EFFECTS OF FIRE ON

PHRAGMITES AUSTRALIS (CAV.) TRIN. EX STEUDEL

AND ASSOCIATED SPECIES AT DELTA MARSH MANITOBA

BY

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A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

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ABSTRACT

In Delta Marsh the responses of a Phragmites australis dominated community were monitored after prescribed burning performed in the spring, summer and fall.

The aerial standing crop produced by Phragmites australis in 1979 in this stand was similar to that reported for similar habitats in other temperate regions. Much of the within stand variation in P. australis performance was explained with reference to a soil moisture gradient within the stand and to the uneven age structure of the stand at different parts of the gradient. P. australis accounted for 91% of the aerial standing crop of the community, which contained seven substorey species. To a greater degree than that of the dominant the performance of the substorey species was related to the moisture gradient. Two upland species (Cirsium arvense and Urtica dioica) occurred more frequently in the drier part of the stand but labiates such as Lycopus asper, Mentha arvensis and Teucrium occidentale were more frequent at intermediate moisture levels.

Several microenvironmental changes occurred after summer burning. Light intensity increased and air and soil temperatures fluctuated more. There was a release of mineral nutrients including nitrate, phosphate and potassium. Reed regrowth began approximately a week after burning and mowing, and continued until frost in late October. The aerial standing crop of regrowth was similar after burning and mowing but shoot

density was greater following mowing. Shoots on summer burned plots were more phenologically advanced than those produced on mowed plots. There was a decline in rhizome reserves following burning and mowing in comparison with the controls. Seeds of several substorey species germinated after burning and mowing which was related to the microenvironmental changes resulting from litter and canopy removal. Of the substorey species C. arvense and U. dioica sprouted regrowth most vigorously following both treatments.

In the 1980 growing season the aerial standing crop of P. australis increased after fall and spring burning but declined following summer burning. Shoot density increased dramatically after all burning treatments due to the production of many smaller vegetative shoots. Flowering shoot density increased after spring burning, but declined after fall and to a greater extent after summer burning. Both flowering and vegetative shoots were shorter and of smaller basal diameter following summer burning, which has potential as a method of controlling P. australis growth. Below-ground production was greater following fall and spring burning but after summer burning was similar to the controls. Changes in the performance of P. australis were related to changes in its morphology and seasonal growth cycle which occurred because of the burning treatments.

After spring and summer burning, with the onset of vernal growth, the total non-structural carbohydrate (TNC) content of P. australis rhizomes declined to lower levels than in the controls but by the end of the growth season rose to higher levels than in the controls. There were differences in the timing of the drop in rhizome reserves related

to differences in the phenological development of the aerial shoots which arose from the rhizomes. The greater decline in reserve levels with the onset of vernal growth after spring burning was related to increased shoot density and in inflorescence production. The decline after summer burning was related to increased shoot density as well as an initally lower TNC level at the begining of the growing season as a result of the production of regrowth in the previous fall.

In the 1980 growing season the magnitude of changes in the dynamics of the plant community depended upon the season of burning. The changes were greatest after summer burning and mowing where the competitive ability of P. australis was reduced. In contrast almost no change in substorey composition or production occurred after spring burning, which enhanced P. australis performance. Fall burning had intermediate effects with increased production of P. australis but there were changes in species composition. The species diversity (based on the biomasses of individual substorey species) increased on summer burned and mowed plots but not on fall or spring burned plots. Species diversity increased following summer burning lun to increased production by C. arvense and due to the establishment of Sonchus arvensis and Atriplex patula which produced considerable biomass.

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ACKNOWLEDGEMENTS

I would like to thank the numerous persons who contributed to the conception, birth and maturation of this thesis.

Foremost I would like to thank my major advisor, Dr. J.M. Shay for her continued encouragement and support. No less encouragement was offered by Dr. T. Booth who served as my supervisor during Dr. Shay's absence and who devoted a great deal of time to this project. The guidance and advice of my other committee members, Drs. D. Punter, J. Reid and A. Storgaard is much appreciated.

I would like to thank Dr. B. Johnston for statistical advice and Mr. Enri Chew for introducing me to MANTES and SCRIPT. Advice on soil and ash analysis was offered by Dr. Racz of the Soil Science Department. Drs. A. Storgaard and R.D. Hill of the Plant Science Department offered me valuable advice on experimental design and tissue analysis techniques respectively.

The staff of the Delta Waterfowl Station provided financial support, equipment and much useful encouragement and advice. In particular thanks go to Dr. B. Batt and Mr. P. Ward for a great number of ideas and much needed encouragement.

Thanks go to the staff of the University Field Station for excellent lodging and meals. I would like to thank the following students and staff for help in my fieldwork, Susan Cosens, Roger Garrard, Marc Lichtenberg, Mike McKernan, Joan Morgan and Mike Watson.

INTRODUCTION

This study describes the responses of an emergent plant community located at Delta Marsh, Manitoba, to prescribed burning carried out at three different times of the year.

Delta marsh stretches along the southern shore of Lake Manitoba and consists of a series of shallow bays separated from the lake by a forested dune ridge. Around these bays extensive stands of marsh emergents such as Phragmites australis, Typha glauca and Scirpus acutus and S. validus have become established. Water is exchanged between the marsh and the lake through a number of channels which cut through the dune ridge.

In the past the extent of the emergent marsh communities has changed in response to periodic fluctuations in the level of Lake Manitoba (Walker, 1965) but such fluctuations have been less extreme since the installation of a control structure at Fairford on the north outlet of the lake in 1961. Thus, interest in methods of managing these communities has arisen. One of the management options which has received some study in the Delta marsh is the use of prescribed burning which centered on P. australis stands (Ward, 1942 and Ward, 1968). The site chosen for detailed study of burning in summer (August 1, 1979), fall (October 11, 1979) and spring (May 11, 1980) was part of an extensive P. australis stand 5.5 ha in area which is located 1.5 km from the Cram Creek channel in the west part of the marsh.

The climate is mild to cool continental (Wier, 1960) with a mean January temperature of -5° C and a mean July temperature of 20° C. Annual preciptation is 52.1 cm with 70% of this falling as rain between April and October.

This study offered a valuable opportunity to integrate the responses of the dominant (both morphological and physiological) with that of the substorey species to the various burning treatments. Changes in community composition and structure could be related to the responses of the dominant.

This thesis is divided into five sections. The first describes the pre-burn aerial production, community composition, and aspects of the dynamics of a plant community dominated by P. australis. The second section describes regrowth on parts of this stand which occured in the autumn of 1979 following burning or mowing. The third section describes the performance of the dominant, P. australis, during 1980 after burning in the summer or fall of 1979 or the spring of 1980. Included are estimates of aerial and below-ground standing crop and shoot morphological measurements. In section four the response of P. australis rhizome reserve levels to the burning treatments are described. The final section deals with the effects of the various burning treatments on the diversity, composition and community aerial standing crop along with the individual responses of the more abundant substorey species.

Chapter I

THE SPECIES COMPOSITION AND PRODUCTION OF A MARSH COMMUNITY

1.1   INTRODUCTION

The primary production of aquatic macrophytes has been the subject of many investigations in Europe but such studies have been less numerous in North America.   There is a paucity of literature concerning the production by macrophytes in prairie marshes.

One of the most studied species in terms of production is reed, Phragmites australis, (Cav.) Trin. ex Steudel (1) because of its importance in the overgrowing of lakes, ponds, and other water bodies (Iwata and Ishizuka,1967; Mochnacka-Lawacz,1975).   Only one study to date (van der Valk,1976) has reported estimates of production by this species in prairie marshes.   P. australis is especially important in Manitoba because of the number of large marshes in which it predominates, forming extensive monotypic stands.

This chapter describes the production, community composition and aspects of community dynamics of a P. australis stand in the Delta marsh, Manitoba. These data were collected as a preliminary step toward a study in which the responses of P. australis to fire were to be investigated.

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(1) Formerly named Phragmites communis Trin. Taxomomic change according to Clayton (1968).

1.2   METHODS

In late July 1979 part of one dense P. australis stand was divided into a grid of twenty, 400 m^2 plots (Figure 1-1). This grid was set out so that it ran perpendicular to a water depth gradient within the stand. The most elevated side of the grid was free of standing water by June and at the lowest lying end the water depth was approximately 30 cm. To evaluate within stand variation, four 0.25 m^2 (0.5 by 0.5 m) quadrats were randomly located within each plot. All living and dead plant material was clipped at ground level and separated as living (2) P. australis, dead P. australis stems and the substorey species combined. Shoot densities of each species within the quadrats were recorded. Additional information collected for P. australis included flowering stem density, and the leaf number and height of the quadrats' tallest shoot. All plant material was oven dried to constant weight at 80° C. The characteristics recorded were compared between moisture levels using analysis of variance (Snedecor and Cochran, 1967).

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(2) Biomass is used to denote living aerial standing crop where below-ground biomass is reported the qualifier below-ground is used.

Figure 1-1. Site preparation at time of August sampling, 1979.

FORSTER'S BAY

TYPHA

→ N →

PHRAGMITES

— 100 m —

WETTER →

B4

B3

B2

B1

HORDEUM-TEUCRIUM
MEADOW

TYPHA
SCIRPUS

TYPHA

BLIND CHANNEL
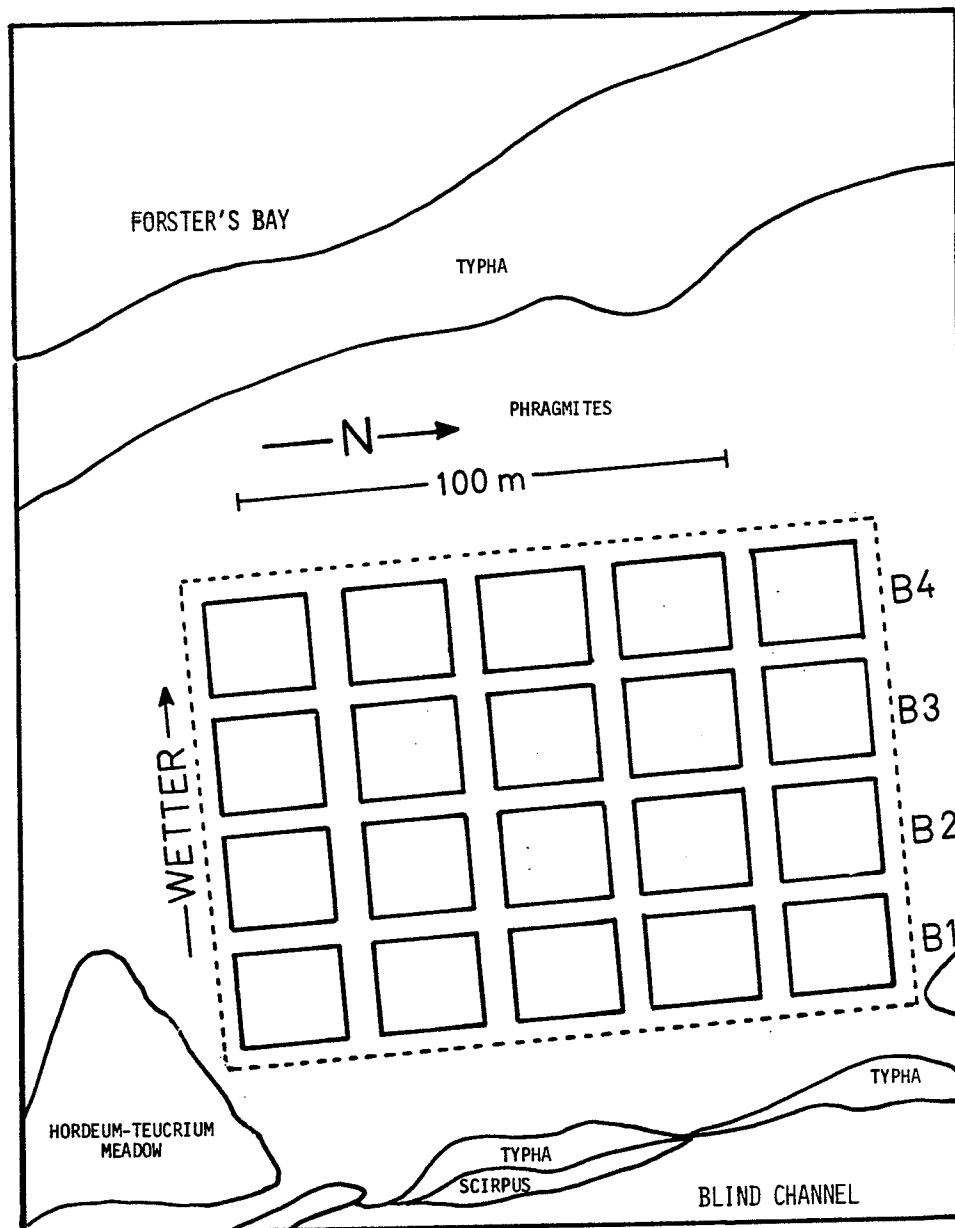
1.3 <u>RESULTS</u>

1.3.1 <u>P. australis</u>

Mean biomass for the stand was 812 $\pm$ 38.4 g/m 2, which was less than the mass of its litter (984 $\pm$ 32.8 g/m 2)   Mean biomass differed significantly (α = .01) between rows of plots at different moisture levels.   This effect was mainly due to lower biomass in the second row of plots, biomass being relatively constant over the other three moisture levels. Litter weight varied significantly (α = .05) between water levels, declining from the first (driest) row of plots to the last (wettest) row.

Mean shoot density was 78.3 $\pm$ 2.9 shoots/m 2 There was a consistent trend where density increased with increasing mositure (α = .01). Flowering density averaged 31.2 $\pm$ 2.4 shoots/m 2,   and varied significantly between moisture levels (α = .001). It was high in the first and third rows of plots but lower in the second and fourth row, there being no consistent trend across moisture levels.

The mean height of the quadrats' tallest shoot was 225.1 $\pm$ 2.4 cm and varied significantly between water levels (α = .0001), due to a dramatic reduction in shoot height in row two.   The mean number of leaves for these shoots was 13.9 $\pm$ 0.1 which did not vary significantly across water levels.

Average weight per stem varied significantly between moisture levels (α = .01), being highest in the driest row and declining toward the wettest row.

There were significant correlations between several of the <u>P.</u> <u>aus</u>-<u>tralis</u> characteristics measured (Table 1-1).

Table 1-1. Correlations between P. australis characteristics.

Characteristics	Correlation (r)	Significance level
Density vs. Biomass	0.680	.0005
Total Density vs. Flowering density	0.533	.0010
Max. Height vs. Biomass	0.478	.0010

1.3.2   Substorey

The combined biomass of substorey species averaged 67.9 g/m 2, which varied between mositure levels (α = .01).   Substorey biomass declined with increasing moisture, except that the mean for row two was somewhat higher than for row one.

There were seven substorey species present in this community (Table 1-2).   The most abundant was Teucrium occidentale Gray which had an average biomass of 25.6 g/m 2 and a density of 19.5 $\pm$ 2.2 shoots/m 2 The density of this species varied across the water level gradient (α = .0001).   Its biomass was lowest in the driest row (one), increased dramatically in row two and declined somewhat in rows three and four. Frequencies of Mentha arvensis L. var. villosa (Benth.) Stewart and Urtica dioica L. were similar but less than that of T. occidentale. Lycopus asper Greene, Cirsium arvense L. (Scop.) and Scutellaria epilobiifolia Hamilton had consecutively lower frequencies.   The frequencies of individual substorey species varied along the moisture gradient. C. arvense and U. dioica decreased in frequency with increasing moisture.   The labiates, including L. asper, M. arvensis and T. occidentale increased with increasing moisture but declined somewhat in the last, wettest, row of plots.

1.3.3   Relationship between P. australis and Substorey

Total substorey biomass was weakly negatively related to the density of P. australis (r = -.252, α=.05) but was not significantly related to its biomass.   There was a stronger relationship between substorey biomass and the weight of P. australis litter (r = -.548, α= .0001).

Table 1-2. Frequencies of substorey species, 1979.

MOISTURE LEVEL

------------------------------- WETTER ------------------------[>

SPECIES	ROW1	ROW2	ROW3	ROW4	OVERALL *
Teucrium occidentale	50	90	100	95	84
Mentha arvensis	25	60	65	45	49
Urtica dioica	80	60	25	25	48
Cirsium arvense	50	36	20	5	26
Lycopus asper	0	30	50	45	31
Scutellaria galericulata	25	15	0	30	19
Stachys palustris	10	0	0	0	3

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* Overall denotes frequency for the whole stand.

Figure 1-2. Relationship between combined dry weight of substorey

species and the dry weight of P. australis litter. Fitted

curve is Y= 66500/X - 12.3.
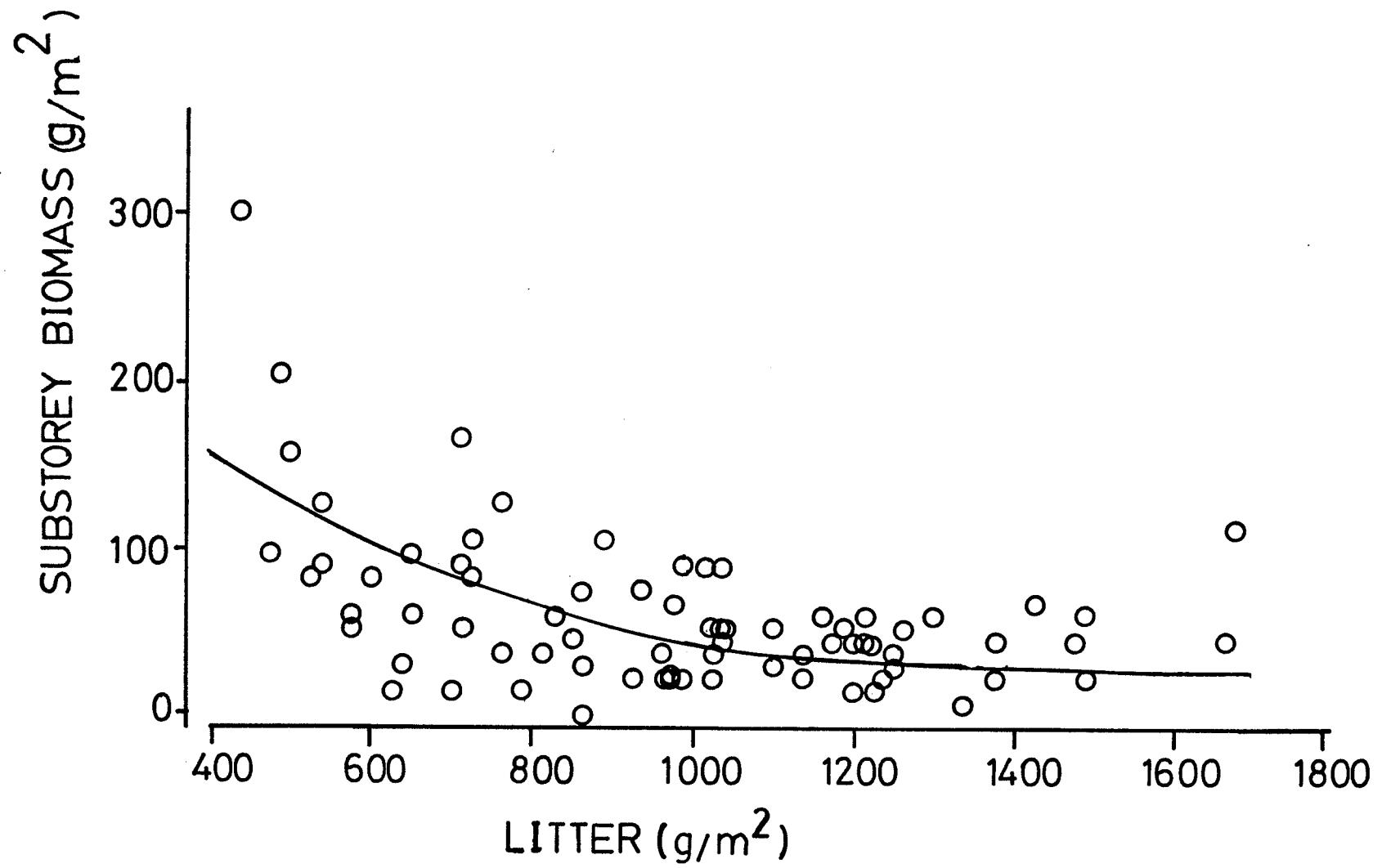
This relationship was curvilinear ($Y = 66500/X - 12.8$) with little constraint on substorey biomass at low litter loadings but a strong constraint at higher litter loadings (Figure 1-2).

1.4   DISCUSSION

1.4.1   Phragmites australis

The biomass of P. australis in this stand is similar to that of Shay (unpublished) for Delta Marsh and to that reported by van der Valk (1976) for an Iowa fen. It was also similar to that reported by van der Toorn (1972) for a riverbank ecotype, by Kvet (1973) for a drier stand, and by Ho (1979) for a mesotrophic stand. Similar P. australis biomasses were also reported by Kowalczeweski and Wasilewski (1966), Mason and Bryant (1975), Anderson (1976) and by Brooker (1976). This biomass is higher than that reported in oligotrophic environments (van der Toorn, 1972 and Mason and Bryant, 1975). Higher P. australis biomasses were reported in estuarine marshes (Hopkinson et al.,1978; Linthurst et al.,1978) and in some eutrophic environments (Dykyjova and Pribil,1972; van der Toorn,1972). Several authors reported that P. australis production increases from the drier to the wetter parts of stands (Buttery and Lambert,1965; Kowalczewski and Wasilewski,1966; Haslam,1972; Dykyjova and Hradecka,1973; and Mochnaka-Lawacz,1974). The within stand differences in biomass seen in my study were due to the thinning of the canopy in the second row of plots. This may have been due to edaphic conditions or perhaps more likely to the uneven age structure of the stand. If invasion of the habitat was from the two channels on the east and west sides of the penninsula studied, then this part of the stand would

be the last to be colonized. Comparable somewhat erratic profiles for P. australis have been reported by several authors (Husak and Kvet,1973; Mochnacka-Lawacz,1974) and by Smith (1973) for Scolochloa festucacea. P. australis declined in performance in row two in terms of maximum height, flowering density, and weight per stem in addition to biomass (see 1.3.1). These may be indications of a younger part of a stand.

Some characteristics exhibited definite reactions to the moisture gradient- including density, which increased with increasing moisture and weight per stem, which declined with increasing moisture. Mochnacka-Lawacz (1974) reported no consistent trends in density with increasing moisture but increasing density with increasing moisture was reported by Buttery and Lambert (1965) and Anderson (1976). Nikolajevski (1971) and Mochnacka-Lawacz (1974) reported that average stem weight declines with increasing water depth. Nikolajevski (1971) found that in deeper water reed stems have less conductive and supportive tissue and larger lumens and therefore average stem weight declines.

Similar correlations between various P. australis characteristics were reported by Ondok (1970 and 1971), with a higher correlation between density and biomass in the drier (r = 0.82) than in the wetter part (r = 0.50) of the same stand. He reported a positive relationship between average height and biomass (r = .329, α =.05). I found a positive correlation between flowering and total density (r= +.533, n= 80) in contrast with Onkok (1970) who found a negative correlation (r= -.740). Haslam (1972) emphasized that many factors such as stand age, moisture regime, and nutrient status can effect the flowering response of P. australis. The very different relationship reported by Ondok may have been due to differences in one or more of these factors.

