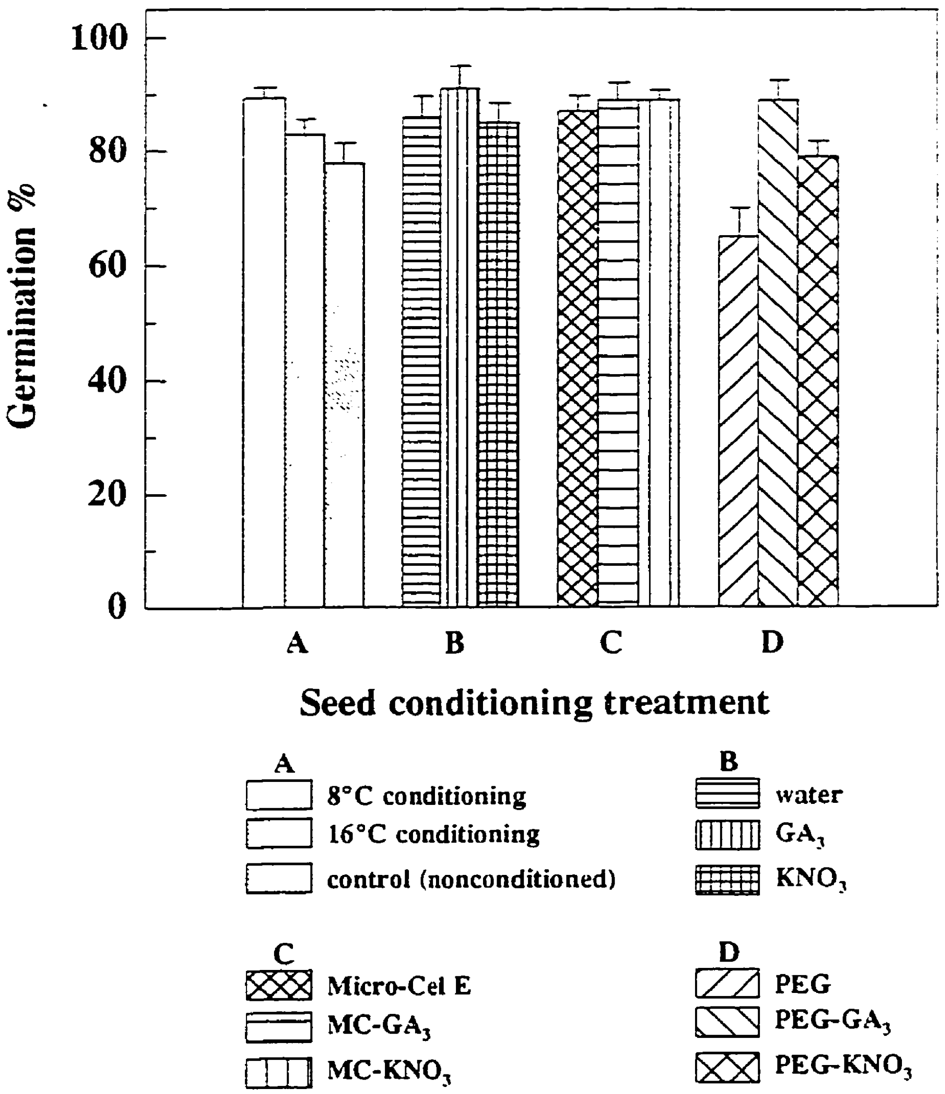

Germination %
100
80
60
40
20
0
A
B
C
D
Seed conditioning treatment
A
8°C conditioning
16°C conditioning
control (nonconditioned)
B
water
GA$_3$
KNO$_3$
C
Micro-Cel E
MC-GA$_3$
MC-KNO$_3$
D
PEG
PEG-GA$_3$
PEG-KNO$_3$

Fig. 7.3: Enhancements in germination by seed conditioning of New Jersey 50 seeds germinated at 16°C. Seeds were osmoconditioned with polyethylene glycol or matriconditioned with Micro-Cel E with or without 1 mM GA_3 or 0.2% KNO_3. Bars extending beyond the symbols denote SE.

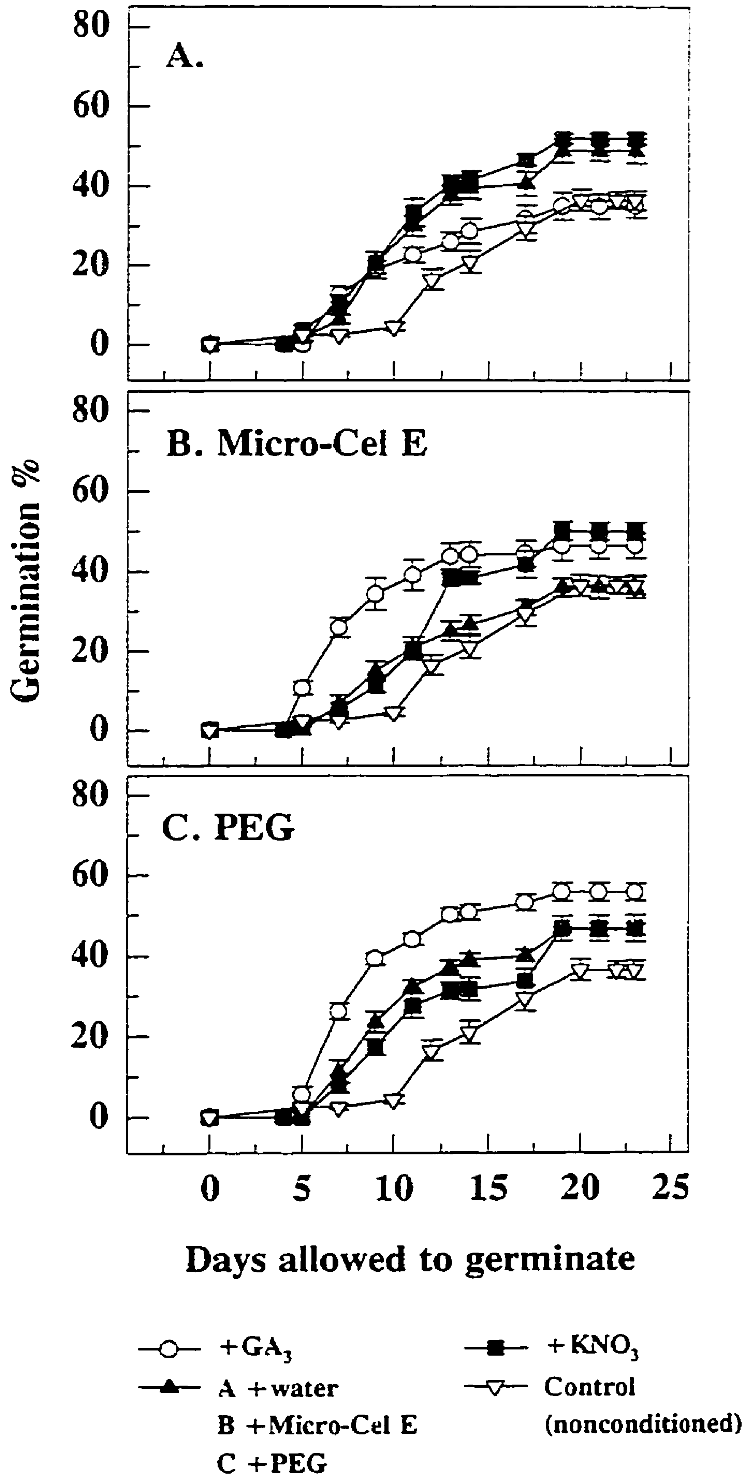

A.
B. Micro-Cel E
C. PEG
Germination %
0
20
40
60
80
0
5
10
15
20
25
Days allowed to germinate
+GA$_3$
A +water
B +Micro-Cel E
C +PEG
+KNO$_3$
Control
(nonconditioned)

Fig. 7.4: Interaction between conditioning mixture and conditioning temperature effects on the germination of New Jersey 50 seeds germinated at 24°C. Bars extending beyond the symbols denote SE.

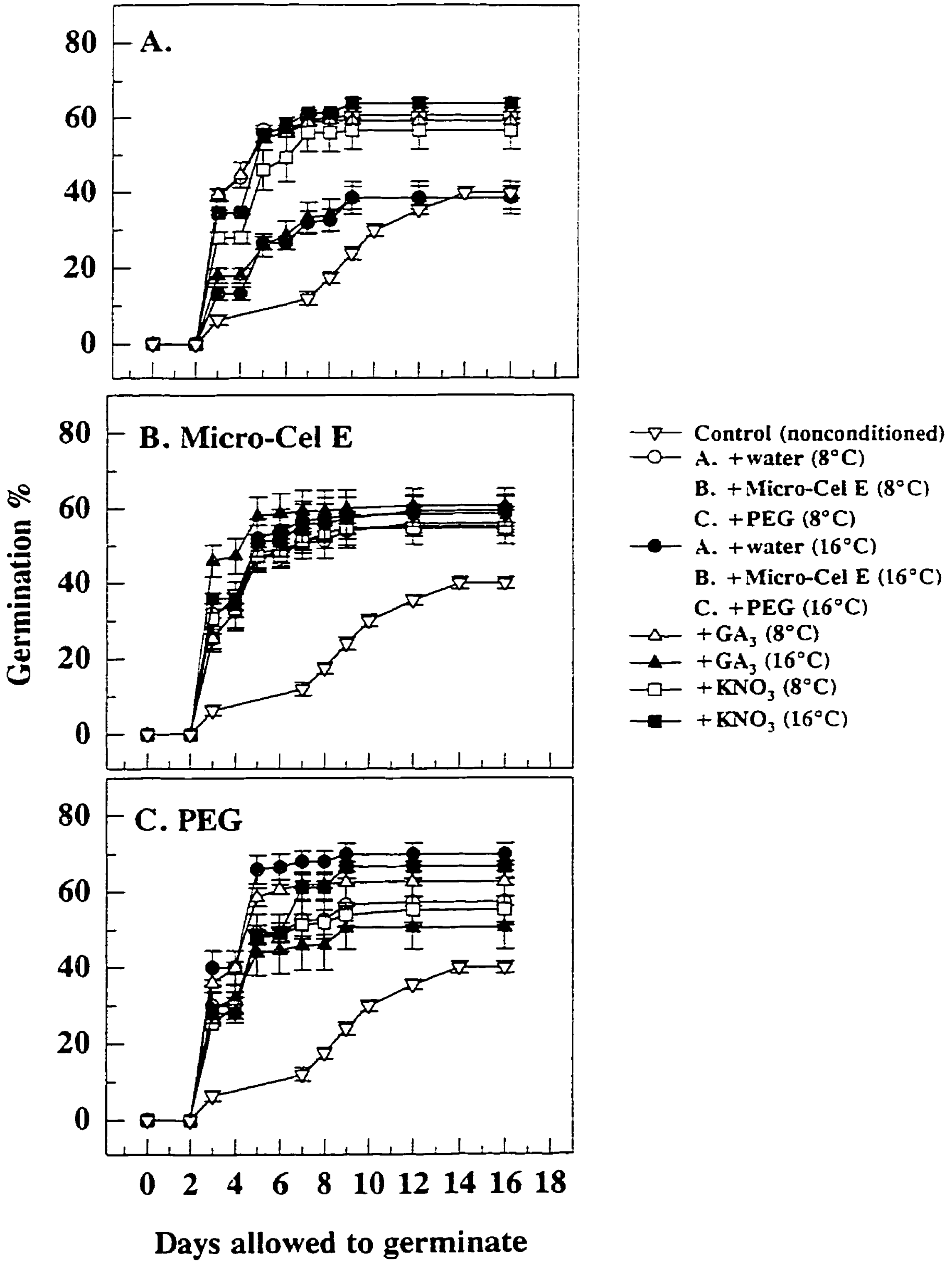
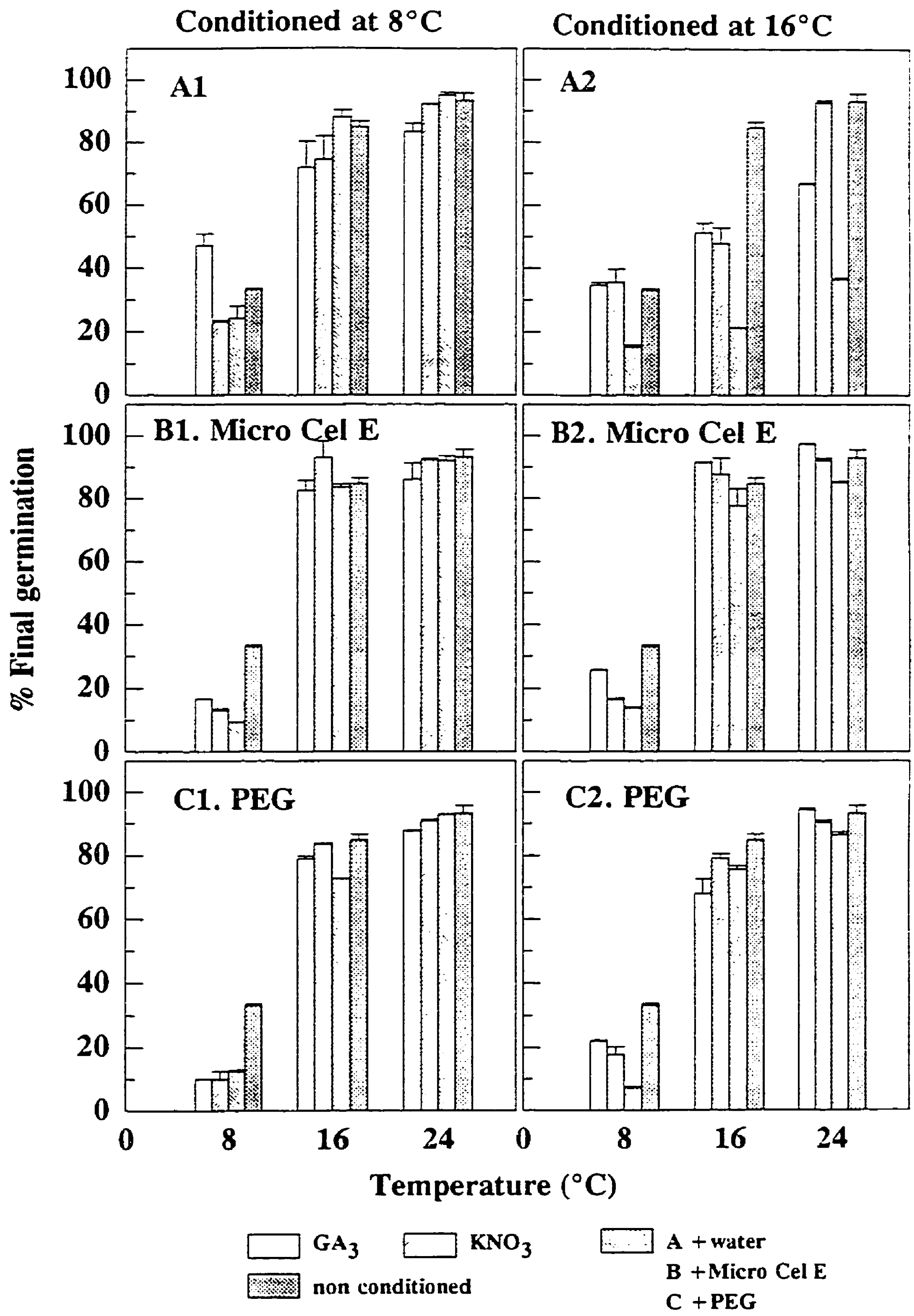
A.
B. Micro-Cel E
C. PEG
Germination %
0
20
40
60
80
0 2 4 6 8 10 12 14 16 18
Days allowed to germinate
Control (nonconditioned)
A. +water (8°C)
B. +Micro-Cel E (8°C)
C. +PEG (8°C)
A. +water (16°C)
B. +Micro-Cel E (16°C)
C. +PEG (16°C)
+GA3 (8°C)
+GA3 (16°C)
+KNO3 (8°C)
+KNO3 (16°C)

Fig. 7.5: The effects of conditioning mixture and temperature during conditioning, and germination temperature on the total germination of Dakota seeds. T-bars extending beyond the bar graphs denote SE.


Conditioned at 8°C
Conditioned at 16°C
A1
A2
B1. Micro Cel E
B2. Micro Cel E
C1. PEG
C2. PEG
% Final germination
0
20
40
60
80
100
0
8
16
24
Temperature (°C)
GA3
KNO3
A +water
B +Micro Cel E
C +PEG
non conditioned

Preface to Chapter 8

Chapter 8 is based on a manuscript submitted for publication to the journal *Biomass and Bioenergy* in 1997.

The modelling of canopy growth started in Chapters 4 and 5 is continued in Chapter 8. More detailed time changes in biomass accumulation, lignocellulose and energy concentrations were monitored. Biomass changes and light interception were used to derive radiation use efficiencies or rates of solar energy capture. These parameters all build the case for use of switchgrass as a biofuel feedstock, and can be used in growth modelling.

Chapter 8

Dry Matter Accumulation, Radiation-Use Efficiency, and Chemical Composition of Switchgrass (*Panicum virgatum* L.) grown in a Short Season Area

8.1. Abstract

Switchgrass (*Panicum virgatum* L.) has been identified as a potential biomass crop in North America. A two-year study was conducted to characterise the growth, estimate radiation-use efficiency (RUE), and evaluate changes in biomass composition of switchgrass at Montréal, Québec. Three cultivars, Cave-in-Rock (CIR), Pathfinder (PF) and Sunburst (SB) were grown in solid stands in a randomised complete block design. Leaf area development, light interception, canopy height, dry matter (DM) accumulation and chemical composition were monitored bi-weekly throughout the growing season. Mean seasonal maximum leaf area indices (LAI) were 6.1, 5.3 and 5.1 for CIR, PF and SB, respectively. By early July of each season, the canopies were intercepting about 90% of the incoming light. Maximum canopy heights were 192.5 cm for CIR, 169.9 for PF and 177.8 for SB. The rates of DM accumulation during the near linear phases of growth were 191.3, 175.5 and 175.4 kg DM ha^{-1} day^{-1} for CIR, PF and SB, respectively. The respective end of season DM yields were 12.2, 11.5 and 10.6 Mg ha^{-1}. Energy contents of the switchgrass averaged 17.4 MJ g^{-1} DM and did not vary among cultivars or during the season. RUE computed, using total incoming solar radiation, for the near linear growth phases averaged 1.07 g MJ^{-1} for CIR, 0.90 for PF and 0.89 for SB. Nitrogen concentration of DM decreased curvilinearly from 25 g kg^{-1} at the beginning of the season to 5 g kg^{-1} DM at season end. Both acid detergent fibre (ADF) and neutral detergent fibre (NDF) contents increased to a maximum in early season after which no changes were detected. The average maximum values of ADF and NDF were 647.6 and 849.0 g kg^{-1} DM for CIR, respectively; 669.1 and 865.2 for PF; 661.8 and 860.9 for SB. Changes in LAI, canopy height, chemical composition and dry matter accumulation could all be described by predictive regression equations. These results indicate the potential of switchgrass as a biomass crop in a short season environment.

8.2. Introduction

Recent years have seen increased interest in warm season grasses as renewable sources of biomass for energy and industrial raw materials. In North America, most of the research programs that have resulted from this interest are located in the southern USA (Woodard and Prine, 1993; Sanderson *et al.*, 1996). Adoption in more northern locations like Canada is limited by the cool temperatures in spring and early summer, and again in fall, resulting in short growing seasons. For example, in eastern Canada maize (*Zea mays* L.) can only be sown beginning in late May (MAPAQ, 1984).

Agronomically, an ideal warm season grass species for these short season areas should have rapid initial leaf area development for high light interception, and therefore high plant growth and yield (Coombs, 1984; Muchow *et al.*, 1990). From a herbaceous feedstock standpoint, lignocellulose, nitrogen and ash are the most important DM constituents. High levels of lignocellulose are desirable for chemical and biofuel production (Trebbi, 1993), and high levels of nitrogen and/or ash reduce chemical output in thermochemical conversions (Agblevor *et al.*, 1992).

In an evaluation of several warm season grass species, switchgrass was identified as having biomass-producing potential in eastern Canada (Madakadze *et al.*, 1996a). This study was conducted in an effort to generate detailed information on the performance of switchgrass in the same environment. Specific objectives were to a) characterise the growth performance of switchgrass, b) estimate the energy yield of switchgrass and measure the efficiency with which solar energy is recovered and stored in dry matter, and c) determine the dry matter composition of switchgrass at different times of the season.

8.3. Materials and Methods

8.3.1. Site and experimental plots

This study was conducted during 1995 and 1996 using three commercial cultivars of switchgrass: Cave-in-Rock, Pathfinder and Sunburst. The plots were located at the Emile A. Lods Research Centre, McGill University, Montréal, Canada (45° 28'N 73° 45'W). The site was on a free draining sandy clay loam (St. Bernard, Typic Hapludalf). The grass plots used were two years old and arranged in a randomised complete block design, with three blocks. The positions of the three cultivars in each block were randomly assigned at establishment. For this study, a total of 600 m^2 per block (200 m^2 for each cultivar) were used. In mid-May of each year, prior to initiation of new growth, residue from the previous season was mowed at a 10-cm stubble height and removed. Each year, the stands also received 50 kg N ha^{-1} as ammonium nitrate, all applied in spring soon after initiation of growth.

8.3.2. Measurements and sampling

Beginning in mid-June, canopy height was measured every two weeks at ten different positions using a metre ruler. Canopy biomass was harvested every two weeks beginning when the canopy height was at least 30 cm. Four quadrats measuring 1 m^2 were harvested at a 10-cm cutting height on pre-allocated positions over the two seasons. Sub-samples from these harvests were dried to constant weight at 70 °C for DM determination and further analysis. At harvests in early and mid July and August, 40 representative tillers were separated into leaf and stem (stem + leaf sheath). These components were then dried at 70 °C and used to compute leaf-to-stem ratios. Tiller numbers were also counted during the first and third weeks of July, and first week of August, each time within four 0.5 m^2 quadrats.

Leaf area and light interception were also measured at the time of harvest. Leaf area index (LAI) and mean tilt angle (MTA) were measured using a Li-COR Plant Canopy Analyser 2000 (Li-COR Inc., Lincoln, Nebraska, USA). As the season advanced, the LAI was measured in 25-cm strata. The final LAI was an average of four independent readings made on the four harvest quadrats. Interception of photosynthetically active radiation (PAR, 400-700 nm) was measured using line quantum sensors (LI-191SA) connected to a LI-1000 Data Logger (both from Li-COR Inc., Lincoln, Nebraska, USA). These PAR measurements were also made on the four harvest quadrats around solar noon (between 1130 and 1430 hours) under clear to slightly hazy sky conditions. Choice of time of measurements followed the demonstration that radiation measured near noon can be representative of integrated daily radiation (Tollenaar and Bruulsema, 1988). Where possible, PAR measurements were also taken at 25-cm strata.

Daily total solar radiation (TSR), temperature, and rainfall totals were collected with an on-station automatic weather station linked to Environment Canada's network of such stations.

8.3.3. Chemical analyses

Subsamples taken from harvested material were analysed for nitrogen (N), acid detergent fibre (ADF) and neutral detergent fibre (NDF). Nitrogen was analysed as Kjeldahl N using the Kjeltec System 1002 Distilling Unit (Tecator, Hoganas, Sweden). The F-200 Fibre Unit with F-56 filter bags (Ankom Tech. Corp., Fairport, New York, USA) was used to analyse for ADF and NDF on a 100°C oven dry matter basis. The energy contents of the grasses at different times of the season were measured using a PARR Adiabatic Calorimeter (PARR Instrument Co., Moline, Illinois, USA). Energy determinations were carried out on samples dried to a constant weight at 70°C.

8.3.4. Statistical analysis

For most of the response variables, repeated measures of analysis (Crowder and Hand, 1990) was performed to test the year, cultivar and sampling date effects and any interactions. Regression analysis was used to fit relationships between DM accumulation and time; DM yield and canopy height; LAI and DM yield; light interception and LAI; N, ADF and NDF and time. The relationships were fitted on means of the three blocks for each cultivar, either for each year or when combined for both years. Where response variables were similar for all three cultivars, relationships were also developed from data pooled over cultivars.

Linear regression models were also used to derive some parameters. Canopy extinction coefficients (*k*) were determined as slopes of linear regression equations (no intercept) between cumulative LAI and the natural log of transmitted PAR. Crop growth rates were determined as the slopes of the near linear phases of DM accumulation over time. Also based on the near linear phase of DM accumulation, RUE was determined in three different ways:

a) weight (g) of DM produced per unit (MJ) of incoming TSR,
b) total energy of DM as fraction of TSR (solar energy recovery)
c) total energy of DM as a fraction of incoming PAR. It was assumed that 0.45 of TSR was total incoming PAR (Meek *et al.*, 1984, Rosenthal *et al.*, 1993).

The derived parameters were determined from regression of data from each year x cultivar x block combination unit. These derived parameters were compared using Analysis of Variance and a protected Least Significance Difference (LSD) test (Steel and Torrie, 1980). All statistical procedures were conducted using Statistical Analysis Systems (SAS) procedures (SAS, 1995).

8.4. Results and Discussion

8.4.1. Environment

Weekly maximum and minimum temperatures, rainfall totals and fortnightly totals of radiation receipt from April through October in 1995 and 1996 are presented in Fig. 8.1. The rate of temperature increase in spring and maximums were generally higher in 1995 than 1996. Increases in temperature lagged behind increases in total radiation receipt. The year 1995 was also characterised by a very dry period in the month of June.