1.4.2   Substorey

The distribution of wetland species along moisture gradients, as shown in table 1-2   for this community, has been shown by many authors (Dix and Smeins,1966;   Husak and Kvet,1970 van der Valk and Bliss,1971; Kvet and Ondok,1973 and Nicholson and Aroyo,1974).   This may be due to differing abilities of these species to tolerate inundation.   Labiates such as Mentha arvensis, Lycopus asper, and Teucrium occidentale appear to be highly tolerant of flooding. M. arvensis and T. occidentale were reported by Dix and Smeins (1966)   to be important marsh meadow species in North Dakota.   C.   arvense and U. dioica are less well adapted to flooding and thus declined in the community with increasing moisture. The composition of this community was similar to that reported by Philips (1976) for two P. australis stands at Delta Marsh and it was more similar to the drier of the two.

1.4.3   Relationship between P. australis and Substorey

The majority of the biomass in this community (91.1 $\pm$ 0.9 %) was contributed by the dominant, P. australis.   Sculthorpe (1967) described the tendency of emergent species to form monodominant stands.   Grime (1973) listed several characteristics of highly competitive species, including a tall growth form, a high relative growth rate, a perennial growth form which includes an extensive system of rhizomes or rootstalks, and a tendency to accumulate large amounts of litter.   Of these characteristics the ability to accumulate litter was the most important competitive mode of P. australis in this community.   Accumulations of litter in excess of living biomass were also reported by Hopkinson et

al. (1978) and by Linthurst et al. (1978). Haslam (1972) stated that the ability of P. australis to accumulate litter was an important means of competition. She suggested that litter prevents the germination and establishment of possible competitors. It is notable that all the species present in this community are perennials and that most of the understorey growth was from rootstocks rather than from seedlings. The biomass of substorey species increased somewhat from the drier to the wetter part of the stand. This parallelled a decline in P. australis litter. Declines in litter with increasing moisture may be due to more rapid decomposition when stem bases are flooded.

The negative correlation between P. australis stem density and understorey biomass probably reflects the effect of light interception by its shoots on the understorey. Light extinction under reed canopies is very rapid (Buttery and Lambert,1965; Haslam,1972; Ondok,1973). This is due to the dense and tall canopy formed by reed, which also gives it competitive advantages. The substorey species begin vernal growth several weeks earlier than the dominant. This may be why they can persist beneath the dense canopy. In a dense reed stand light intensity in May and June at heights less than one metre were much greater than later in the growing season when the canopy had developed (Buttery and Lambert,1965). Buttery and Lambert suggested this was why Glyceria maxima (Hartm.) Holmb. can compete with P. australis. Substorey biomass declined in the wettest row of plots where reed density was highest, probably because of the combined effects of water levels in addition to competition with P. australis.

1.5 SUMMARY

The dominant in this community is clearly P. australis which accounts for 91% of the total biomass. This stand appears to be relatively homogeneous in both Phragmites performance and in species composition. Within stand variation is due to a water level gradient and perhaps to variation in the time since colonization by the dominant. The production by P. australis is similar to that reported for similar habitats throughout temperate zones. P. australis controls the development of the substorey as a result of accumulating litter and by intercepting light with its tall and dense canopy.

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Chapter II

INFLUENCE OF SUMMER MOWING AND BURNING ON STAND REGENERATION

2.1 INTRODUCTION

Reed, _Phragmites australis_ (Cav.) Trin. ex Steudel, constitutes much of the emergent cover of the Delta Marsh. Where it forms extensive dense stands, habitat diversity is reduced for wildlife. It is therefore desirable to find some means of thinning these dense stands in order to enhance wildlife production and diversity. Several methods have been attempted to control reed growth including mowing (Ward,1942; Haslam,1968; Husak,1970: Dkykjova and Husak,1973; Mochnacka-Lawacz,1974), herbicide application (Brooker,1976), cultivation (Ward,1868; Haslam,1968) and burning (Ward,1942; Ward,1968). These measures were applied during the growth season to deplete the plant's reserves and weaken its regrowth.

Several authors have described regrowth following summer mowing (Dykyjova and Husak,1973; Mochnacka-Lawacz,1974). The first authors compared regrowth after cutting in a terrestrial and inundated stand and concluded that cutting more than once in a summer would give better control. The latter author described regrowth after cutting three times in the same summer and in addition to morphological and productivity data determined the mineral contents of the regrowth.

This chapter describes regrowth on burned and mowed parts of a dense reed stand in the Delta Marsh, and some of the microenvironmental

changes occurring after fire. These data were collected as part of a larger study quantifying the effect of season of burning on the perform- ance of P. australis. The pre-burn production and community composition of this stand is described in Chapter 1.

2.2 METHODS

In early August of 1979 four 400m^2 (20m by 20m) experimental plots were burned and a part (25m^2) of four others were mowed as near as possible to ground level, and the material raked off (Figure 2-1). These treatments were applied once within each of four rows of experi- mental plots which were earlier set out along a moisture gradient within the stand. These rows of plots were used as blocks with the treatments randomized within each. The purpose of the mowing treatment was to sep- arate the effects of canopy removal, heating during fire, and that of the release of nutrients from the ash. In addition, two control meas- ures for P. australis could be evaluated.

On September 21 regrowth was sampled from burned and mowed plots using four 0.25 m^2 quadrats per plot. P. australis regrowth was clip- ped at ground level from these quadrats and oven dried at 80° C, and shoot density was recorded. The height to topmost unfolded leaf and basal diameter of each shoot was recorded as was its leaf number. Shoots were separated into three components (leaf blades, leaf sheaths, and stems) for analysis of their mineral content. The nutrients assayed were total P, K, Ca, and Mg. Cations were determined by atomic absorb- tion on diluted acid extracts after dry ashing. Total P was determined using the Vanadate-Molybdate-yellow method (Chapman and Pratt,1961).

Figure 2-1. Study site after summer burning and mowing. Note- 'M' represents areas which were mowed and raked in early August.

FORSTER'S BAY

TYPHA

N→

PHRAGMITES

100 m

WETTER→

		CONTROL		SUMMER BURN
	M			
	CONTROL	M	SUMMER BURN	
CONTROL		SUMMER BURN		M
	SUMMER BURN			CONTROL M

HORDEUM-TEUCRIUM MEADOW

TYPHA

SCIRPUS

TYPHA

BLIND CHANNEL
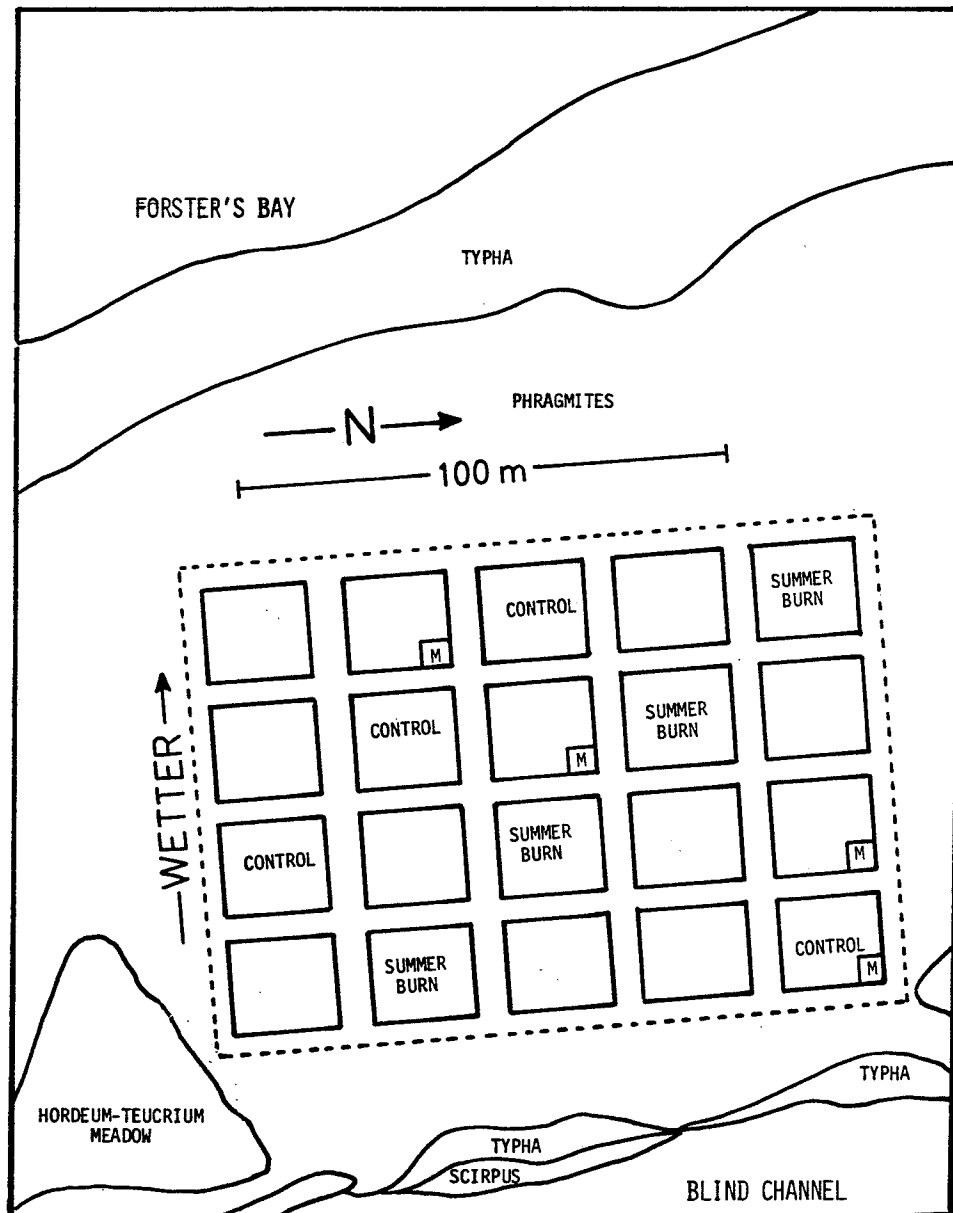
Rhizomes were excavated from burned, mowed, and control plots on November 1 and analysed for their Total Nonstructural Carbohydrate (TNC) content as outlined in Chapter 5.

The densities of substorey species were counted within the same 0.24 m^2 quadrats, seedlings and regrowth stems being counted separately.

Several environmental measurements were made in the week following burning including soil and air temperature (Grant temperature recorder), solar radiation (pyrheliometer), and relative humidity (hygrothermograph). One of each instrument was positioned on a burned and control plot. For the temperature profiles two thermistor probes were set at 100cm and 50cm above the soil surface, two at the soil surface, two at a depth of 5 cm in the soil and two at a depth of 10 cm in the soil. The hygrothermograph and pyreheliometer were placed on the soil surface with a similar orientation. In the control, care was taken not to disturb the living stems and the litter.

Soil samples were taken at three dates after burning (August 14, 24 and September 8). The samples were blocks of soil 20 by 10 cm in area and 15 cm in depth. These samples were cut into three 5cm deep sections and oven dried at 50° C to constant weight. Samples were separated from roots and rhizome material and passed through a 2mm mesh screen before being sent to the Manitoba Provincal Soils Testing Laboratory for analysis which included extractable nitrate, phosphate, and K and conductivity.

2.3   RESULTS

2.3.1   Environmental Changes

2.3.1.1   Physical Characteristics

Temperatures at 100cm and 50cm above the soil, at the soil surface and at 5 cm below the surface showed more extreme fluctuations on the burned area than in the control (Figures 2-2 and 2-3). Solar radiation was increased on the burned area where the canopy and litter had been removed by burning (Figure 2-4a). Diurnal cycles in soil and air temperatures were closely tied to incident solar radiation, peaking near noon and dropping towards the night. Mean humidity was similar on the burned and the control plot but it was much more variable (Figure 2-4b). Humidity was negatively related to solar radiation, dropping near mid-day and rising at dusk.

2.3.1.2   Chemical Characteristics

There were significant changes in all the chemical soil characteristics studied (Table 2-1). Phosphate increased after burning, showing a strong treatment effect in the analysis of variance (Table 2-2). Date, depth and block also had significant effects. The treatment by block interaction was due to higher phosphate concentration at all moisture levels except the wettest (Figure 2-5a). The difference between burned and control plots was mainly in the 0-5 cm level (Figure 2-5b), causing a treatment by depth interaction. There was little difference between burned and control plots at the first date but a great difference by August 24, causing a treatment by date interaction (Figure 2-5c).

Figure 2-2. Air temperature recorded for a three day period on a
burned and a control plot at a height of 100 cm and 50 cm.
Values are means from two probes. Measurements made using
Grant Model B thermistor with recorder.

Open circles - Burn

Closed Triangles - Control
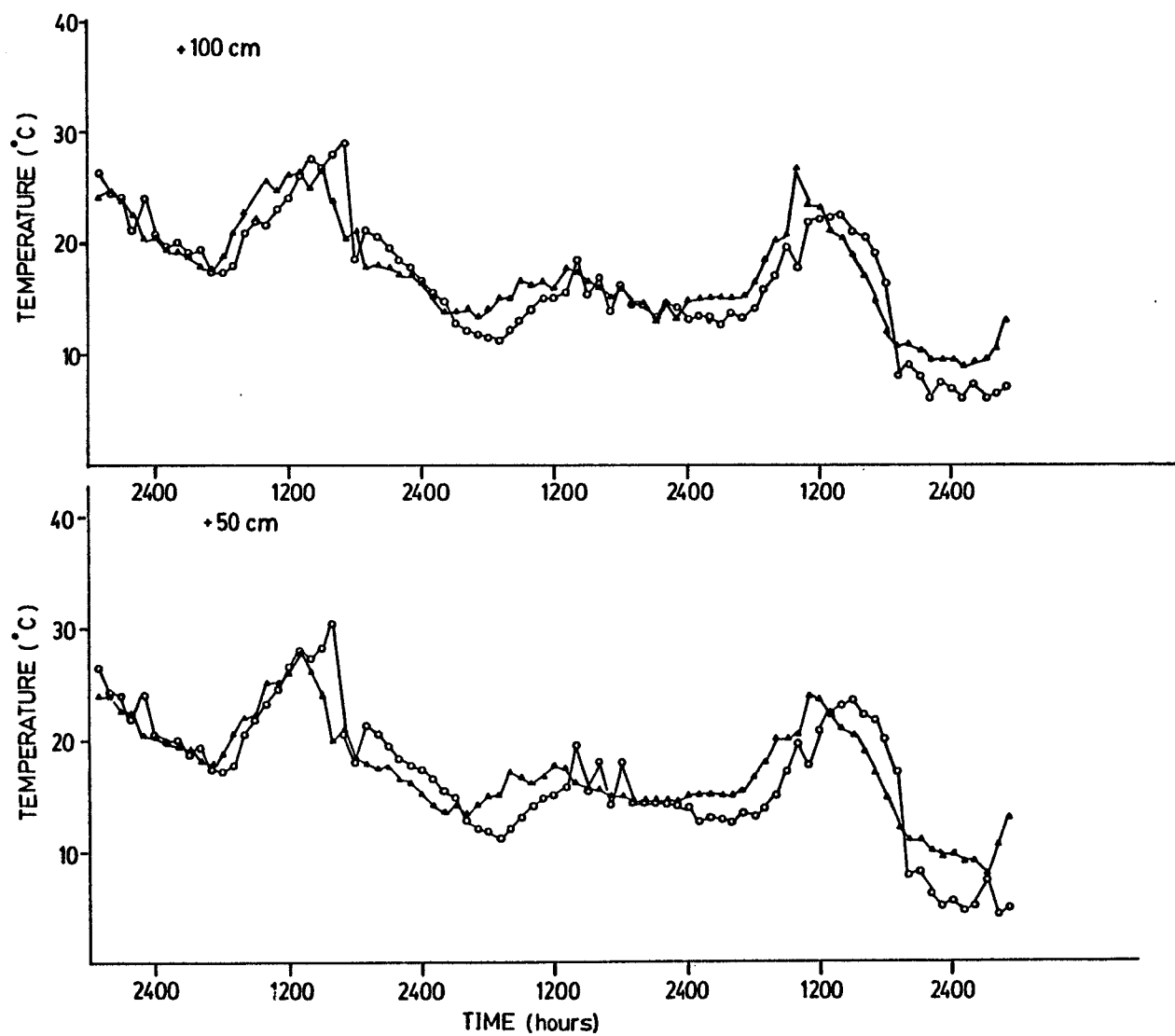
Figure 2-3 Soil temperatures recorded for a three day period on a burned and a control plot at soil surface and at a depth of 5 cm. Values are means from two probes. Measurements made using Grant Model B thermistor with recorder.

Open circles - Burn

Closed Triangles - Control

SOIL SURFACE

TEMPERATURE (°C)

TIME (hours)

-5cm

TEMPERATURE (°C)

TIME (hours)
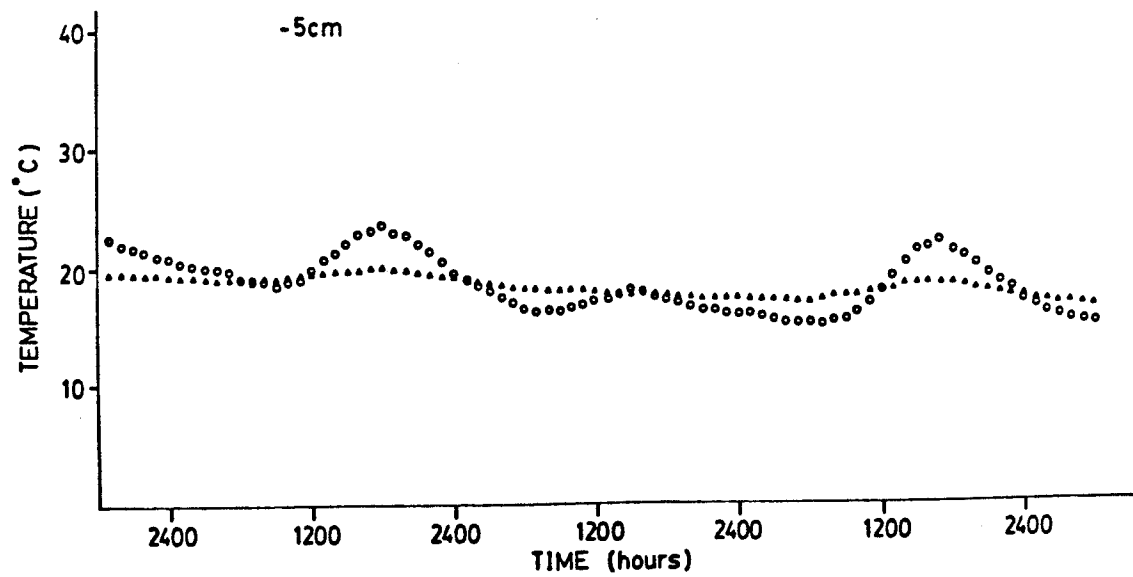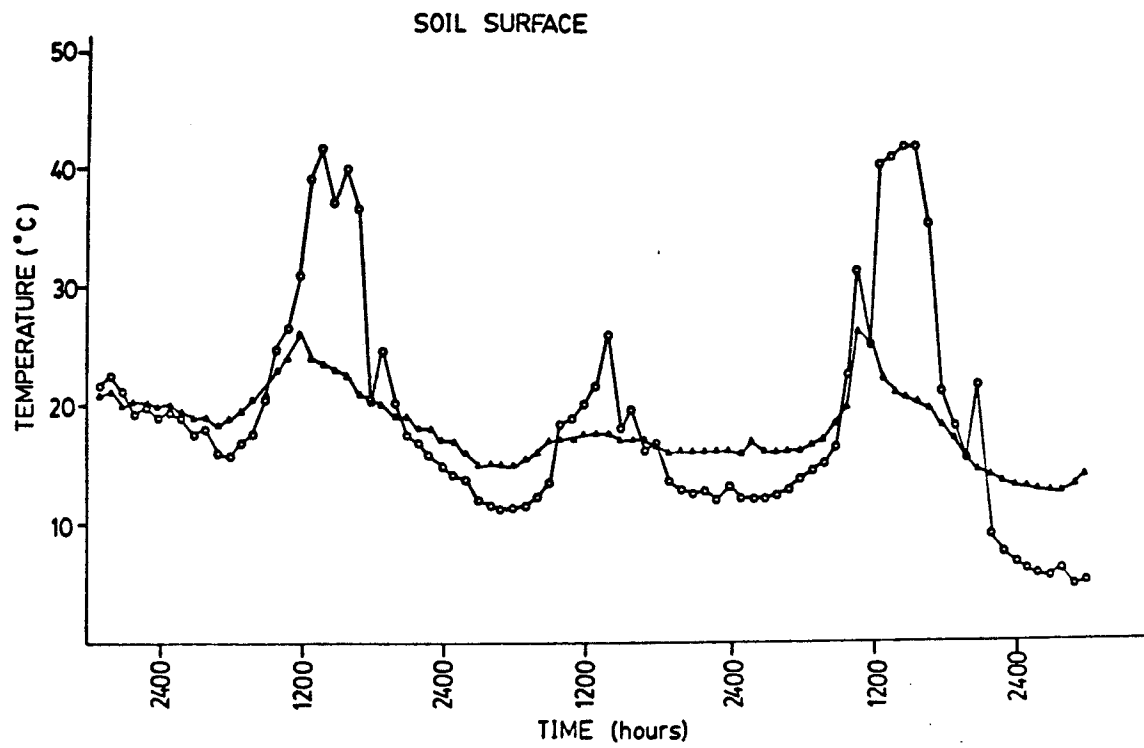
Figure 2-4a. Solar radiation recorded at 10 cm above the soil surface

for a three day period on a burned and control plot, using

Belfort pyreheliometers.

Figure 2-4b. Relative humidity recorded for a three day period on a

burned and control plot at 10 cm above the soil surface,

using Weather Measure H311 hygrothermographs.
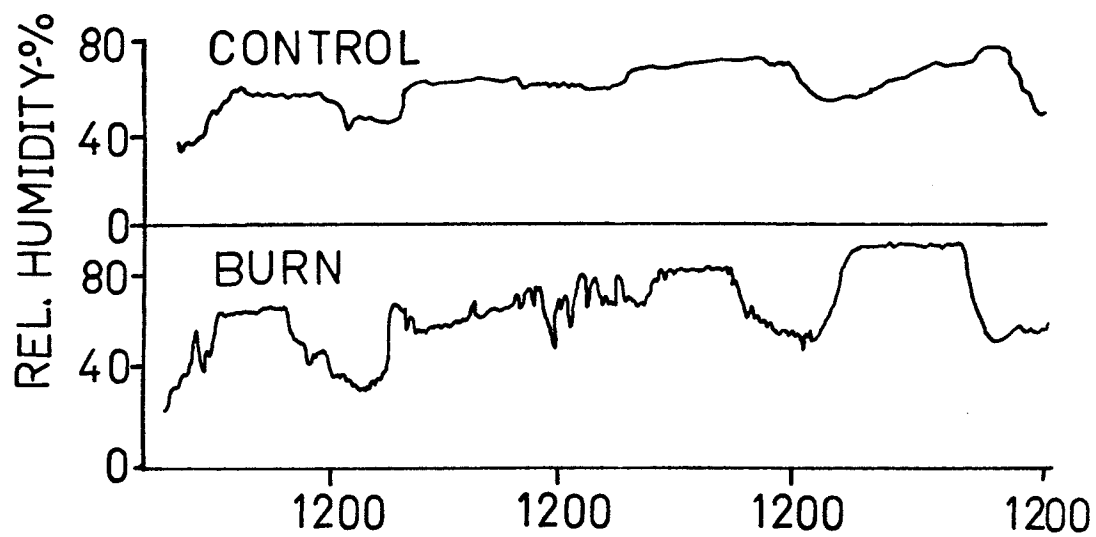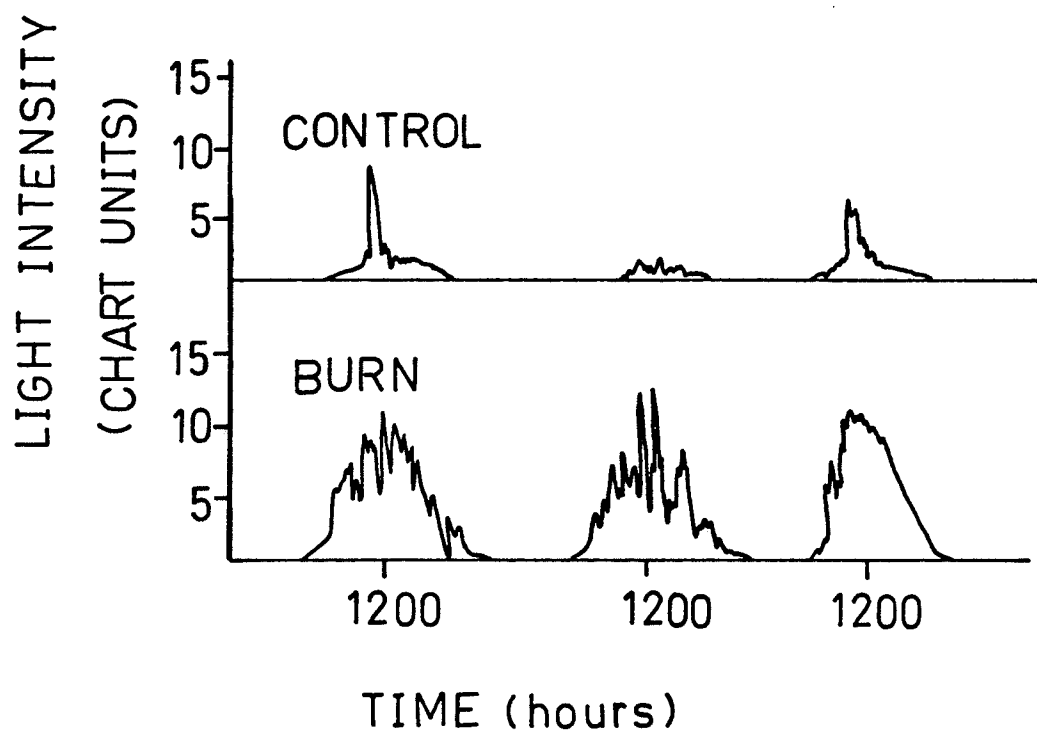
Table 2-1. Means for Soil Chemical Characteristics.

TREATMENT

CHARACTERISTIC	BURN	CONTROL
Nitrate (ppm)	40.8 ± 2.3	30.4 ± 1.7
Phosphate (ppm)	30.0 ± 1.6	24.7 ± 0.9
Potassium (ppm)	400 ± 21.0	365 ± 17.3
Conductivity (mmohs/cm)	2.9 ± 0.1	1.8 ± 0.1

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* Values are means with standard errors.

Mean soil nitrate increased on burned plots (Table 2-1) and there were also significant date, depth and block effects for nitrate (Table 2-3). The mean nitrate concentration was higher at all moisture levels except block 4, causing a significant interaction between block and treatment (Figure 2-5d). nitrate concentration was higher after burning at all depths (Figure 2-5e), so that the interaction between treatment and depth was relatively small. There was no difference between burn and control nitrate concentrations at the first date, but after burning, nitrate increased rapidly after the first sample period (Figure 2-5f), causing the treatment by date interaction.

There was a lesser difference in soil K between burned and control plots (Tables 2-1 and 2-4). Most of the variation in K was due to a decrease with increasing depth which occurred in both control and treated plots. There was no significant block or date effect for this characteristic. The treatment by The treatment by depth interaction was strong and was due to significant increases in K after burning, occurring only at the 0-5 cm depth (Figure 2-6).

There was a significant increase in conductivity on the burned plots (Tables 2-1 and 2-5), and a strong depth effect as for K (Table 2-4). Conductivity increased with increasing soil moisture, causing a significant block effect. None of the interactions were highly significant.

Table 2-2. Analysis of variance for soil extractable phosphate.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
TREATMENT	1	1,089.6	1,089.6	23.89	.0001
DATE	2	3,323.5	1,661.8	36.39	.0001
DEPTH	2	3,581.9	1,790.9	39.21	.0001
BLOCK	3	636.6	212.2	4.68	.0050
TREAT*DATE	2	937.3	468.6	10.26	.0001
TREAT*DEPTH	2	1,053.0	526.5	11.53	.0001
DATE*DEPTH	4	215.4	53.9	1.18	.3273
TREAT*BLOCK	3	1,319.7	439.9	9.63	.0001
DATE*BLOCK	6	473.1	78.9	1.73	.1271
DEPTH*BLOCK	6	408.5	68.1	1.49	.1935
TREAT*DATE*DEPTH	4	313.8	78.4	1.72	.1555
TREAT*DATE*BLOCK	6	1,315.6	219.3	4.80	.0004
TREAT*DEPTH*BLOCK	6	659.3	109.9	2.41	.0356
DATE*DEPTH*BLOCK	12	427.3	35.6	0.78	.6692
TREAT*DATE*DEPTH* BLOCK	12	595.2	49.6	1.09	.3848
ERROR	72	3,288.4	45.7		
TOTAL	143	19,932.1			

Figure 2-5a. Mean extractable soil phosphate on a control and burned plots at different moisture levels (blocks) and averaged over depths and dates.

Figure 2-5b. Mean extractable soil phosphate on control and burned plots at different depths, averaged over moisture levels (blocks) and dates.

Figure 2-5c. Mean extractable soil phosphate on control and burned plots at different dates, averaged over moisture levels (blocks) and depths.

Figure 2-5d. Mean extractable soil nitrate on control and burned plots at different moisture levels (blocks), averaged over depths and dates.

Figure 2-5e. Mean extractable soil nitrate on control and burned plots at different depths, averaged over moisture levels (blocks) and dates.

Figure 2-5f. Mean extractable soil nitrate on control and burned plots at different dates, averaged over moisture levels (blocks) and depths.

Note- Open circles represent burn values and closed circles represent control values.
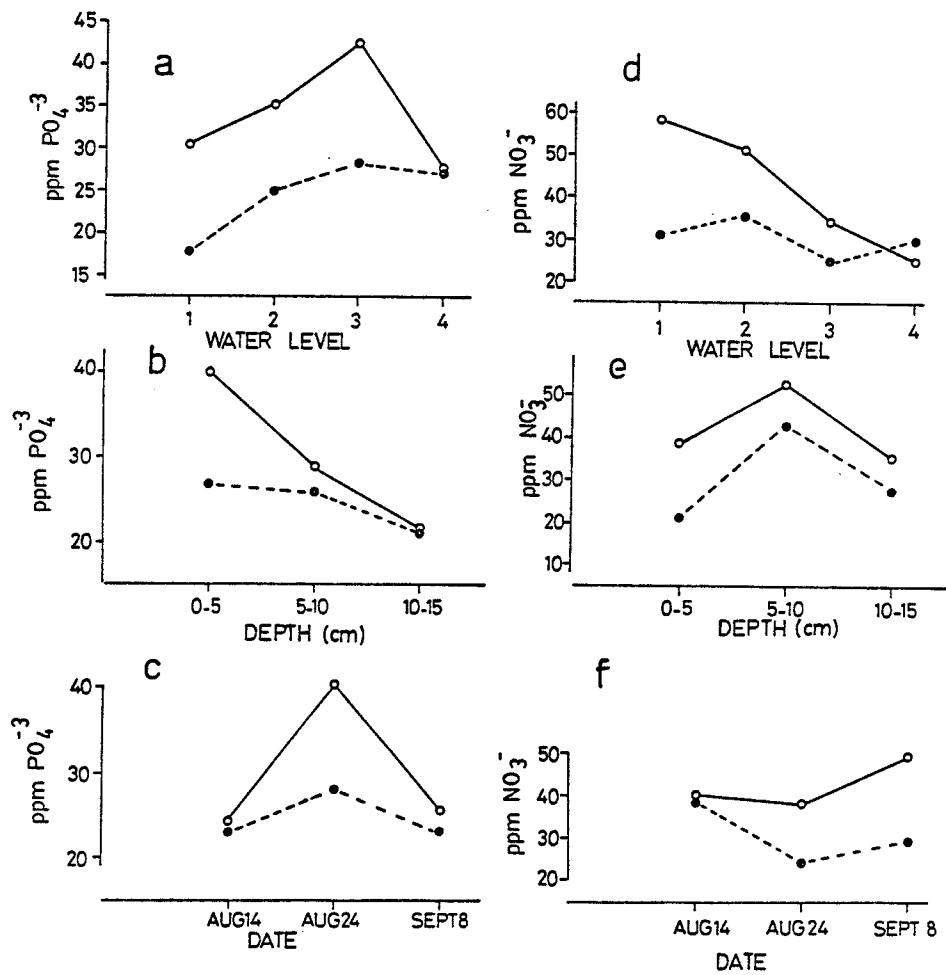
Table 2-3. Analysis of variance for extractable soil nitrate.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
TREATMENT	1	5,081.3	5,081.3	47.60	.0001
DATE	2	1,969.9	1,984.9	39.23	.0003
DEPTH	2	9,259.4	4,629.7	43.37	.0001
BLOCK	3	9.078.4	4,629.7	28.35	.0001
TREAT*DATE	2	1,992.2	996.1	9.33	.0002
TREAT*DEPTH	2	1,620.4	310.2	12.91	.0611
DATE*DEPTH	4	1,154.7	288.7	2.70	.0370
TREAT*BLOCK	3	4,789.0	1,596.3	14.95	.0001
DATE*BLOCK	6	2,250.0	375.0	3.51	.0042
DEPTH*BLOCK	6	828.3	138.1	1.29	.2713
TREAT*DATE*DEPTH	4	762.7	190.7	1.79	.1410
TREAT*DATE*BLOCK	6	1,306.2	217.7	2.40	.0713
TREAT*DEPTH*BLOCK	6	1,573.1	131.1	1.23	.2813
DATE*DEPTH*BLOCK	12	1,573.1	131.1	1.23	.2813
TREAT*DATE*DEPTH* BLOCK	12	1,149.6	95.8	0.90	.5535
ERROR	72	7,685.5	106.7		
TOTAL	143	51,242.0			

Table 2-4. Analysis of variance for extractable soil potassium.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
TREATMENT	1	34,720.1	34,720.1	5.61	.0205
DATE	2	4,357.5	2,178.8	0.35	.7045
DEPTH	2	2,732,637.1	1,366,318.5	220.75	.0001
BLOCK	3	30,084.3	10,028.1	1.62	.1922
TREAT*DATE	2	45,399.0	22,699.0	3.66	.0306
TREAT*DEPTH	2	84,236.7	42,118.4	6.80	.0020
DATE*DEPTH	4	12,213.3	3,053.0	0.49	.7406
TREAT*BLOCK	3	16,154.3	5,384.8	0.87	.4608
DATE*BLOCK	6	121,269.8	20,211.6	3.27	.0068
DEPTH*BLOCK	6	62,316.4	10,385.9	1.68	.1388
TREAT*DATE*DEPTH	4	8,903.5	2,225.9	0.36	.8365
TREAT*DATE*BLOCK	6	42,322.2	7,053.7	1.14	.3484
TREAT*DEPTH*BLOCK	6	7,398.7	1,233.1	0.20	.9760
DATE*DEPTH*BLOCK	12	25,157.1	2,096.4	0.34	.9791
TREAT*DATE*DEPTH* BLOCK	12	29.789.9	2,482.5	0.40	.9588
ERROR	72	445,637.0	6,189.4		
TOTAL	143	3,699,530.0			

Figure 2-6. Mean extractable soil potassium on control and burned plots at different depths, averaged over moisture levels and dates.

Note- Open circles represent burn values and closed circles control values.
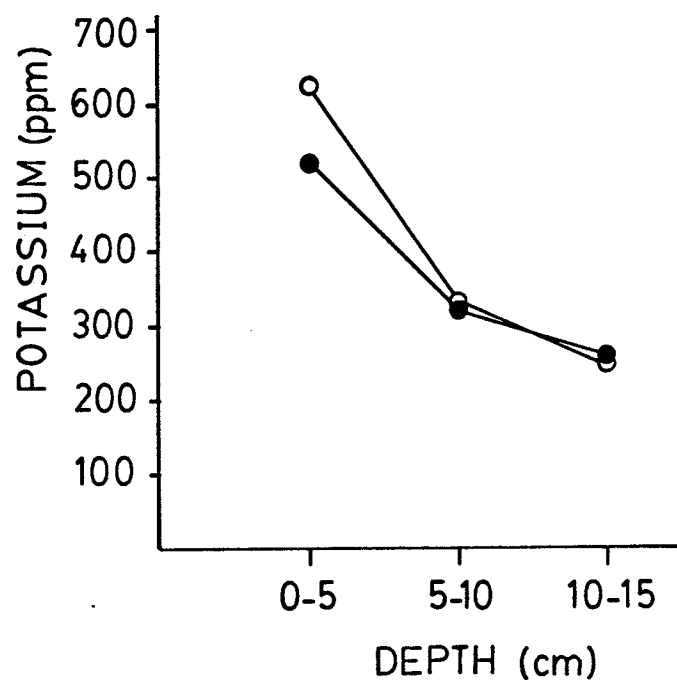
Table 2-5. Analysis of variance for soil conductivity.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
TREATMENT	1	41.28	41.28	52.65	.0001
DATE	2	2.41	1.21	1.54	.2218
DEPTH	2	27.31	13.66	17.24	.0001
BLOCK	3	15.53	5.18	6.60	.0005
TREAT*DATE	2	2.86	1.43	1.82	.1693
TREAT*DEPTH	2	4.23	2.12	2.70	.0740
DATE*DEPTH	4	0.84	0.21	0.27	.8987
TREAT*BLOCK	3	11.75	3.92	4.99	.0033
DATE*BLOCK	6	10.41	1.74	2.21	.0513
DEPTH*BLOCK	6	1.60	0.27	0.34	.9132
TREAT*DATE*DEPTH	4	3.35	0.84	1.07	.3785
TREAT*DATE*BLOCK	6	6.42	1.07	1.36	.2409
TREAT*DEPTH*BLOCK	6	0.99	0.17	0.21	.9723
DATE*DEPTH*BLOCK	12	3.98	0.33	0.42	.9497
TREAT*DATE*DEPTH* BLOCK	12	2.80	0.23	0.30	.9879
ERROR	72	56.46	0.78		
TOTAL	143	192.24			

2.3.2   Reed Regrowth

2.3.2.1   Shoot Biomass, Density and Morphology

Reed regrowth appeared less than a week after both mowing and burn-
ing and by September 21 had an average height of 58 cm on the burned and
47 cm on the mowed plots (Table 2-6).   The biomass of regrowth on burned
plots was 18.6% of preburn and on mowed plots 18.0% of preburn.   Density
declined by 10% after mowing and 17% after burning.   Biomass of regrowth
did not   differ between   burned and   mowed plots   but shoot   density was
higher (α = .05)   on mowed plots.   On the average regrowth shoots were
taller (α = .0005), had a greater basal diameter (α = .025) and had more
leaves (α =.0005) on burned than mowed plots (Table 2-7).

2.3.2.2   Shoot Mineral Contents

The concentrations   of P and K   varied between plant   parts,   being
highest in leaves, intermediate in leaf sheaths and lowest in stems (Ta-
ble 2-8).   Shoots from burned plots had   lower P and K in their leaves,
sheaths and stems than those from mowed plots (Table 2-9).   The Ca con-
tent of all plant organs except   sheaths was not significantly different
after the two treatments.   The Mg content   of leaves and stems was sig-
nificantly different after the two treatments. Leaf Mg content was high-
er after burning and stem content lower after burning than mowing.

2.3.2.3   Rhizome Reserves

On November1 there were significant   differences in the TNC content
of rhizomes due to treatments (Table   2-10).   Rhizome reserves were re-
duced after burning   and mowing,   with a greater   reduction after mowing
(Table 2-11).

Table 2-6. Reed regrowth after summer burning and mowing.

TREATMENT

CHARACTERISTIC	BURN	MOW
MEAN HEIGHT (cm)	57.5	46.5
MEAN LEAF NO.	5.7	4.3
BASAL DIAMETER (mm)	4.8	4.5
DENSITY (Shoots/m^2)	71.7	92.8
BIOMASS g/m^2)	146.0	120.0

Table 2-7. Analyses of variance for P. australis regrowth, 1979.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
HEIGHT					
TREATMENT	1	952.7	952.7	21.89	.0001
BLOCK	3	172.6	57.5	1.32	.2904
TxB	3	615.5	205.1	4.71	.0100
ERROR	24	1044.6	43.5		
TOTAL	31	1355.4			
LEAF NUMBER					
TREATMENT	1	14.44	14.44	123.71	.0001
BLOCK	3	5.61	1.87	16.02	.0001
TxB	3	1.58	0.53	4.52	.0119
ERROR	24	2.80	0.12		
TOTAL	31	24.43			
BASAL DIAMETER					
YEAR	1	0.845	0.845	6.43	.0182
BLOCK	3	4.844	1.615	12.28	.0001
TxB	3	0.525	0.175	1.33	.2875
ERROR	24	3.155	0.131		
TOTAL	31	9.369			
DENSITY					
TREATMENT	1	231.13	231.13	5.09	.0334
BLOCK	3	231.00	71.00	1.56	.2240
TxB	3	28.38	9.45	0.21	.8896
ERROR	24	1089.50	45.40		
TOTAL	31	1562.01			

Table 2-8. Analyses of variance shoot phosphorus and potassium.

SOURCE OF VARIATION	D.F.	SUM SQUARES	F calc.	Pr > F
		PHOSPHORUS		
TREATMENT	1	0.0450	54.43	.0001
PART	2	0.5538	335.03	.0001
BLOCK	3	0.1006	40.57	.0001
TREAT*PART	2	0.0067	4.06	.0214
TREAT*BLOCK	3	0.0479	16.45	.0001
PART*BLOCK	6	0.0143	2.88	.0142
T*P*B	6	0.0202	4.08	.0014
ERROR	72	0.0595		
TOTAL	95	0.8409		
		POTASSIUM		
TREATMENT	1	3.598	49.96	.0001
PART	2	14.810	112.58	.0001
BLOCK	3	10.056	50.96	.0001
TREAT*PART	2	1.887	14.34	.0001
TREAT*BLOCK	3	0.745	3.77	.0142
PART*BLOCK	6	3.317	8.40	.0001
T*P*B	6	5.227	13.34	.0001
ERROR	72	4.736		
TOTAL	95	44.087		

Table 2-9 Mineral contents of various _Phragmites_ organs after two experimental treatments. Values are mean and std. error, expressed as percent of dry weight.

MINERAL	LEAF		SHEATH		STEM	
	MOW	BURN	MOW	BURN	MOW	BURN
CALCIUM	0.276 ± 0.018	0.284 ± 0.012	0.208 ± 0.009	0.180 ± 0.008	0.048 ± 0.001	0.051 ± 0.004
MAGNESIUM	0.154 ± 0.007	0.169 ± 0.006	0.126 ± 0.009	0.110 ± 0.004	0.500 ± 0.003	0.043 ± 0.002
PHOS PHORUS	0.345 ± 0.012	0.291 ± 0.009	0.206 ± 0.015	0.161 ± 0.013	0.161 ± 0.015	0.120 ± 0.012
POTASSIUM	2.75 ± 0.123	2.16 ± 0.071	1.53 ± 0.118	1.51 ± 0.124	2.02 ± 0.137	1.49 ± 0.182

Table 2-10. Analysis of Variance for T.N.C. after 3 Treatments, 1979.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
TREATMENT	2	480.20	240.10	38.11	.0001
BLOCK	3	16.42	5.47	0.87	.4464
TxB	16	44.76	7.46	1.18	.3372
ERROR	35	220.49	6.30		
TOTAL	46	761.87			

Table 2-11. Mean T.N.C. content of rhizomes after 3 treatments, 1979.

CHARACTERISTIC

TREATMENT	MEAN	STDERR
CONTROL	37.2	0.65
BURN	32.5	0.75
MOW	29.3	0.45

2.3.3 Substorey Regrowth

2.3.3.1 Seedlings

The removal of litter and the P. australis canopy by fire or mowing produced conditions favorable for the germination of seeds of certain species (Table 2-12). After burning the highest seedling frequencies were for Sonchus arvensis L. and Urtica dioica L.. Atriplex patula L. and Cirsium arvense (L.) Scop. had intermediate frequencies and Mentha arvensis L. var villosa (Benth.) Stewart and Teucrium occidentale Gray low frequencies. After mowing high frequencies of S. arvensis and U. dioica also occurred but M. arvensis and C. arvense had higher frequencies than after burning. The frequency of A. patula was lower after mowing than burning and the frequencies of M. arvensis and Lycopus asper Greene were higher.

After burning A. patula and U. dioica had the highest seedling densities, with that of S. arvensis intermediate and other species having low seedling densities. S. arvensis seedling density was similar after the two treatments but that of C. arvense was higher after mowing than burning. Following both treatments there were differences in seedling densities along the water depth gradient (Table 2-12) with C. arvense being most abundant in row 1 (driest), S. arvensis and U. dioica being densest in row 2 and A. patula being most abundant in row 3 (wetter).

2.3.3.2 Regrowth from Rhizomes

In comparison with preburn densities the number of replacement shoots was less for all species except C. arvense (Table 2-13). After mowing there was also a reduction in the densities of all substorey

Table 2-12. Seedling frequencies (%) and densities ($\#/m^2$).

SPECIES	DENSITY		FREQUENCY	
	BURN	MOW	BURN	MOW
Atriplex patula	49.2	2.3	56	19
Cirsium arvense	6.8	16.0	56	69
Mentha arvensis	4.8	7.3	19	56
Lycopus asper	0.0	0.3	0	6
Sonchus arvensis	15.2	12.8	81	63
Teucrium occidentale	2.0	0.5	6	3
Urtica dioica	76.8	26.8	75	63

Table 2-13. % Change in Substorey Densities, Preburn to Regrowth.

TREATMENT

SPECIES	BURN	MOW
Teucrium occidentale	-75.0	-96.4
Lycopus asper	-36.9	-80.2
Mentha arvensis	-12.5	-87.5
Urtica dioica	-37.0	+186.7
Cirsium arvense	+60.0	+350.0

Table 2-14 Substorey Regrowth, Density (Shoots/m 2).

TREATMENT

SPECIES	BURN	MOW
Teucrium occidentale	5.0	0.5
Lycopus asper	2.3	1.3
Mentha arvensis	3.5	1.5
Urtica dioica	6.8	23.8
Cirsium arvense	4.0	7.0

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species except C. arvense and U. dioica. After burning L. asper, M. arvensis and T. occidentale had greater regrowth (Table 2-14), but after mowing densities of of C. arvense and U. dioica were higher.

2.4 DISCUSSION

2.4.1 Environmental Changes

2.4.1.1 Physical Characteristics

Only Hoffpauir (1961) has reported the effects of marsh burning on subsequent soil temperatures. He found no increase in soil temperature where the soil surface was flooded but a significant increase where the water table was below the soil surface. In my study soil temperatures were measured only in the driest plot, and it may be that there was no change in the wettest (intermittently flooded) plot. Several authors have reported increased soil temperatures after burning in terrestrial habitats. In aspen woodlands Smith and James (1978) found that soil temperature at the surface, at -5 and -10 cm increased. In prairies Hulbert (1969) reported that soil temperatures increased by 1-5 $^{\circ}$C. following both burning and the removal of litter by mowing and raking. Sharrow and Wright (1977) also found increased soil temperatures at a depth of 7.5 cm after burning and mowing, but found a greater increase after burning than mowing. This is the first report to date of diurnal fluctuations in soil temperature following burning. My data shows that not only is the mean soil surface temperature increased but there are much larger diurnal fluctuations in soil temperature following burning. A more severe environment following removal of litter by burning was shown by Old (1969) in terms of humidity, and temperature profiles. She

created environmental indicies which summarized the increasingly severe environment when vegetation and litter was removed. Buttery and Lambert (1965) and Ondok (1973) reported that light extinction was rapid beneath P. australis canopies. My data shows this and also that light intensity increased dramatically when the canopy and litter were removed by burning.