8.4.2. Dry matter accumulation

The year x cultivar x date of harvest interactions were significant at the 0.05 level of probability. Trends in DM accumulation of CIR, PF and SB are presented by year in Fig. 8.2. The slowed growth due to the June 1995 drought is apparent between days 60 and 90 after May 1st. In 1996, the increases in DM were relatively smoother than in 1995. There were differences in the length of the near-linear phases in DM accumulation and the eventual decline in DM as the season advanced. Timing of the decline in DM accumulation was earliest with SB followed by PF and lastly CIR. This was also the order the cultivars matured in this environment. The average end of season yields were 12.2, 11.5 and 10.6 Mg ha^{-1} for CIR, PF and SB, respectively.

The increases in dry matter with time were accompanied by increases in tiller densities, (Fig. 8.3). Seasonal maximum tiller numbers were 873, 1009 and 871 tillers

m^{-2} for CIR, PF and SB respectively. The generally high tiller densities for PF at each sampling time did not translate into highest yields because PF tillers were narrower and their leaves smaller than were those of either CIR or SB (data not presented). Tiller numbers reported by Redfearn *et al.* (1997) are higher for PF (1200-1500 m^{-2}) and comparable for CIR (800-1000 m^{-2}) to those in this study. The average end of year yields are comparable to the four-year averages of several switchgrass cultivars (9.2-12.3 Mg ha^{-1}) reported by Jung *et al.* (1990) in the northeastern USA. This range was for treatments receiving 75 kg ha^{-1} N. The yield for Pathfinder (the only cultivar common to both their study and this one) averaged 9.1 Mg ha^{-1}. Sanderson et al. (1996) also reported switchgrass yields ranging from 5.4 to 26 Mg ha^{-1} in the southern USA, PF and CIR yielding 9.8 and 5.4-9.5 Mg ha^{-1}, respectively. Our yields are generally in the upper end of the reported ranges. It is not clear why CIR and PF yielded well in a more temperature limiting environment.

Using repeated-measures analysis the changes in DM over the season followed second degree polynomials. The fitted relationships for each year x cultivar combination are presented in Table 8.1. The near linear phases of DM accumulation lasted 40 to 50 days. The statistical analysis and means of the crop growth rates are presented in Table 8.2. The growth rates were higher in 1996 than 1995, partly because of initial slow growth due to the June 1995 drought. However, cultivar means were not different. Stout and Jung (1995) reported switchgrass growth rates over 45 days varying from 157 to 211 kg ha^{-1} day^{-1} depending on fertiliser, soil type and environment. Our results fall within this range. Woodard and Prine (1993) reported high growth rates, of between 213 and 256 kg ha^{-1} day^{-1}, for warm season grass species of the genera *Pennisetum* and *Saccharum* during linear growth phases of 140-196 days under subtropical conditions (Florida, USA).

8.4.3. Canopy height

In both years, canopy height increased throughout the early and mid season (Fig. 4). In 1995, increases in height were very slow during the June drought. Rate of recovery was different among the cultivars with SB taking a longer period to resume height growth.

Clear separation in canopy height only occurred during the mid to late season. Maximal seasonal heights were 188 and 197 cm for CIR in 1995 and 1996, respectively; 175 and 164.7 for PF; and 175 and 181 for SB. For all cultivars, third order polynomials fitted the 1996 changes in height as a function of time. Similar analysis did not result in acceptable equations for the height changes in 1995. Heights ranging from 89-120 cm were measured by Jung *et al.* (1990) at head emergence (possibly before attaining maximum canopy height) and are lower than the maximum heights we are reporting.

In general, dry matter accumulation was linearly related to canopy height (Fig. 8.5). In 1995, the coefficients of determination of the fitted relationships were lower than in 1996 (Table 8.1) due to reduced growth during the drought. Drought stress affected both DM accumulation and height increases (Fig. 8.2 and 8.4). While the fitted line in 1995 (Fig. 8.5) might suggest that DM accumulated without corresponding height increases, the realistic interpretation is that both growth variables experienced a 'quiescent' phase, due to drought stress, after which growth resumed.

8.4.4. Leaf area index

There was a significant ($p<0.05$) year x cultivar x sampling date interaction for LAI. LAI development was faster in the spring of 1995 than 1996 (Fig. 8.6). This was probably due to the warmer temperatures in spring of 1995. CIR had the highest LAI in both years (5.9 and 6.3 in 1995 and 1996, respectively). The season maxima for PF and SB were 5.1, 5.5 and 5.1 and 5 for 1995 and 1996, respectively. After attainment of maximum LAI, there were cultivar differences in its decline. Except for CIR in 1995, which fitted a quadratic relationship, all LAI fitted third order polynomials over time (Table 8.1).

PAR interception values were above 90 % by the first week of July in both years for all cultivars. These values remained above 90 % until near the end of the season. Maximum interception values (Table 8.3) were obtained at different times for the three cultivars. The criterion of 95 % light interception at noon for critical LAI, suggested by Brougham (1958), could only be applied to CIR; at maximum LAI, CIR intercepted 95 % of incoming PAR. Averaged over the two seasons the relationship between light interception and LAI (Fig. 8.7A) was quadratic for CIR and linear for PF and SB (equations presented in Table 8.1). This suggests greater scope for improvements in PF and SB than in CIR. However, the model fitting the relationship between LAI and DM yield was linear for CIR (Fig. 8.7B) and quadratic for PF and SB. Using the definition for optimum LAI given by Davis (1971)(LAI at which rate of DM accumulation is maximum but declines with higher LAI), the optimal LAI values are 4.7 and 4.5 for PF and SB respectively. Taken together, data presented in Fig. 8.7A and B seem contradictory. Beyond an LAI value of 4, light interception did not increase substantially for CIR, yet at an LAI of close to 6, DM yield was still increasing linearly. Reverse trends were noted for PF and SB. Average mean tilt angles were not different among cultivars and the minor differences in extinction coefficients (Table 8.3) are not sufficient to explain this disparity. Leaf area distribution might have played a role in this discrepancy. When stratified by height CIR had higher proportions of leaf area at the top of the canopy (Fig. 8.8) compared with both PF and SB. It is argued that maximum rates of photosynthesis are usually found in the top part of the canopy (Woodward, 1971), possibly making it an advantage to have high leaf area proportions in the top portion of the canopy. This data might also be a reflection of biochemical differences in terms of photosynthetic rates, and light intensities at which the photosynthetic compensation point occurs.

8.4.5. Radiation-use efficiency

Radiation-use efficiency (RUE) means computed for the near linear phases of DM accumulation are also presented in Table 8.2. The RUE was computed both as the dry matter-solar energy quotient and as the energy content of biomass per unit area divided by total solar energy input during crop growth. While the year and cultivar effects were significant ($p<0.05$), the interaction component was not. RUE was higher in 1996 than 1995 and the cultivar ranking was CIR > PF = SB. When the RUEs were computed using PAR as the denominator (instead of TSR), the absolute values were, on average, 100 to 120 % higher. The RUE values of 1.11 - 1.25 g DM MJ^{-1}

based on TSR (2.54 - 2.9 based on PAR) for *Pennisetum* and *Saccharum* spp. (Woodard *et al.*, 1993) are higher than those we are reporting. Solar energy recovery of these species ranged from 1.7 to 2.4%, switchgrass values in our study fit in the lower end of this range. Despite species differences, subtropical conditions are generally more favourable to warm season grasses. Kiniry *et al.* (1989) reported RUE values based on PAR ranging from 2.1-4.5 g MJ^{-1} for maize and 2.1-3.8 for sorghum. These values are closer to the switchgrass values of our study.

8.4.6. Chemical composition

The trends in chemical composition with time were similar for NDF, ADF and N in all three cultivars (Fig. 8.9). While there were no differences among the cultivars for ADF and N, CIR had lower NDF levels for much of the growing season. In general, concentrations of ADF and NDF increased linearly to a maximum 80 and 90 days after May 1st, respectively. The average maximum values were for, CIR 647.6 and 849.0 g kg^{-1} DM ADF and NDF, respectively; for PF 669.1 and 865.2; and for SB 661.8 and 860.9. Beyond these maxima, ADF and NDF concentrations remained constant. This shift in phases of fibre deposition occurs during internode elongation (Sanderson and Wolf, 1995a). The trends for NDF are similar to those reported from the study of Sanderson and Wolf (1995b) at Stephenville, Texas. They reported maximum NDF values of 744-758 and 660 g kg^{-1} DM for Alamo switchgrass and CIR, respectively. However, at their other site, Blacksburg, Virginia, both ADF and NDF continued to increase, albeit slowly, after the initial period of rapid increase. The changes in ADF and NDF over time fitted linear plateau analysis (Draper and Smith, 1981) using intersecting straight lines, one before and the other after attainment of the maxima. However, linear regressions on the natural log transformed data (log X)(Steel and Torrie, 1980) were preferred because they offered singular predictive equations with good fits (Table 8.4).

Nitrogen concentrations decreased curvilinearly from 25 to 5 g kg^{-1} of DM. Sanderson and Wolf (1995b) found that N content decreased curvilinearly from 25 to 6-2 g kg^{-1} DM depending on the site. Jung *et al.* (1990) reported a range of 8-10.5 g N

kg^{-1} DM at head emergence for switchgrass cultivars receiving 0 or 75 kg N ha^{-1}. This is comparable to the N contents in this study at the same stage of development, about day 98 for CIR, 100 for PF and 90 for SB (Fig. 8.9). Linear models were fitted to semi-natural log transformed (log Y) data. These changes in chemical constituents were related to changes in biomass components. For all three cultivars the proportion of leaves relative to stems decreased with time (Fig. 8.10). As more stem material constituted biomass the fibre contents increased and N decreased. This was closely related to stem elongation in late vegetative and reproductive phases of plant growth. Unlike forage production, in herbaceous biomass-feedstock production high lignocellulose and low N contents are desired (Sanderson *et al.*, 1996). Although high levels of lignocellulose were realised at the end of the season, it might be necessary to pretreat the biomass to further reduce N contents. For example, the biomass can be left in the field over winter to leach N and other soluble constituents.

8.4.7. Energy yield

Energy content per unit weight was relatively constant for all the cultivars (Fig. 8.11). The seasonal average energy contents were 17.7, 17.4 and 17.4 kJ g^{-1} DM for CIR, PF and SB, respectively. These energy values are within the range 17.1-18.2 kJ g^{-1} DM reported for the bunchgrass species studied by Woodard *et al.* (1993). The energy contents in the present study are on the lower end of the range 17.8-19.3 reported for several tropical grasses by Butterworth (1964).

Total energy yield per hectare at the end of the season was calculated by multiplying end of season yield and the energy content per unit weight at that time, Table 8.5. Crude oil equivalent yield was then calculated by dividing total energy yield by the energy content of a barrel of oil (6090 MJ for a 158.8-L barrel, Woodard and Prine, 1993). The equivalent of between 30 and 36 barrels of crude oil per ha were realised from the switchgrass stands. Because energy content per unit weight of plant DM does not seem to vary widely, yield per unit area is likely to be the largest determinant of total energy yield. Woodard and Prine (1993) reported crude oil equivalents of 124-156 barrels ha^{-1} in *Pennisetum* and *Saccharum* spp. These grasses yielded between 37 and 53 Mg ha^{-1} at the end of the season, 3 to 4 times higher than switchgrass yields in the present study.

8.5. Conclusions

Seasonal dry matter yields of the switchgrass cultivars CIR, PF and SB averaged 12.2, 11.5 and 11.0 Mg ha^{-1}, respectively. The respective DM accumulation rates in the near linear phases of growth were 191.3, 175.5 and 175.4 kg ha^{-1} day^{-1}. Seasonal DM accumulation could be described by quadratic equations. Radiation-use efficiency values ranged from 0.89 to 1.07 g MJ^{-1} of total solar radiation. The energy content of the DM produced averaged 17.5 kJ g^{-1} and did not vary with time during the season. The crude oil equivalent of the end of season yields ranged from 30 to 36 barrels ha^{-1}. These results indicate the potential of switchgrass as a biomass crop even in short growing season areas.

Table 8.1: Regression equations for various parameters of switchgrass cultivars grown in a short season area. Data were pooled over 1995 and 1996 seasons where no year is indicated.

Cultivar	Year	n	Equation	rMSE[†]	r^2[‡]
Dry matter yield (Y, Mg ha^{-1}) vs. time (X, days)					
Cave-in-Rock	1995	8	$Y = -10.58 + 0.35X - 1.29E{-}3X^2$[¶]	0.82	0.97
	1996	8	$Y = -21.22 + 0.55X - 2.16E{-}3X^2$	0.89	0.97
Pathfinder	1995	8	$Y = -11.02 + 0.35X - 1.29E{-}3X^2$	0.80	0.97
	1996	8	$Y = -16.24 + 0.43X - 1.59E{-}3X^2$	0.55	0.98
Sunburst	1995	8	$Y = -9.04 + 0.30X - 1.11E{-}3X^2$	0.76	0.96
	1996	8	$Y = -18.32 + 0.50X - 2.07E{-}3X^2$	0.87	0.96
Combined[#]	1995	24	$Y = -10.21 + 0.33X - 1.23E{-}3X^2$	0.79	0.95
	1996	24	$Y = -18.59 + 0.49X - 1.94E{-}3X^2$	0.96	0.94
Dry Matter yield (Y, Mg ha^{-1}) vs. canopy height (X, cm)					
Cave-in-Rock	1995	6	$Y = 0.95 + 0.63X$	1.65	0.86
	1996	6	$Y = -0.74 + 0.073X$	0.25	0.99
Pathfinder	1995	6	$Y = 0.86 + 0.068X$	1.82	0.82
	1996	6	$Y = -1.35 + 0.081X$	0.80	0.97
Sunburst	1995	6	$Y = 0.28 + 0.064X$	1.38	0.87
	1996	6	$Y = -0.34 + 0.071X$	0.77	0.97
Combined	1995	18	$Y = 0.77 + 0.064X$	1.48	0.84
	1996	18	$Y = -0.72 + 0.074X$	0.62	0.98
LAI[§] (Y) vs. dry matter yield (X, Mg ha^{-1})					
Cave-in-Rock		7	$Y = 2.10 + 0.28X$	0.40	0.91
Pathfinder		7	$Y = 1.35 + 0.68X - 0.034X^2$	0.36	0.87
Sunburst		7	$Y = 0.59 + 0.84X - 0.044X^2$	0.39	0.85
Light interception (Y) vs. LAI (X)					
Cave-in-Rock		9	$Y = 40.94 + 19.76X - 1.92X^2$	4.84	0.85
Pathfinder		9	$Y = 8.34 + 32.10X - 3.04X^2$	2.86	0.99
Sunburst		9	$Y = 26.63 + 13.63X$	3.23	0.97

[†] root mean square error [‡] coefficient of determination [¶] $E{-}3 = x10^{-3}$
[#] pooled over cultivars [§] leaf area index

Table 8.2: Crop growth rate, radiation-use efficiency, and solar energy recovery of switchgrass cultivars grown in south-western Québec.

Parameter	Crop growth rate (kg ha^{-1} day^{-1})	Radiation-use efficiency	
		(g MJ^{-1})	Solar Energy Recovery (%)
ANOVA model r^2	0 .77	0.93	0.97
cv (%)	13.88	10.93	6.94
cultivar	ns	*	*
year	*	***	***
cultivar * year	ns	ns	ns
Year: 1995	161.40b	0.77b (1.59)[‡]	1.39b (2.77)
1996	200.08a[†]	1.14a (2.51)	2.01a (4.45)
LSD	28.94	0.12	0.13
Cultivar			
Cave-in-Rock	191.29a	1.07a (2.20)	1.84a (3.84)
Pathfinder	175.54a	0.90b (2.00)	1.65b (3.52)
Sunburst	175.39a	0.89b (1.96)	1.61b (3.46)
LSD	35.44	0.15	0.16

[†] year or cultivar means in each column followed by different letters differ significantly ($P<0.05$) by an ANOVA protected LSD test.

[‡] numbers in brackets indicate the respective value if only photosynthetically active radiation was used in the computation. The pattern of differences was the same with the same letters denoting differences

Table 8.3: Seasonal maximum light interception levels, mean tilt angles and light extinction coefficients of switchgrass cultivars grown at Montréal, Québec.

Parameter	Year	Cultivar			LSD
		Cave-in-Rock	Pathfinder	Sunburst	
Maximum PAR interception (%)	1995	95 (July 24)[†]	94 (July 7)	92 (July 7)	
	1996	95 (August 6)	94 (July 22)	94 (July22)	
Mean tilt angle (° from the horizontal)[‡]	1995	54	56	58	8.60
	1996	61	60	59	3.80
Extinction coefficient (*k*)[‡]	1995	-0.57	-0.55	-0.44	-0.04
	1996	-0.50	-0.53	-0.54	-0.05

[†] dates in parenthesis indicate the first time the level of interception was recorded

[‡] average of the period mid July to end of August

Table 8.4: Regression equations for nitrogen, acid detergent fibre and neutral detergent fibre of switchgrass cultivars grown in a short season area.

Cultivar	Year	n	Equation	rMSE[†]	r^2[‡]
Nitrogen (Y, g kg^{-1}) vs. Time (X, days)					
Cave-in-Rock		14	$Y = 8.29e^{-1.35X}$	0.14	0.94
Pathfinder		14	$Y = 8.85e^{-1.48X}$	0.13	0.96
Sunburst		14	$Y = 9.21e^{-1.56X}$	0.21	0.90
Combined[#]		42	$Y = 8.78e^{-1.47X}$	0.16	0.93
Acid detergent fibre (Y, g kg^{-1}) vs. time (X, days)					
Cave-in-Rock		7	$e^Y = 134.34X^{108.37}$	33.50	0.67
Pathfinder		7	$e^Y = 1.45.83X^{111.13}$	33.78	0.68
Sunburst		7	$e^Y = 195.33X^{98.25}$	35.67	0.59
Combined		21	$e^Y = 158.50X^{105.92}$	32.19	0.62
Neutral detergent fibre (Y, g kg^{-1}) vs. time (X, days)					
Cave-in-Rock		7	$e^Y = 283.58X^{119.52}$	13.94	0.93
Pathfinder		7	$e^Y = 571.10X^{62.27}$	13.48	0.80
Sunburst		7	$e^Y = 480.24X^{80.45}$	19.70	0.76
Combined		21	$e^Y = 444.97X^{87.41}$	22.88	0.69

[†] root mean square error [‡] coefficient of determination [#] pooled over cultivars

Table 8.5: Mean end of season yields, energy concentrations, and crude oil equivalents of switchgrass cultivars grown at Montréal, Québec

Cultivar	Energy concentration (kJ g $^{-1}$)			End of season yield (kg ha $^{-1}$)			Crude oil equivalent (barrels)[‡]		
	1995	1996	Mean	1995	1996	Mean	1995	1996	Mean
Cave-in-Rock	17.49	17.88	17.69a[†]	12 595.41	11 785.08	12 191.25a	36.19	35.17	35.68a
Pathfinder	16.93	17.13	17.03a	11482.83	11 592.62	11 537.73ab	31.92	32.68	32.30ab
Sunburst	17.59	17.52	17.56a	11 309.79	9 875.61	10 592.70b	32.66	28.45	30.56b
Mean	17.34a[†]	17.51a		11 796.01a	11 084.44a		33.59a	32.10a	

[†] cultivar or year means followed by different letters differ significantly at $p<0.05$

[‡] it was assumed that a 158.8-L barrel contains 6090 MJ of energy

Fig. 8.1: Mean maximum and minimum temperatures, rainfall and total radiation receipt for 1995 and 1996 at the Emile A. Lods Research Centre, Montréal, Québec.

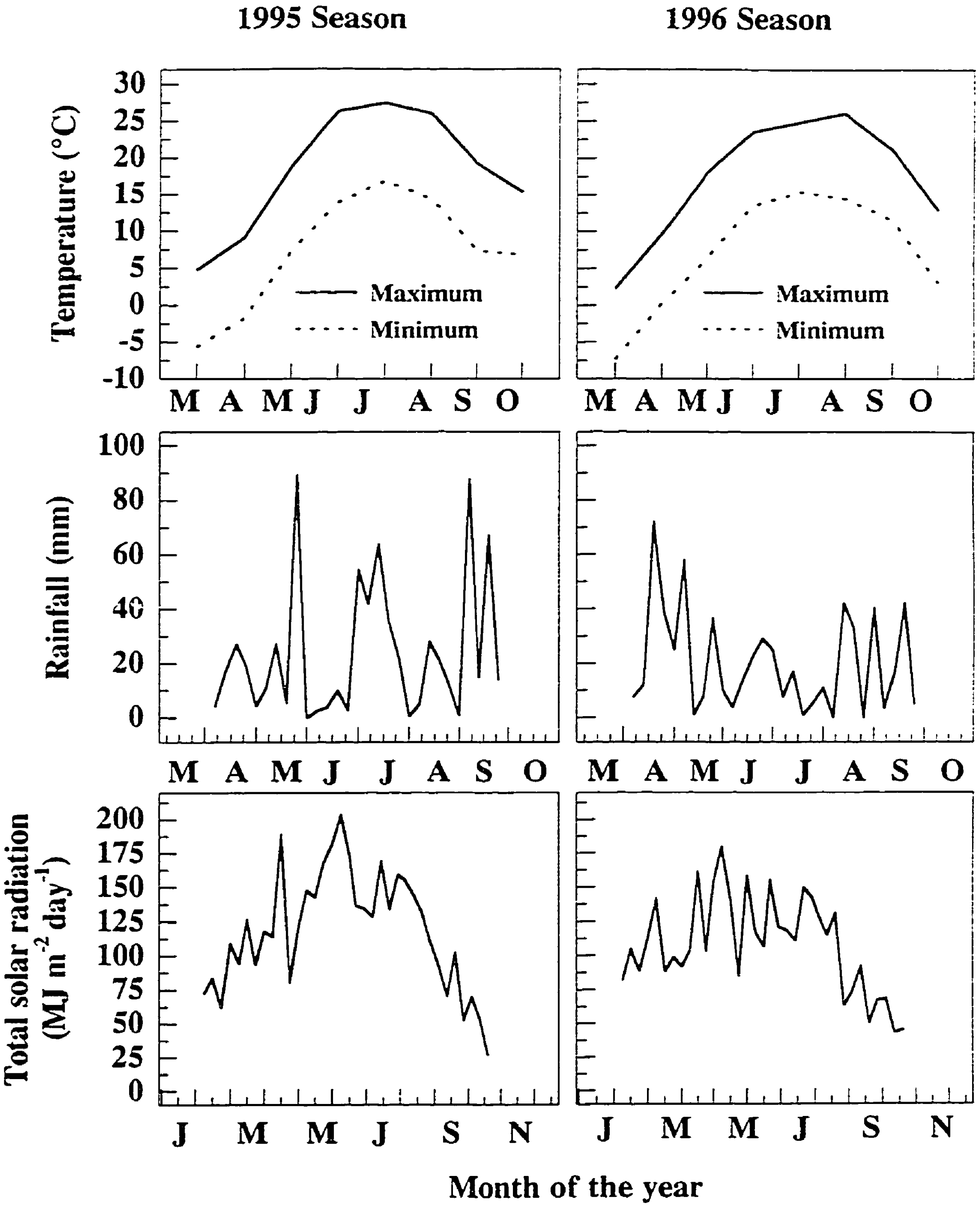
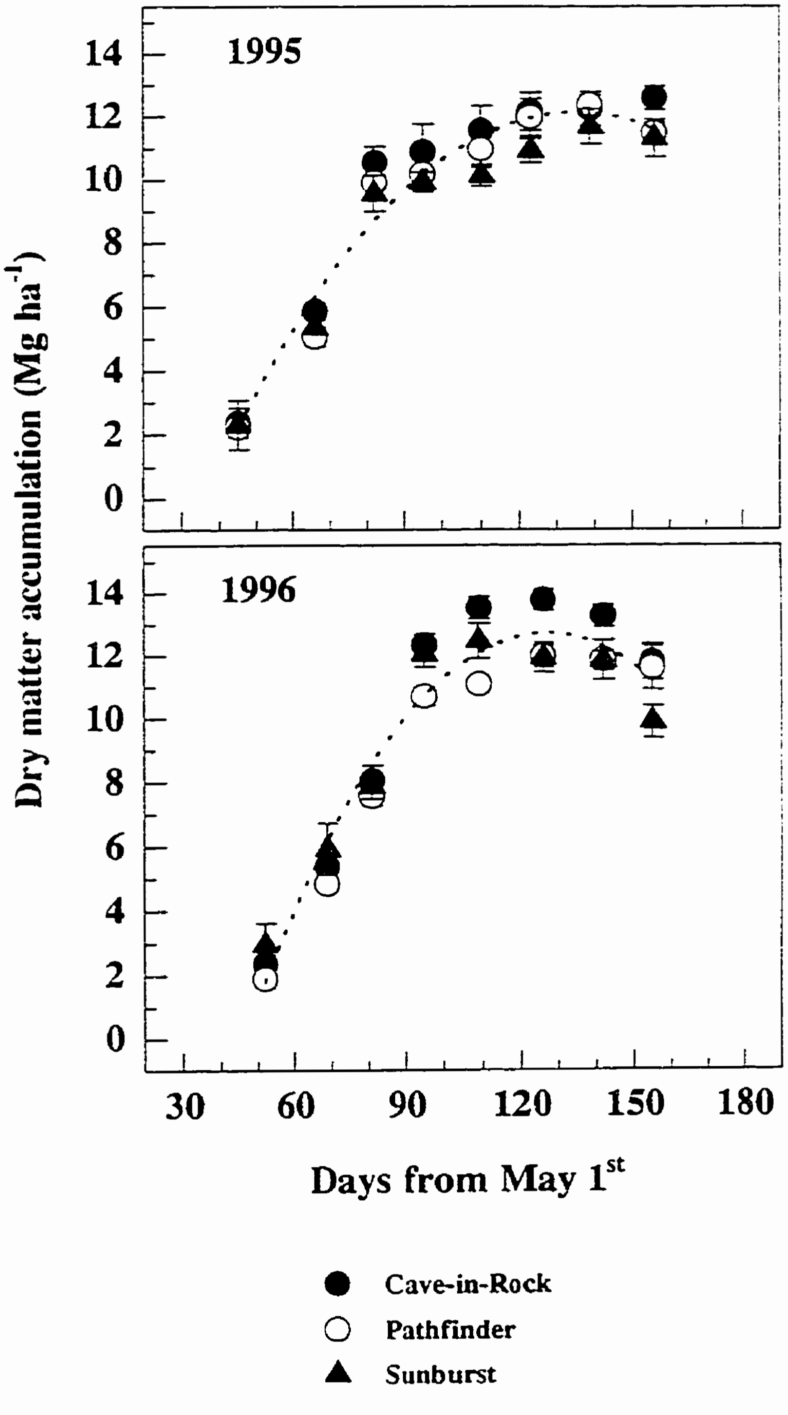

1995 Season
1996 Season
Temperature (°C)
30
25
20
15
10
5
0
-5
-10
Maximum
Minimum
M A M J J A S O
Rainfall (mm)
100
80
60
40
20
0
M A M J J A S O
Total solar radiation (MJ m^{-2} day^{-1})
200
175
150
125
100
75
50
25
0
J M M J S N
Month of the year

Fig. 8.2: Dry matter accumulation with time for three cultivars of switchgrass during the 1995 and 1996 growing seasons at Montréal, Québec. The dotted curves were fitted by regression using the combined data set. Regression equations fitted for each cultivar and to the combined data are presented in Table 8.1. Bars extending beyond symbols denote SE.