2.4.1.2 Chemical Characteristics

Hoffpauir (1961) found significant increases in soil calcium, conductivity, phosphate and K immediately following the burning of Spartina marshes in Louisiana. He found that most of these changes were short lived and hypothesized that these nutrients had been taken up by the regrowing plants. He also tied the increases to the nutrient content of the ash and suggested that all the increases observed could be accounted for by their release from the ash. I also determined the calcium, magnesium, K and P content of the ash (Table 2-15). Inputs of nutrients from the ash can explain the increases in phosphate, and K I observed following fire. It is especially notable that increases in phosphate and K were mainly in the surface (0-5 cm) layer of soil, this layer being largely silt and clay and had a very low organic matter content. The increases in phosphate and K observed at the surface level, therefore must have been due to their release from the ash rather than to accelerated organic matter decomposition. In contrast nitrate increased most in the second soil layer, which was high in organic matter. This increase was then due to more rapid mineralization as a result of higher soil temperatures.

Table 2-15. Nutrient content of ash.

CHARACTERISTIC	MINERAL			
	CALCIUM	MAGNESIUM	POTASSIUM	PHOSPHORUS
Ash Content (% dw)	0.939	0.354	0.695	0.443
Nutrient Input (g/m^2)	1.22	0.598	0.904	0.576

I found that there was no immediate increase in nitrate on the burned plots. This may have been because a certain amount of time was required for the soil to heat up after burning. As described above there was no increase in nitrate or phosphate in the wettest plot. This plot was periodically inundated throughout the period in which soil chemistry was studied. It may be that the phosphate released from the ash was removed in sheet runoff from this area when waters declined. In the case of nitrate the inundation may have prevented an increase in soil temperature which is the hypothesized reason for nitrate release. Sharrow and Wright (1977) tied the release of mineral N after burning to subsequent increases in soil temperatures and more rapid mineralization as a result of enhanced microbial decomposition. Several other authors have reported a release of soil nutrients after burning in other ecosystems. Smith and James (1978) reported increased calcium, magnesium and K concentrations at a depth of 0-5 cm in the soil of an aspen woodland following burning. Smith (1970) found an increase in the phosphate and K content of the soil of coniferous forest following burning and Beaton (1959) noted an increase in phosphate in a similar habitat following burning. In tallgrass prairie Owensby and Wyrell (1973) found increased soil calcium, magnesium and K following burning but no consistent increase in nitrate or phosphate. In heathlands releases of calcium, phosphate and K following burning were reported in the surface organic layers of the soil (Allen,1964; Allen et al.,1969). In my study the release of nutrients from ash may have stimulated growth to a greater extent on the burned than the mowed plots and contributed to the more rapid phenological development of P. australis shoots observed after this treatment.

2.4.2   Reed Regrowth

2.4.2.1   Shoot Biomass, Density and Morphology

As shown above, the biomass of regrowth was much less than that of the original crop. This is similar to the response after mowing found by Dykyjova and Husak (1973) for a dry stand and by Mochnacka-Lawacz (1974). The former authors found that in a flooded stand the biomass of regrowth produced after mowing was almost equal to that of the intact stand. No reports have been found of the regrowth following summer burning but my study indicates that it is very similar to that after mowing.

My study showed that the density of regrowth following both mowing and burning was similar to the initial stand density, although burning resulted in slightly fewer stems. The density of regrowth after burning was less than after mowing and in all morphological characteristics shoots averaged larger after burning than mowing. This was because more branch shoots developed after mowing, from stem nodes at or just below the soil surface. Fire damaged the lateral buds at these nodes so that regrowth on burned plots was mainly due to a break in the dormancy of overwintering buds located near the soil surface. Furthermore it may be that the release of nutrients described after burning stimulated the regrowth shoots to develop more rapidly after burning than after mowing. All indications were that regrowth shoots after burning were more phenologically advanced than after mowing (height and leaf number). Dykyjova and Husak (1973) found that in a dry stand the density of regrowth was similar to the original stand density, as did Mochnacka-Lawacz (1974). In a flooded stand the former authors found that the density of regrowth

was almost twice that of the original. Haslam (1968) stated that re-growth is usually less dense after summer mowing than after summer burn-ing. My data shows the opposite.

2.4.2.2 Shoot Mineral Content

The mineral content of regrowth shoots after mowing and burning was similar to those noted by Mochnaka-Lawacz (1974) after mowing. She found that in comparison with intact stands harvested at the same time regrowth shoots were higher in the minerals characteristic of young spring growth (K, N, Mg, and P) and lower in those characteristic of older shoots (Ca, Si, total ash). She found that, similar to my find-ings, leaves were higher in N,P and K than stems but similar in Ca con-tent. The differences in the mineral contents of shoots that I found after burning and mowing were probably due to more rapid phenological development following burning. Shoots from burned plots had lower con-tents of those minerals characteristic of immature shoots (P and K). Bailey and O'Neill (1972) showed that the N and P content of reed shoots declines with age.

2.4.2.3 Rhizome Reserves

The TNC contents of rhizomes were reduced after both burning and mowing in comparison with controls at the end of the growth season. This indicated that both treatments would deleteriously effect reed growth in the next (1980) growing season. The lower TNC content follow-ing mowing in comparison to burning may have been related to the higher shoot density.

2.4.3 Substorey Regrowth

2.4.3.1 Seedlings

The appearance of seedlings after mowing and burning may be related to some of the microenvironmental changes which occurred as a result of the removal of the canopy and litter. Light intensity and soil temperature were shown to be lower on the control plots. Germination of C. arvense, L. asper and S. arvensis seeds either requires or are enhanced by high light intensities (Descheid and Schultz,1960; Thompson,1969; and Kumar and Irvine, 1971; and Wilson,1979). The germination of Lycopus also requires fluctuating temperatures (Thompson,1969). Germination of C. arvense (Kumar and Irvine,1971; Wilson,1979) and S. arvensis (Dersheid and Schultz,1960) are also enhanced by fluctuating temperatures. Beneath the litter layer light intensity is probably low and so the removal of litter by fire would trigger the germination of light requiring seeds. It was shown above that fluctuations in temperature both at the soil surface and at a depth of 5 cm were increased after burning and this would further enhance the germination of these species. There were higher A. patula seedling densities following burning than mowing. Seeds of this species are of two types, soft and hard coated (Beadle,1952) and the germination of hard coated seeds is low without scarification. Burning may damage the seed coat of A. patula thus contributing to greater germination following burning than mowing.

2.4.3.2 Regrowth from Rhizomes

C. arvense and U. dioica sprouted the greatest number of regrowth shoots in comparison to their original density. Both species have ro-

bust perennial rhizomes (Grime and Lloyd,1973; Basset et.al.,1977). The labiate species have less robust rhizomes and would be expected to regrow less profusely after burning or mowing, as was observed.

2.5 CONCLUSIONS

Several microenvironmental changes were observed after burning, including increased light intensity and more fluctuating temperatures and humidity. Following burning there was a release of nutrients including nitrate, phosphate and K.

Reed regrowth following both mowing and burning began soon after the treatments were applied and by mid-September shoots were well developed. The biomass of regrowth following the two treatments was similar but higher shoot densities followed mowing. Shoots from burned plots were more phenologically advanced than those from mowed plots. Regrowth shoots were high in mineral content in comparison to the values recorded in the literature for mature shoots. There was a decline in rhizome reserves following both treatments which occurred to a greater degree following mowing.

Many seeds germinated following both burning and mowing and this was related to the microenvironmental changes which occurred as a result of removing the canopy and litter. Of the substorey species C. arvense and U. dioica sprouted regrowth shoots most vigorously and this was related to their more robust rhizomes.

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Chapter III

POSTFIRE PERFORMANCE OF PHRAGMITES AUSTRALIS

3.1   INTRODUCTION

The use of prescribed burning to manage the production and species composition of native prairie vegetation has received intensive study in the past several decades. Prescribed burning, if wisely used, is both a 'natural' and an inexpensive grassland management tool and has been used to manage ecological preserves (Lloyd,1968).   However, prescribed burning in prairie marshes has not received the attention that it has in upland grassland communities.   Some early accounts (Cartwright, 1942) emphasized the dangers inherent in marsh burning caused by the buildup of extremely heavy fuel loadings in certain marsh communities.   Other authors (Ward,1942; Hoffpauir,1961;Ward,1968;Haslam,1969a) have indicated that marsh fires are both controllable and useful in their effects.

Reports have been made of the effects of fire on a number of different marsh dominants such as the reed, Phragmites australis (Cav.) Trin. ex Steudel (Ward,1942; Schlichtmeir,1967;   Ward,1968;   Haslam,1969a), whitetop Scolochloa festucacea (Wild.) Link (Smith,1973) and wiregrass Spartina patens (Ait.) Muhl.   (Hoffpauir,1961). Marsh fires have been carried out specifically to manage marsh dominants for forage (Smith,1973) or to produce reed for the thatching industry in Britain (Haslam,1969a).   Other marsh fires described were set with the objective of improving marsh wildlife habitat (Ward,1942;   Hoff-

pauir,1961; Zonteck,1966; Sclichtmeir,1967; Ward,1968; Perkins,1969). In marshes, plant succession often trends toward monodominant communities and burning was seen as a way to increase habitat diversity and thus wildlife use.

One of the marsh species whose responses to fire has received some study is reed, Phragmites australis (Ward,1942;Sclichtmeir, 1967; Ward,1968, Haslam,1969a). These reports are descriptive in nature and contain few detailed data. They indicate that P. australis responds differently to burning in different seasons. The present study was designed to quantify the postfire performance of Phragmites australis following fires set in mid-summer, at the peak of growth; in the fall, after senescence; and in the spring, before the commencement of growth.

3.2 METHODS

3.2.1 Site Preparation

Within a dense P. australis stand a grid of twenty 20m by 20m plots was delimited with a system of 5m wide firebreaks (Figure 3-1). Four different treatments (control, summer 1979 burn, fall 1979 burn, and spring 1980 burn) were assigned four times each in a randomized complete block design. Rows of north to south oriented plots were used as blocks. This accounted for a significant portion of the within site variation in P. australis performance due to an east to west oriented moisture gradient within the stand. Four plots were burned on August 1,1979 four on October 7,1979 and four on May 11,1980.

Figure 3-1. Study site, spring 1980.

FORSTER'S BAY

TYPHA

PHRAGMITES

N→

100 m

SPRING BURN		M	CONTROL	FALL BURN	SUMMER BURN
	CONTROL	SPRING BURN M	SUMMER BURN	FALL BURN
CONTROL		SUMMER BURN	FALL BURN	SPRING BURN M
FALL BURN	SUMMER BURN	SPRING BURN		CONTROL M

HORDEUM-TEUCRIUM MEADOW

TYPHA

TYPHA
SCIRPUS

BLIND CHANNEL
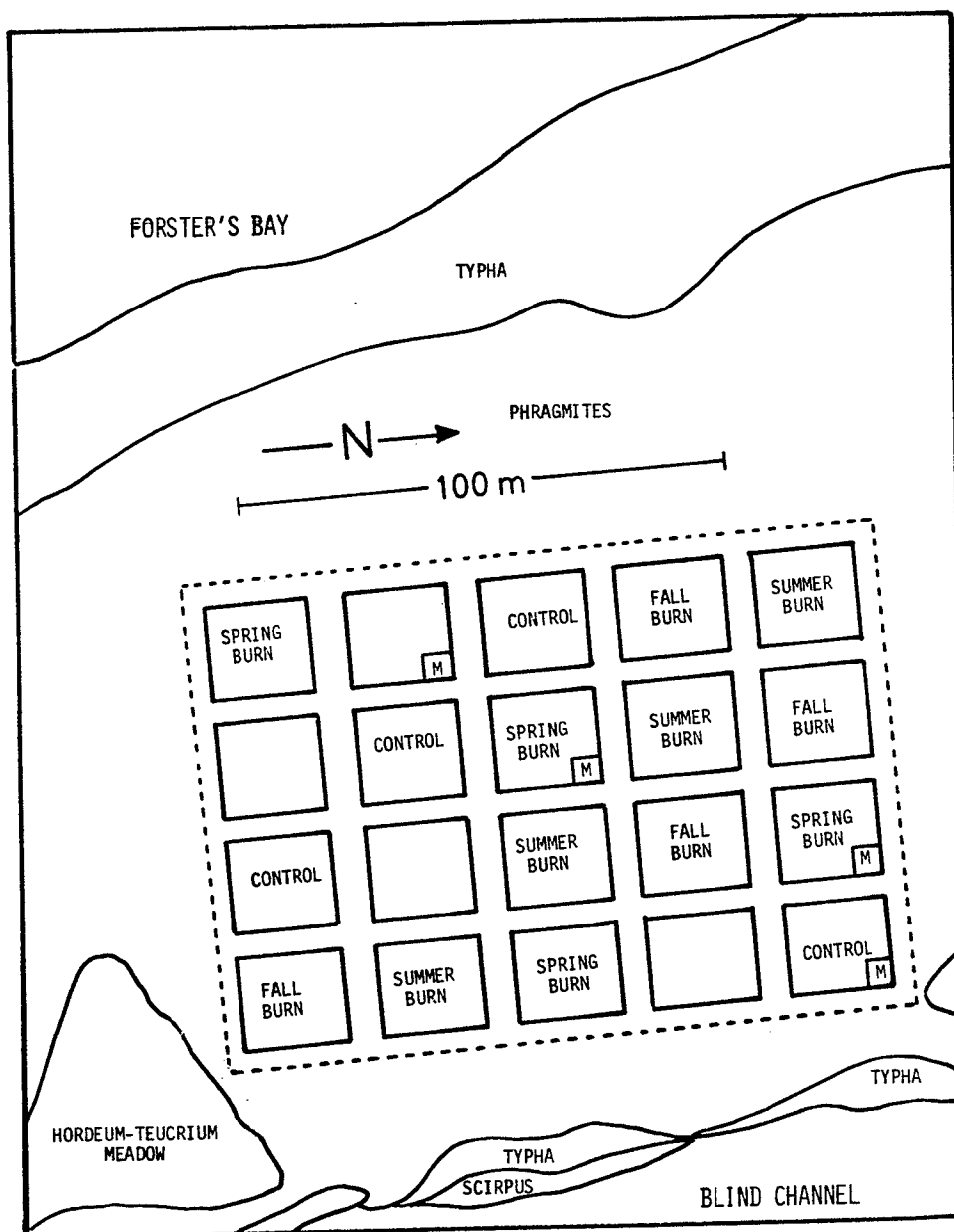
3.2.2   Firing Techniques

To prevent wildfires the canes in the fire breaks were cut and re-
moved.   The stubble was soaked with water pumped from an adjacent chan-
nel before burning. Backfires were set on the leeward side of the plots
before the major fire was set with the wind. Spring and fall fires were
set on fairly calm days but fires would not maintain themselves with a
windspeed of less than 10 Kmph in the summer.

3.2.3   Shoot Density and Biomass

Seasonal trends in P. australis shoot biomass, (3) and in total and
flowering shoot density, and in average stem weight were followed on the
treated and control plots throughout the 1980 growing season.   In May
three sampling stations were randomly located within each plot (Figure
3-1). Biweekly from May 15 to September 15 a $0.5m^2$ (71 by 71 cm) quad-
rat was located at each sampling station.   Sampling periods ranged from
3 to 5 days with the 1st or 15th of the month as the midpoint.   From
within these quadrats P. australis shoots were clipped at ground level,
counted, bagged and dried at 80° C to constant weight.   Average stem
weight was calculated.   Flowering stem density was recorded from their
formation in early July until senescence.   On August 15, flowering and
vegetative shoots were harvested and weighed separately,   to determine
the relative importance of these two stem types to total production in
the variously treated plots.   On August 1 inflorescences were clipped,
dried and weighed from three $1.5m^2$ quadrats per plot and average in-

_____

(3) Biomass is used to denote living aerial standing crop and where the
    qualifier below-ground is used this refers to the living standing
    crop of subterranean organs.

florescence weight calculated.

3.2.4   Shoot Morphology

Flowering shoot morphology was compared under all treatments during the August 1 sampling period by randomly choosing five flowering shoots from those collected in each of three $1.5m^2$ quadrats per plot, the total number approximating 60 shoots per treatment. The larger quadrat size was necessary because of the much reduced flowering stem density after summer burning. Characteristics measured for each shoot included height to flag leaf, length of the inflorescence, basal diameter, leaf number and largest leaf length. Vegetative shoots were also sampled with the height to the topmost unfolded leaf and the basal diameter of each being recorded.

3.2.5   Below-ground Standing Crop

Below-ground biomass of P. australis under the four treatments was sampled from Sept. 15 to Sept. 20,1980. Each sample consisted of a block of soil 25 by 50 cm in surface dimensions and 30 cm in depth. Three samples were taken per plot at random points along a transect running in a north to south direction through the center of the plots. The belowground material was washed free of soil in lake water and divided into four categories before oven drying at $80°$ C. Included were; 'new' roots and rhizomes (approximating this year's production), 'old' stem bases, rhizomes and roots, stem bases of this year's shoots, and dead P. australis material. New rhizomes were separated on the basis of position and color.

Figure 3-2. Experimental design for the sampling of aerial biomass and
density throughout the 1980 growing season. showing
randomized complete block design (north to south rows of
plots being blocks).

C-Control

F-Fall Burn

SP-Spring Burn

SU-Summer Burn

EXPERIMENTAL DESIGN

* SAMPLING STATION

New roots were those attached to new rhizomes as well as those attached to this year's stem bases. Old stem bases, roots and rhizomes were darker in color but were white in their centers and were firm which differentiated them from dead material.

3.3 DATA ANALYSIS

Aerial biomass, total, flowering and vegetative stem density percentage of stems flowering and weight per stem were compared by treatments and blocks across sampling periods. Sampling stations over time were the main plots and stations at any one time were the split plots (Steele and Torrie, 1960). Density data from June 15 to September 15 inclusive were used in the analysis. Analysis of variance for biomass and weight per stem excluded the September 15 data because after senescence a different set of factors are involved in changes in stem weight. Flowering and vegetative density and percent flowering were compared using data collected from August 15 to September 15 inclusive. The August 1 data was not included as different sampling stations were used at this time.

Flowering and vegetative biomass collected on August 15 were compared by analysis of variance across treatments with a randomized complete block design. Stem morphological characteristics were compared across treatments using a completely randomized design and Duncan's Multiple Range test was used to compare treatment means. Differences in belowground biomass were tested using a randomized complete block design. Calculations were made using the S.A.S (Helwig and Council,1979) or B.M.D.P. (Dixon and Brown,1977) statistical packages.

3.4   RESULTS AND DISCUSSION

3.4.1   Shoot Biomass

3.4.1.1   Total Shoot Biomass

There was a strong treatment effect shown in the analysis of variance for biomass throughout the 1980 growing season (Figure 3-2, Table 3-1).   There was also a strong block effect and a significant treatment by block interaction.   This interaction was due to different growth of P. australis on the control plots where biomass increased dramatically with increasing soil moisture.   In treated plots biomass was relatively stable over blocks (water levels).   After all treatments biomass increased with time from emergence, reflecting canopy development but there was a strong interaction between treatment and time.   Biomass was higher on summer and fall burned plots early in the season, but by July 15 a consistent trend emerged where biomass was greater on spring and fall burned plots than in the controls,   but lower than in the controls on summer burned plots. This was related to earlier shoot emergence and more rapid early season growth on burned plots, especially on summer and fall burned plots (Table 3-2).   Phenological differences were greater early in the season but less apparent by the initiation of flowering.

Ward (1968) and Haslam (1969a)   did not include production data in their descriptions of fire responses by P. australis Smith (1972) found that fall burning of Scolochloa festucacea increased biomass in the subsequent growth season. He also found that there was no clear trend in the effects of water levels on S. festucacea production.   The increases in P. australis production observed in my study are similar to those observed by many authors for tallgrass prairie species such as big blues-

tem *Andropogon gerardi* Vitman (Gay and Dwyer,1965; Owensby and Anderson

1967; Hulbert,1969; Old,1969; Owensby,1970 and Peet et al.,1975). All

these authors reported increased production by *A. gerardi* following

spring burning. Hulbert (1969) and Old (1969) showed that much of this

response could be duplicated by removing the standing litter. Peet et

al. (1975) tied increased production to warmer soil temperatures and

greater light penetration which allowed better growth from emergence un-

til late June on burned plots. Smith (1972) noted a similar early emer-

gence in *S. festucacea*. Enhanced growth of *P. australis* in our study was

probably due to similar environmental changes to those recorded by Smith

in *Scolochloa* marshes after burning.

3.4.1.2 Flowering vs Vegetative Shoot Biomass

Based on the August 15 sampling (Figure 3-3, Table 3-3) flowering

stem biomass was approximately equal on spring burned and control plots,

but was much reduced after fall and summer burning. Trends in inflores-

cence yields (Figure 3-4) are similar to those for flowering stem densi-

ties (see below), with an increase after spring burning but a decline

after fall and summer burning. Flowering stem biomass did not increase

after spring burning in spite of increased flowering shoot density (see

below). Old (1969) reported increased flowering stem biomass on tall-

grass prairie after spring burning but did not indicate if vegetative

biomass also increased. Vegetative biomass was greatly increased by all

burning treatments (Figure 3-3, Table 3-3) reflecting increased stem

densities (see below). Vegetative stem biomass was greatest on fall

burned plots. Vegetative biomass was similar after spring and summer

burning.

Figure 3-3. Seasonal trends for P. australis mean aerial biomass
collected from differently treated sets of plots throughout
the 1980 growing season.   Values are means with standard
errors.
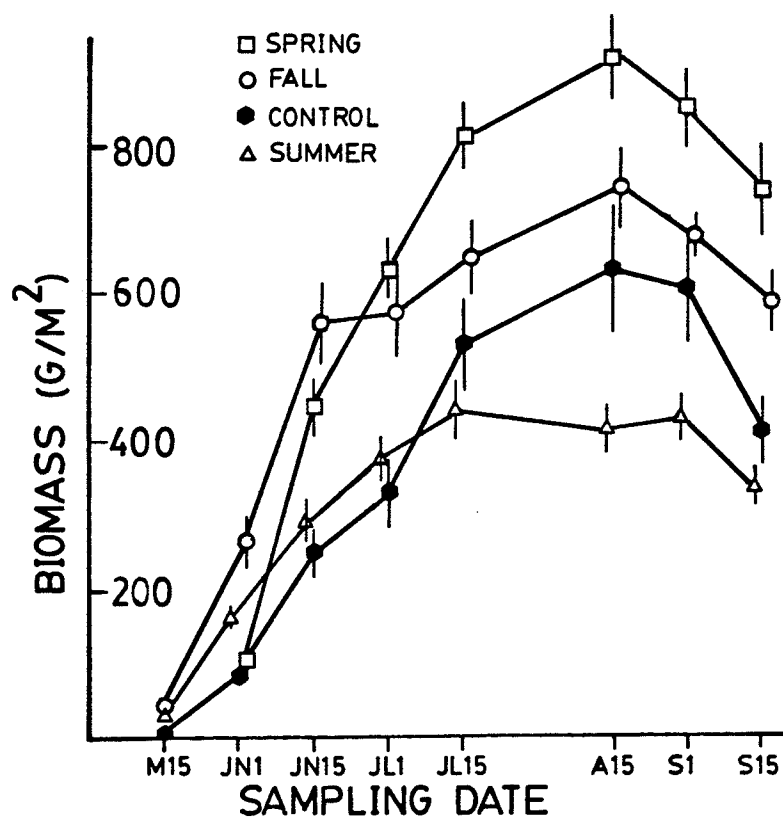
Table 3-1. Analysis of variance for <u>P</u>. <u>australis</u> biomass, 1980.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
Treatment	3	4,290,044	1,430,015	66.24	.0001
Block	3	1,061,480	353,827	16.39	.0001
Treat x Block	9	1,160,632	128,959	5.97	.0001
Error # 1	32	690,882	21,590		
Time	4	2,835,853	708,842	42.72	.0001
Treat x Time	12	755,842	62,987	3.80	.0001
Block x Time	12	186,923	15,557	0.94	.5109
Treat x Block x Time	36	797,177	22,144	1.33	.1543
Error # 2	128	2,124,115	16,595		
Total	239	13,902,948			

Table 3-2. Phenological development of shoots after 4 treatments.