Dry matter accumulation (Mg ha^{-1})
1995
1996
0
2
4
6
8
10
12
14
30
60
90
120
150
180
Days from May 1st
● Cave-in-Rock
○ Pathfinder
▲ Sunburst

Fig. 8.3: Mean tiller numbers of switchgrass cultivars at three sampling dates at Montréal, Québec. Each bar is an average of three blocks and two years for each cultivar and the T-bars on each bar graph denote SE.

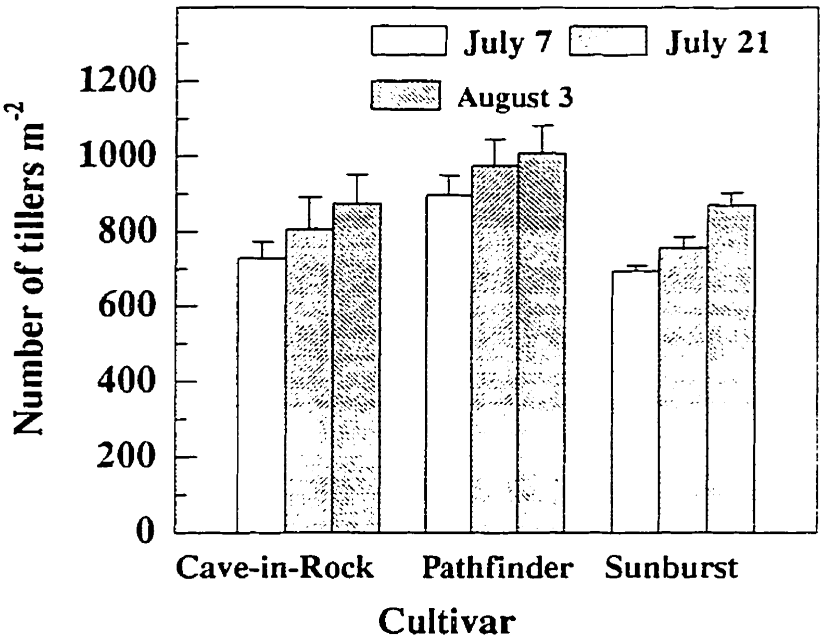
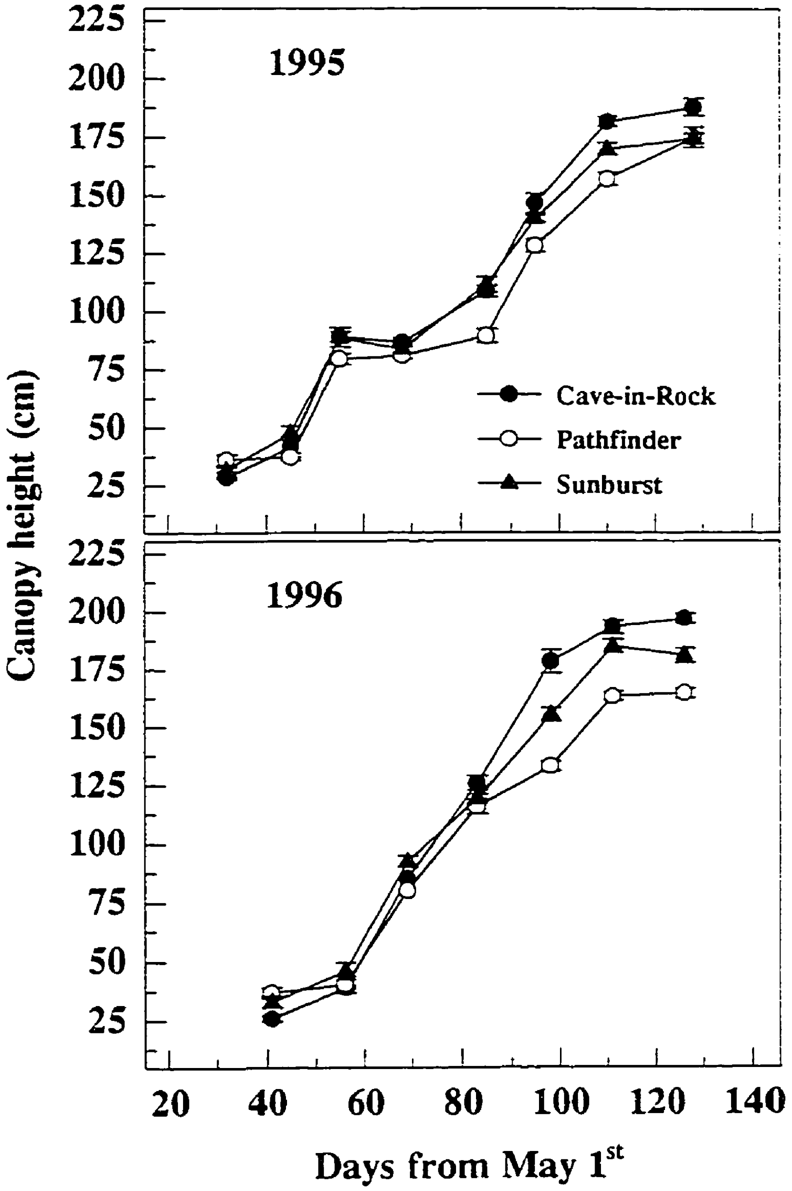

July 7
July 21
August 3
Number of tillers m^{-2}
0
200
400
600
800
1000
1200
Cave-in-Rock
Pathfinder
Sunburst
Cultivar

Fig. 8.4: Canopy heights of Cave-in-Rock, Pathfinder and Sunburst switchgrass during the 1995 and 1996 growing seasons at Montréal, Québec. Regression analyses of height on time did not yield acceptable equations for the 1995 data. Bars extending beyond symbols denote SE.



● Cave-in-Rock (1996)
$Y = 212.32 - 10.64X + 0.18X^2 - 7.56X^3$; $r^2 = 0.99$

○ Pathfinder (1996)
$Y = 146.69 - 6.61X + 0.11X^2 - 4.77X^3$; $r^2 = 0.99$

▲ Sunburst (1996)
$Y = 144.44 - 7.01X + 0.13X^2 - 5.39X^3$; $r^2 = 0.99$

Fig. 8.5: Relationship between dry matter accumulation and canopy height for three cultivars of switchgrass during the 1995 and 1996 growing seasons at Montréal, Québec. The dotted curves were fitted by regression using the combined data set. Regression equations fitted for each cultivar and to the combined data are presented in Table 8.1. Bars extending beyond symbols denote SE.

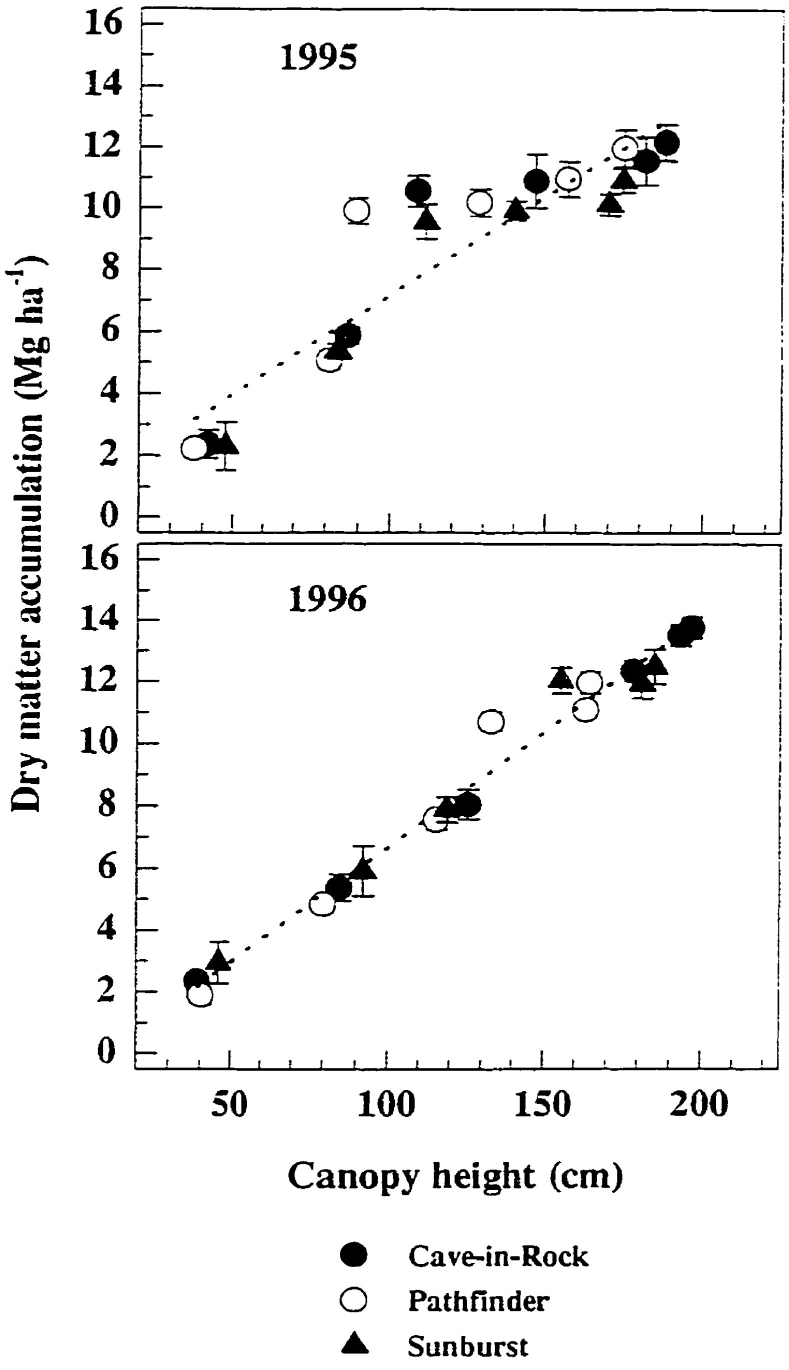

16
14
12
10
8
6
4
2
0
1995
16
14
12
10
8
6
4
2
0
1996
Dry matter accumulation (Mg ha^{-1})
50
100
150
200
Canopy height (cm)
● Cave-in-Rock
○ Pathfinder
▲ Sunburst

Fig. 8.6: Leaf area development of switchgrass cultivars during the 1995 and 1996 growing seasons at Montréal, Québec. Bars extending beyond symbols denote SE.

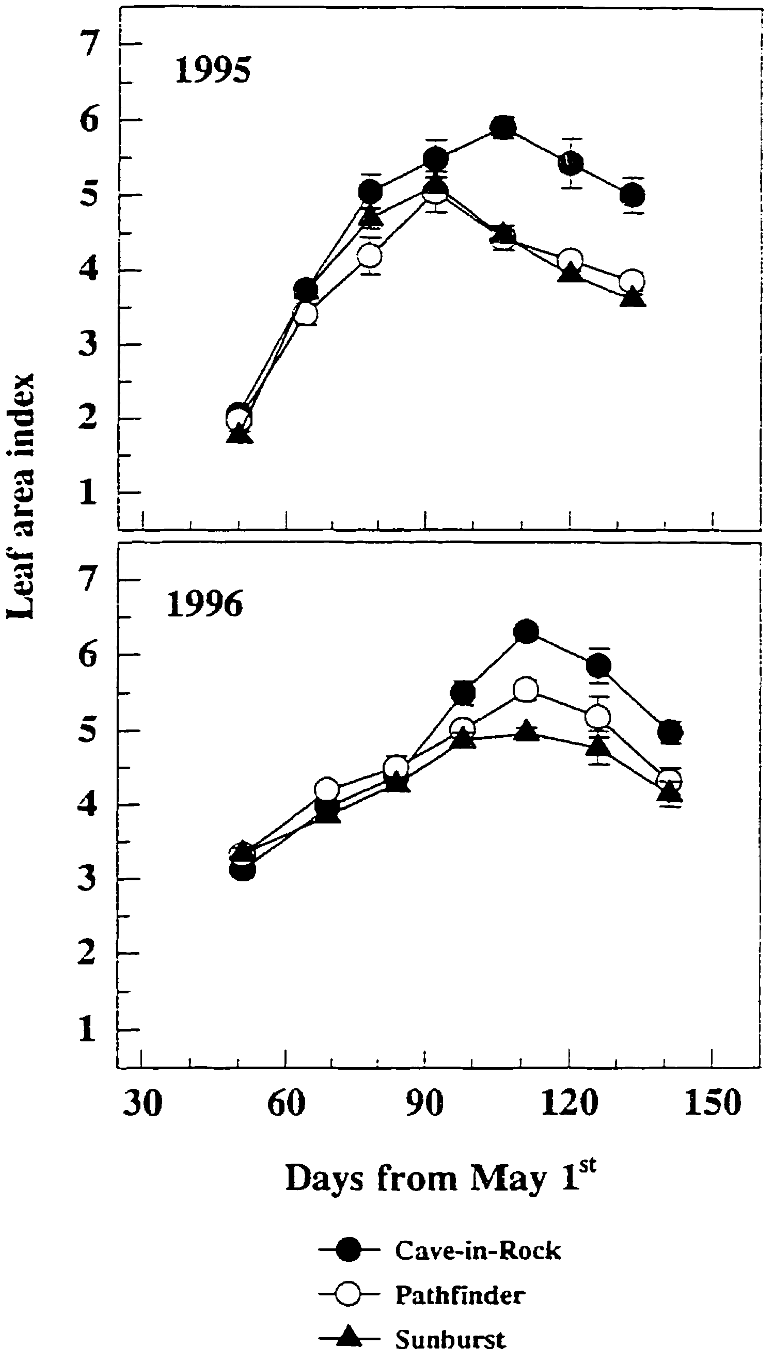

1995
1996
Leaf area index
7
6
5
4
3
2
1
30
60
90
120
150
Days from May 1st
Cave-in-Rock
Pathfinder
Sunburst

Fig. 8.7: Relationships between leaf area index and a) light interception and b) dry matter yield of three switchgrass cultivars at Montréal, Québec. Data were combined for 1995 and 1996. Regression equations fitted to these Relationships are presented in Table 8.1. Bars extending beyond symbols denote SE.

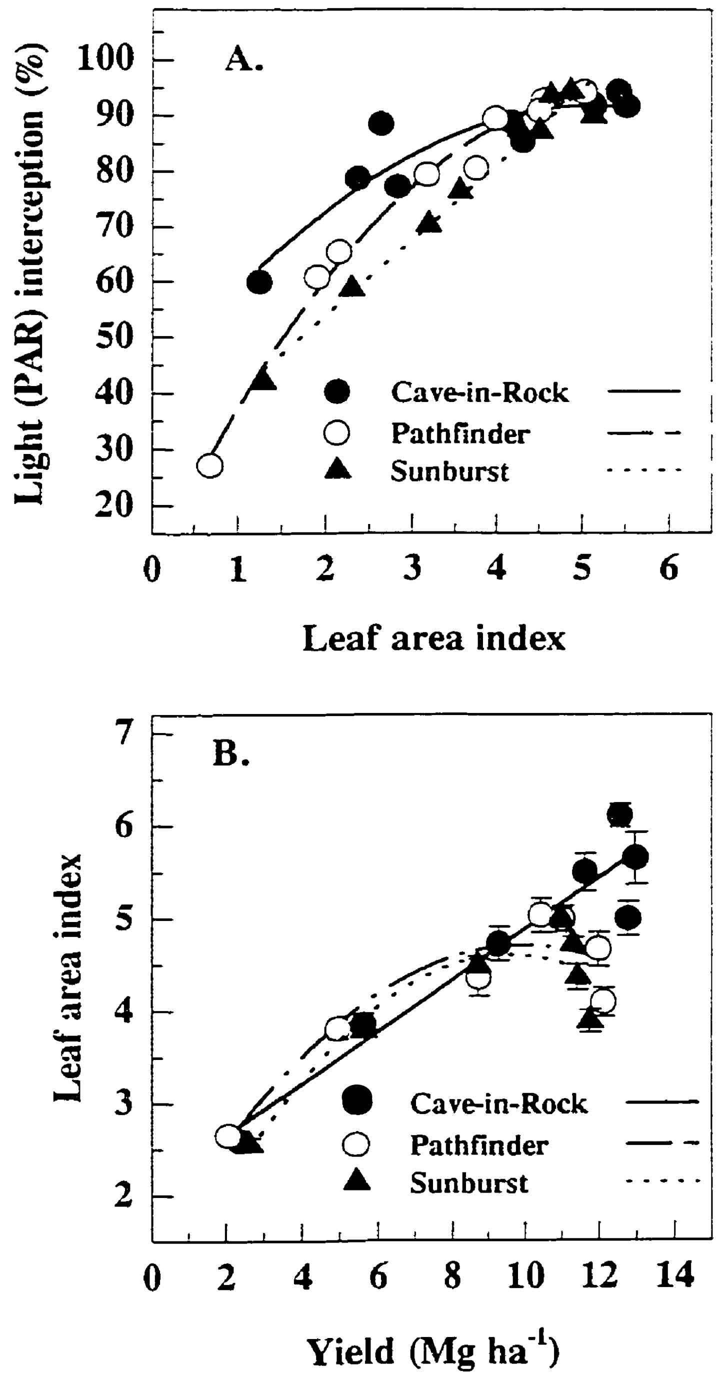

A.
Light (PAR) interception (%)
100
90
80
70
60
50
40
30
20
0
1
2
3
4
5
6
Leaf area index
Cave-in-Rock
Pathfinder
Sunburst
B.
Leaf area index
7
6
5
4
3
2
0
2
4
6
8
10
12
14
Yield (Mg ha-1)
Cave-in-Rock
Pathfinder
Sunburst

Fig. 8.8: Mean vertical distribution of total leaf area of Cave-in-Rock, Pathfinder and Sunburst switchgrass in late-July of 1995 at Montréal, Québec. Values were obtained by difference between successive height strata within the canopy. This was typical for the mid-late periods of both seasons. Bars extending beyond each symbol denote SE.

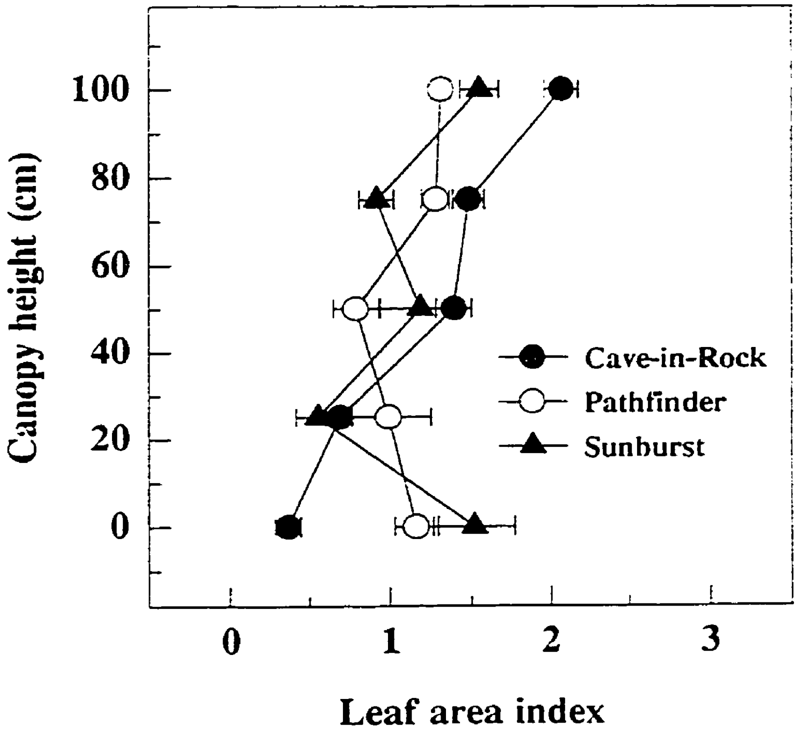

Canopy height (cm)
100
80
60
40
20
0
0
1
2
3
Leaf area index
Cave-in-Rock
Pathfinder
Sunburst

Fig. 8.9: Concentration of acid detergent fibre, neutral detergent fibre and nitrogen in cultivars of switchgrass grown at Montréal, Québec. Each point is an average of the two years. Fitted regression equations for all graphs, using combined data, are presented in Table 8.4. Bars extending beyond symbols denote SE.

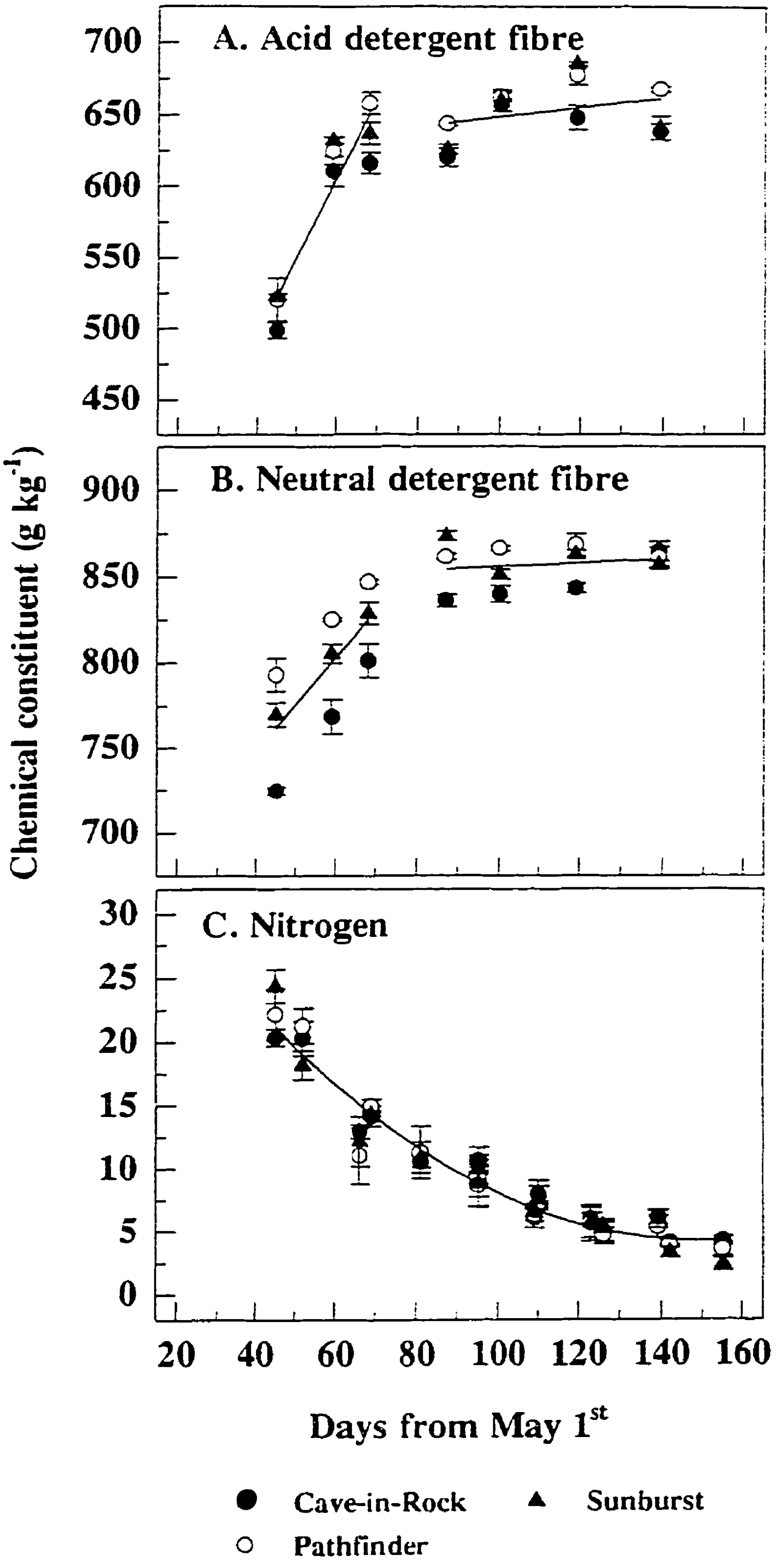

A. Acid detergent fibre
700
650
600
550
500
450
B. Neutral detergent fibre
900
850
800
750
700
C. Nitrogen
30
25
20
15
10
5
0
20
40
60
80
100
120
140
160
Chemical constituent (g kg^{-1})
Days from May 1st
● Cave-in-Rock
▲ Sunburst
○ Pathfinder

Fig. 8.10: Changes in leaf to stem ratios of three switchgrass cultivars grown at Montréal, Québec. Each point is an average of the two years, 1995 and 1996. Bars extending beyond symbols denote SE.

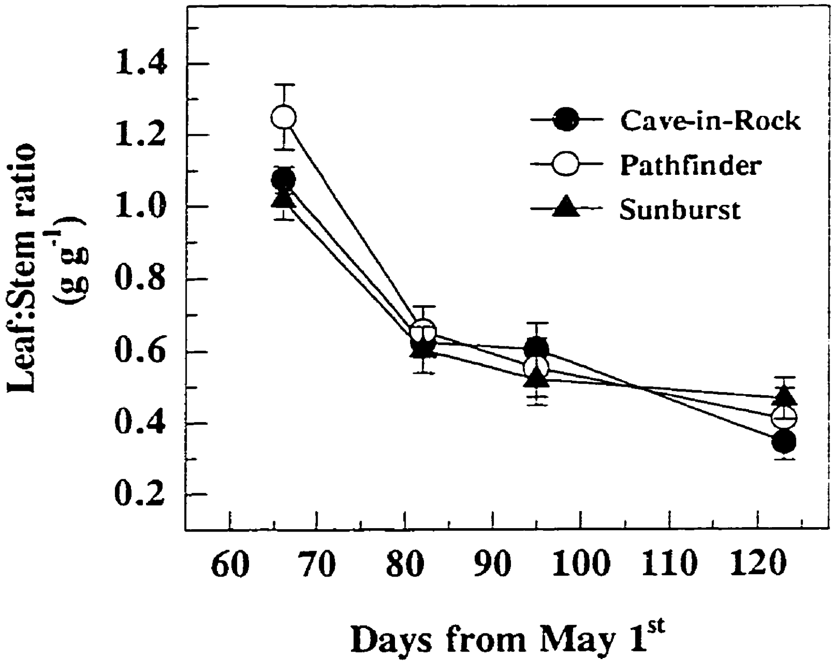
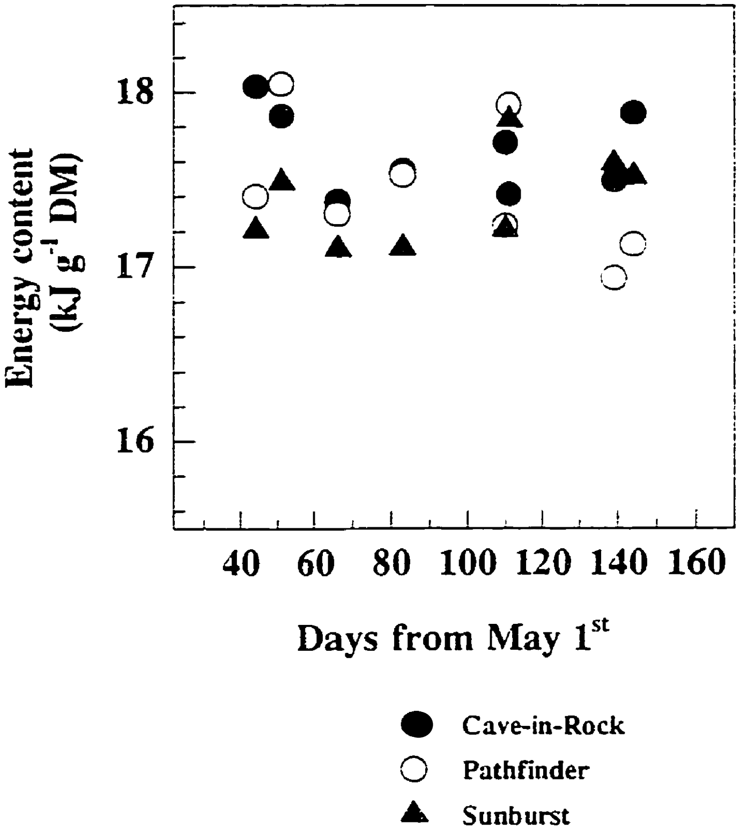

Leaf:Stem ratio
(g g-1)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
60
70
80
90
100
110
120
Days from May 1st
Cave-in-Rock
Pathfinder
Sunburst

Fig. 8.11: Energy content of three switchgrass cultivars grown at Montreal, Quebec. The data was combined for the two seasons (1995 and 1996) for each cultivar.


Energy content (kJ g^{-1} DM)
18
17
16
40
60
80
100
120
140
160
Days from May 1st
● Cave-in-Rock
○ Pathfinder
▲ Sunburst

Preface to Chapter 9

Chapter 9 is based on a manuscript submitted for publication to the *Journal of Production Agriculture* in 1997.

The discussion so far has largely covered aspects of biomass production. In forage production systems there is some form of defoliation during the growth of the forage plant. This is either through grazing or cutting for hay and/or silage. The effects of harvest schedule and N fertilisation on yield and quality are presented in this chapter. The chapter ends with a discussion on the potential of switchgrass in livestock production systems.

Chapter 9

Effect of Nitrogen Fertilisation and Cutting Frequency on Yield and Nitrogen concentration of Switchgrass (*Panicum virgatum* L.) grown in a Short Season Area.

9.1. Abstract

Adapted warm season grasses have potential for both summer forage and biomass production in eastern Canada. A field study was conducted in 1995 and 1996 to determine the response of switchgrass (*Panicum virgatum* L.) cv Cave-in-Rock (CIR), Pathfinder (PF) and Sunburst (SB), to nitrogen (N) fertilisation at 0, 75 or 150 kg ha^{-1}, and three harvest schedules. The grass was harvested at 4 or 6-week intervals (4-wk and 6-wk, respectively) or left uncut until the end of the season. These treatments were combined in a split-plot design in each of three blocks on a sandy clay loam. Herbage yield, canopy height, herbage N content and leaf chlorophyll meter readings were determined at each harvest for the cutting schedules, and chlorophyll meter readings and N contents from herbage samples of the uncut stands every two weeks. Herbage yields were influenced by a cultivar x N x harvest schedule interaction in 1996 while in 1995 only the two-way interactions between cultivar x harvest schedule and N x harvest schedule were significant ($p<0.05$). Total yield ranking for the harvest regimes was uncut > 6-wk > 4-wk with their respective mean yields being 11, 10 and 8 Mg ha^{-1} for CIR; 10, 8 and 6 for PF; and 11, 8 and 7 for SB. Increased N fertilisation increased yields in a diminishing returns manner. N contents increased with fertilisation and varied with harvest and year, but not with cultivar. Mean N concentrations were 12.4, 13.9 and 15.4 g kg^{-1} DM for the 0, 75 and 150 N levels, respectively, under the 4-wk system. Corresponding values were 10.1, 11.6 and 12.9 for the 6-wk system. End of season N contents for the uncut regime averaged 5.4, 6.0 and 7.6 g kg^{-1} DM in increasing order of N fertilisation. These nitrogen concentrations were linearly related to chlorophyll meter readings, which also had positive correlation with dry matter yields. The results indicate that switchgrass can be used in both grazed

or hay forage systems in eastern Canada.

9.2. Introduction

Warm season grasses can be used for both summer forage and biomass production in temperate regions (Jung *et al.*, 1990; Berg, 1995; Sanderson *et al.*, 1996). Despite high fibre contents, these grasses have relatively high intakes and support substantial daily animal liveweight gains (Vona *et al.*, 1984; Anderson *et al.*, 1988). Nitrogen availability has been shown to be the most limiting factor in production of these grasses (Woodhouse and Griffith, 1974; Berg, 1990). Available information suggests limited N applications are made to warm season grass stands because of: a) invasion of stands by weedy species (Pettit and Deering, 1974; Reid *et al.*, 1993), and b) poor persistence of the grasses under intensive defoliation systems that occur with high N fertilised forages. This is despite the demonstration by Burns *et al.* (1984) that switchgrass is tolerant of severe grazing pressure when fertilised at 500 kg N ha^{-1}, an economically questionable rate.

Evaluations of N sufficiency or management strategies can now be easily achieved in a non-destructive way, by using a hand held-leaf chlorophyll meter (SPAD 502, Minolta Corp., NJ). This technique is based on the fact that leaf chloroplasts contain 70% of leaf N, and as a result, chlorophyll content is well correlated with N content (Wood *et al.*. 1992). Use of this relationship has been demonstrated in several crops, for example corn (*Zea mays* L.; Piekielek and Fox, 1992; Ma and Dwyer, 1997), rice (*Oryza sativa* L.; Turner and Jund, 1991) and wheat (*Triticum aestivum* L.; Reeves *et al.*, 1993).

In earlier studies, we evaluated maximal herbage production and growth of uncut canopies in south-western Québec (Madakadze *et al.* 1996a, 1996b). These evaluations were more suited to biomass production than forage. Defoliation patterns largely affect stand persistence and total herbage yield of warm season grasses (Belesky and Fedders, 1995; Brejda *et al.*, 1996). Intensely clipped or frequently harvested grass stands eventually show stand loss. This is a result of removal of large proportions of meristematic tissue under infrequent and intense defoliation while frequent defoliations do not allow for sufficient recovery. There is a paucity of information to guide development of defoliation and fertilisation management regimes. This study was conducted to determine the response of switchgrass to N fertilisation and different harvest schedules. We also tested whether leaf chlorophyll meter readings were related to tissue N content and herbage yield in this grass species.

9.3. Materials and Methods

9.3.1. Site and experimental layout

This study was conducted during 1995 and 1996 on two-year old stands of CIR, PF and SB. The site was a free draining sandy clay loam (St. Bernard, Typic Hapludalf) located at the Emile A. Lods Research Centre, McGill University, Montréal, Québec, Canada (45° 28'N 73° 45'W). The station was equipped with an automated weather station which was used to collect temperature and rainfall data. The grass stands used were established in spring of 1993 at a seeding rate of 12 g ha^{-1}. The stands were fertilised with 40 kg N ha^{-1} in the establishment year, but received no fertilisation in 1994. The 1993 growth was cut and removed in spring of 1994.

The experimental plots were arranged in a split-plot design with three blocks, the three cultivars formed the main plots. Within each main plot treatment, combinations of three N fertiliser levels and four harvest schedules were applied randomly. N fertiliser was applied as ammonium nitrate at 0, 75 or 150 kg ha^{-1} yr^{-1} and the plots were harvested at 2, 4, or 6 week intervals beginning when there was at least 80% ground cover and a canopy height of 25 cm. A fourth harvest schedule entailed harvesting the plots once at the end of the season. The 2-wk harvest schedule was discontinued halfway into the first season because of heavy weed infestation. Fertiliser application was split into two equal dressings for the 4-wk and 6-wk harvest regimes, with one application soon after initiation of growth and a second after the first cut. For the uncut plots, fertiliser was applied in one application at the beginning of the season. The plots measured 4 m x 3 m. Each spring, before the initiation of new growth, surface plant residues from the previous season were cut at a 15-cm stubble height and removed.

9.3.2. Measurements

Canopy height and ground cover scores were assessed twice a week during the spring to enable scheduling of harvests, after which canopy heights only were measured at each harvest. Herbage dry matter yield estimates were obtained from three 0.5 m^2 quadrats within each plot. Harvests were made at a 15-cm stubble height. Except for the last harvests, which were towards the end of the season, after each harvest the whole plot was mowed to 15 cm and the herbage removed. Herbage subsamples were oven-dried to constant weight at 70 °C for DM determination and kept for further analysis. Subsamples were also taken from the uncut plots at two-week intervals. SPAD 502 chlorophyll meter readings were taken at each harvest and every two weeks in the uncut plots. Three such readings were taken on the top most fully expanded leaf of each of 10 tillers in each plot being sampled. Nitrogen was analysed as Kjeldahl N.

9.3.3. Statistical Analysis

The data were subjected to analysis of variance (Steel and Torrie, 1980). Seasonal total herbage yields were analysed with subplot variation being partitioned for N and harvest regime and their respective interactions. Herbage yields were also analysed separately for the 4-wk and 6-wk regimes with partitioning of subplot variation for N and harvest date/cut number and the respective interactions. Chemical analysis data were analysed separately for each harvest regime. Where possible, means separation was done using the protected Least Significant Difference (LSD) test. The two-weekly SPAD readings and N contents from the uncut plots were subjected to repeated measures analysis (Crowder and Hand, 1990). All statistical analyses were conducted using SAS General Linear Models procedures (SAS, 1995).

9.4. Results and Discussion

9.4.1. Environment

The mean weekly maximum and minimum temperatures and weekly rainfall totals are presented in Fig. 9.1. Spring was warmer in 1995 than 1996. However, late season minimum temperatures were higher in 1996 resulting in a relatively longer growing season. Rainfall was relatively more evenly distributed in 1996 than in 1995, which was very dry in the month of June. Table 9.1 presents the harvest dates by year. Only two harvests were possible in 1995 under the 4-wk regime, largely because of a shorter growing season.

9.4.2. Herbage yields

Seasonal total herbage dry matter (DM) yields showed a significant ($p<0.05$) cultivar x harvest regime interaction in both years and a N x harvest regime interaction in 1995 only. Table 9.2 presents the cultivar x harvest schedule means for both years. Total herbage yields were generally higher in 1995 than 1996. Yields from the uncut regime were, on average, higher than the seasonal totals from the other two harvest regimes. Except for SB in 1995 and PF in 1996, the 6-wk regime had higher yields than the 4-wk one. The interaction between cultivar and harvest regime resulted from the different magnitudes of the respective differences among harvest regimes for each cultivar. For example, total yields were not different for 4 and 6-wk regimes for SB in 1995, in 1996 the differences between 6-wk and uncut regimes and between 4 and 6-wk regimes for CIR and PF, respectively. In 1995, responses to N fertiliser were linear. The first cut yielded more than the second for both the 4 and 6-wk regimes. The N x harvest regime interaction was significant because of differential increases in herbage yields in response to increasing N. There were large proportional and absolute increases in total yield (Table 9.3) due to application of 75 kg N ha^{-1} for both the cut and uncut systems. However, when N level was increased from 75-150, increases in herbage yields were higher under the 6-wk than either the 4-wk or uncut regimes. Greater increases occurred due to the 0-75 than the 75-150 N kg ha^{-1} level increase for the individual cuts, under both the 4 and 6-wk regimes. Diminishing returns with increasing N application levels is common in crops (Hall *et al.* 1982; Sinclair and Horie, 1989). In 1996, the three-way interactions between cultivar, N and cut-number were significant for both the 4-wk and 6-wk regimes. This interaction occurred because of different responses to increased N fertilisation (Fig. 9.2). In general, herbage yields increased with increasing N level but the absolute increases and rates of increase were different for the various cultivar x harvest regime x cut number combinations. In the uncut (biomass production) system, there were no cultivar differences in the average yields, but yield increased with N fertilisation. Choice of level of N to apply will be influenced by the economics at the time of production.

Increased switchgrass yields following N fertilisation have also been reported in studies from various North American regions (Hall *et al.* 1982; Stout *et al.*, 1988; Jung *et al.*, 1990; Reid *et al.*, 1993). In these studies, switchgrass response to N was dependent on cultivar or ecotype and stand age. Hall *et al.* (1982) reported yields ranging from 4 to 8 Mg ha^{-1} for Blackwell switchgrass receiving 0 to 150 kg N ha^{-1}, in a two cut system. Yields ranged from 6.9-7.8 and 9.1-12.3 Mg ha^{-1} in a two-cut system for several switchgrass cultivars receiving 0 and 75 kg N ha^{-1}, respectively (Jung *et al.*, 1990). The two-cut systems in these two studies are equivalent to our 6-wk regime, whose yields are comparable with the reported values. Responses to N in the range 0-150 kg ha^{-1} were largely linear in our study and quadratic in the study of Hall *et al.* (1982). It would seem some factor(s) limited responses to N fertilisation in their study.

Switchgrass yields were also reported to increase with delayed 1st cut (Andersen *et al.*, 1989; Belesky and Fedders, 1995). However, yields at the 2nd cut declined as a result of increased delay of the 1st cut. These two studies also highlighted the importance of scheduling harvests based on canopy considerations. Depending on specific environment and/or management, plants harvested frequently may not be able to replenish carbohydrates required for new growth. With the exception of the 2-wk schedule that was eliminated early in the study, there were no obvious detrimental effects from the cutting regimes in our study. Yield decreases from 1995 to 1996 were probably due to stand age, because they also occurred in the 0 N level treatments. Reid *et al.* (1993) reported switchgrass stands (cv Trailblazer) that became more open with increased fertilisation (75 and 150 kg N ha^{-1}). These stands were invaded with broad-leaf weeds, which were absent in 0-N treatments. Other than in the discontinued 2-wk regime, all plots remained weed free. We contend that weed infestation in the discontinued treatments was largely due to reduced vigour following from the frequent clippings.

9.4.3. Canopy height

Fitting predictive equations to the relationships between herbage yields and canopy height produced mixed results, depending on year, harvest regime, and cut number (Table 9.4). Coefficients of determination for predictive models ranged from 0.35 to 0.81 for the 4-wk and 0.28 to 0.80 for the 6-wk harvests. Cut 1 under the 6-wk regime had a lower coefficient of determination than cut 2 in both years. It is probable that by the time cut 1 was made the stands were already past the near-linear phases of growth. Drought stress in June 1995 might also have contributed to the poor relationship between yield and height for cut 1 of this year. Some of the intercepts were significantly different from zero (Table 9.4). Negative intercepts in this case, do not have biological meaning and therefore indicate that in these particular instances there was deviation from linearity early in the growth cycle or when data were combined for all cuts.

9.4.4. Nitrogen content

N concentrations in the two-weekly samples taken from uncut plots declined with the season in an increasingly curvilinear nature (Fig. 9.3). Using the contrast option in repeated measures analysis, the large differences due to N level early in the seasons were non existent by day 80 after June 1st. In the cut regimes, N concentration of herbage was greatly influenced by N fertilisation. For most treatment combinations, only the effects due to N level were significant. Cultivar effects were also significant for the first cut under the 6-wk regime in 1995, when the average for SB (9.7 g N kg^{-1} DM) was higher than for CIR (8.9) and PF (8.5). The average N concentrations are presented in Table 9.5. Fertilisation with 150 kg N ha^{-1} resulted in the highest herbage N concentrations, although in some cases these were not statistically different from those of the other N levels. Under the 4-wk regime, N concentrations at all N levels increased from 1st cut to the 2nd , the increases being more dramatic in 1995 than 1996. However, N concentrations declined at cut 3 relative to cut 2 or 1. The general increase in N concentrations from cut 1 to 2 was also noted for the 6-wk regime. N concentrations were also higher in the 4-wk than 6-wk regime, and in the first cuts of 1996 than 1995. These differences do not seem to have been due to carryover effects from the previous season because they also occurred when no N fertiliser was applied. End of season N concentrations for uncut herbage ranged from 5.1-9.2 g kg^{-1} DM. In 1996, the effects of N level were not evident while in 1995 higher N concentrations were obtained from plots fertilised at the 150 N level.

Jung *et al.* (1990) reported N concentrations ranging from 8.0-8.4 and 9.0-10.5 g kg^{-1} DM for 1st harvest switchgrass (early heading) receiving 0 and 75 kg N ha^{-1}, respectively. These values are comparable to our 6-wk values for cuts 1 and 2 in 1995 but lower than those in 1996. Vona *et al.* (1984) also reported crude protein (CP) concentrations ranging from 5-13.6 % DM for various switchgrass hays depending on actual date of harvest, early cut material had higher CP concentrations than the late cut. For the same approximate dates of harvests, these CP concentrations are comparable to the N concentrations we are reporting for both the 4 and 6-wk regimes.

There is no definitive explanation for the increase in N concentrations from cut 1 to 2 in both years. The periods preceding cut 1 in both harvest schedules were characterised by high canopy growth with near-linear phases of leaf area index (LAI) and dry matter increases. It is possible that there was a trade-off between leaf N concentrations and LAI as demonstrated by Sinclair and Horie (1989) and Anten *et al.* (1995). At low levels of available N (below optimum), it has been shown that several plant species have a lower N content per unit area, as a trade-off for a larger leaf area to maximise biomass accumulation. This is an optimisation phenomenon because, while increased LAI allows for more light interception, reduced leaf N content results in reduced photosynthetic rates. In our study, responses to N were largely linear suggesting our highest level was still below the optimum. It is also possible that root N uptake did not match the high canopy growth rates creating the low levels of available N for growth, or the N was largely stored in roots and stem bases for use when N needs cannot be met by root N uptake (Thornton *et al.*, 1994; Volenenc *et al.*, 1996). Drought in June 1995 might have also contributed to lower N concentrations in cut 1 herbage of 1995. Plant tissues produced under high temperatures and/or low soil moisture contain less N and more fibre regardless of tissue age or stage of development (Hendrickson and Robinson, 1982; Hendrickson *et al*, 1997). The relatively cooler and wet spring of 1996 would partly account for higher 1996 cut 1 N concentrations than in 1995. N concentrations in the 4-wk regime were higher than those in the 6-wk because of increased stem tissue fibre due to increased maturity in the latter (Griffin and Jung, 1983; Hendrickson *et al.*, 1997).

9.4.5. Chlorophyll meter readings

The SPAD 502 readings taken every two weeks did not follow the decline in nitrogen concentrations of the corresponding herbage (Fig. 9.4). Using Fig. 9.4 B and D and reading the plots from left to right (N content declining from highest levels in early season) the SPAD meter readings increased to a maximum beyond which they declined rapidly. The initial increase in the readings was in spite of decreasing total herbage N concentration. On a temporal basis (Fig. 9.4 A and C, reading with increasing time), the SPAD meter readings increased through 80 days after June 1st followed by a decline (mirror images of B and D, respectively). This discrepancy between data in Fig. 9.3 and Fig. 9.4 reflect differential partitioning of N within the plant. Because SPAD meter readings were taken on the top most fully expanded leaf, the data suggest that as the plant grows, more tissue N is found in the top leaves. This is supported by Field (1983), and also Hirose and Werger (1987) who reported that at a given LAI and total amount of canopy N, there is an optimisation pattern of N allocation which allows for highest leaf N content in the most illuminated regions of the canopy. This in turn would allow for maximum canopy photosynthesis. N content of these top leaves would therefore be higher than the average for the whole plant, which would include senescing leaves. The maximum readings correspond to various reproductive stages in the three cultivars. By day 80 after June 1st, SB was in the early stages of grain filling; CIR in late anthesis, while PF was in mid anthesis. Increased N contents in the top leaves are required to support the increased photosynthetic activity at this stage of plant development. These relationships between SPAD meter readings and

N contents of uncut herbage suggest potential use of leaf chlorophyll content to monitor or predict N availability for seed production in switchgrass.

Nitrogen concentrations of herbage in the vegetative phase, harvested at 4-wk and 6-wk intervals, were linearly related to SPAD meter readings (Fig. 9.5). This relationship was best for cut 1 under the 4-wk harvest schedule. Zero or 'negative' N contents are biologically impossible in living plant tissues. Our ranges of SPAD meter readings and N contents were not sufficiently low to allow fitting of zero-intercept models. Therefore, we would like to emphasise that the predictive equations (Fig. 9.5) are valid only for the ranges indicated and the respective growth phases of the plants. While there was no correlation between dry matter yield and SPAD meter readings for 4-wk cut 1, correlation was positive for cuts 2 and 3 and for both cuts under the 6-wk harvest regime (Fig. 9.6).

Use of SPAD meter readings in N management has been demonstrated mostly for grain crops like maize (Ma and Dwyer, 1997), wheat (Reeves *et al.* 1993) and rice (Turner and Jund, 1991) and on a limited scale in forage crops. In tall fescue (*Festuca arundinacea* Schreb.; Kantety *et al.*, 1996) and in timothy (*Phleum pratense* L.; Virtatenen and Peltonen, 1996) positive correlations between SPAD meter readings and herbage yield have been demonstrated. These forage crops are both C_3 photosynthetic system species. We are reporting the potential use of SPAD meter readings in a C_4 forage species.

9.4.6. Livestock production potential

In livestock production, grazing at 4-wk intervals would provide animals with high quality forage. Mullahey *et al.* (1992) reported that this herbage contains 50% (21% for smooth bromegrass, *Bromus inermis* Leyss.) of its N as rumen-undegradable protein (RUDP) that is available postruminally. Given the high nitrogen concentrations we are reporting, the herbage could easily support growing steers or cow-calf systems. In growing steers grazing a mixed stand of big bluestem (*Andropogon gerardii* Vitman) and switchgrass, Hafley *et al.* (1993) reported high herbage RUDP values of up to 54%. They showed that low levels of rumen degradable protein (RDP) might limit animal performance, something which was corrected by minimal supplementation. However, our study is based on clipping and simple extrapolation to grazing are vitiated by, firstly, N recycling under grazing; and secondly, possible differences in plant physiological responses to clipping than grazing. The 6-wk harvest regime is ideal for hay production. Based on our data, 1.0-2.6 and 1.7-3.6 Mg ha^{-1} would be available for grazing in late summer/early fall under the 4 and 6-wk regimes respectively. Yield differences among cultivars at this time suggest differences in carrying capacities per ha. Potential also exists for using SPAD meter readings to time forage N fertilisation and utilisation.