PHENOSTAGE	TREATMENT			
	CONTROL	SPRING	SUMMER	FALL
Emergence	May 26	May 19	May 2	May 2
'2 Leaf' Stage	May 31	May 31	May 21	May 21
'5 Leaf' Stage	June 14	June 14	June 4	June 4
Floral Inititation	July 8	July 8	July 1	July 1
Anthesis	August 18	August 18	August 18	August 18

Figure 3-4. Aerial P. australis biomass sampled after four treatments on August 15, 1980 and divided into flowering and non-flowering shoots. Values are means with standard errors.

PHRAGMITES BIOMASS Aug. 15. 1980

MEAN BIOMASS (g /m²)

KEY

FLOWERING
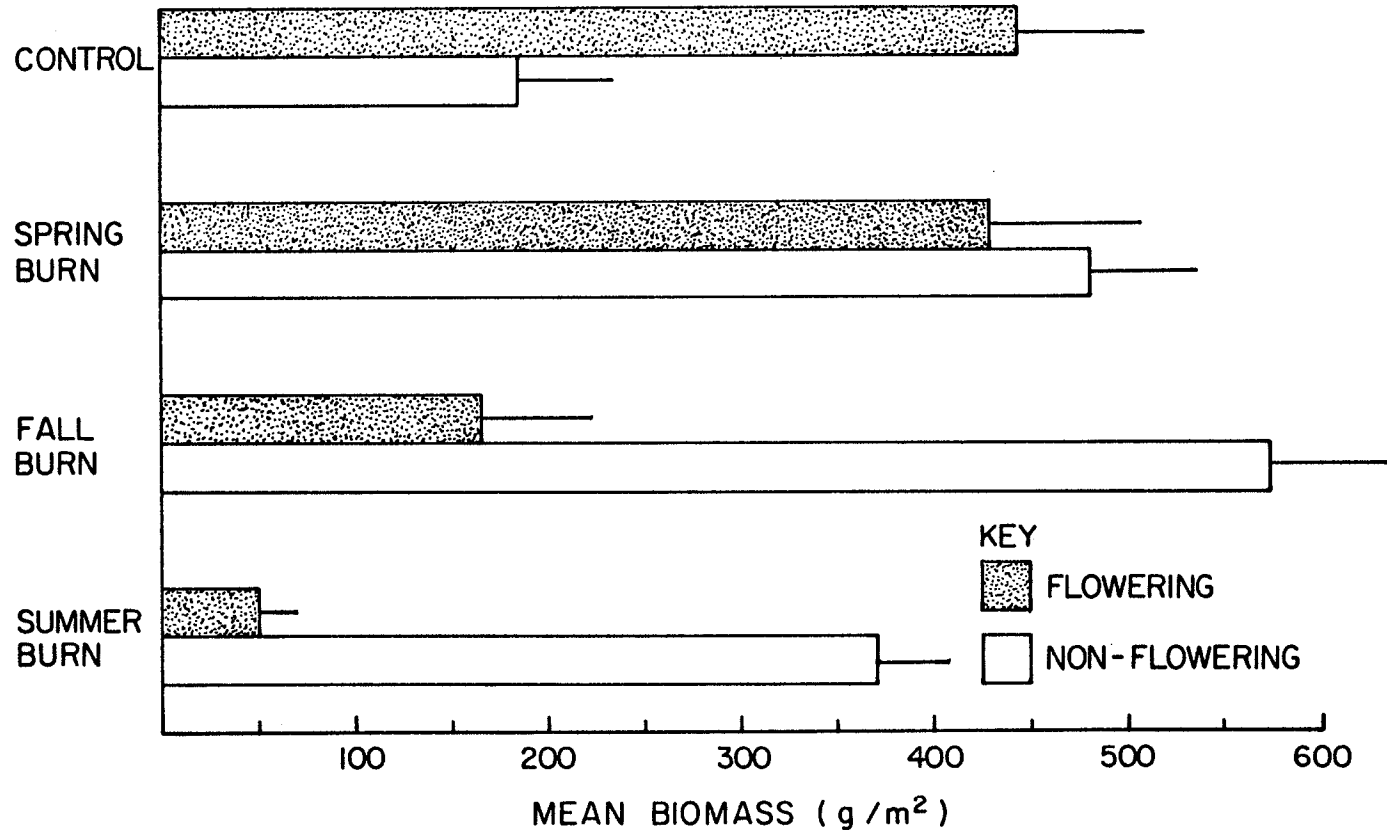
NON-FLOWERING

Table 3-3. Compartmentalized $\underline{P}$. $\underline{australis}$ biomass, August 15 1980.

CHARACTERISTIC   TREATMENT MEAN *

	Control	Summer	Fall	Spring
Flowering Biomass (g/m^2)	445.6a	49.2b	166.2b	431.9a
Vegetative Biomass (g/m^2)	187.3c	376.8b	575.2a	482.6ab
Total Biomass (g/m^2)	632.9b	416.9c	741.4b	914.6a

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* Means followed by the same letter are not different at $\alpha = .05$, Duncan's Multiple Range test.

Figure 3-5. Inflorescence weights from differently treated sets of plots, based on twelve 1.5m quadrats per treatment.

Sp - Spring burn

Su - Summer burn

F - Fall burn

C - Control
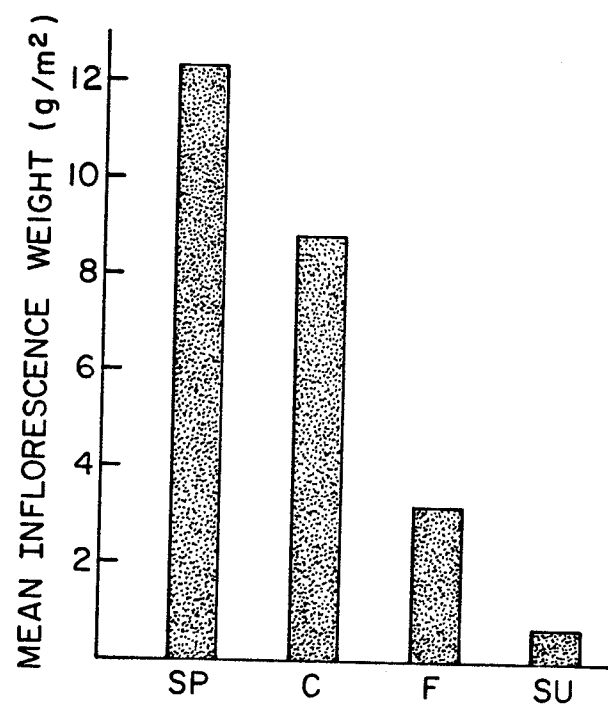
Figure 3-6. Seasonal trends for P. australis shoot density after four

experimental treatments throughout the 1980 growing season.

Values are means and standard errors. The bold horizontal

lines represent mean post-emergence density.
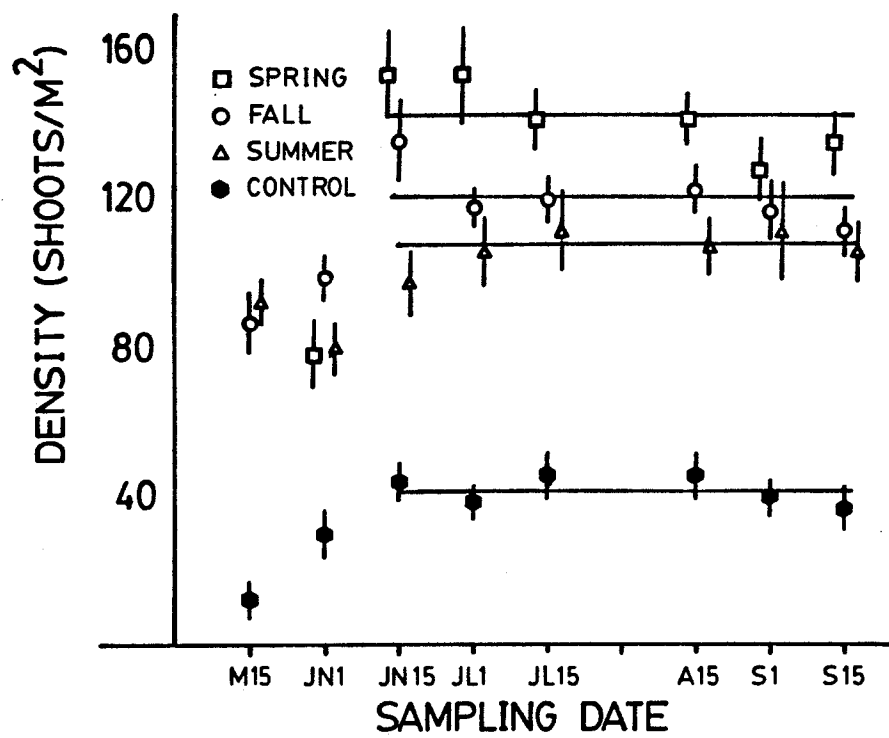
3.4.2   Shoot Density

3.4.2.1   Total Density

Following the initial emergence period (after June 15) there was no significant change in shoot density after any treatment (Figure 3-5) but there was an extremely strong treatment effect (Table 3-4) in density. The main difference was due to the dramatic increase in shoot density on burned plots when compared with controls (Figure 3-5). Differences between sets of plots burned at the various times were of lesser magnitude. Spring burned plots had a slightly higher density than fall or summer burned plots. Total stem density also showed an extremely strong block effect (Table 3-4). Density was low in block 1 (driest) and increased with increasing moisture (i.e. toward block 4). Density did not respond similarily to the moisture gradient after all treatments (i.e. there was a treatment by block interaction). In the control plot set density increased steadily with increasing moisture. After all burning treatments density was low in the first (driest) row of plots but remained fairly stable over blocks 2,3 and 4.

Increased stem density of Scolochloa festucacea in the year following burning was reported by Smith (1972). Haslam (1969a) reported that Phragmites australis density increases dramatically after spring burning but presented no data to support these observations. She suggested that spring burning breaks internal dormancy and thus allows the simultaneous emergence of all overwintering and axillary buds. Numerous authors (Hulbert,1969; Old,1969; Peet et al.,1975) reported that the density of Andropogon gerardi increased following spring burning.

Table 3-4. Analysis of variance for total $\underline{P}$. $\underline{australis}$ density.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
Treatment	3	410,160	136,720	120.78	.0001
Block	3	20,330	6,777	5.99	.0025
Treat x Block	9	29,623	3,291	2.91	.0124
Error # 1	32	36,228	1,132		
Time	5	4,062	812	1.88	.0992
Treat x Time	15	9,246	616	1.43	.1394
Block x Time	15	13,802	920	2.13	.0109
Treat x Block x Time	45	37,796	840	1.95	.0014
Error # 2	160	69,047	432		
Total	287	630,293			

Figure 3-7. Seasonal trends for % of P. australis shoots flowering throughout 1980. Values are means and standard errors.
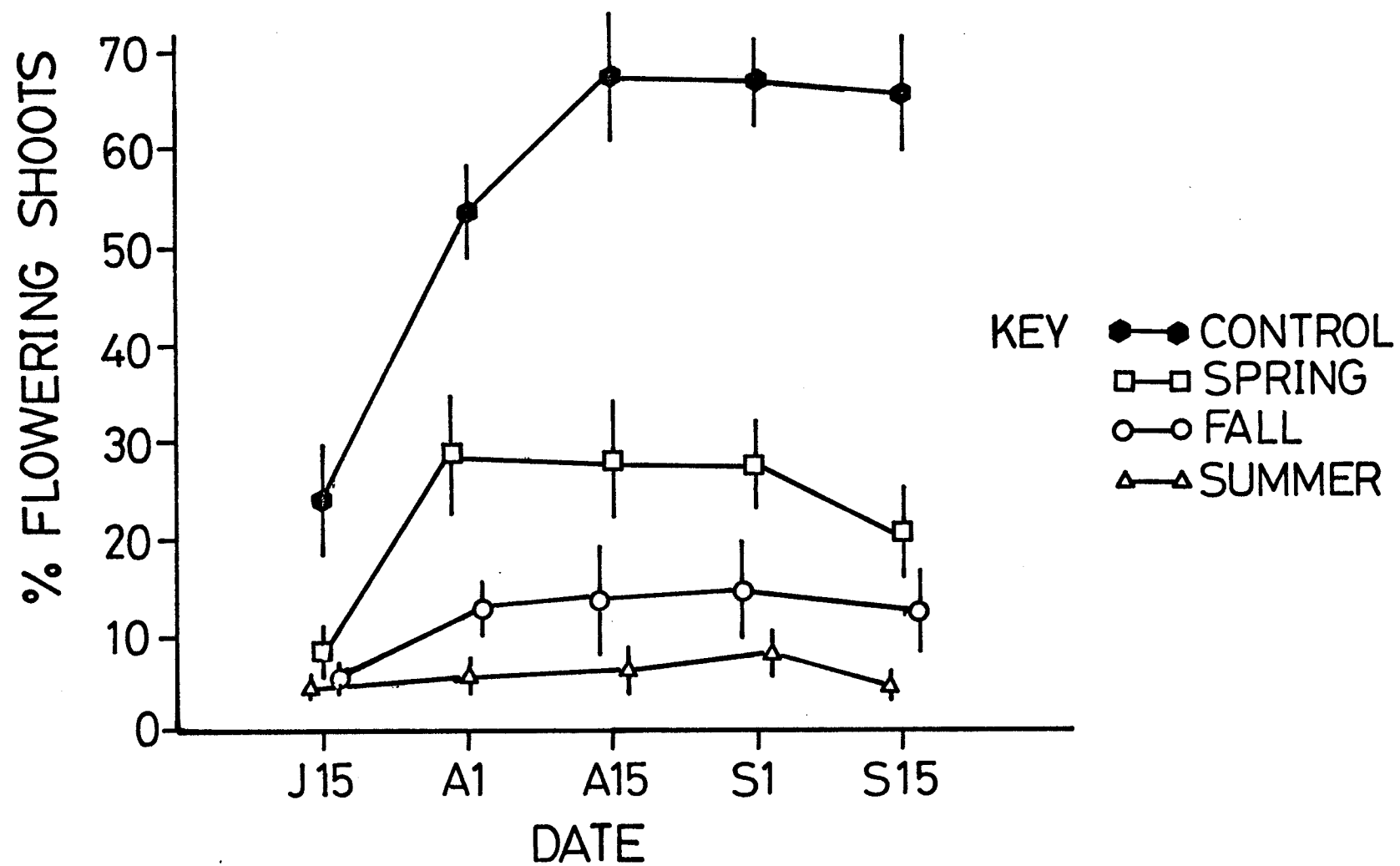
3.4.2.2   Percent flowering

The percentage of stems flowering was greatly reduced after all burning treatments (Figure 3-6).   In the analysis of variance this showed as a strong treatment effect (Table 3-5).   Percent flowering was less reduced after spring burning than after fall and summer burning. There was little change in the mean values for any treatment from August 15 to September 15 (i.e. no time effect).   There was a strong block effect, with percent flowering being highest in the first (driest) row, dropping in row two and increasing slightly in rows three and four. Percentage flowering responded differently to the moisture gradient in control than in burned plots (significant interaction).   In contrast to burned plots percent flowering on control plots was highest in the wettest plot, where there was a noticeable increase in stem density.   Haslam (1971) suggested that percent flowering was a good performance characteristic.   In optimum conditions smaller shoots flower as well as the larger shoots which almost always flower regardless of conditions. It may be that flowering stem density is a more sensitive performance indicator than percentage flowering as vegetative stem density appears to be influenced by slight disturbances.

3.4.2.3   Flowering density

Flowering stem density increased slightly after spring burning in comparison with the controls, but declined dramatically after fall and to a greater extent after summer burning (Figure 3-7).   This is shown as a significant treatment effect (Table 3-6).   There was also a strong block effect for this characteristic, which was almost as strong as the treat-

ment effect, mainly due to a reduction in flowering stem density in row two. Flowering stem density declined to a smaller extent after fall and summer burning in row one than in the wetter rows of plots. There was a strong time effect for this characteristic, with flowering density declining after August 15. This may have been due to abscisson of inflorescences with senescence or to the great spatial variability shown by this characteristic. Several authors (Dix and Butler,1954; Kucera and Ehrenreich,1962; Hadley and Kieckhefer,1963; and Old,1969) have shown increases in the flowering stem density of warm season tallgrass prairie species such as Andropogon gerardi. Increased inflorescence production was related to the removal of litter by fire through an experiment in which flowering stem production was compared on clipped and burned plots with controls (Old,1969). Phragmites australis responds in a similar way to spring burning. All shoots are capable of flowering but priority is given to those which develop from over-wintering buds (Haslam,1971). Reduction in flowering stem densities following summer and fall burning can be tied to the status of these buds. After summer burning overwintering buds lost their dormancy and developed immediately, permitting a second crop of shoots before frost. Few new overwintering buds developed before frost so that few were present to develop into flowering shoots in 1980. After fall burning there may have been high mortality of overwintering buds due to an earlier and deeper penetrating ground frost. There was greatly reduced snow accumulation during the winter of 1979 on fall burned plots which had few standing stems to trap the snow. Mean snow depth on fall burned plots was 22 cm compared with 66 cm on control plots in mid Febuary of 1979.

Table 3-5. Analysis of variance for % P. australis shoots flowering.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
Treatment	3	173,680	24,560	110.31	.0001
Block	3	12,404	4,135	18.57	.0001
Treat x Block	9	9,318	1,035	4.65	.0006
Error # 1	32	7,125	223		
Time	2	292	146	1.92	.1549
Treat x Time	6	358	60	0.78	.5864
Block x Time	6	613	102	1.34	.2516
Treat x Block x Time	18	1,995	111	1.46	.1371
Error # 2	64	4,871	76		
Total	143	110,654			

Figure 3-8. Seasonal trends for mean P. australis Flowering shoot
density throughout 1980. Values are mean with standard
errors.
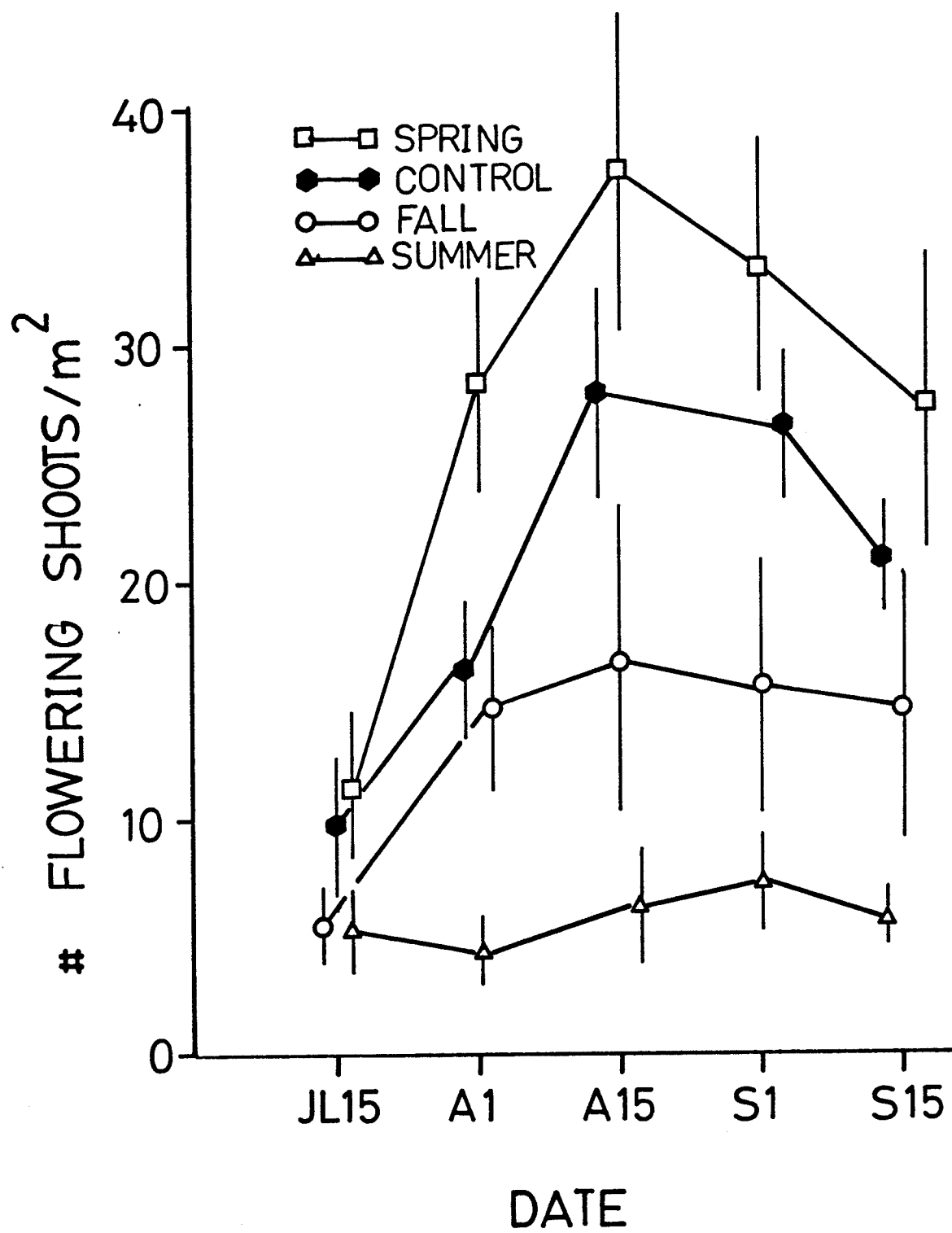
Table 3-6. Analysis of variance for flowering shoot density.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
Treatment	3	9,495	3,165	51.04	.0001
Block	3	6,688	2,229	35.95	.0001
Treat x Block	9	8,011	890	14.35	.0001
Error # 1	32	1,984	62		
Time	2	5,724	2,862	43.49	.0001
Treat x Time	6	2,392	399	6.06	.0001
Block x Time	6	2,699	450	6.83	.0001
Treat x Block x Time	18	3,517	195	2.97	.0007
Error # 2	64	4,214	66		
Total	143	44,725			

Smith (1972) did not report the effect of fire on inflorescence production in <u>Scolochloa</u> <u>festucacea</u> but suggested that frost could destroy floral primordia and that removal of litter by fire may increase frost damage.

3.4.2.4 Vegetative Density

There was a much stronger treatment effect for vegetative stem density than for flowering density (Tables 3-7 and 3-6). Vegetative density increased greatly after all burning treatments in comparison with the controls, but was not different between burning treatments. The greater portion of the strong treatment effect for total density thus appears to be due to this increase in vegetative density after all burning treatments. The enhancement of flowering density by spring burning adds to the treatment effect making it even stronger.

3.4.3 Mean Weight per Stem

3.4.3.1 Overall mean Stem Weight

A strong treatment effect showed in the analysis of variance for mean weight per stem (Table 3-8), due to a large decline in mean stem weight after all burning treatments. Average stem weight was similar after spring and fall burning, but was reduced to a greater extent after summer burning. There was a strong block effect for this characteristic, which was mainly due to smaller stems in block 2 after all treatments. There was also a significant treatment by block interaction, mainly due to a drop in mean stem weight on the wettest fall-burned plot. As with biomass, time had a strong effect (Table 3-8) since aver-

age stem weight stabilized earlier on all burned plots in comparison with the controls (Figure 3-8). There was a significant time by treatment interaction, probably due to phenological differences in shoots on burned and control plots. Haslam (1969a) stated that replacement shoots after burning are smaller than normal, but offered little data. She hypothesized that they were smaller because spring-formed buds arise higher on the rhizome system. They are smaller because buds arising higher receive a lesser share of rhizome reserves than those arising lower. My findings (Chapter 4) indicate that during the emergence period there is a considerably greater utilization of rhizome reserves on spring-burned than on control plots. On spring-burned plots there may be competition among shoots for energy during the emergence period which produces shorter individual shoots. Similar to my findings for P. australis Willims et al. (1980) found that the tillers of Agropyron spicatum (Pursh.) Scribn. and Sm. were lighter on burned than control plots.

3.4.3.2 Flowering and Vegetative Stem Weight

Mean vegetative stem weight was less (Figure 3-9) than mean flowering stem weight after all treatments. Average flowering stem weight was less after all burning treatments than in the controls, with those from spring, fall and summer burned plots becoming successively lighter. Weight per vegetative shoot also declined after all burning treatments. Vegetative stems were heavier after fall burning than after spring burning, and lightest after summer burning. These weight differences are reflected in morphological differences in stems from the different treatments as described below.

Table 3-7. Analysis of variance for vegetative shoot density.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
Treatment	3	199,552	66,517	87.87	.0001
Block	3	36,148	12,049	15.92	.0001
Treat x Block	9	26,942	2,994	3.95	.0081
Error # 1	32	24,223	757		
Time	2	9,837	4,919	12.25	.0001
Treat x Time	6	4,473	746	1.86	.1021
Block x Time	6	16,483	1,081	2.69	.0215
Treat x Block x Time	18	39,143	508	1.27	.2408
Error # 2	64	25,691	25,691		
Total	143	342,493			

Table 3-8. Analysis of variance for mean $\underline{P}$. $\underline{australis}$ shoot weight.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
Treatment	3	1,909	636.4	333.20	.0001
Block	3	93	30.9	5.99	.0025
Treat x Block	9	55	6.1	3.20	.0071
Error # 1	32	61	1.9		
Time	4	537	134.3	3.20	.0001
Treat x Time	12	350	29.2	16.73	.0001
Block x Time	12	43	43.6	2.05	.0246
Treat x Block x Time	36	52	1.5	0.83	.3502
Error # 2	128	223	1.7		
Total	239	3,324			

Figure 3-9. Seasonal trends for mean P. australis stem weight after

four treatments in the 1980 growing season. Values are

means with 95% confidence intervals for the twelve samples

per period. This variable was calculated as the ratio of

quadrat biomass to density.
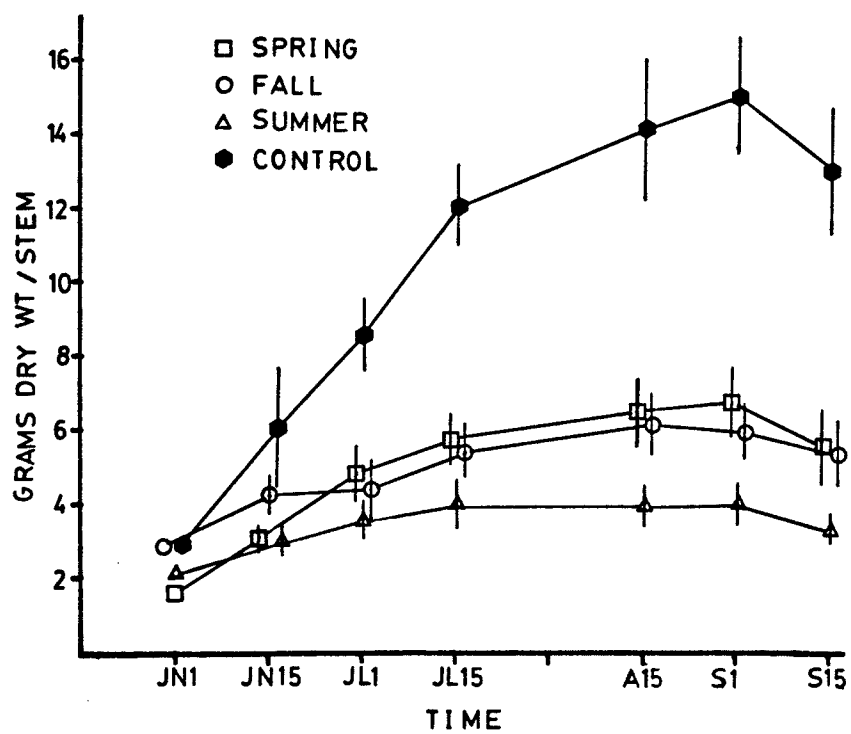
Figure 3-10. Mean weight per stem of different types of P. australis stems. Values are the total biomass of a stem type collected on August 15,1980 from 12 quadrats divided by their total density.

PHRAGMITES STEM WEIGHT Aug. 15. 1980

KEY:
ALL STEMS
FLOWERING STEMS
NON-FLOWERING STEMS

MEAN WEIGHT / STEM (g)

TREATMENT

CONTROL SPRING BURN FALL BURN SUMMER BURN
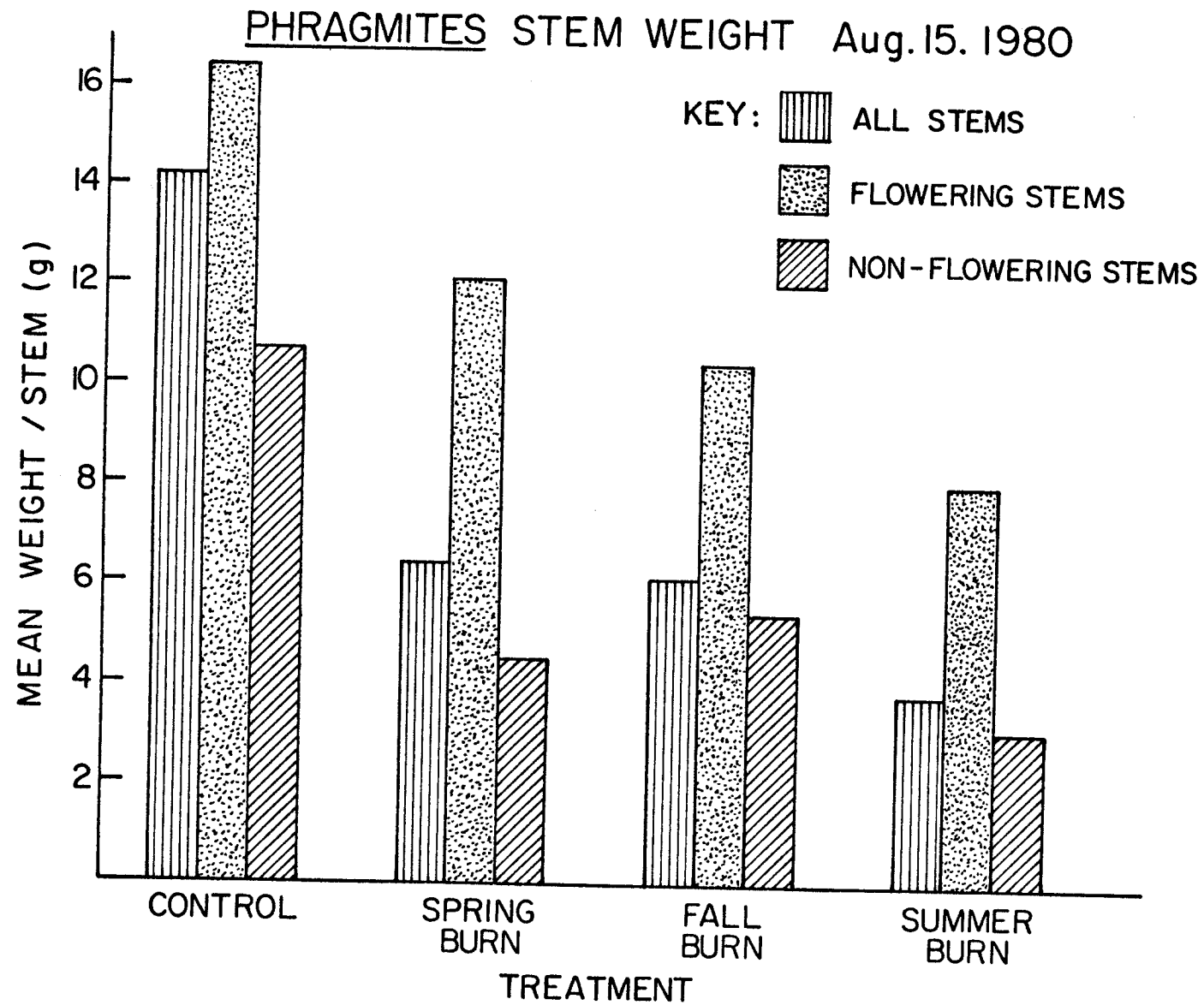
3.4.4   Shoot Morphology

3.4.4.1   Flowering Shoots

The most dramatic morphological difference between treatments was a decline in stem height which occurred to progressively greater extents after spring, fall and summer burning respectively (Table 3-9). According to Haslam (1973) the potential height of a shoot is determined by the width of the bud from which it originates but the degree of this expression can be affected by environmental conditions during elongation. Where density increased without environmental improvement (as after burning) shoots narrow more rapidly and final height declines. P. australis shows a similar decline in height after burning to that reported for Andropogon gerardi noted by Hulbert (1969). There was a shift in the shape of the frequency distribution for height (Figure 3-10) depending on treatment. The distribution became more negatively skewed with fall and summer burning but more positively skewed with spring burning. Haslam (1973) stated that a negatively skewed height distribution indicated a sub-optimal population and a positive skew indicated an optimal population. This suggests that performance of P. australis was enhanced by spring but hampered by summer and fall burning. The greatest spread in shoot height occurred after spring burning. This suggests that some control mechanism has been removed by burning. High concentrations of auxin-like substances have been extracted from the tips of vertical rhizomes (Haslam,1973). Damage of the buds at the tips of these rhizomes would lead to loss of apical dominance and lateral buds on the rhizomes and stem bases would develop. As these buds would be variable in size there would be much more varied shoot heights after burning.

Figure 3-11. Frequency distribution of stem height for flowering shoots sampled from differently treated plots on August 1-10, 1980.

FLOWERING STEMS

CONTROL
n=60

FALL BURN
n=58

SPRING
BURN
n=60

SUMMER
BURN
n=38

NUMBER OF SHOOTS
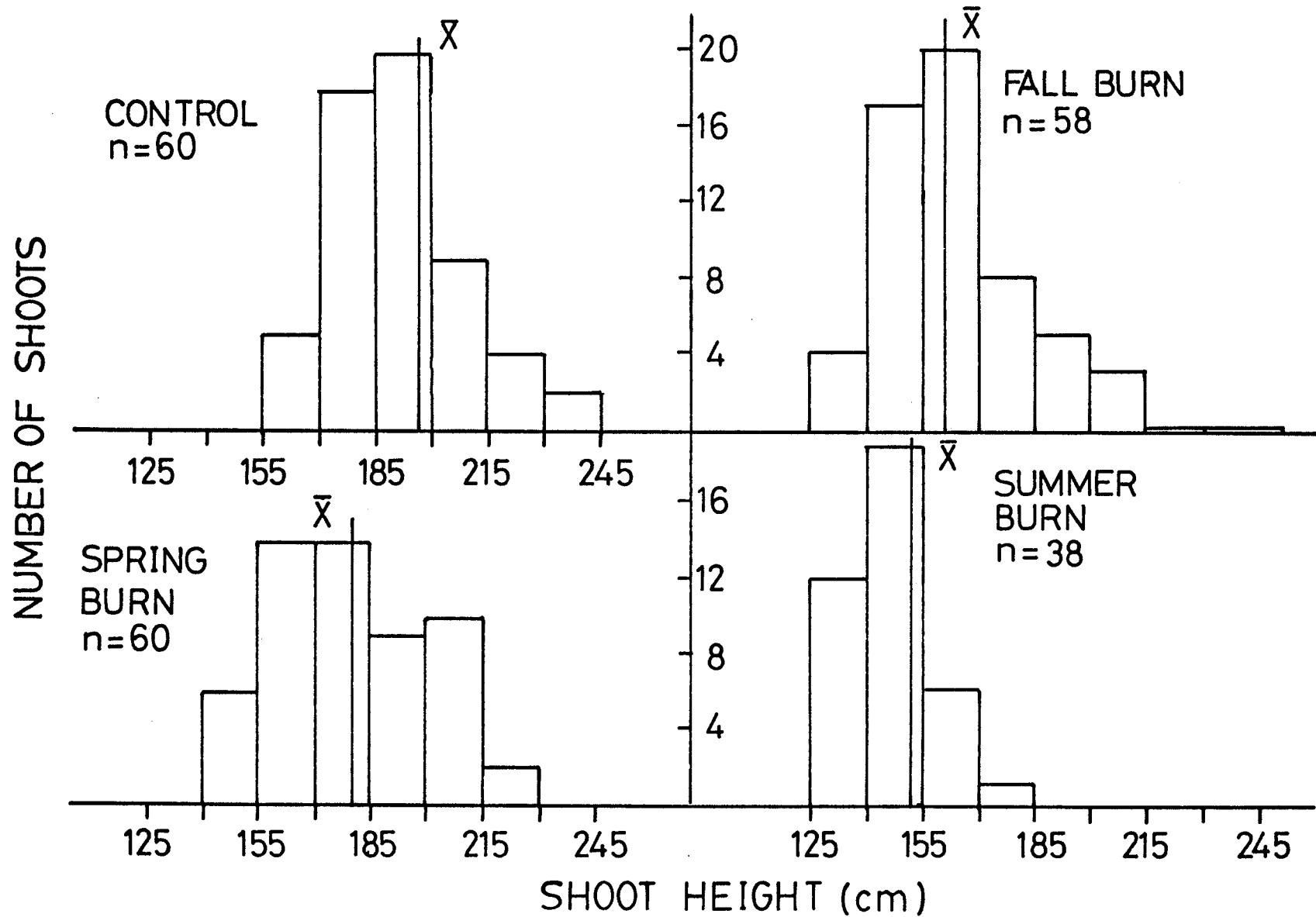
SHOOT HEIGHT (cm)

Table 3-9. P. australis flowering shoot morphology after 4 treatments.

_____

CHARACTERISTIC	TREATMENT MEAN *			
	Control	Summer	Fall	Spring
Height (cm)	191.3a	148.1d	161.5c	179.0b
Basal Diameter (cm)	6.57b	5.72c	6.78ab	7.14a
Inflorescence Length (cm)	16.9a	12.9b	13.8b	17.1a
Leaf Length (cm)	34.1a	31.6b	32.0b	34.1a
Leaf Number	14.3a	13.4b	13.8ab	13.6b

_____

* Means followed by the same letter are not different at α = .05, Duncan's Multiple Range test.

Inflorescence length and largest leaf length decreased after summer and fall burning but not after spring burning. Anderson and Bailey (1980) reported a reduction in leaf length of a number of mixed grass prairie grasses following burning. Shoot basal diameters were reduced (Table 3-9) after summer burning but not after spring or fall burning. The number of leaves per flowering stem declined slightly after all burning treatments and to the greatest extent after summer burning. Average inflorescence weights declined after spring burning but to a much greater extent after fall and summer burning (Figure 3-11). This corresponded to the reduction in inflorescence length after these treatments (see above). Haslam (1973) tied the size of an inflorescence to the height of a shoot, the larger shoots bearing larger inflorescences. This observation is supported by our data as reduction in shoot height after burning was related to reduced inflorescence length and weight.

3.4.4.2 Vegetative Shoots

Vegetative shoots were both shorter and of lesser basal diameter than flowering shoots after all treatments (Table 3-10). Vegetative shoots were much reduced in height by all burning treatments as were flowering shoots. Vegetative shoots from controls were actually taller than flowering shoots from summer burned plots (Table 3-10). Vegetative shoots from fall-burned plots were taller than those from either spring or summer burned plots.

Figure 3-12. Average weight per P. australis inflorescence sampled after different treatments. Values are the total weight of inflorescences divided by the total number sampled.
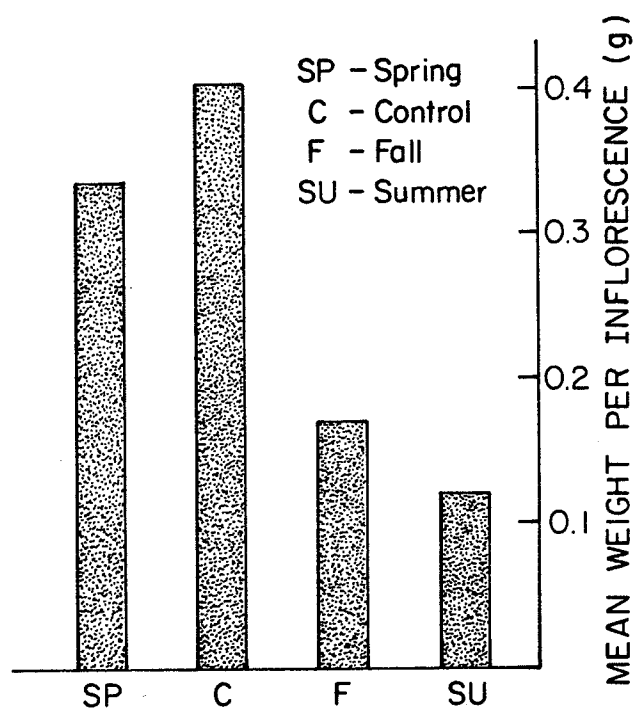
Table 3-10. Vegetative vs. flowering shoot morphology, after 4
treatments, Sept. 1 1980.

CHARACTERISTIC	STEM TYPE	TREATMENT MEAN *			
		Control	Summer	Fall	Spring
Height (cm)	Flowering	210.5a	164.4e	195.7b	189.0c
	Vegetative	182.5d	140.2g	163.0e	151.3f
Basal Diameter	Flowering	7.12b	6.41bc	9.36a	6.99b
	Vegetative	5.24cde	5.00e	6.09bc	5.24de

----

* Means followed by the same letter are not
different at α = .05, Duncan's Multiple Range test.

Figure 3-13. Diagramatic representation of shoot origins in early September of 1980 after three treatments. Roots have not been included to show shoot origins more clearly. Shoots open at the top represent living shoots and those closed at the top represent the bases of shoots which grew in previous years.

SUMMER
BURNED

SOIL
SURFACE

3   2   1 0

SPRING
BURNED

SOIL
SURFACE

3   2   1 0

CONTROL
(UNBURNED)

SOIL
SURFACE

3   2   1 0

RHIZOME AGE (YEARS)

10 cm
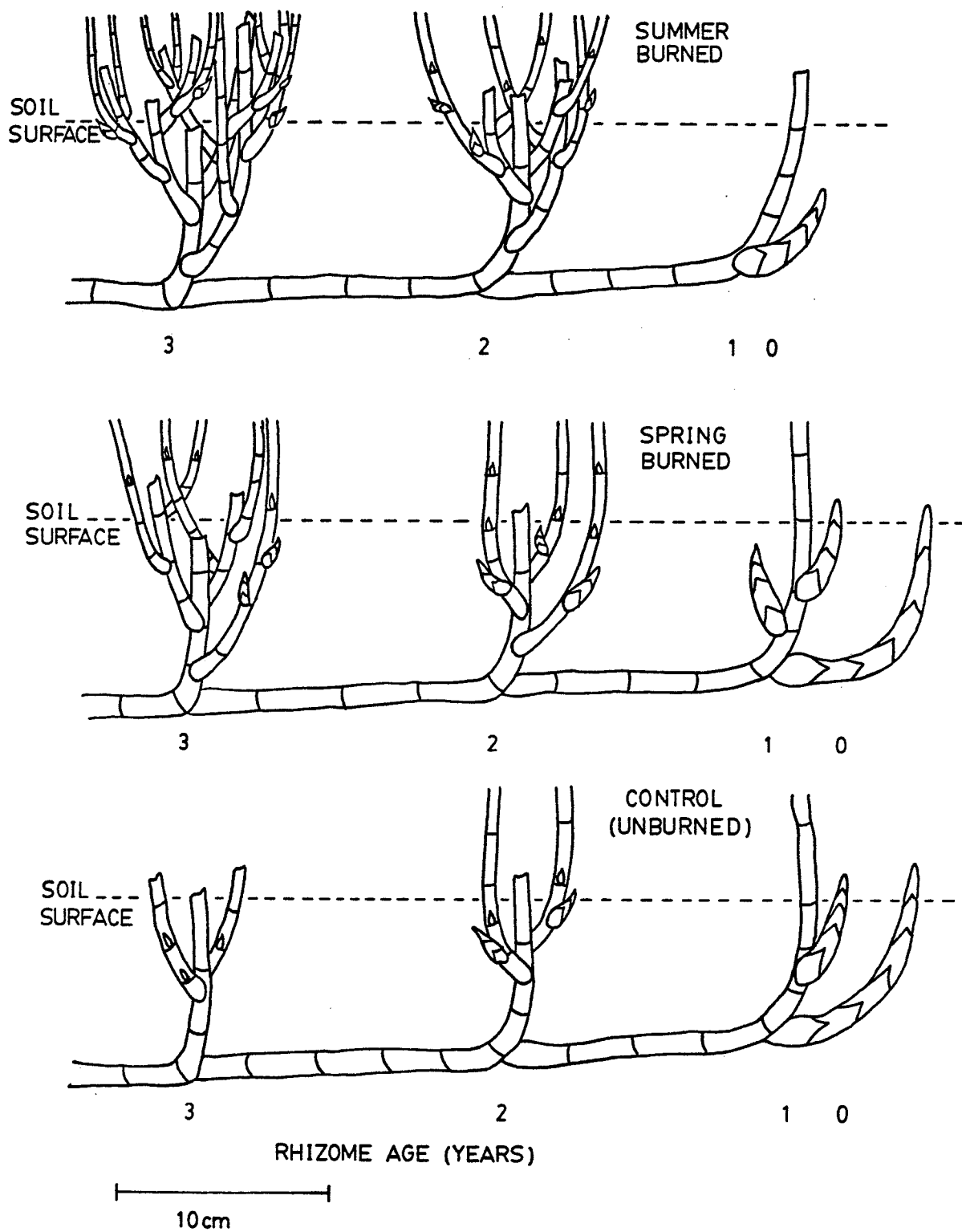
The average basal diameter of vegetative shoots from fall burned plots was greater than from the controls (Table 3-10). Mean basal diameters were similar to the controls on spring and summer burned plots. Vegetative stems from fall burned plots were thus very stocky for their height. This may have been because the floral primordia of most overwintering buds were damaged by frost. If this were the case many of the vegetative stems on fall burned plots may have been from these larger buds.

Many of the changes in shoot production, density, and morphology after the three burning treatments can be explained by considering the growth form of P. australis and how this is affected by burning at the various times.