9.5. Conclusions

Our results indicate that switchgrass can be grown and harvested successfully at least twice in south-western Québec. Successive cuts yielded less that the preceding ones. A 6-wk harvest regime resulted in more herbage yield than a 4-wk regime. Nitrogen fertilisation increased both herbage yields and nitrogen contents under the cutting systems and herbage yield only under the biomass option. High quality forage is available for grazing under the 4-wk system while the 6-wk system is better suited for hay production. Chlorophyll meter readings were linearly related to herbage N content and correlated with herbage yield within cutting systems. These readings have potential in guiding N management for seed production and forage utilisation strategies.

Table 9.1: Harvest dates of switchgrass by year and target harvest schedule

Harvest schedule	Year	
	1995	1996
4 weeks apart		
cut 1	12 July	08 July
cut 2	18 August	05 August
cut 3	—	04 September
6 weeks apart		
cut 1	22 July	22 July
cut 2	02 September	03 September
End of season cut	16 September	22 September

Table 9.2: Dry matter yield of switchgrass cultivars as influenced by harvest schedule at Montréal, Québec. Data were averaged over the three fertiliser levels.

Cultivar	Harvest schedule	Seasonal total dry matter yield (Mg ha^{-1})[‡]	
		1995	1996
Cave-in-Rock	4 weeeks	7.87d	8.16c
	6 weeks	10.89b	9.29b
	End of season	12.33a[†]	9.56ab
Pathfinder	4 weeeks	6.03e	6.45d
	6 weeks	9.02c	6.90d
	End of season	10.86b	9.87a
Sunburst	4 weeeks	7.43d	5.84e
	6 weeks	8.10d	7.64c
	End of season	11.35b	9.78ab
	LSD	0.73	0.54
	CV (%)	8.18	6.87

[†] means in each column followed by different letters differ significantly ($p<0.05$) using an Anova protected Least Significant Difference (LSD) test

[‡] total yield of all harvests where there were more than one harvest

Table 9.3: Dry matter yield of switchgrass as influenced by harvest schedule and nitrogen fertilisation at Montréal, Québec, 1995. Data were averaged over the three cultivars.

Harvest schedule	N level (kg ha^{-1})	Dry matter yield (Mg ha^{-1})		
		Cut 1	Cut 2	Total
4 weeks	0	3.66c	1.31c	4.97G
	75	5.29b (44)[*]	2.11b (61)	7.40F (49)
	150	6.33a[†] (20)	2.63a (25)	8.96E (21)
LSD[‡]	0.38			
6 weeks	0	4.64c	2.01c	6.65F
	75	6.70b (44)	2.64b (31)	9.34DE (41)
	150	8.40a (25)	3.62a (27)	12.02B (29)
LSD[‡]	0.48			
End of season	0	—	—	9.99D
	75	—	—	11.16C (12)
	150	—	—	13.39A[§] (20)
LSD				0.79

[†] means in each column, within each harvest schedule, followed by different lower case letters differ significantly ($p<0.05$) using an Anova protected Least Significant Difference (LSD) test

[‡] LSD value common to both cut 1 and 2 within each harvest schedule

[§] total yield values across harvest schedules followed by different upper case letters differ significantly ($p<0.05$) using a protected LSD test

[*] number in parenthesis indicates percentage increase over the next lower level of N

Table 9.4: The regression parameters of dry matter yield (Mg ha^{-1}) against canopy height (cm) of switchgrass grown at Montréal, Québec. Data were combined for three cultivars and three N levels.

Harvest schedule		Predictive equation	r^2	Significance of coefficient	
				b_0[‡]	b_1[¶]
4 weeks					
1995	cut1	Yld = -2.31 + 0.088Height	0.54	ns[#]	*
	cut2	Yld = -2.27 + 0.068Height	0.68	ns	**
	combined[†]	Yld = -5.10 + 0.118Height	0.81	***	***
1996	cut 1	Yld = -3.93 + 0.104Height	0.60	ns	*
	cut 2	Yld = -1.90 + 0.069Height	0.68	ns	*
	cut 3	Yld = 0.68 + 0.015Height	0.35	ns	ns
	combined	Yld = -0.51 + 0.042Height	0.52	ns	***
6 weeks					
1995	cut 1	Yld = -1.28 + 0.085Height	0.28	ns	ns
	cut 2	Yld = -0.37 + 0.041Height	0.50	ns	*
	combined	Yld = -3.69 + 0.099Height	0.47	ns	**
1996	cut 1	Yld = -1.64 + 0.069Height	0.47	ns	*
	cut 2	Yld = -4.26 + 0.089Height	0.80	*	**
	combined	Yld = -4.31 + 0.093Height	0.66	**	***

[†] data combined for all cuts within year and harvest schedule

[‡] intercept of predictive equation; [¶] coefficient of the regressor variable (slope)

[#] not significantly different from zero ($p < 0.05$)

*, ** and *** statistically different from zero at $p<0.05$, 0.01 and 0.001, respectively

Table 9.5: Dry matter nitrogen concentration of switchgrass as influenced by harvest schedule and nitrogen fertilisation at Montréal, Québec. Data were averaged over the three cultivars.

Harvest schedule	N level (kg ha^{-1})	Nitrogen concentration (g kg^{-1} DM)				
		1995		1996		
		Cut 1	Cut 2	Cut 1	Cut 2	Cut 3
4 weeks	0	9.41b	13.53b	14.88a	15.58c	10.39b
	75	9.78b	14.18b	15.09a	18.91b	12.89a
	150	10.94a[†]	15.18a	17.23a	20.22a	14.43a
LSD		1.28	1.00	2.79	1.12	1.70
6 weeks	0	8.32b	8.75a	10.89b	12.53b	
	75	9.30a	9.67a	13.52a	13.87b	
	150	9.51a	10.22a	14.88a	16.91a	
LSD		0.72	0.51	1.72	1.61	
End of season[‡]	0		5.96b			5.08a
	75		6.58b			5.39a
	150		9.16a			5.95a
LSD			1.96			0.90

[†] means in each column, within each harvest schedule, followed by a different letter differ significantly ($p<0.05$) using an ANOVA protected Least Significant Difference (LSD) test

[‡] only one cut made at the end of the season

Fig. 9.1: Mean weekly maximum and minimum temperatures and weekly rainfall totals for 1995 and 1996 at the Emile A. Lods Research Centre, Montréal, Québec.

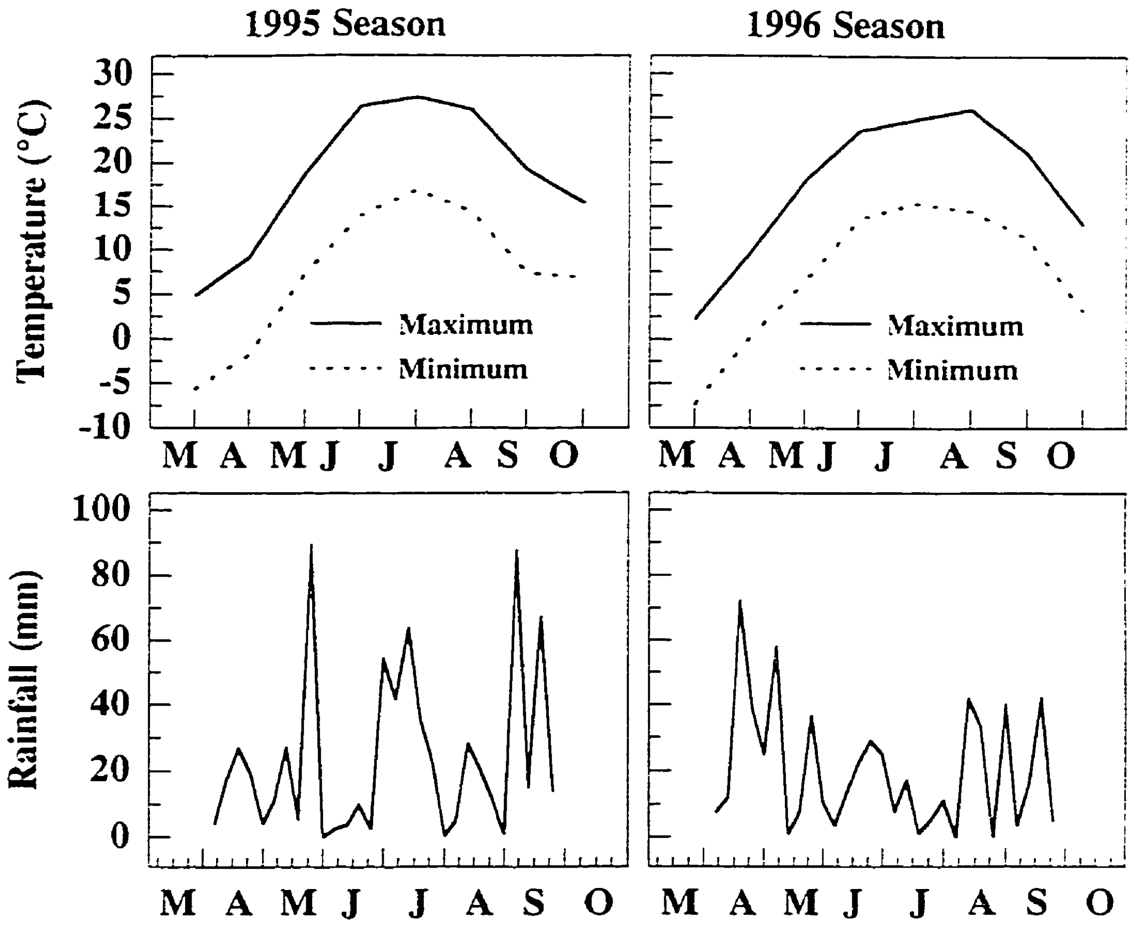

1995 Season
1996 Season
Temperature (°C)
30
25
20
15
10
5
0
-5
-10
Maximum
Minimum
Maximum
Minimum
M A M J J A S O
M A M J J A S O
Rainfall (mm)
100
80
60
40
20
0
M A M J J A S O
M A M J J A S O

Fig. 9.2: Herbage dry matter yield of switchgrass as influenced by nitrogen fertilisation and harvest frequency at Montréal. 1996. Bars extending beyond symbols denote SE.

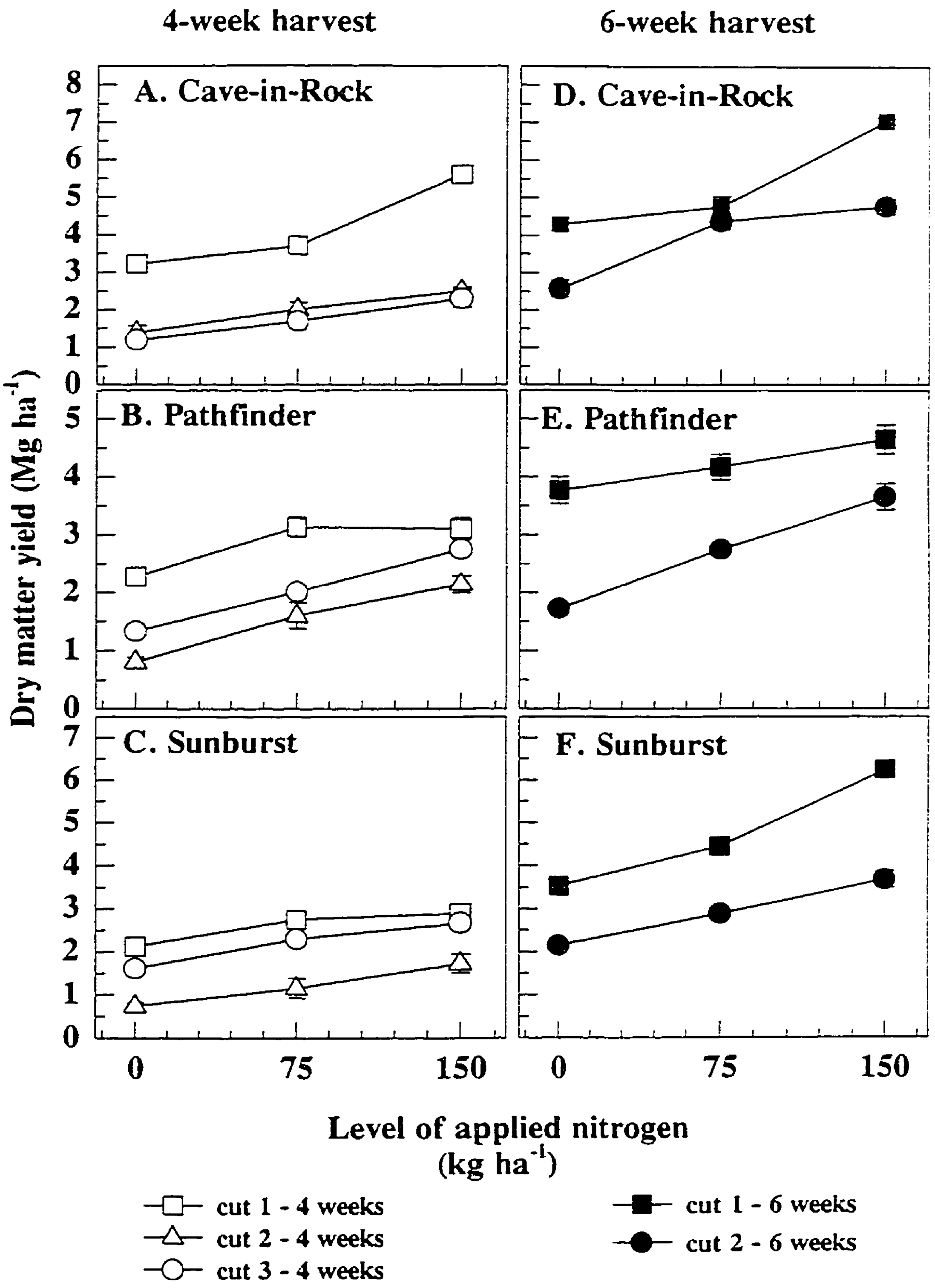

4-week harvest
6-week harvest
A. Cave-in-Rock
B. Pathfinder
C. Sunburst
D. Cave-in-Rock
E. Pathfinder
F. Sunburst
Dry matter yield (Mg ha^{-1})
0
1
2
3
4
5
6
7
8
0
75
150
Level of applied nitrogen (kg ha^{-1})
cut 1 - 4 weeks
cut 2 - 4 weeks
cut 3 - 4 weeks
cut 1 - 6 weeks
cut 2 - 6 weeks

Fig. 9.3: Changes in herbage nitrogen concentration with time of uncut switchgrass fertilised at different rates of nitrogen, Montréal, Québec. The data were averaged across cultivar and year. Bars extending beyond symbols denote SE.

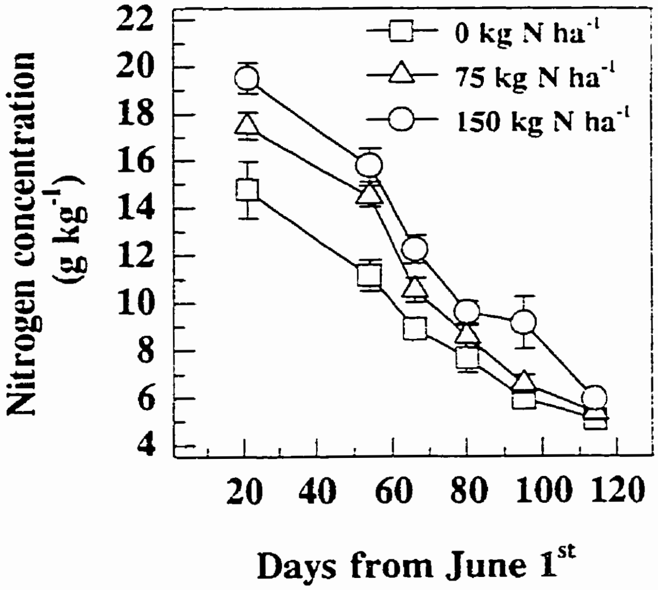

0 kg N ha^{-1}
75 kg N ha^{-1}
150 kg N ha^{-1}
Nitrogen concentration (g kg^{-1})
22
20
18
16
14
12
10
8
6
4
20
40
60
80
100
120
Days from June 1st

Fig. 9.4: Seasonal changes in chlorophyll meter readings of uncut switchgrass and their relationship to seasonal changes in herbage nitrogen concentration as influenced by: A and B, cultivar; C and D, fertiliser level. Readings were taken on the top most fully expanded leaves. Bars extending beyond symbols denote SE.

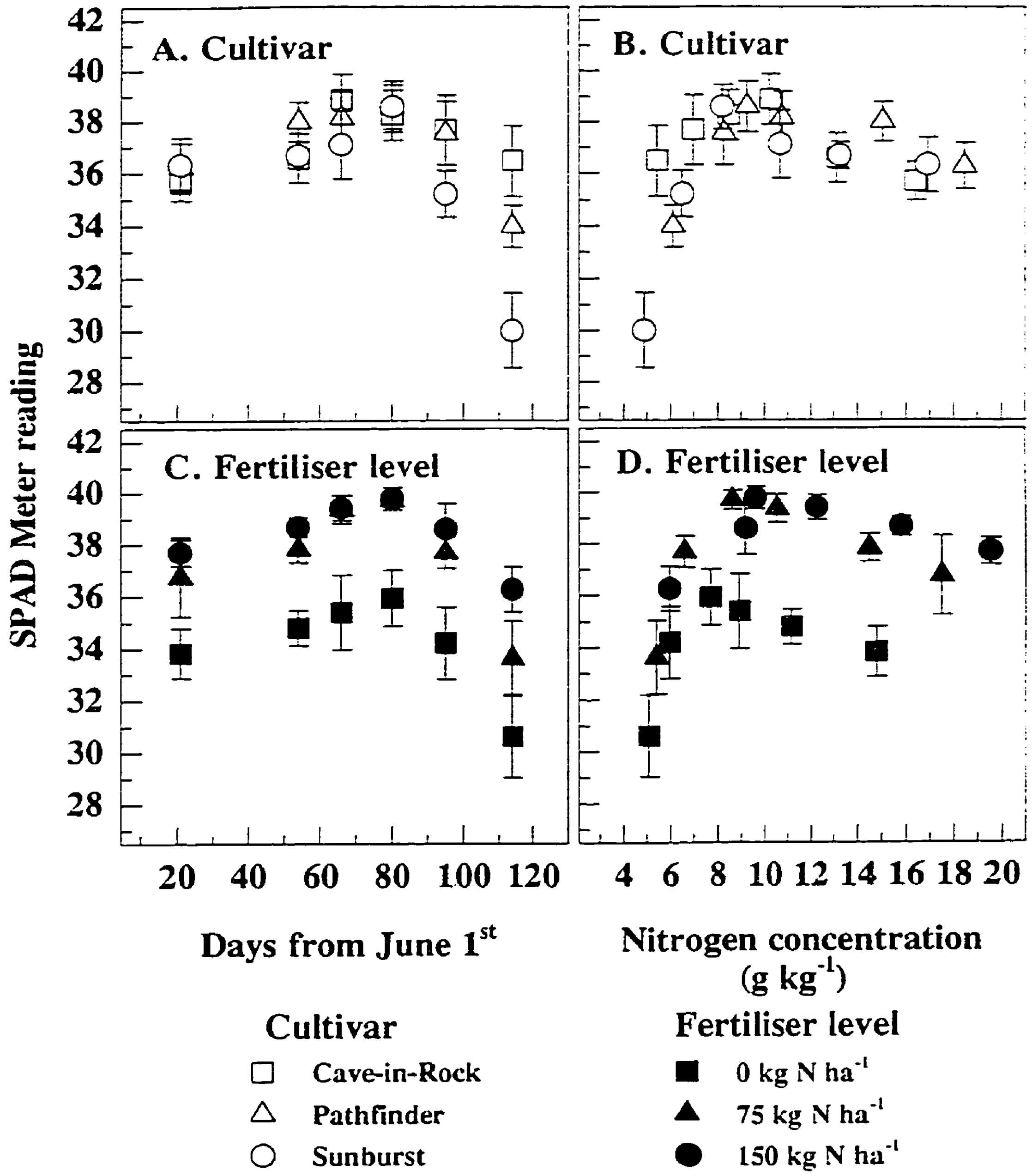

A. Cultivar
B. Cultivar
C. Fertiliser level
D. Fertiliser level
SPAD Meter reading
42
40
38
36
34
32
30
28
20 40 60 80 100 120
Days from June 1st
4 6 8 10 12 14 16 18 20
Nitrogen concentration (g kg-1)
Cultivar
□ Cave-in-Rock
△ Pathfinder
○ Sunburst
Fertiliser level
■ 0 kg N ha-1
▲ 75 kg N ha-1
● 150 kg N ha-1

Fig. 9.5: Herbage nitrogen concentration as a function of chlorophyll meter readings for switchgrass harvested at A) four week intervals, and B) six week intervals. Data were combined for three cultivars and three N levels of fertilisation. Bars extending beyond symbols denote SE.

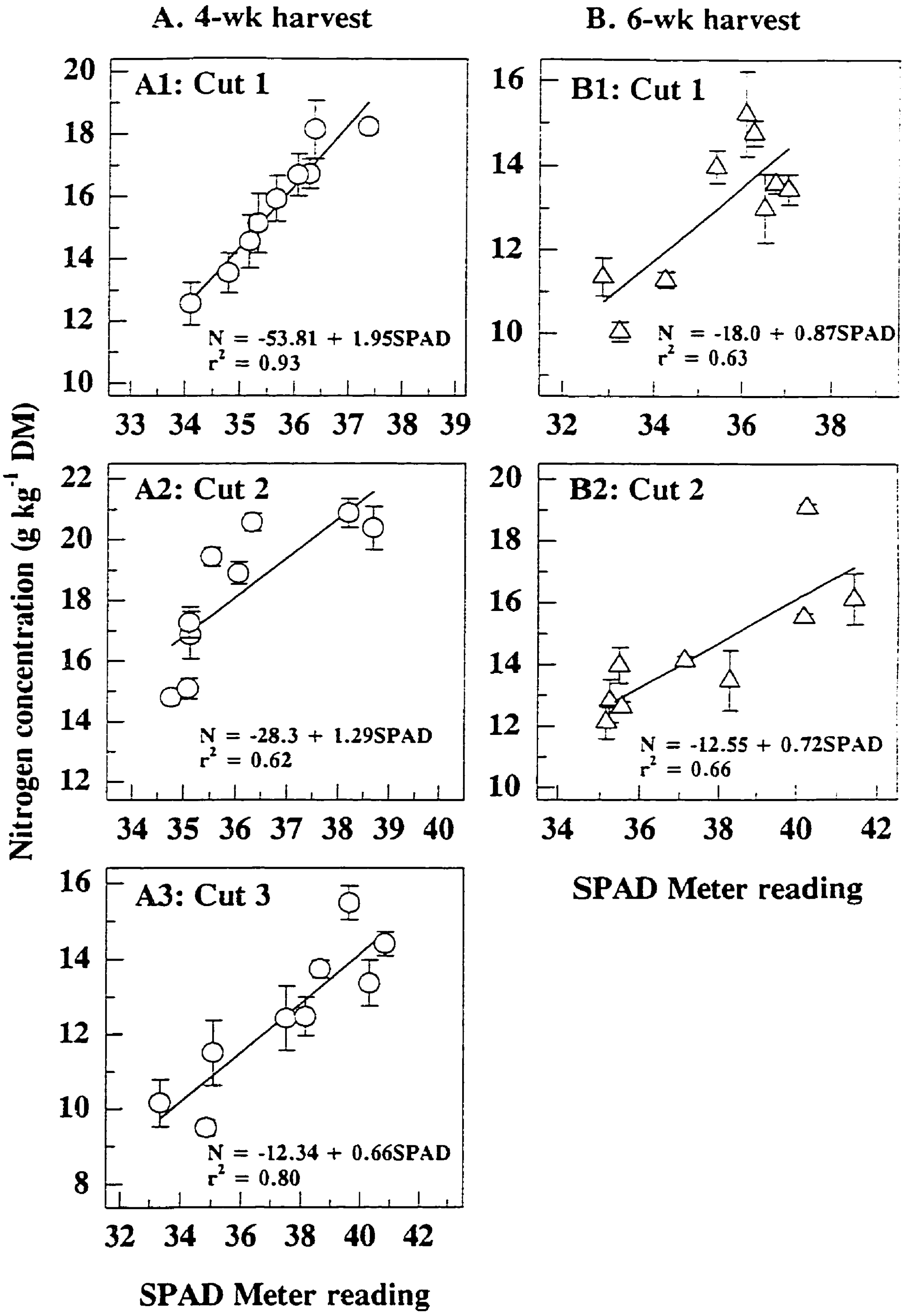
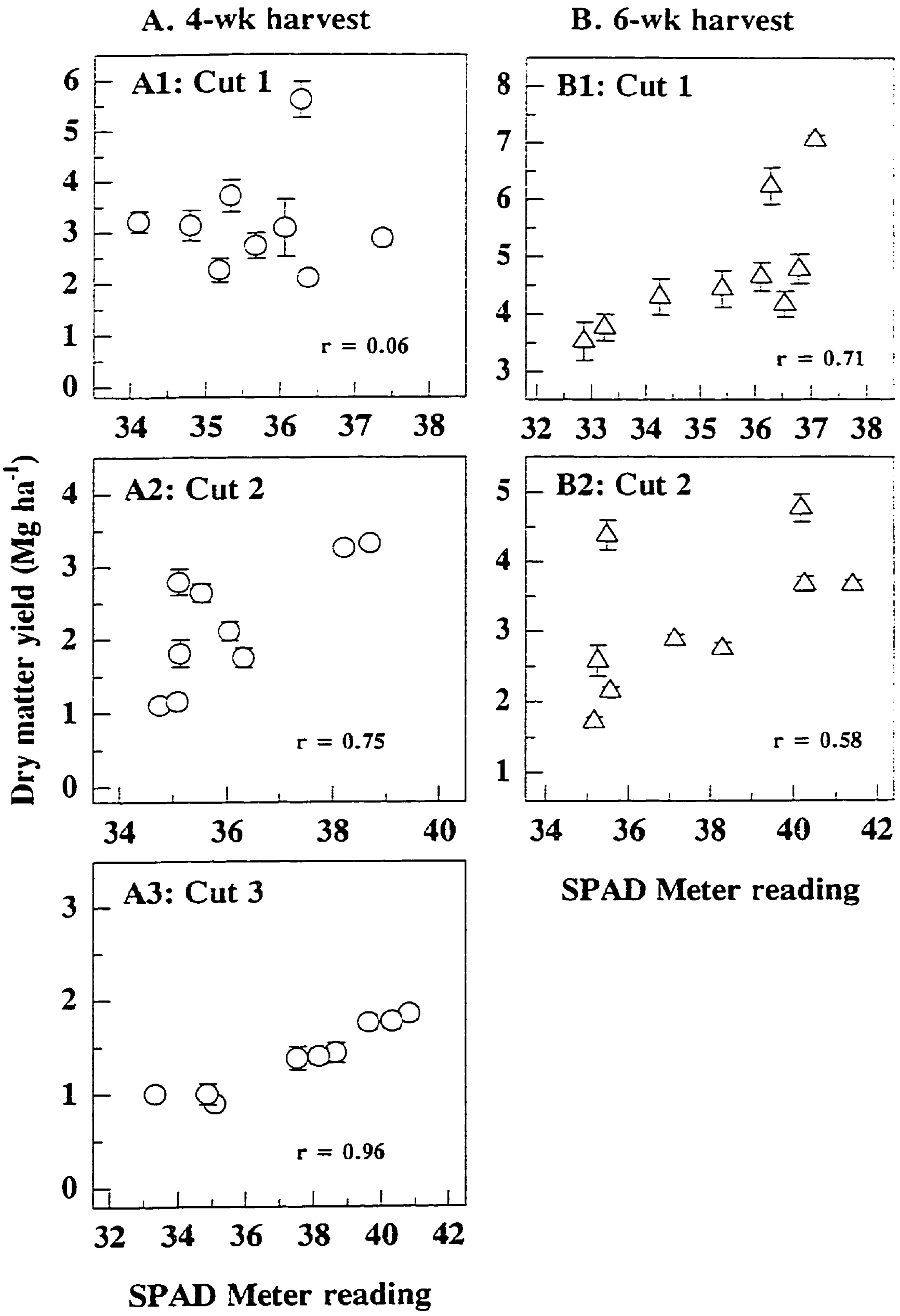