3.4.5   General Discussion of Shoot Origins
3.4.5.1   Growth form of Phragmites

Several authors (Buttery and Lambert,1965a; Walker, 1965; Haslam,1969c) have described the growth form of P. australis. There are four stem types; horizontal rhizomes,vertical rhizomes,aerial shoots and legehalme (long runners). The first three types occur in all stands and arise from one another in an ordered pattern (Figure 3-12). Horizontal rhizomes are the least differentiated type, branches of which turn up (vertical rhizomes) and form a large terminal bud. These buds are normally formed in July and remain dormant overwinter after which they develop into the largest aerial stems in the stand. There is a system of sympodial branching, whereby a bud develops at the base of this vertical rhizome and a new horizontal rhizome is formed. Any axillary bud on P.

australis stems can develop into a horizontal, vertical or an aerial stem depending on environmental conditions, but buds usually develop into a certain stem type governed by their position in the plant.

Aerial stems are annual but their basal internodes remain viable after the senescence of the aerial part and may form additional aerial shoots in subsequent years from axillary buds. Due to this branching, clumps of stems develop after a number of years. There is a system of apical dominance in these stem types whereby the large stems which terminate vertical rhizomes exert a control over the density of aerial stems. These shoots are the tallest in the stand and are more likely to flower than those formed from old aerial shoot bases. It is hypothesized that fire may damage the apicies of the buds which will develop into these shoots so that apical dominance is reduced and many more stems develop at the 2nd, or 3rd order of branching. Some of these shoots may flower in addition to 1st order stems if conditions are appropriate.

3.4.5.2   Summer Burning

Summer burning kills all the aboveground parts of aerial stems and releases the normal overwinter dormancy of terminal buds so that a replacement crop of shoots is produced (Figure 3-12). Shoots may also be produced from the bases of aerial stems if their basal internodes are not killed. This crop of stems is killed by frost before senescence occurs and few new overwintering buds are formed. In the following spring, buds are formed at the 3rd, 4th or 5th order of branching from aerial stem bases. Therefore the crop of shoots is much reduced in

height and few flower. Harper (1977) coined the term 'bud bank' to describe the reserve of growing points present on perennial plants. In terms of this analogy it could be said that as a net result of summer burning the bud bank has been depleted of its larger depositors and its reserves are drastically reduced. Attempts to set back P. australis growth by applying such control measures as burning or mowing during the growing season would be even more valuable if applied several times. Haslam (1969c) suggested that branching of stem base clumps cannot occur beyond the 6th degree, so that killing subsequent crops of shoots would eventually result in the erradication of the stand.

3.4.5.3 Spring Burning

Spring burning appears to remove apical dominance in the stand so that many 2nd and 3rd degree shoots arise. Since many of these can flower, flowering shoot density increases. In addition many smaller stems are added to the crop increasing production. Whether the large shoots which arise from overwintering terminal buds develop properly or form inflorescences after spring burning was not adequately investigated and requires further study.

3.4.5.4 Fall Burning

Fall burning has somewhat intermediate effects between spring and summer burning. The large overwintering buds may be influenced by frost so that some do not develop, and those that do develop into shoots that may not flower. Many small shoots arise at higher degrees of branching as after spring burning. The net result is that production is somewhat

increased over the controls, but flowering declines. Vegetative stem biomass is highest after this treatment as many of the larger stems do not flower.

3.4.5.5 Shoot Aggregations and Shoot Origins

Confirmation that these are the actual trends is presented in Figure 3-13, which includes maps of points of shoot origin in a quadrat representative of each treatment. A greater degree of aggregation is apparent in burned than control plots. This reflects branching from old stem bases. Clumps are largest after summer burning where the degree of branching was greatest. In the controls shoots are largely solitary in origin, arising from large terminal buds. After spring and to some extent fall burning there is a mixture of solitary (terminal) and clumped (branch) shoots.

3.4.6 Below-ground Biomass

'New' belowground biomass was greater on spring and fall burned plots than in the controls (Figure 3-14), but was similar on summer burned plots and controls. The number of overwintering buds followed similar trends (Figure 3-15). This pattern is also apparent for 'old' biomass, which calls into doubt the statement that burning in spring and fall increases belowground production. If new belowground biomass depends on old then greater new biomass after fall and spring burning may be only a reflection of initial preburn differences.

Figure 3-14. Maps of 1980 shoot origins within representative quadrats

from variously treated plots. These were mapped during

August 1-10, while shoots were being collected for

measurement. Each 1m quadrat was divided into 256

equally-sized sections using a grid which was placed over

the cut stem bases.

FALL   CONTROL

SPRING   SUMMER

1m
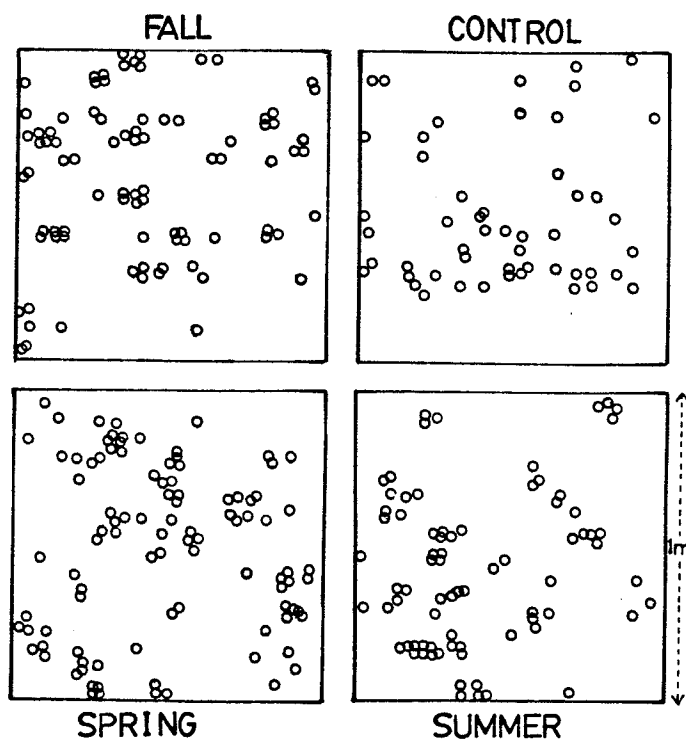
Figure 3-15. Mean below-ground biomass of P. australis collected Sept.
15-20 from differently treated sets of plots and divided
according to 1980 and previous year's production. Values
are means and standard errors.

BELOW-GROUND BIOMASS (g/m^2)
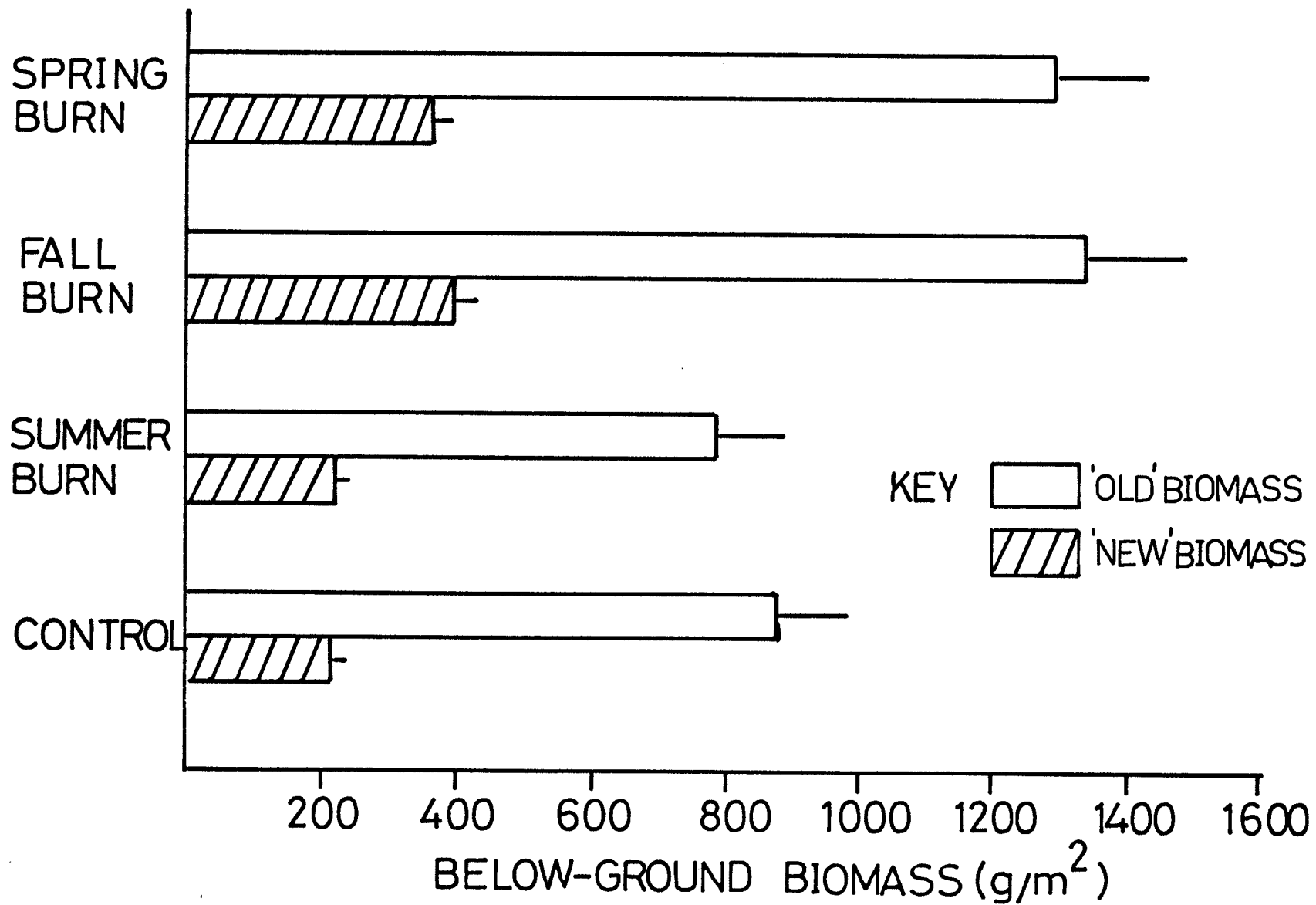
Figure 3-16. Mean density of P. australis buds excavated in September
on differently treated sets of plots. Values are means and
standard errors.

SPRING BURN

FALL BURN

SUMMER BURN

CONTROL

50   100   150   200

BUDS/m^2
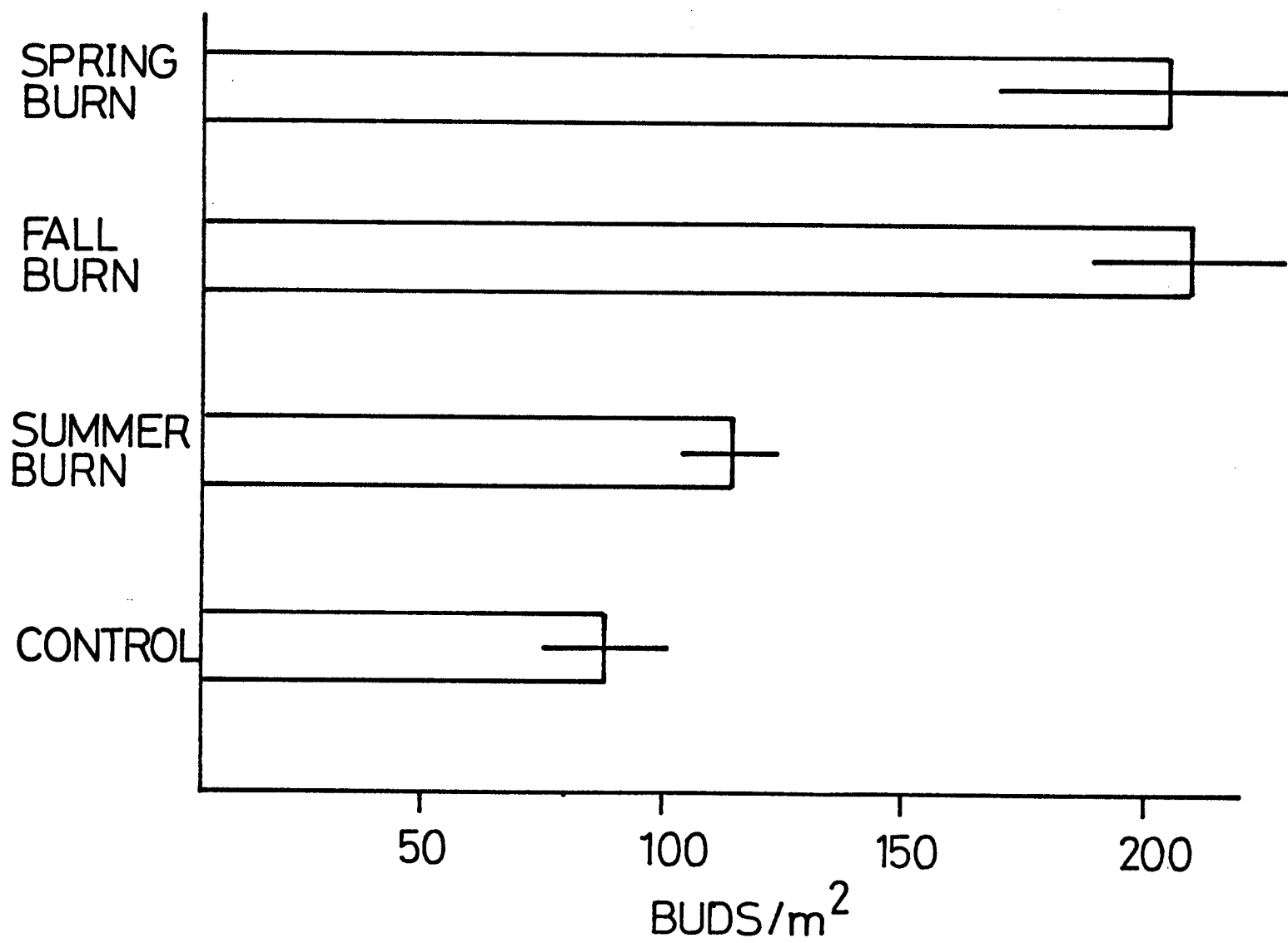
Analysis of covariance (using old biomass as a covariate for new biom-
ass) indicates that there is only a weak (α = .05) treatment effect for
new biomass. One of the first reports of the effects of experimental
manipulation on the production of a marsh dominant was that involving
fertilization of Spartina alterniflora Loisel (Viala and Teal,1976).
Their study reported no change in below-ground production in spite of
much increased aerial production. There was no increase in belowground
biomass accompanying increased aerial production of Agropyron gerardi
following spring burning (Old,1969). However Kucera and Dahlman (1968)
reported greater belowground biomass on plots of A. gerardi which had
been spring burned for a number of years in comparison to that on plots
which had not been burned and on which litter was allowed to accumulate.
The decline was mainly in rhizome biomass. They associated declining
density and biomass which accompanied the buildup of litter with this
decline in rhizome production. It is likely that a similar trend would
occur in P. australis. If spring burning were repeated there would pro-
bably be an increase in rhizome production but if it were only done once
litter would buildup in subsequent years and production would decline.

3.5 CONCLUSIONS

Spring burning appears to enhance the performance of Phragmites
australis, considering such performance characteristics as biomass,
flowering stem density, and the shape of the frequency distribution for
height. Spring burning could then be used to assist the spread of reed
where it is sparse and cover is lacking for wildlife use. If reed is to
be harvested for some economic use such as thatch (Haslam,1969a) or cel-

lulose production (de la Cruz,1978) spring burning can be used to increase density and production. Summer burning is deleterious to P. australis performance in terms of aerial biomass, flowering shoot density and shoot height. This supports Ward's (1968) statement that summer burning can be used to thin dense P. australis stands and increase habitat diversity for wildlife. Fall burning has intermediate effects in that P. australis aerial biomass increases slightly but flowering shoot density declines and the shoot height declines. Fall burning may not be compatible with good water management as snow accumulation is much decreased in winter on fall burned plots.

This study documented the suggestion of several other authors that burning at different times of the year has different effects on the growth of P. australis. If any of these burning regimes is repeated for a number of years the effects of the season of burning would probably show up even more strongly.

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Chapter IV

EFFECTS OF FIRE ON PHRAGMITES RHIZOME RESERVES

4.1   INTRODUCTION

Perennial grasses are known to store considerable amounts of energy
in their below-ground organs in the form of non-structural carbohydrates
(White,1973). In Phragmites australis (Cav.) Trin. ex Steudel these re-
serves are in the form of sucrose and starch (Smith,1969).   Reserves in
P. australis are stored mainly in the extensive rhizome system (Fia-
la,1976).

Non-structural carbohydrates are mobilized rapidly in the spring
with the commencement of growth and are equally important in regrowth
after defoliation. High levels of these reserves have also been associ-
ated with good winter survival of temperate grasses (White,1973).

Agriculturalists have studied the effects of such management prac-
tices as clipping (Weinmann,1961;White,1973)   and burning (Owensby et
al.,1970) on the reserves of forage and rangeland species. Seasonal re-
serve patterns have been followed for a number of wetland species such
as Typha glauca Godr. (Linde et.al.,1976) Carex lacustris Willd.   (Ro-
seff and Bernard,1979), and P. australis (Fiala,1976); but to date no
study has been made of the effects of management practices on the re-
serves of wetland plants. It has been hypothesized that declines of re-
serve carbohydrates of wetland species such as Typha glauca to manage-
ment may have profound effects on their control,(Linde et.al.,1976).

The use of fire as a management tool in marshes has received little attention. The purpose of this study was to investigate the response of P. australis rhizome reserve levels to controlled burning carried out in three different seasons. Parts of a dense P. australis stand located in the Delta Marsh, Manitoba, were burned at one of three times (on August 1, 1979; October 7,1979; or April 11, 1980). Nonstructural carbohydrate levels were assayed on rhizome samples from the treated plots and controls throughout the period of May 1 to September 15 of 1980. This paper describes part of a larger study of the effects of fire on P. australis.

4.2 METHODS

4.2.1 Sampling Schedule

The design of the burning experiment is described in Chapter 3, with the exception that four 5 m^2 plots were mowed concurrently with the summer burning carried out in 1979. Sixteen samples were collected on November 1, 1979 from the plots which had been burned and mowed that summer and from control plots. Biweekly from May 1 to July 15 and on August 15 of 1980 and September 15 P. australis rhizome samples were collected from a monolith of soil approximately 0.025 m^2 in area and 30 cm in depth surrounding the densest clump of stem bases in quadrats being sampled for aerial standing crop. Twelve samples were collected at each date from each treatment.

4.2.2   Sample Preparation

Samples were washed clean of soil in water,   separated into 'new' and 'old' rhizomes as outlined by Fiala,(1976), and oven dried to constant weight at 80° C. Samples were then ground through the 1mm mesh of a Wiley mill and stored in sealed plastic bags.

4.2.3   Carbohydrate Assay

To perform the carbohydrate assay,   200 mg samples were refluxed with 10 ml of 0.2N HCl in a covered 15 cm test tube in a water bath for one hour.   The liquid was hot filtered through Whatman #1 15cm filter paper to remove the residue and made up to a volume of 100 ml.   An aliquot was removed,diluted further, and assayed colorimetrically using the phenol-sulphuric acid method of Dubois et al. (1956).   The absorbance values were converted to glucose equivalents by comparison with a standard curve prepared with reagent grade glucose.   Values were converted to percentage nonstructural carbohydrates.   Analyses of variance were performed between experimental treatments and Duncan's Multiple Range test was used to compare mean percentage values at each sampling date (Helwig and Council,1979).

4.3   RESULTS

4.3.1   New Rhizomes

There were no significant differences between treatments in the percent T.N.C. in new rhizomes (Figure 4-1a), at any of the three sampling dates.   The T.N.C. content of new rhizomes rose rapidly from the time of their formation, then levelled off later in the season.

Figure 4-1a. Mean Total Nonstructural Carbohydrate (TNC) contents of

1980 rhizomes (new rhizomes) throughout the 1980 growing

season.   Values are means for 12 samples per treatment per

date.

Figure 4-1b. Mean TNC contents of rhizomes produced in previous years

(old rhizomes) throughout the 1980 growing season.   Values

are means with 95% confidence intervals for different

treatments.

'NEW' RHIZOMES

'OLD' RHIZOMES

□---□ SPRING
o·······o FALL
△-·-△ SUMMER
●——● CONTROL

% NONSTRUCTURAL CARBOHYDRATES

% T.N.C.

DATE
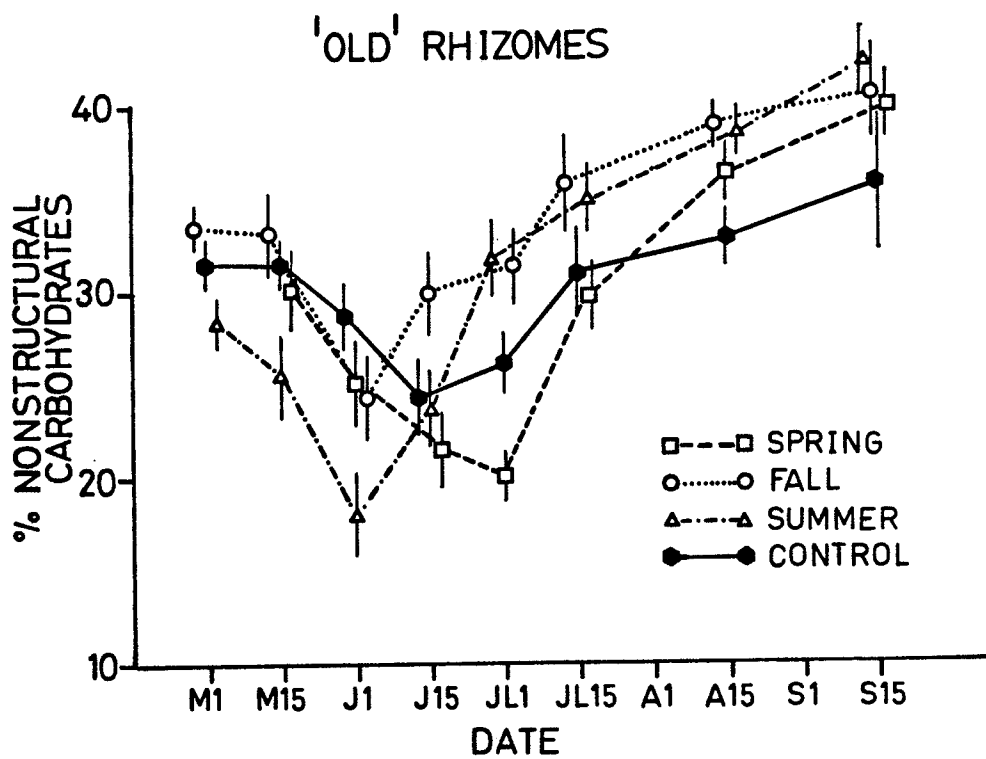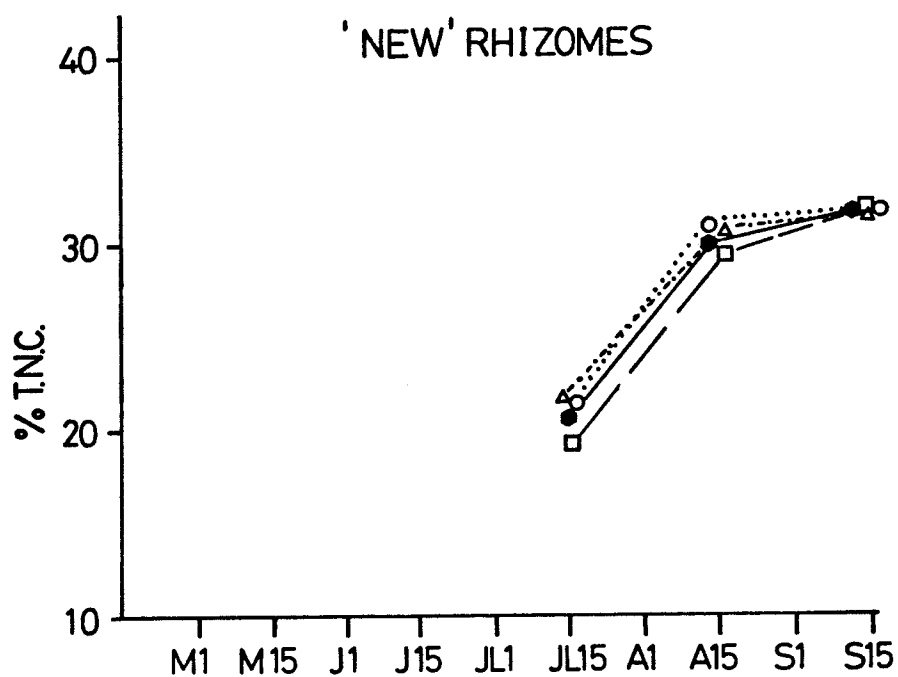
4.3.2 Old Rhizomes

The data from old rhizomes show many differences and interesting trends. On summer burned plots the mean T.N.C. content of old rhizomes was significantly lower on May 1,1980, before the onset of growth, in comparison with the controls or fall burned plots (Figure 4-1b, and Table 4-1). This is a continuation of differences noticed in October of 1979 where the T.N.C. content of rhizomes from both summer burned (X = 32.5 $\pm$ 0.75%) and summer mowed (X = 29.3 $\pm$ 0.45%) was lower than on control plots (X = 37.2 $\pm$ 0.65%). There was a decline in the percent T.N.C. of old rhizomes with the onset of shoot growth,after all treatments and in the controls. This fell to a minimum value after which the values rose steadily until the final sampling period (Figure 4-1b). The minimum value was lower on plots burned in the previous summer and spring, than in the controls. Minima were similar on fall burned and control plots. The time at which the minimum T.N.C. value was reached varied, being June 1 in summer and fall burns, June 15 in controls, and July 1 for spring burned plots. By September 15 the T.N.C. content of rhizomes collected from all burning treatments was similar,but higher than in the controls. The rate at which storage reserves accumulated immediately after the minimum was more rapid after burn treatments than in the controls.