A. 4-wk harvest
B. 6-wk harvest
A1: Cut 1
N = -53.81 + 1.95SPAD
r² = 0.93
20
18
16
14
12
10
33 34 35 36 37 38 39
B1: Cut 1
N = -18.0 + 0.87SPAD
r² = 0.63
16
14
12
10
32 34 36 38
A2: Cut 2
N = -28.3 + 1.29SPAD
r² = 0.62
22
20
18
16
14
12
34 35 36 37 38 39 40
B2: Cut 2
N = -12.55 + 0.72SPAD
r² = 0.66
20
18
16
14
12
10
34 36 38 40 42
A3: Cut 3
N = -12.34 + 0.66SPAD
r² = 0.80
16
14
12
10
8
32 34 36 38 40 42
Nitrogen concentration (g kg⁻¹ DM)
SPAD Meter reading
SPAD Meter reading

Fig. 9.6: Correlation of the chlorophyll meter readings with herbage dry matter yield for switchgrass harvested at A) four week intervals, and B) six week intervals. Data were combined for three cultivars and three N levels of fertilisation. Bars extending beyond symbols denote SE.


A. 4-wk harvest
B. 6-wk harvest
A1: Cut 1
r = 0.06
B1: Cut 1
r = 0.71
A2: Cut 2
r = 0.75
B2: Cut 2
r = 0.58
A3: Cut 3
r = 0.96
Dry matter yield (Mg ha^{-1})
SPAD Meter reading
SPAD Meter reading
0
1
2
3
4
5
6
7
8
32
33
34
35
36
37
38
40
42

Preface to Chapter 10

Chapter 10 is based on a technical report initially prepared for the Pulp and Paper Research Institute of Canada and subsequently submitted for publication to the journal *Bioresource Technology*, in 1997.

The prospects for energy production were discussed in Chapter 8, and for livestock production in Chapter 9. Pulp and paper production is one suggested end use of biomass from warm season grasses. The results of mild kraft pulping are presented in this chapter. Key pulp characteristics are presented and discussed.

Chapter 10

Kraft Pulping Characteristics and Pulp Properties of Different Warm Season (C_4) Grasses

10.1. Abstract

Non-wood fibres are increasingly being used in the pulp and paper industry to help meet the increasing world demand for paper, and as a result of escalating wood costs. Their use also helps to reduce demand on declining forest reserves. In this study, several warm season grasses, prairie sandreed (*Calmovilfa longifolia* (Hook.) Scribn.), cordgrass (*Spartina pectinata* L.), big bluestem (*Andropogon gerardii* Vitman), hybrid pennisetum (*Pennisetum purpureum* Schum.), and switchgrass (*Panicum virgatum* L. cv. Cave-in-Rock (CIR), Pathfinder (PF) and New Jersey 50 (NJ50), were evaluated as potential raw materials for pulp and paper production. Raw material chemical composition, kraft pulp yield and properties, and fibre characteristics were evaluated. All these grasses were easily pulped under a mild kraft process, with pulp yields ranging from 44 to 51%, and kappa numbers ranging from 9 to 16. The weight-weighted fibre length ranged from 1.29 to 1.43 mm, the highest value being recorded for big bluestem. Pulp freeness ranged from 139 mL for hybrid pennisetum to 411 for NJ50. Sandreed, NJ50, and big bluestem had high tear indices of 7.49, 7.12 and 7.07 mN.m^2 g^{-1}, respectively. Only the hybrid pennisetum, cordgrass, and sandreed had burst indices above 5.0 kPa.m^2 g^{-1} (5.85, 5.68 and 5.22 kPa.m^2 g^{-1}, respectively). Other physical and strength properties are also presented.

10.2. Introduction

10.2.1. The case for non-wood fibre

Wood is largely the conventional raw material for pulp and paper production in the world with over 90 % of the world production (155 million tonnes, (FAO, 1994)) being produced in developed countries. In the developing world, fibre is mainly produced from non-wood sources (accounting for 97 % of world non-wood pulp production). Despite these production statistics there is an ever increasing interest in non-wood fibres even in seemingly forest rich regions like Canada and the USA. In the developed world, this interest has been largely driven by external factors like increasing environmental awareness and recycling issues. Over the years, there have been increased concerns with regard to forest preservation and reduction of carbon monoxide and dioxide emissions associated with burning of waste and agricultural residues (McCloskey, 1995; Wislon, 1996). Surplus food supply has also called for alternative uses of agricultural land to food production. More recently, market conditions and wood fibre shortages in areas like the North American west coast (Jacobs *et al.*, 1996) coupled with high prices for recyclable waste paper have also increased interest in non-wood fibre sources.

Non-wood fibre sources offer several advantages in addressing this situation. For one, they can be produced annually in agricultural systems (renewable resource) compared with the long growth cycles for wood. Non-wood fibre sources, especially grasses, have lower lignin contents, and they are more easily delignified, requiring milder and faster cooking conditions, than wood sources (Paavilainen, 1994). The resultant pulp can be used in every grade of paper and board, fibreboard and composite materials (Hurter, 1990). In the developing world, increased research into non-wood fibres is a result of increased paper demand in these regions (Wilson, 1996) as well as an increased effort to design environmentally-efficient mills.

10.2.2. *Warm season grasses in North America*

Recent years have seen increased interest in warm season grasses in North America for summer forage, soil conservation and biomass production (Jung *et al.*, 1990; Stout and Jung, 1995; Sanderson *et al.*, 1996). These grasses are characterised by high optimal temperatures for photosynthesis (Edwards and Walker, 1983) and thrive during the summer months when high temperatures limit production from cool season (C_3) plants. However, these grasses have been adopted to only a limited scale in Canada. Much of Canada is characterised by cool temperatures in spring and early summer and again in fall, resulting in a short growing season. However, mid summer conditions can be too warm for cool season grasses, and suitable for warm season ones. In a four year field evaluation several warm season grass species showed potential in south-western Québec (Madakadze *et al.*, 1996a). Several North American collections of switchgrass, big bluestem, prairie sandreed, cordgrass and indian grass (*Sorghastrum nutans* L. (Nash)) were evaluated in that study. These collections exhibited differences in morphological development, dry matter yield, and tissue proportions of the dry matter. As a result, different collections showed potential for forage or biomass production. Biomass produced from such sources can be used for energy and industrial chemical production and/or pulp and paper raw materials.

The objective of this study was to evaluate kraft pulping characteristics and pulp properties of switchgrass, sandreed, cordgrass, big bluestem and hybrid pennisetum.

10.3. Materials and Methods

10.3.1. Pulping and pulp processing

The grass collections used in this study were Cave-in-Rock, Pathfinder and New Jersey 50 switchgrasses, Niagara big bluestem, CWNC cordgrass, PI 477011 sandreed and SDPN3 hybrid pennisetum. A summary of their agronomic characteristics is presented in Table 10.1. These grasses were grown at the Emile A. Lods Research Centre, McGill University, Ste Anne-de-Bellevue, Québec, Canada. They were harvested in mid-October of 1995, air dried, and kept in loose bales until required. Before pulping the grasses were cut into about 2 cm long pieces and washed with water to remove adhering soil particles, air dried, and stored with less than 15% moisture content.

Kraft pulp from each entry was prepared by pulping 200 g (oven dry weight) grass using a 14 % active alkali (AA) and 20 % sulphidity using a 5:1 liquid to grass ratio, excluding moisture. The pulping was done in 2-L rotating bomb digesters at a cooking temperature of 160 °C, being allowed 60 minutes to reach this temperature, and another 60 minutes at this temperature. After collecting about 150 mL of black liquor for analysis, the cooked grasses were disintegrated in a Cowles mixer (Louis Allis Co., Milwaukee, Wisconsin, USA) for two minutes followed by thorough washing with tap water. The pulp was soaked in tap water overnight followed by screening on a vibrating flat screen with 0.2 mm wide slots. The screened pulp was captured on a 450 mesh screen, small enough to retain fines. The pulp was concentrated by a centrifuge to about 30% solids and weighed. Rejects and a subsample of the pulp were dried to constant weight at 105 °C for determination of dry weight. Three independent cooks, including pulp processing, were conducted for each entry.

10.3.2. Chemical analyses and physical testing

Subsamples of the raw materials were analysed for ash, nitrogen(N), lignin, pentosans and extractives using Standard Tests Methods of the Canadian Pulp and Paper Association (CPPA, 1994). Black liquor was analysed for residual effective alkali (EA) and sulphides using the ABC test (TAPPI, 1992). Ultraviolet spectroscopy analysis of dilute (1:1000) black liquor samples were conducted using 0.1 N NaOH as the diluent. Pulp physical properties (freeness, bulk and density) were also determined using standard CPPA procedures. Fibres from the screened pulp were characterised using the Kajaani FS 200 optic fibre analyser and the Bauer-McNett classifier. Kappa numbers were determined on screened pulp. Optical and scanning electron microscopy were also used to characterise the pulp and pulp handsheets.

10.4. Results and Discussion

10.4.1. Chemical composition

The chemical composition of the raw materials is presented in Table 10.2. The low N contents of these grasses is typical of material harvested at the end of the season. Plant material composition/quality changes during the course of the season. Nitrogen content declines as the season advances while structural components like cellulose, hemicellulose and lignin increase (Jung *et al.*, 1990; Sanderson and Wolf, 1996b). The increase in structural components reaches a maximum during flowering.

Pennisetum had the lowest lignin content while the other entries averaged 23%. These values are, on average, higher than in wheat straw (*Triticum* spp., 17.1%; Montane *et al.*, 1996) or kenaf (*Hibiscus* spp., 14.7%; Mittal, 1990), comparable to those for bamboo (*Bambusa* spp. L., 23 %) and lower than for wood based materials (26-30 %; Moore, 1996). These grasses have high proportions of higher molecular weight cellulose and hemicellulose (α and γ cellulose fractions, respectively). Pentosan contents are comparable to those of hardwoods (19-25 %, Technical Association of Pulp and Paper Industries (TAPPI) standard) and kenaf (20.2 %, Mittal, 1990). Both cold and hot water extractives were higher for the hybrid pennisetum and the sandreed than the other entries, suggesting higher of inorganic compounds, tannins, gums, sugars and colouring matter, and starches in the former.

The ash content average of 5% was lower than the 9% reported for reed canary grass (*Phalaris arundinacea* L.) and comparable to the 5.4% for wheat straw (Pahkala *et al.*, 1994). These ash contents are still high, especially given the higher acid insoluble ash than in wood, for industrial processing. Due to the nature of field operations, these raw materials would inevitably contain soil. In our case, ash contents were reduced by 1-2 % by washing before pulping. This indicates that processing economics (with reference to reduced ash in recycled chemicals) can be improved by thorough cleaning of the raw materials. Based on the relatively low lignin contents in Table 10.2 these grasses should be easier to pulp than wood.

10.4.2. Pulping

Table 10.3 summarises the pulping results obtained using the mild kraft conditions. Judging by the low amount of rejects and kappa numbers the different grasses were well pulped. The pulping results were subjected to analysis of variance (ANOVA) with variation being partitioned for entry and cook, followed by a Least Significant Difference(LSD test $p<0.05$) using SAS procedures. New Jersey 50 (NJ50) had the highest total yield and sandreed the least. The total yields were also compared at a kappa number of 13.3 (numerical average for all pulps), and assuming a a total yield reduction of 0.15% per kappa number. For these adjusted total yields NJ50, big bluestem and pennisetum were not different (51.1, 51.1 and 50.6%, respectively, Table 10.3). Differences in rejects, kappa numbers and residual alkali partly reflect differences in pulping kinetics of the individual grasses. Cordgrass and sandreed were characterised by low total yield and rejects and relatively higher kappa numbers. Residual alkali was also low for these two entries. It is probable that for these two grasses there was increased solubilisation of dry matter constituents (other than lignin) which resulted in greater consumption of alkali. Given the high viscosity values for these two species, the high consumption of alkali was not from fibre degradation but more likely, solubilisation of the high leaf portions (Table 10.1). It was also interesting to note that there were no sulphides detected in the black liquor following pennisetum pulping, in each of the three different cooks. Put together, differences in rejects, kappa numbers, and residual EA and sulphides between species suggest that the pulping conditions and white liquor concentrations nedd to be optimised for each species.

The UV and short wavelength visible spectra (190 to 800 nm), of the diluted black liquors are shown in Fig. 10.1. Generally, the spectra showed one pronounced peak at about 220 nm and another at about 288 nm (292 nm for pennisetum). A third weakly defined peak was present at 334 nm for pennisetum and at 354 nm for cordgrass and sandreed. These differences reflect differences in chemical bonding in the different lignins. In general, they resemble the UV spectrum for pure pine lignin in the same solvent.

10.4.3. Fibre characteristics

NJ50 and big bluestem had higher arithmetic, length-weighted and weight-weighted means than the other entries (Table 10.4). These length-weighted fibre lengths are comparable to those of reed canary grass (0.8-0.9 mm) and wheat straw (0.8 mm) reported by Paavilainen and Togilsson (1994). In general, the arithmetic mean lengths of fibres for the seven grasses were on the lower end of the range 0.26-1.32 mm for various wheat straws, shorter than 0.54 mm for eucalyptus (*Eucalyptus* spp.) and 0.62 mm for Canadian aspen (*Populus spp.*) pulps cited by Jacobs *et al.* (1996). The mean weight-weighted fibre lengths of the grasses were higher than for the two cited wood pulps (0.69 and 0.80 mm for eucalyptus and aspen, respectively) . The fibre distribution curves for the pulps (Fig. 10.2) indicate a high proportion of short fibres. The distribution curves for pennisetum were narrower than any of the other pulps indicating a relatively higher degree of fibre uniformity. The Kajaani proportions of fines (P<0.2 mm) ranged from 44 to 53 %, with values for pennisetum, sandreed and CIR above 50 %. However, these proportions were not all the same as the Bauer-McNett proportions of fines (Fig. 10.3). For Pathfinder (PF), cordgrass, and sandreed values from these two methods were similar while for CIR, NJ50, big bluestem and pennisetum the Kajaani proportion of fines were greater than those from the Bauer-McNett classification. Except for CIR (which had a high 48/100 and low 100/200 proportions), the combined Bauer-McNett 100/200 and 200 fractions approximated the Kajaani proportion of fines.

The light micrographs of the pulps and the surface and cross section scanning electron micrographs of different handsheets are presented in Figs. 10.4, 10.5 and 10.6, respectively. In Fig. 10.4, as in most non-wood pulps (Hua and Xi. 1988). several cell types could be distinguished. In addition to the fibres, the other cell types that were evident include narrow epidermal cells with hook-like serrulate margins; parenchyma cells that ranged from ball-shaped to barrel-shaped; vessel elements with or without pitting, and with open ends. In general the fibres were narrow and slender. Pennisetum and sandreed pulps showed high proportions of fines and/or non fibre contents. The serrulate epidermal cells and open ended vessel elements were clearer in the surface SEM micrographs (Fig. 10.5). Differences in sheet density/porosity are were also evident from these surface micrographs, pennisetum being characterised by high density sheets. The cross sectional SEM revealed differences in sheet consolidation. Density of the sheets increased in the order PF < sandreed < cordgrass < NJ50 < big bluestem < pennisetum (Fig. 10.6). Pennisetum also had less variation in sheet density. In all cases, density was higher near the sheet surfaces, a result of the pressure applied during sheet making.

10.4.4. Physical and strength properties

The pulp physical properties are also summarised in Table 10.4. NJ50 and PF had the highest freeness and pennisetum the lowest (411, 407 and 139 mL, respectively). These freeness values could be explained partly by differences in apparent density. Pennisetum also displayed the lowest bulk (specific volume) and thickness of handsheets produced from any of the entries. The thickest handsheets were recorded for CIR and PF. Except for pennisetum, bulk values for the grass pulps in our study are higher than reported values for corn stalk and wheat straw (1.52 and 1.41 $cm^3\ g^{-1}$, respectively)(Lavoie *et al.*, 1996).

The strength properties presented in Table 10.5 were compared statistically using a protected LSD ($p<0.05$) following a one factor ANOVA (Steel and Torrie, 1980), using SAS procedures. The burst index was highest for pennisetum and cordgrass followed closely by sandreed. For the switchgrasses, the average burst index was 4.15 $kPa.m^2\ g^{-1}$, lower than for big bluestem. Cordgrass and pennisetum also had the highest breaking lengths and the switchgrasses the lowest, averaging 7.6 km. However, while cordgrass maintained a high ranking in zero-span breaking length (Z-span), pennisetum had the lowest value. Switchgrass cultivars averaged 76 $N.m\ g^{-1}$ in tensile strength and sandreed, big bluestem, pennisetum and cordgrass had 8, 14, 23 and 23 % more. Although cordgrass and pennisetum had similar tensile strengths more energy was required to rupture pennisetum sheets (TEA index). The relationships between tear index and Z-span, tensile strength and fibre length, α-cellulose and tensile index are presented in Fig. 10.7. Tensile strength was linearly ($r^2 = 0.72$) related to the proportion of

α-cellulose in the raw materials. The log-log relationship between tear index and z-span breaking length was also linear ($r^2 = 0.65$) while the coefficient of determination for a linear fit to the plot of tear index against weight-weighted length was low at 0.27. Pennisetum pulp also had air resistance values more than 50 times higher than the average (19 s 100 mL^{-1}) of the other entries. The tear and burst indices we are reporting were higher to than for corn stalk (4.0 $mN.m^2\ g^{-1}$ and 3.8 $kPa.m^2\ g^{-1}$, respectively) and comparable to those reported for wheat straw, 5.2 and 5.9, respectively (Lavoie *et al.*, 1996). The high burst and tensile indices recorded for pennisetum and cordgrass are in the lower end of the ranges (burst, 5.9-7.15 $kPa.m^2\ g^{-1}$

and tensile, 94 - 108 Nm g^{-1}) reported for coniferous kraft pulps (Akhtaruzzaman and Shafi, 1995).

The optical properties presented in Table 10.6 were determined on unbleached pulps and handsheets. The following points need to be taken into consideration when interpreting these results: a) many of these properties can easily be manipulated by various bleaching treatments, and b) the paper making processes will greatly determine the final optical properties. Both these considerations are beyond the scope of this study. Pulp brightness ranged from 26 to 36% with NJ50 pulp being brightest. In general, these pulps should be very easy to bleach. The recorded brightness compares well with that of kraft pulp of jute (*Corchorus* spp.) (18.3-27.6 %; Akhtaruzzman and Shafi (1995)) but lower than that of linseed (*Linum usitalissimum* L.) stalks (43-53 %), pulped at the same alkali charge (Shaikh *et al.*, 1992). Opacity values were lowest for big bluestem and pennisetum, the margin of difference between highest and lowest being larger in the TAPPI than the ISO scale. The relationship between coarseness and the light scattering ability of the different handsheets is illustrated in Fig. 10.8. Pulps with low coarseness are more effective in scattering light. This follows directly from the inverse proportionality of total refractive surfaces and coarseness (Karenlampi *et al.*, 1994).

10.5. Conclusion

Chemical analysis of seven warm season grasses showed Klason lignin values ranging from 17.7 to 24% which are in the typical range for non-wood materials. They can be pulped easily with the conventional kraft pulping process. Pulping yields of 44 to 51% were obtained, with kappa numbers ranging from 9.2 to 15, using 14% AA and 1 hour cooking at 160 °C. The pulp from these grasses was characterised by short fibres and high proportions of fines. If substituted for hardwoods this pulp could provide good printability properties to paper. The pulp can also be used in speciality products like tea bags, filters, cigarette paper, and bank notes.

Species differences were evident in both pulping characteristics and pulp properties. Further studies on optimisation of pulping conditions would be needed for successful adoption of each species. Though the grasses used in this study were produced under the same environmental conditions, it is conceivable to have fluctuations in pulping characteristics as influenced by growing conditions. Soil type, fertilisation, plant age, and climate are factors that affect chemical compositions of plant material.

Table 10.1: A summary of the main agronomic characteristics of seven warm season grasses

Entry	Seasonal maximum height (cm)	Average tiller diameter (cm)	Leaf:Stem ratio (%)	Dry matter Yield (Mg/ha)
Cave-in-Rock	166	0.47	28.21	12.58
Pathfinder[†]	149	0.46	30.31	11.06
New Jersey 50	172	0.50	21.11	12.92
Big Bluestem	147	0.47	29.17	8.49
Cordgrass	222	0.77	50.00	13.95
Sandreed	186	0.56	52.27	5.64
Hybrid Pennisetum	240	2.22	49.60	-----[‡]

[†] material used was a population selected for biomass yield from the original Pathfinder by A. McElroy, Agriculture and Agri-Food Canada, Ottawa.

[‡] yield not determined at the Emile A. Lods Research Centre (averaged 30 Mg ha^{-1}, from senior author's work under subtropical conditions)

Table 10.2: Chemical composition of different warm season grasses

Chemical component (%)	Cave-in-Rock	Pathfinder	New Jersey 50	Big Bluestem	Cordgrass	Sandreed	Pennisetum
Nitrogen	0.69	0.66	0.63	0.85	0.52	0.83	0.84
Ash	4.83	4.36	4.97	5.44	5.18	5.41	4.23
Acid insoluble ash	1.74	2.11	2.29	1.98	2.42	3.46	0.83
Klason lignin	23.89	23.68	23.69	23.48	22.84	23.10	17.70
Cellulose[†]							
α	41.20	39.60	41.10	44.10	42.70	41.80	45.60
β	2.20	1.30	1.70	1.30	1.40	1.80	1.50
γ	30.50	32.30	30.50	28.50	29.70	28.40	29.70
Pentosans	22.90	22.30	24.00	23.00	22.60	20.60	21.50
Extractives							
cold water	1.91	3.90	1.50	2.10	2.50	5.00	9.90
hot water	3.80	3.60	2.30	2.10	3.90	7.20	10.90
1% NaOH	34.70	39.10	37.10	38.50	41.50	45.90	44.60
acetone	1.19	1.75	1.28	1.70	1.82	3.15	2.70

[†] presented as proportion of total cellulose corrected for lignin and ash

Table 10.3: Pulping characteristics of different warm season grasses

Entry	Total Yield (%)	Rejects (%)	Kappa number	Viscosity (mPa's)	Residual chemicals ($g\ L^{-1}$ as Na_2O)	
					EA[†]	Sulphides
Cave-in-Rock	47.98d (47.65)[¶]	1.18a	15.47a	30.00d	3.32c	0.34bc
Pathfinder	49.36c (49.24)	0.62bc	14.01b	37.40bc	3.21c	1.58a
New Jersey 50	51.01a[‡] (51.09)	0.65bc	12.77c	39.80ab	3.69b	1.87a
Big bluestem	50.53b (51.07)	0.82ab	9.70d	38.00bc	2.87d	1.71a
Cordgrass	47.63d (47.26)	0.40c	15.73a	40.70ab	1.32e	1.87a
Sandreed	44.11e (43.68)	0.67bc	16.13a	41.97a	1.11e	0.77b
Pennisetum	50.01b (50.63)	0.60bc	9.17d	35.00c	4.16a	0.00c
CV (%)	0.64	29.35	2.93	5.15	4.38	21.17
LSD (0.05)	0.56	0.37	0.69	3.44	0.22	0.44

[†] effective alkali

[‡] means within a column followed by different letters differ significantly at $p<0.05$, using a protected LSD test

[¶] values in parenthesis are calculated total yields at a kappa number of 13.28 (average) and assuming a reduction of total yield of 0.15 % per kappa number

Table 10.4: Fibre characteristics and pulp physical properties of different warm season grasses

Parameter	Cave-in-Rock	Pathfinder	New Jersey 50	Big bluestem	Cordgrass	Sandreed	Pennisetum
Fibre length† (mm)							
Arithmetic mean	0.32	0.35	0.36	0.36	0.34	0.32	0.30
Length weighted mean	0.76	0.80	0.81	0.81	0.75	0.81	0.75
Weight weighted mean	1.31	1.35	1.38	1.43	1.29	1.39	1.33
Coarseness ($mg\ m^{-1}$)	0.086	0.078	0.075	0.073	0.070	0.070	0.080
P<0.2mm‡ (%)	50.36	47.20	44.53	44.22	46.60	52.08	54.97
Physical properties							
CSF (mL)¶	335.00	407.00	411.00	338.00	295.00	275.00	139.00
Grammage ($g\ m^{-2}$)	61.60	59.10	59.50	59.90	59.10	57.70	60.20
Specific volume ($cm^3\ g^{-1}$)	2.03	2.09	1.92	1.90	1.99	2.03	1.47
Apparent density ($g\ cm^{-3}$)	0.50	0.48	0.52	0.53	0.50	0.49	0.68
Caliper (mm)	125.00	124.00	115.00	114.00	118.00	117.00	89.00

† as measured by the Kajaani FS 200 optic fibre analyser

‡ proportion of fibres less than 0.2mm

¶ Canadian Standard Freeness

Table 10.5: Strength properties of standard handsheets of different warm season grasses

Parameter	Cave-in-Rock	Pathfinder	New Jersey 50	Big bluestem	Cordgrass	Sandreed	Pennisetum
Burst Index (kPam^2 g^{-1})	4.06d	4.16d	4.22d	4.88c	5.68a	5.22b	5.85a
Tear index (mN.m^2 g^{-1})	5.64d	6.67c	7.12b	7.07b	6.81bc	7.49a	4.40e
Breaking length (km)	7.75d	7.74d	7.64d	8.87b	9.53a	8.37c	9.51a
Elastic modulus (km)	811.4a[†]	779.30b	758.40b	809.30a	766.00b	723.50c	776.00b
Z-span breaking length (km)	15.11c	16.19b	16.34ab	16.79ab	17.08a	15.96b	14.83c
Breaking energy (Scott bond, J m^{-2})	385bc	334.30c	362.80c	400.00b	439.50a	412.00ab	.....[‡]
Tensile Index (N.m g^{-1})	75.98d	74.88d	75.0d	87.00b	93.49a	82.05c	93.25a
Stretch (%)	1.96d	2.03d	2.03d	2.18c	2.46b	2.43b	2.86a
TEA index (mJ g^{-1})	985.53d	996.70d	997.26d	1226.22c	1483.26b	1312.83c	1812.91a
Air resistance (Gurley, s 100mL^{-1})	22.34b	10.54b	12.32b	32.78b	21.08b	16.18b	1019.02a

[†] means within a row followed by different letters differ significantly at $p<0.05$, using a protected LSD test

[‡] sample too strong

Table 10.6: Optical properties of pulp from different warm season grasses

Entry	Brightness (%)	Opacity (%) ISO[†]	TAPPI[‡]	Light scattering coefficient ($m^2 kg^{-1}$)	Light absoption coefficient ($m^2 kg^{-1}$)
Cave-in-Rock	27.59c	98.21b	94.73b	27.32e	14.33a
Pathfinder	29.30b	97.71c	93.65c	28.85d	13.14b
New Jersey 50	35.53a	96.13e	90.85d	30.47c	9.17d
Big bluestem	28.86bc	98.04b	94.29bc	27.83e	14.24a
Cordgrass	28.41cd	98.52a	95.86a	32.80b	14.62a
Sandreed	27.87cd	98.52a	95.95a	34.58a	14.63a
Pennisetum	26.15f	96.76d	91.06d	25.04f	11.92b
CV (%)	1.55	0.21	0.52	2.51	2.58
LSD (0.05)	0.59	0.27	0.68	0.96	0.44

[†] International Standards Organisation
[‡] Technical Association of Pulp and Paper Industries

Fig. 10.1: The ultraviolet and short wavelength visible spectra of lignin from warm season grasses following kraft pulping

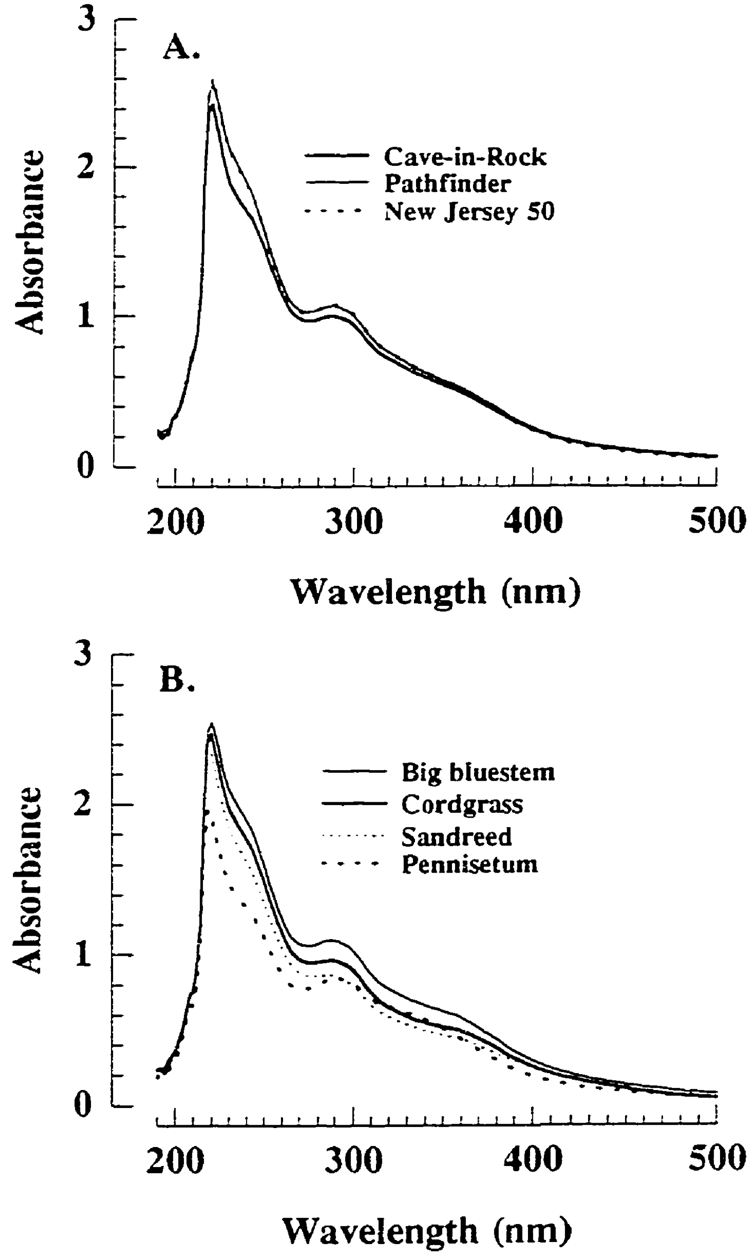

A.
Absorbance
3
2
1
0
200
300
400
500
Wavelength (nm)
Cave-in-Rock
Pathfinder
New Jersey 50
B.
Absorbance
3
2
1
0
200
300
400
500
Wavelength (nm)
Big bluestem
Cordgrass
Sandreed
Pennisetum

Fig. 10.2: The length- and weight-weighted fibre distributions of different grass species using the Kajaani FS-200 optic fibre analyser

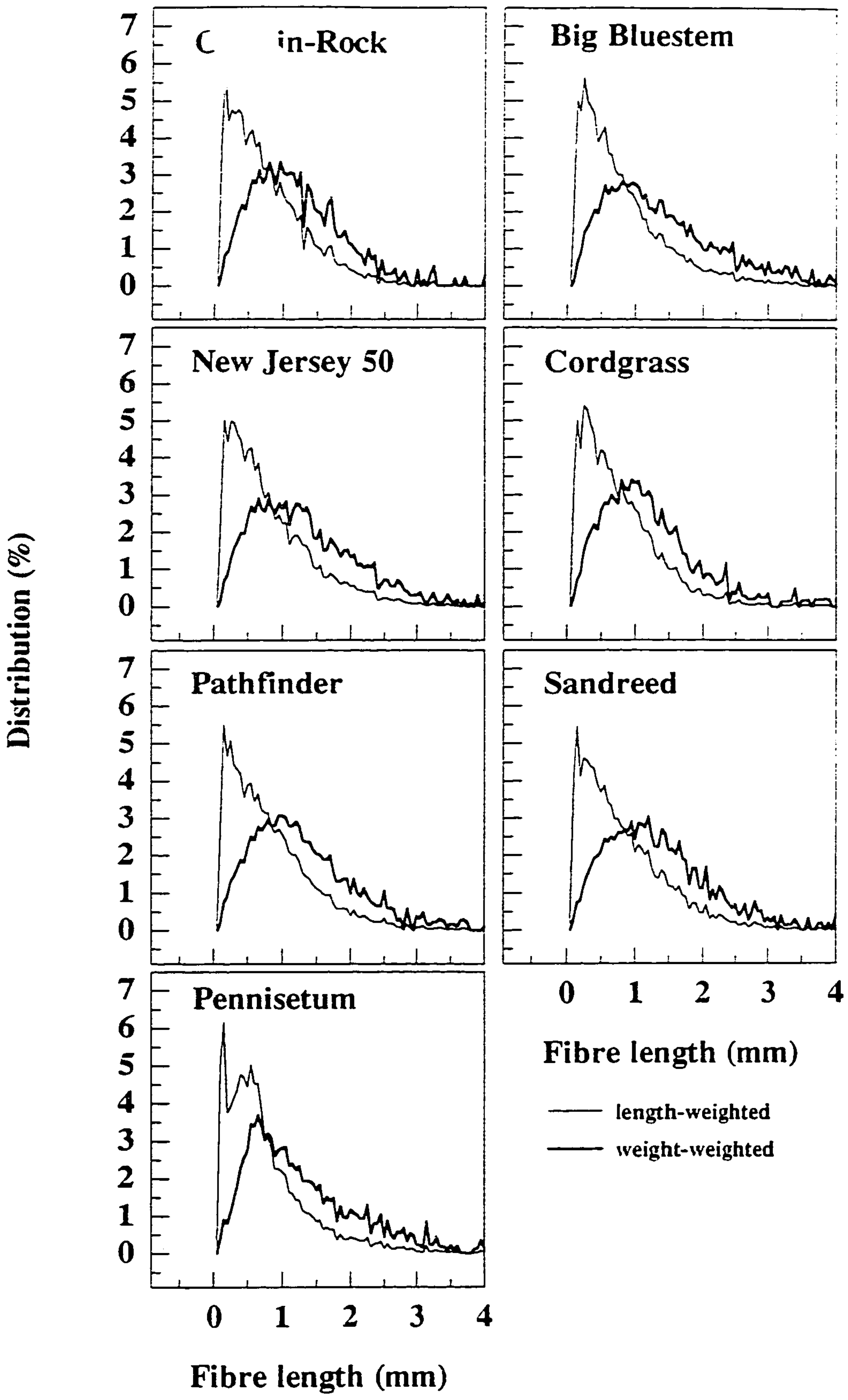

C in-Rock
Big Bluestem
New Jersey 50
Cordgrass
Pathfinder
Sandreed
Pennisetum
Distribution (%)
0
1
2
3
4
5
6
7
Fibre length (mm)
0
1
2
3
4
length-weighted
weight-weighted

Fig. 10.3: The Bauer-McNett fibre classification for warm season grasses after kraft pulping

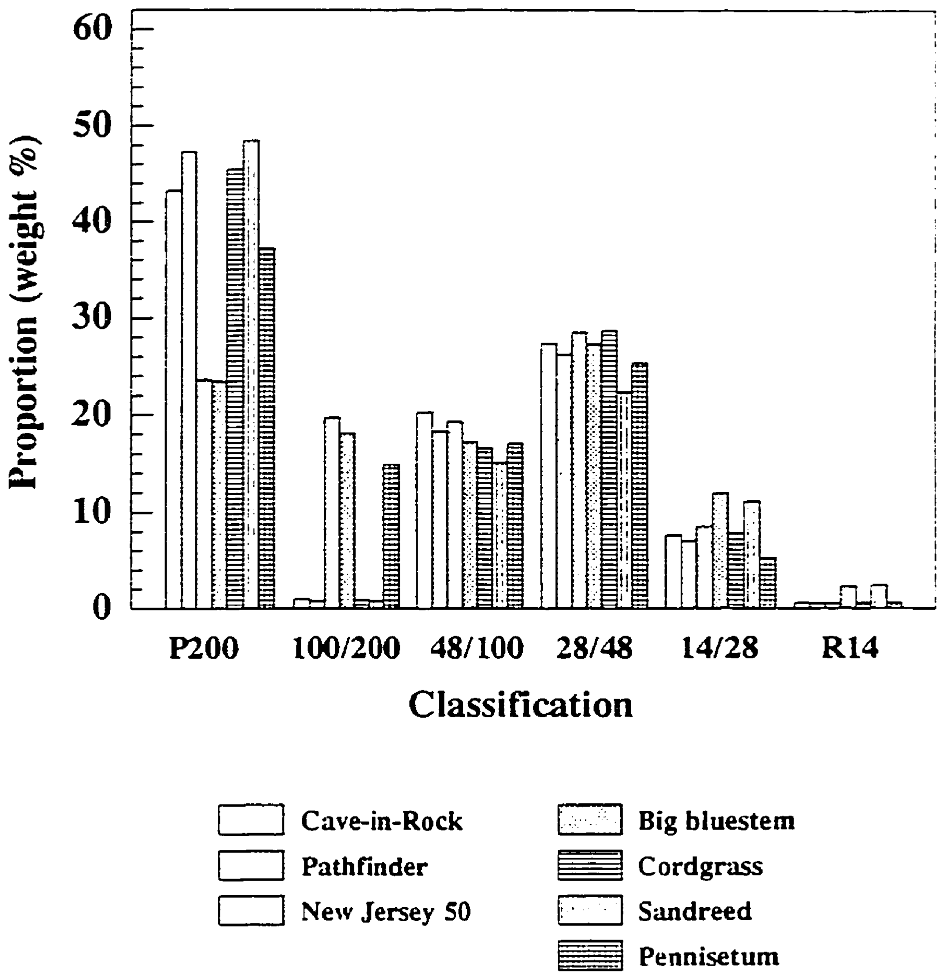

Proportion (weight %)
60
50
40
30
20
10
0
P200
100/200
48/100
28/48
14/28
R14
Classification
Cave-in-Rock
Pathfinder
New Jersey 50
Big bluestem
Cordgrass
Sandreed
Pennisetum

Fig. 10.4: Light micrographs (x93) of different kraft pulps from warm season grasses. The different cell types identified in the pulp are: e = epidermal cell; f = fibre; p = parenchyma cell; v = vessel element; pv = pitted vessel element; sv = spiral vessel element.

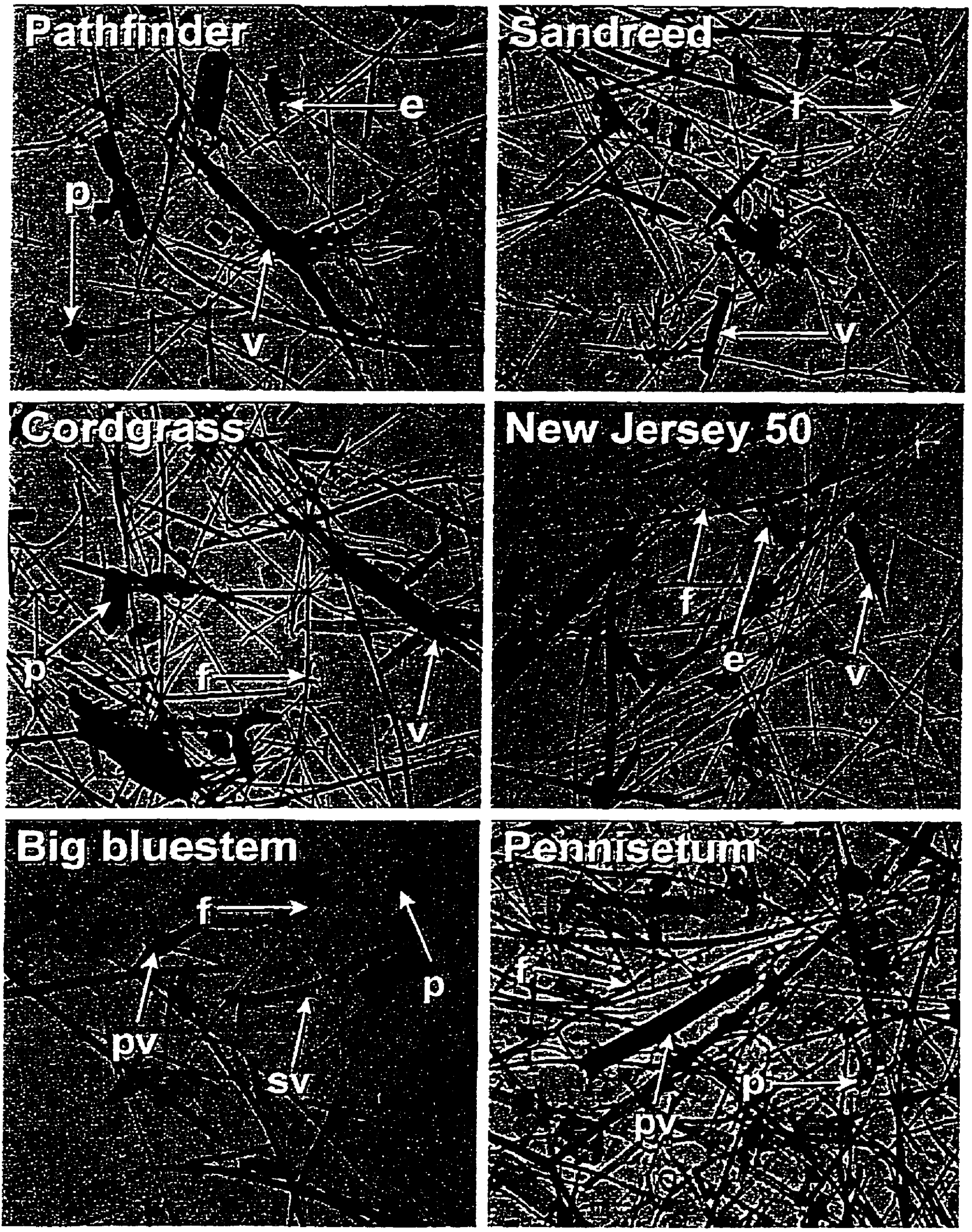

Pathfinder
e
p
v
Sandreed
f
v
Cordgrass
p
f
v
New Jersey 50
f
e
v
Big bluestem
f
p
pv
sv
Pennisetum
f
pv
p

Fig. 10.5: Surface scanning electron micrographs of pulp handsheets of different warm season grasses. Bar at the bottom of each micrograph represents 100 μm. The different cell types identified are as described for Fig. 10.4.

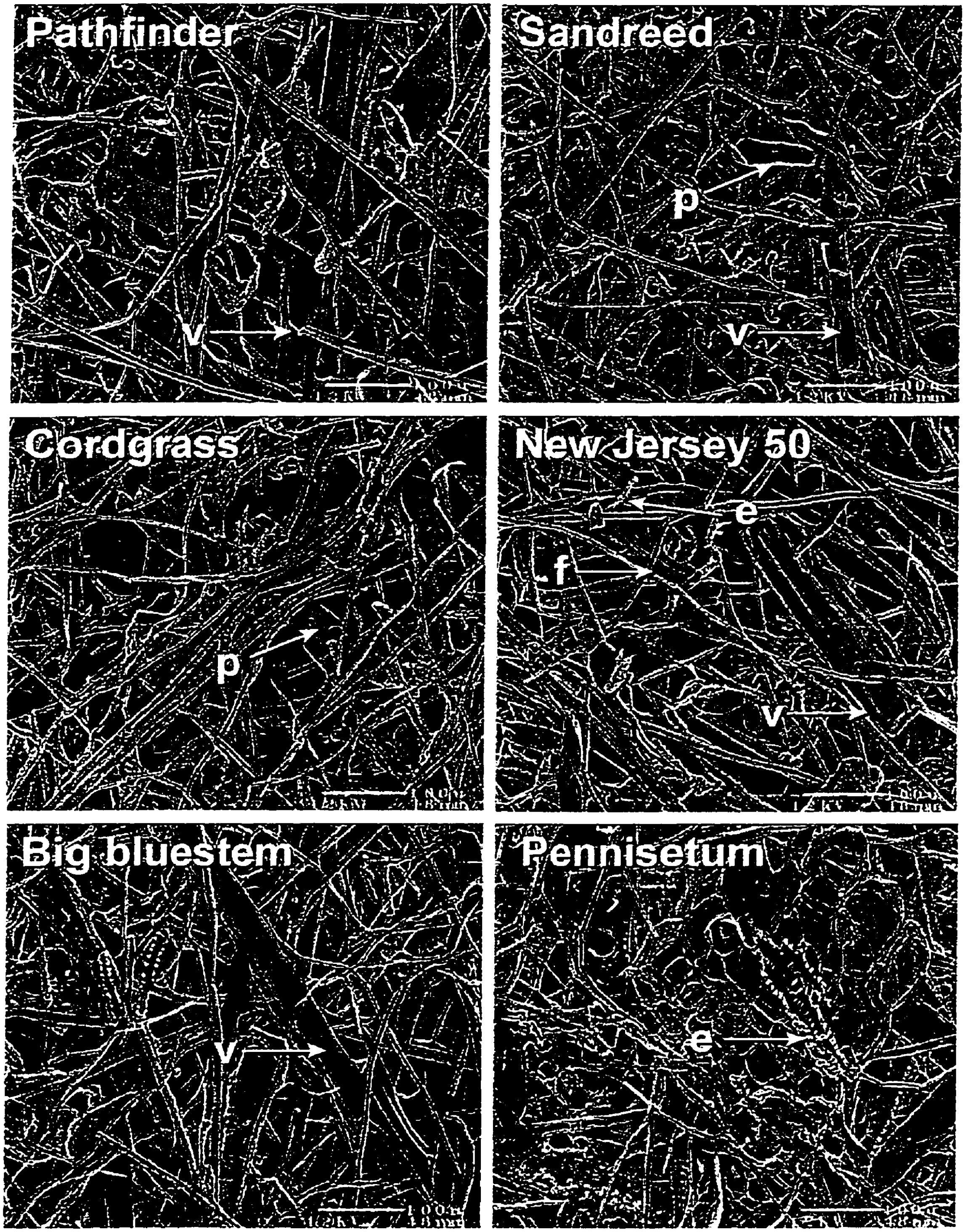

Pathfinder
v
Sandreed
p
v
Cordgrass
p
New Jersey 50
e
f
v
Big bluestem
v
Pennisetum
e

Fig. 10.6: Cross-section micrographs of pulp handsheets of different warm season grasses. Bars at the bottom of each micrograph represents 100 μm.

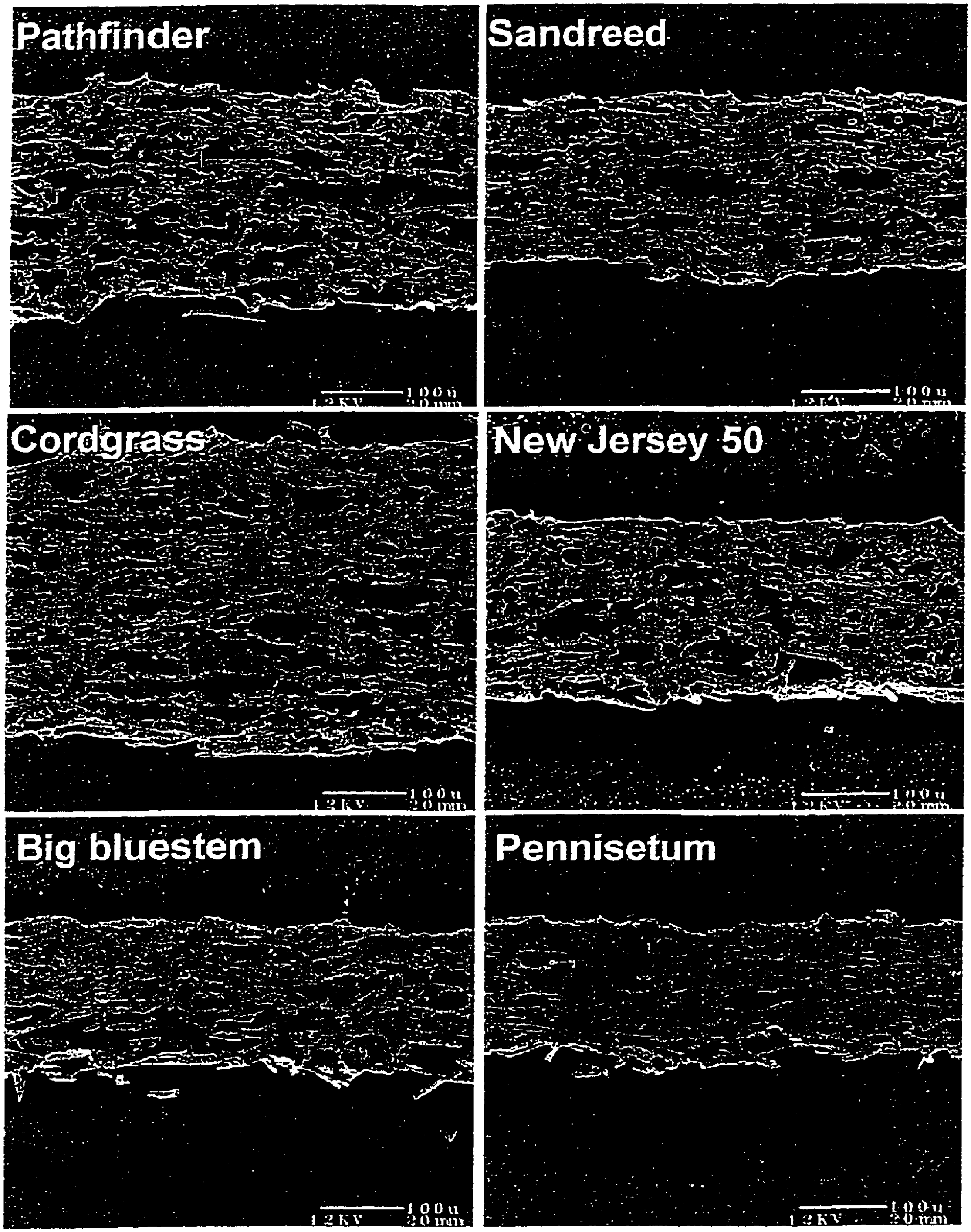

Pathfinder
Sandreed
Cordgrass
New Jersey 50
Big bluestem
Pennisetum
100u
12KV
20mm

Fig. 10.7: Tear index as a function of A) fibre length, B) Zero-span breaking length, and C) tensile index and D) tensile index as a function of cellulose content for various warm season grasses. The analyses were based on unbeaten pulp with CSF values of 335, 407, 411, 338, 295, 275 and 139 mL for Cave-in-Rock, Pathfinder, New Jersey 50, Big bluestem, Cordgrass, Sandreed and Pennisetum, respectively.

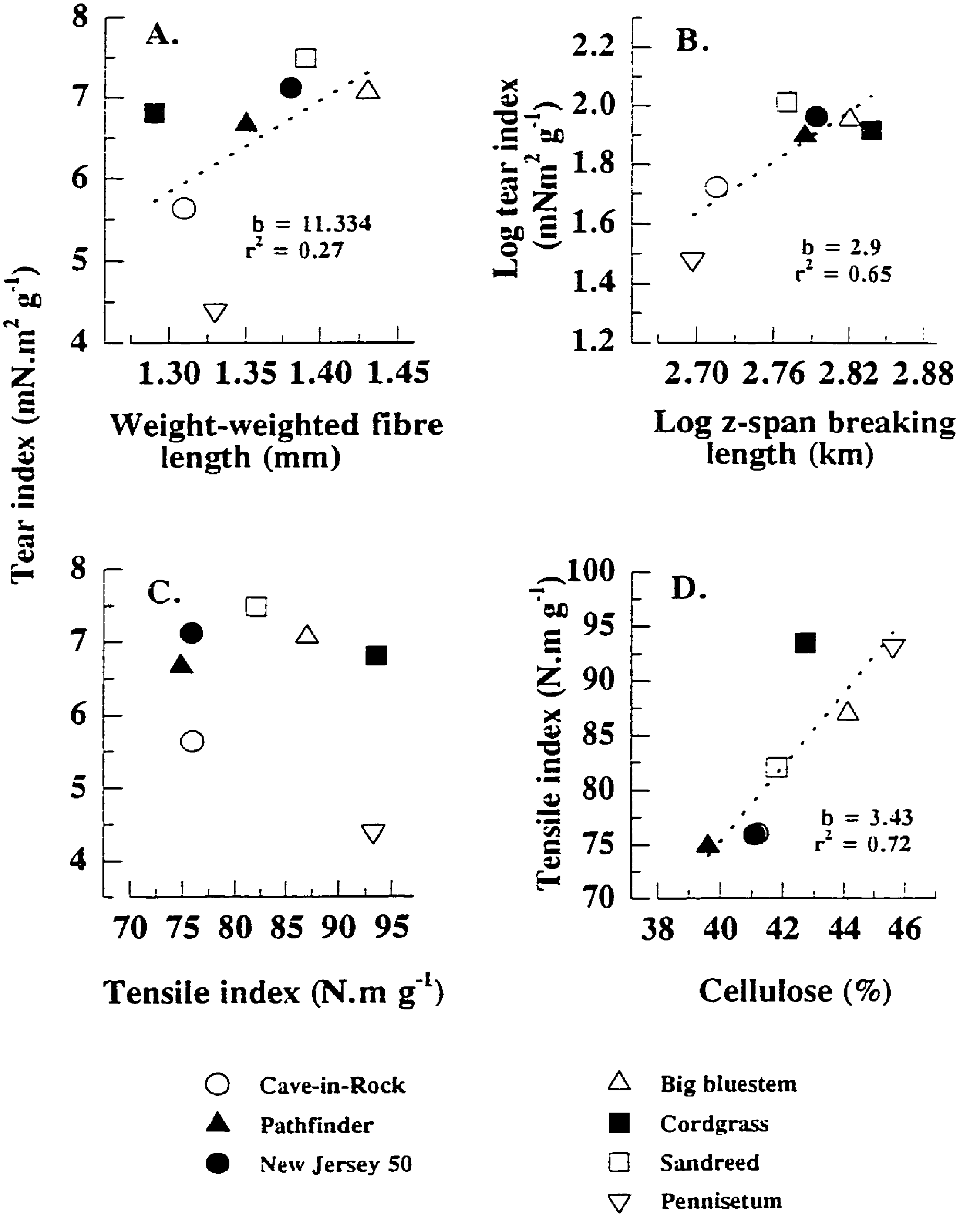
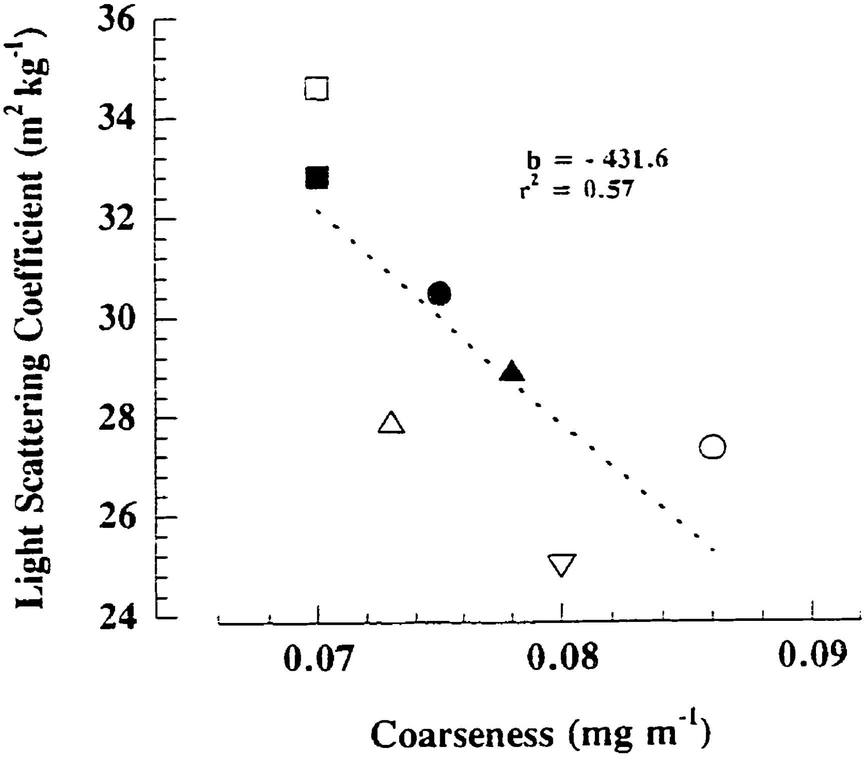

A.
B.
C.
D.
Tear index (mN.m^2 g^{-1})
Weight-weighted fibre length (mm)
1.30 1.35 1.40 1.45
8 7 6 5 4
b = 11.334
r^2 = 0.27
Log tear index (mNm^2 g^{-1})
2.2 2.0 1.8 1.6 1.4 1.2
Log z-span breaking length (km)
2.70 2.76 2.82 2.88
b = 2.9
r^2 = 0.65
Tensile index (N.m g^{-1})
70 75 80 85 90 95
Tensile index (N.m g^{-1})
100 95 90 85 80 75 70
Cellulose (%)
38 40 42 44 46
b = 3.43
r^2 = 0.72
○ Cave-in-Rock
▲ Pathfinder
● New Jersey 50
△ Big bluestem
■ Cordgrass
□ Sandreed
▽ Pennisetum

Fig. 10.8: The relationship between light-scattering coefficient and coarseness for unbleached warm season grass pulps.



Light Scattering Coefficient ($m^2\,kg^{-1}$)
36
34
32
30
28
26
24
b = - 431.6
r^2 = 0.57
0.07
0.08
0.09
Coarseness ($mg\,m^{-1}$)

Chapter 11

General Discussion

The general objective of this study was to evaluate performance of warm season grasses in a short growing season area. There was no information to guide choice of collections to evaluate, and therefore, the strategy was initially to evaluate as many collections as was feasible at the time. This was done in a space planted nursery, which allows for screening of a large number of entries on a small area of land, and allows the entries the greatest opportunity to express their potential because of reduced competition. In Chapter 3, a total of 22 entries within five species, were evaluated. One entry proved not be winter hardy and was discarded; the remaining 21 showed differences in phenological development, tiller size, leaf numbers per tiller and tiller heights. This initial evaluation provided base information on the growth patterns of these grasses. Chapter 3 confirms a great deal of diversity in developmental patterns. Entries varied in times spring growth was initiated, growth rates, tiller numbers, maturity and yield. Prairie cordgrass (CWNC) had the ideal features of early growth in spring and late maturity. Further experimentation with this entry was limited by seed availability. Differences in early season growth and yield are partly explained by differences in base temperatures and growth rate constants (Chapter 6).

Performance in space planted nurseries is usually modified by canopy conditions when the plants are grown as solid swards (as in most production systems). Chapters 4, 5, 8 and 9 evaluated performances of a few entries under solid sward conditions. Under these conditions height, tiller leaf number, and LAI could be described in terms of accumulated growing degree-days. The r^2 values for pooled LAI data were higher than those for tiller leaf number, suggesting LAI is a better parameter to monitor during evaluations. Redfearn *et al.* (1997) reported strong association ($r = 0.67$) between LAI and yield and suggested LAI (and not individual traits like leaf number) as a potential phenotypic selection criterion for increasing total yield. Our results indicate linear relationships between total yield with LAI ($r^2 = 0.85 - 0.91$) and with leaf area duration ($r^2 = 0.64 - 0.69$). The longer the leaf area duration the higher was the yield.

In grasses, a slow rate of leaf appearance was identified as the primary developmental trait associated with a long duration of vegetative growth (Van Esbroeck *et al.*, 1997). This is supported by the changes in tiller leaf numbers in Chapter 4 and LAI in Chapters 5 and 8 for entries like Cave-in-Rock. Each internode elongates for the same time as the associated leaf (Rickman and Klepper, 1995), therefore in the collections we evaluated, with 50 - 80 % of biomass coming from stems (leaf to stem ratios, Chapter 3), a slow rate of leaf appearance maximises carbon accumulation per internode and therefore total biomass production. The tall and wide tillers for entries like Blackwell and Cave-in-Rock switchgrasses in Chapters 3 and 4 and the respective yields in Chapter 5, corroborate this line of thinking. The entries that had faster rates of leaf appearance like North Dakota, ND3743, and Pathfinder were characterised by finer tillers and, in the case of Pathfinder, high tiller numbers. These entries were also earlier maturing and lower yielding.

Higher total yields were also associated with extended periods of linear growth (Chapters 4, 5 and 8) with the outstanding entry being Cave-in-Rock. Differences in canopy architecture indicated in Chapters 5 and 8, and the varying lengths of near-linear phases of growth, stress the need to account for phenotypic and ontogenetic differences in the LAI- light interception relationships, especially when developing models to estimate biomass production or radiation-use efficiencies.

The strong relationships between height, tiller leaf number, and accumulated growing degree-days; leaf area duration (based on accumulated growing degree-days) and total yield suggest the use of thermal time to normalise seasonal yield data and produce production curves with wider applications. Growth analysis based on thermal-time could be used to remove differences in observed experimental or site forage/biomass yields due to season length or temperature. For our region, supporting information on select soil and site characteristics (e.g. soil moisture holding capacity and soil organic matter/fertility) as well as biomass yields is needed to develop such a universal growth model.

Although growth analysis could be predicted from thermal-time (GDD), development of models is further complicated by inter- and intra-specific variations in base temperatures for germination and growth. Failure to achieve successful establishment due to low spring temperatures could be alleviated in some genotypes by using various seed treatments. In this study, we focussed on temperature and length of growing season. Much research has been reported which also shows total forage/biomass yield produced to be a function of water and soil nutrient availabilities (Stout *et al.*, 1988; Jung *et al.*, 1990, Staley *et al.*, 1991).

Chemical composition (including energy concentration) was relatively constant from year to year and varied only narrowly among cultivars in switchgrass (Chapter 8). This could also be predicted using time required for development. Sanderson and Wolf (1995b) also reported little variation in chemical composition due to year and cultivar. Increase in lignocellulose concentration was biphasic (an early rapid phase followed by slower increases or a plateau). The shift from the first phase to the second occurs at internode elongation (Sanderson and Wolf, 1995a) (shown to occur after approximately 6 weeks of growth in Chapter 9). Given that dry matter accumulation is curvilinear (Chapter 8) and the observations by Sladden *et al.* (1994) that greatest increases in yield occur in late July to early August, it might be worth harvesting for biomass in late July (closer to our 6-wk cutting schedule). At this time lignocellulose concentration and DM do not show appreciable increases. The regrowth can be utilised by grazing. However, this should be weighed against the benefits of allowing the herbage to mature, to minimise concentrations of inorganic elements in the feedstock (Sanderson *et al.*, 1996). Increased N fertilisation did not necessarily increase N concentration in uncut herbage.

Our results also show the potential of two indirect management tools: estimation of DM using canopy height and N concentrations using chlorophyll meter readings. These can be very useful non-destructive field assessments for biomass accumulation or quality of forage during the season.

Warm season grasses have potential for use in energy, pulp and paper production. Short fibres form a potential raw material for papers requiring good printing qualities (Hurter, 1990). However, relative to woods, the full fibre potential of grasses is developed in one season. Yield and, to a lesser extent, quality of the fibre are directly influenced by the weather/climate and growing conditions of the season. Another potential problem is the short harvest season (usually at the end of growing season). Therefore there is need to store harvested material for year round mill/plant production. There is no option for leaving the herbage in the field for another year if, for example, field production exceeds mill requirements.

Based on the variations in maturity (Chapters 3 and 4) and high biomass yields, even from early maturing genotypes, it might be desirable to grow different genotypes or species during the same year. This would spread the harvest season over a longer time. The harvest season could also be spread by adopting a two-cut system. The often cited drawback of high ash and dirt in herbaceous feedstock can be countered by leaving the biomass standing in the field through winter, with little loss of yield in some years (Sanderson *et al.*, 1996). In addition, modern processing plants include good cleaning systems to remove dirt, dust and /or trash, and in-field separators are currently being tested in the USA (McCloskey, 1995). These are reported to remove large proportions of leaves as well.

On the whole, warm season grasses have potential for both forage and industrial uses even in short seasons like those experienced in eastern Canada. They offer a sustainable option in energy and paper production and in soil conservation. A wide diversity of these grasses was demonstrated in this study and more evaluations are required regarding the adaptability of these grasses, and to address potential logistical problems related to production and utilisation in industrial use.

Chapter 12

General Conclusions and Rejection/Acceptance of Hypotheses

The following conclusions may be drawn based on the findings in this thesis:

1) Warm season grasses of diverse places of origin overwinter in eastern Canada. Despite divergence in areas of origin 24 of the 25 entries used in the different field experiments survived the cold winters.

Thus, Hypothesis 1 is accepted.

2) Considerable variation exists with respect to deadening and early season growth, and differences in places of origin explain some of this variation.

Thus, Hypothesis 2 is accepted.

3) Warm season grasses showed inter- and intraspecific differences in base temperatures for germination and growth. Base temperatures for germination were higher than for growth.

Thus, Hypothesis 3 is accepted.

4) All entries matured and set seed. Some matured and were dormant in late summer, and others in early fall. Durations of individual penological phases varied among the collections evaluated.

Thus, Hypothesis 4 is accepted.

5) There were differences in canopy architecture for the entries evaluated. These differences included temporal development and maximum values of LAI. The differences were linked to leaf number and size, and plant height.

Thus, Hypothesis 5 is accepted.

6) High radiation-use efficiency and biomass yield could be realised in the short seasons of eastern Canada. Differences were influenced by place of origin and phenological development.

Thus, Hypothesis 6 is accepted.

7) N concentration declined curvilineally with time, while lignocelluloses increased to a plateau in mid season. The grasses had high levels of fibre suitable for industrial processing and undesirably high ash contents.

8) At least two cuts per season are possible in eastern Canada, and if accumulation of thermal time is sufficient, a third cut is possible. Cutting at 6-wk intervals resulted in higher yields than at 4-wk intervals. Both systems yielded less than an uncut system.

Thus, Hypothesis 7 is accepted.

9) Moderate levels of N fertilisation increased yield and forage quality of switchgrass.

Thus, Hypothesis 8 is accepted.

10) N concentration in herbage could be monitored using chlorophyll metre readings. In uncut herbage, chlorophyll metre readings reflected preferential N allocation in the plant.

11) Warm season grasses produce short fibres after mild kraft pulping. Individual fibre lengths and distribution, and drainage of the pulps were influenced by species and cultivar in the case of switchgrass.

Thus, Hypothesis 10 is accepted

Chapter 13

Contributions to Knowledge

The work presented in this thesis represents the first systematic effort to evaluate warm season grasses in Canada. Developmental patterns of several warm season grasses are now documented by this thesis and should guide further work into the various aspects of warm season grass production. The specific contributions this thesis makes are:

1) Documentation of phenological development of several warm season grasses and that a) they can mature in northern latitudes like Canada, and

b) they overwinter under the cold (up to -30°C) Canadian winters despite a wide divergence in places of origin, which included relatively warmer regions. This documentation provides well-described characterisations for breeding and genetic study.

2) With regards to base temperatures, this work not only documents base temperatures for different warm season grasses but also,

a) proves that there are differences among species and cultivars. No single value can work for all, and

b) shows differences in base temperatures between developmental stages. These can be adopted in growth models and afford the chance to be more accurate in predictive models.

3) Documentation of growth rate constants for various grass species. These can be used in growth models and in explaining differences in field observations.

4) Provision of thermal-time models describing height growth, leaf number, and LAI in warm season grasses.

5) The radiation-use efficiencies reported in this study are a first for the species, in general, and specifically under a short growing season.

6) The study is the first formal reporting of warm season grass herbage yields in the region of study (and to my knowledge in eastern Canada).

7) The study documents successful multiple harvest strategies for switchgrass

even in a short season area.

8) The study provides documentation of seasonal changes in fibre and N concentrations under low N inputs and in a short growing season.

9) The study demonstrates the potential use of chlorophyll meter readings in the management of warm season grasses.

10) The study demonstrates variation in canopy architecture especially among switchgrass populations, supporting the case for using canopy leaf area as a phenotypic selection criterion.

11)The pulping work is also a first in providing detailed pulping characteristics of various warm season grasses in North America. Most of the previous effort has been devoted to wheat straw.

Chapter 14

Suggestions for Future Research

1) There is obviously a need for testing in a wider range of environments including marginal areas and areas prone to erosion.

2) There is considerable genetic variation for biomass productivity. Of the many key parameters related to the plant canopy, only leaf area and its duration were studied. More studies are required to understand other aspects like canopy photosynthesis and carbon allocation.

3) The factors determining early season growth, especially the temperature photoperiod interactions, need to be studied. This might open up chances of lengthening the growing season for selected species through breeding.

4) In seed physiology, differences in dormancy and seedling vigour seem to be genetic. Altering seed dormancy through breeding and the influence of incorporating this trait with other productivity traits needs to be studied.

5) Evaluation of warm season grasses using animals needs to be done. Of particular importance is the response of these grasses to grazing.

6) More studies on the use of chlorophyll meter in forage management should be conducted. These studies might include timing of sampling and the leaf position on the tiller.

7) Economic evaluation of the warm season grass technology, at least in pulp and paper making needs investigation.

8) In this study, inferences were made regarding potential use of warm season grasses as liquid fuels, based on energy content of the herbage. The ideal situation would be to study liquid fuels after hydrolysis.

Chapter 15

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IMAGE EVALUATION
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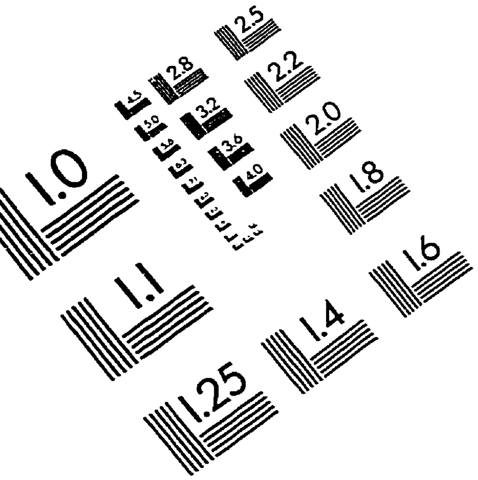

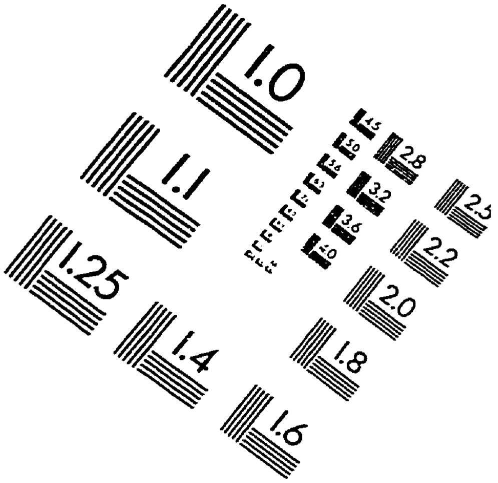

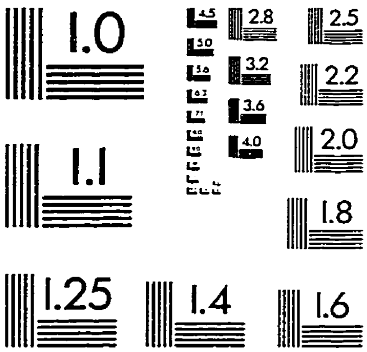

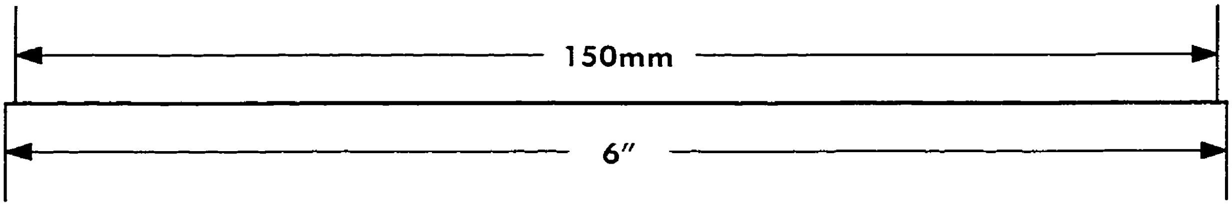

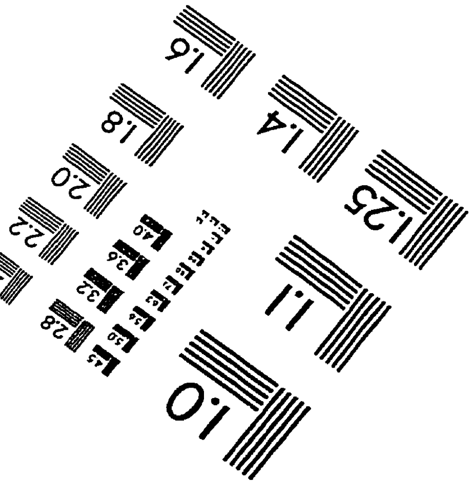

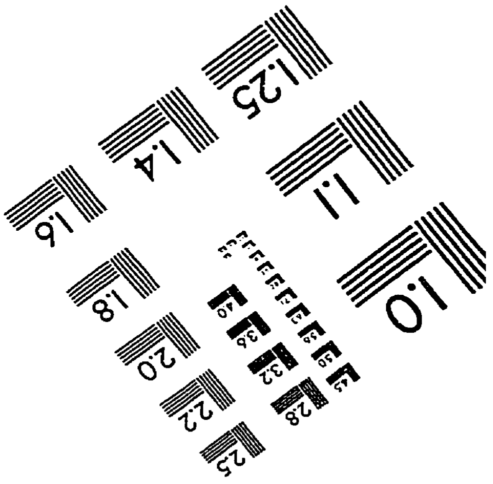

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