Table 4-1. % total nonstructural carbohydrate content of old P.
australis
rhizomes, 1980 growing season.

PERIOD   TREATMENT MEAN

	CONTROL	SUMMER	FALL	SPRING	DF**	F CALC.
May 1	31.6a	28.4c	33.4a	–	2, 52	16.45
May 15	31.3ab	25.7c	33.1a	30.2b	3, 52	15.70
June 1	28.8a	18.1c	24.2b	25.1b	3, 44	20.72
June 15	24.3b	23.7bc	28.9a	21.5c	3, 44	11.89
July 1	26.1b	31.8a	31.5a	20.1c	3, 43	52.42
July 15	31.9b	35.0a	35.7a	29.6b	3, 43	7.28
August 15	32.8c	38.5a	38.9a	36.3b	3, 43	19.93
September 15	35.7b	42.3a	40.6a	39.9a	3, 43	5.73

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* Means followed by different letters are significantly different at α =
.05, by Duncan's Multiple Range Test.
** Degrees of freedom for treatment followed by degrees of freedom for
error.

4.4   DISCUSSION

4.4.1   TNC Levels   Autumn 1979

Both summer burning and summer mowing of P. australis, carried out in early August 1979, lead to a reduction of T.N.C. levels by that fall. This reduction was still apparent before the commencement of growth (May 1,1980) in the following spring. Reduction in the nonstructural carbohydrate content of rhizomes of Typha glauca after mid-suummer mowing was predicted by Linde et al.(1976) but this experiment is the first test of this hypothesis for any wetland species.

4.4.2   TNC Levels- 1980 Growing Season

The decline in reserves with the onset of growth in the untreated controls in 1980 shows similar patterns to those documented by Fiala (1976) for both old and new P. australis rhizomes. The values recorded in my study are several percentages lower than those of Fiala. This may have been due to the more severe hydrolysis procedure used by Fiala where samples were refluxed for 3 hours in 2% HCl before the determination of reducing sugars. Declines of approximately 8% in the reserves of old rhizomes in P. australis are small in comparison with the declines of 35% shown in Typha glauca (Linde et.al.,1976) but of similar magnitude to those observed in Carex lacustris (Roseff and Bernard,1979). A significant decline in the T.N.C. contents of old rhizomes occurred after all burning treatments with the onset of growth. This suggests that none of the burning treatments interfered with normal carbohydrate translocation by P. australis.

After all treatments, the dates on which the minimum T.N.C. values for old rhizomes were recorded were related to the phenological development of shoots. Shoots emerged earlier after summer burning and fall burning (May 2) than after spring burning (May 19) or in controls (May 26). This corresponded with an earlier drop in T.N.C. on summer and fall burned plots. On control and spring burns, where emergence was later, the minimum T.N.C. value was also reached later.

Lower minimum T.N.C. values were reached after summer and spring burning than in the controls. These may be linked with the increased vegetative shoot density observed after all burning treatments (Chapter 3). The production of the many buds for these small vegetative spring shoots may have required additional energy in contrast to the controls where only large shoots were produced from preformed over-wintering buds. This would especially be the case on summer burned plots where few overwintering buds were present and almost the entire standing crop for 1980 had to develop from buds formed in the spring. The further decline in July on spring burned plots may be related to the increased flowering response recorded on these plots (Chapter 3). Inflorescence production may have served as an additional drain on photosynthate thus delaying the downward movement of storage products. Owensby et al. (1970) noted that lower reserve levels were reached in the rhizomes of Andropogon gerardi on spring burned plots in comparison with untreated controls. This was tied to a higher rate of shoot growth after spring burning.

That the minimum T.N.C. values after fall burning are not less than the controls is rather anomalous and deserves further study. If

increased density leads to a greater decline in reserves then rhizome reserves on fall-burned plots should have declined further than the controls.

This study indicates that burning leads to a greater accumulation of storage products in old rhizomes by the time of shoot senescence. No measurements were made of leaf area of the P. australis canopies after the various treatments. It may be that the leaf area or photosynthetic efficiency of the canopies increased due to the increased stem densities observed after burning, especially after spring burning. In addition significantly reduced flowering responses were observed on plots burned in the summer and fall of 1979 (Chapter 3). This may account for the more rapid restoration of reserve levels in rhizomes after these two treatments.

An increase in autumn reserve carbohydrates in response to spring burning was reported for big bluestem, Andropogon gerardi (Owensby et al.,1970) but this difference disappeared by October. My study indicated that in P. australis significantly higer reserve levels were maintained after all burning treatments until mid September. No samples were collected after September 15 so T.N.C. values on controls may have later risen to equal those recorded on burned plots.

4.5   CONCLUSIONS

Either mowing or burning of Phragmites australis in early August reduced reserve levels of rhizomes entering the winter. This was predicted by Linde et al. (1976) who stated that the best time for control measures for Typha glauca would be in early July when rhizome reserves

were at their minimum. From the control data it appears that using this criterion the best time to apply control measures to P. australis is in mid June. Additional control measures could be applied in the second season. Possibly, mowing done at approximately June 1 of the second season would provide more intensive control of P. australis in the Delta Marsh.

Spring burning causes significant declines in rhizome reserves but these are restored later in the season. Following spring burning, mowing could be carried out on approximately July 1 of the same season to cause a further drain in rhizome reserves due to regrowth before frost.

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Chapter V

THE EFFECTS OF FIRE ON A MARSH PLANT COMMUNITY

5.1   INTRODUCTION

The effects of fire on marsh plant communities have has received little study.   Work to date suggests that fire has an important influence on the density and production of marsh dominants (Ward,1968;Smith,1972) and on the species composition of marsh meadow communities (Auclair et. al.,1973).

Fire has been used to manage dense stands of reed, Phragmites australis, (Cav.) Trin. ex Steudel for wildlife in North America (Ward,1942; Ward,1968; Schlichtmeir,1967)and in the production of reed for thatching in Britain (Haslam,1969a,1969b). These reports indicated that the postfire response of P. australis varied according to season of burning, but few quantitative data were presented to substantiate these observations.

P. australis is highly competitive with other marsh dominants such as Glyceria maxima (Hartm.) Holmb. (Buttery and Lambert,1965), Typha angustifolia L. (Fiala and Kvet,1971;van der Toorn,1972) and Scirpus maritimus L. (van der Toorn,1972) when water levels and nutrient conditions favor its growth. Mixed stands are common both at the wet and dry ends of its habitat range with competition the major factor limiting its spread in dry sites (Haslam,1971).

The role of the dominant in determining the environment of other members of a plant community was emphasized by Watt (1964). In a mixed P. australis stand any change in the performance of the dominant due to fire should elicit a response from the substorey species. If summer, fall, and spring burning have differing effects on P. australis they should also have differing effects on substorey production and species composition.

This paper will outline the responses of a mixed P. australis community to prescribed burning at three times; early August 1979 (during the peak of growth), October 1979 (after winter dormancy had been established) and May 1980 (before growth of the dominant commenced). This study was complicated by a gradual drop in marsh water levels from 1979 to 1980. van der Valk (1981) defined two states in which wetlands exist, that with standing water (flooded) and that without standing water (drawndown). Changes in the species composition of marsh plant communities during drawdowns have been documented by a number of authors (Harris and Marshall,1963; Walker,1965; Meeks,1969; van der Valk and Davis,1978). Following a drawdown changes in the production, diversity and structure of a marsh were reported by van der Valk and Davis (1976), but no such detailed study has been made during the drawdown year itself.

5.2   STUDY SITE

The study site lies in the Delta Marsh, located along the southern shore of Lake Manitoba in south central Manitoba (50° 11'N.Lat. and 98° 23'W.Long.). Delta Marsh consists of a series of shallow bays separated from Lake Manitoba by a forested dune ridge. Much of the emergent cover of the marsh consists of dense stands of P. australis. At the wet end of these stands P. australis mixes with Typha glauca Godr. and at the drier end with various wet meadow communities such as that dominated by Scolochloa festucacea (Willd.) Link. Few substorey species are present at the wetter end of the range where P. australis dominates but an increasingly diverse substorey develops beneath the P. australis canopy as the average period of inundation declines.

One dense P. australis stand, located on an arm of higher land between a bay and a channel (Figure 5-1). was chosen for the detailed study of postfire responses. A further channel had been dredged out to the north, creating a peninsula. There was an elevation gradient of approximately 30 cm between the wet and dry ends of the stand. Water levels in this part of the marsh fluctuate with wind tides from the Lake. Water is exchanged through the Cram Creek outlet, approximately 1.5 km to the northwest of the study site. This site was inundated as late as June in 1979 but only the lower end was periodically flooded by the autumn when high wind tides formed. Throughout the 1980 growing season the site was free of standing water.

Figure 5-1.   Location of study site.

1 STUDY SITE
2 FORSTERS BAY
3 BLIND CHANNEL
4 CRAM CREEK
5 PORTAGE DIVERSION
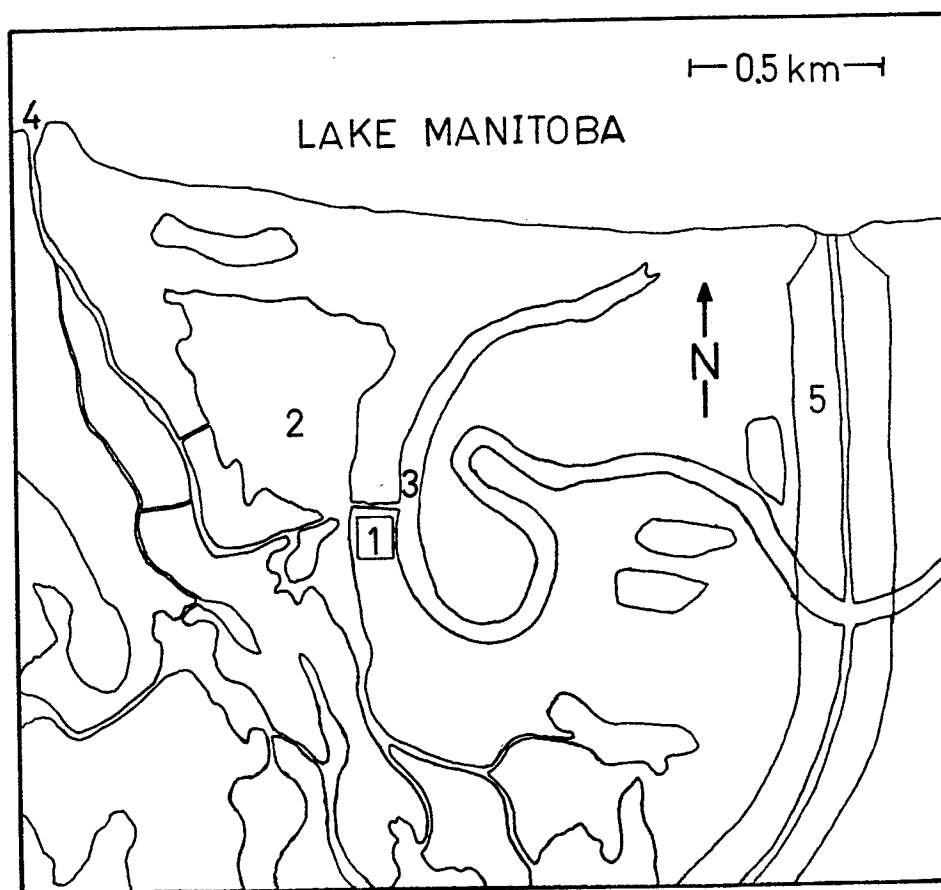
5.3   METHODS

5.3.1   1979 Season

In July 1979 part of the chosen stand was divided into a grid of twenty 400 m^2 (20m by 20m) experimental plots by cutting a series of 5m wide firebreaks (Figure 3-1).

To collect pre-burn data for later comparisons as well as to evaluate within site variation, four 0.25m^2 (0.5m by 0.5m) quadrats were randomly located within each of the plots in late July 1979. All living and dead plant material was clipped at ground level and separated as living P. australis, dead P. australis stems, and the combined substorey species for oven drying at 80° C to constant weight. Shoot densities of each species within the quadrats were recorded.

Plots were assigned an experimental treatment in a randomized complete block design with blocks of plots arranged perpendicular to the moisture gradient. Four plots were burned in the first week of August,1979, four on October 7 1979, and four on May 11,1980. A 25m^2 (5m by 5m) portion of four plots was mowed and raked concurrently with the summer burning. Four plots were left untreated as controls.

Regrowth and seedling densities of all species were recorded on summer burned and summer mowed plots in four 0.25m^2 quadrats per plot on September 21, 1979.

5.3.2   1980 Season

In the first week of August 1980 substorey species in treated and control plots were sampled using three 2m^2 (1m by 2m) quadrats per plot. These were placed at random points along transects running

through the center of the plots and parallel to the moisture gradient. All plants were clipped at ground level and separated by species before oven drying to constant weight at 80° C. P. australis stems were clipped from a $0.5m^2$ (2.7m by 0.7m) quadrat nested within the larger quadrat. The density of each species was recorded in the larger quadrat. One such quadrat was sampled from each of the $25m^2$ areas mowed in the previous summer.

5.3.3 Data Analysis

Floristic similarities between groups of plots assigned different experimental treatments were summarized by calculating Sorensen's (1948) indicies of similarity using the densities of all substorey plants recorded in the 1979 sampling and the substorey species biomasses recorded in the 1980 sampling.

The compartmentalized biomass data was used to calculate a diversity index ,H', (Shannon and Weaver,1949) for each $2m^2$ quadrat. The evenness component,J', was calculated by the formula $J' = H'/\ln s$ (Pielou,1966). It was assumed that this quadrat size would include the minimum area of the plant community after any treatment and at any elevation, so that the three samples from any treatment elevation combination could then be used to estimate the diversity (H), species number (S) and evenness (J) of the plant community under these conditions. In this chapter the symbols H, J and S will be used to denote the population means for diversity, evenness, and species number respectively and H', J' and s to indicate the sample means. Of a number of diversity indices available the Shannon index was used because it is more sensitive to changes

in the abundance of the less abundant species in a community (De-
jong,1975). This characteristic was desirable because of the extreme
disparity between in production the dominant and that of any substorey
species.

Analyses of variance were performed on the values of diversity and
evenness and on the species numbers recorded to evaluate differences due
to treatments and elevation (Snedecor and Cochran,1967). The total com-
munity biomass, substorey biomass and $\underline{P}$. $\underline{australis}$ biomass as well as
the percentage of the total $\underline{P}$. $\underline{australis}$ were similarily compared. Sub-
storey biomass was categorized according to whether species were 'na-
tive' or 'disturbance' species. The criterion used to differentiate
these groups was whether the species could produce robust, reproductive-
ly mature stocks in the control plots. These comparisons were performed
using the SAS statistical packages (Helwig and Council,1979).

5.4   RESULTS AND DISCUSSION

5.4.1   Diversity

5.4.1.1   Diversity Indices

Diversity, (H) evenness (J) and species number (S) were all signif-
icantly affected (α = .0001) by the experimental treatments (Table
5-1). There were significant moisture level effects for all character-
istics but no significant interactions of treatments with moisture lev-
els. Summer burning significantly increased the Shannon diversity,
evenness, and species number (Figure 5-2, Table 5-2). This was the
source of the treatment effect. There was no significant change in div-
ersity, evenness or species number on spring or fall burned plots.

Table 5-1   Analyses of Variance for Diversity Characteristics of the Community.

CHARACTERISTIC	SOURCE OF VAR.	D.F.	S.S.	M.S.	F	Pr>F
Diversity	Treatment	3	4.12	1.37	35.50	.0001
	Block	3	1.40	0.47	12.06	.0001
	Treat. by Block	9	0.33	0.37	00.96	.4934
	Error	32	1.24	0.04		
	Total	47	7.10			
Evenness	Treatment	3	0.661	0.220	17.43	.0001
	Block	3	0.412	0.137	10.87	.0001
	Treat. by Block	9	0.160	0.018	01.41	.2266
	Error	32	0.405	0.013		
	Total	47	1.600			
Species No	Treatment	3	077.90	25.97	14.66	.0001
	Block	3	016.23	05.41	03.05	.0424
	Treat. by Block	9	031.69	03.52	01.99	.0741
	Error	32	056.67	01.77		
	Total	47	182.48			

Figure 5-2a. Shannon and Weaver diversity indicies for various treatments, calculated using species biomasses collected August 1-10, 1980. Values are means with 95% confidence intervals.

Figure 5-2b. Number of species per $2m^2$ quadrat after different treatments. Values are means with 95% confidence intervals.

SHANNON DIVERSITY INDEX

MEAN NO. SPECIES
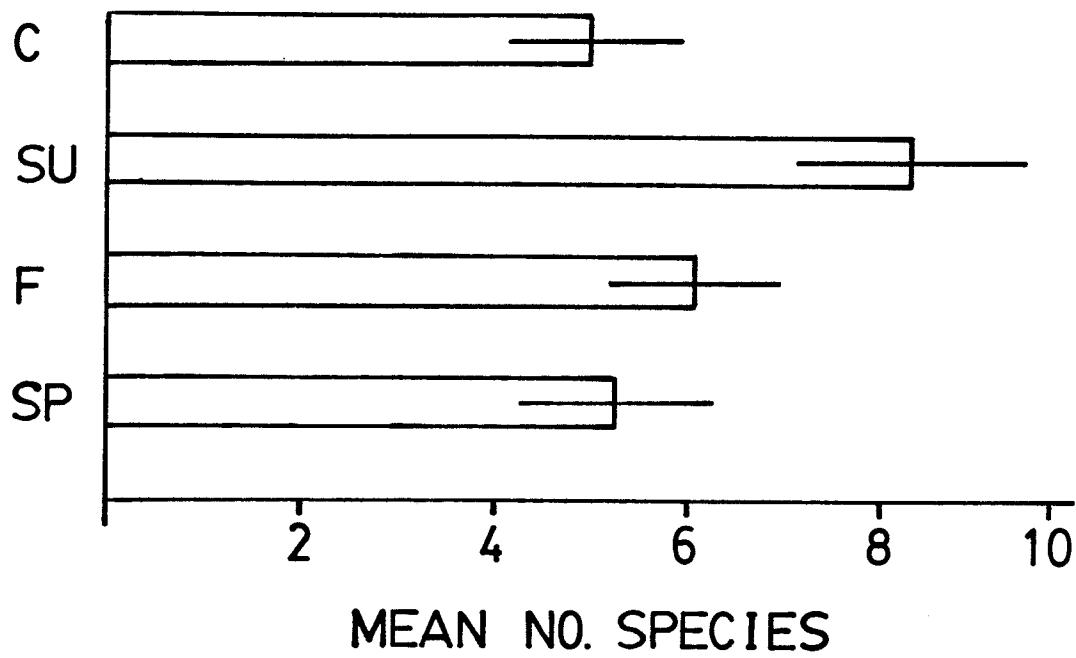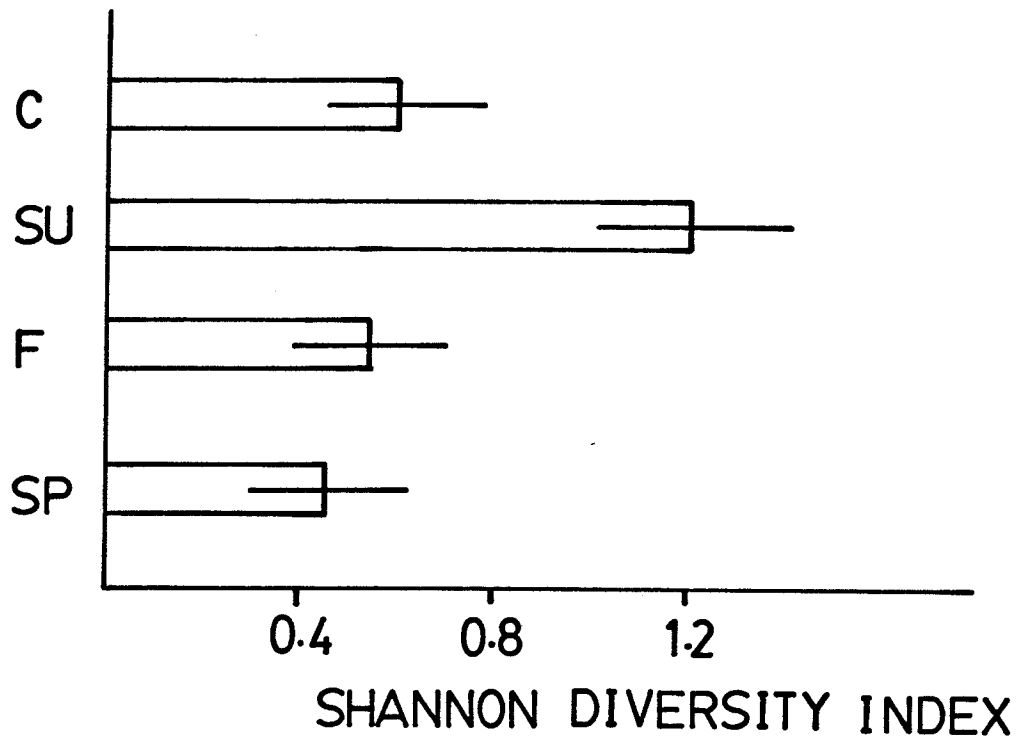
Table 5-2   Mean Diversity Characteristics of the Community after 4 Treatments.

Characteristic	L.S.D. *	TREATMENT MEAN **			
		Control	Summer	Fall	Spring
Shannon Diversity (H′)	0.227	0.603 ± .075b	1.205 ± .091a	0.550 ± .072b	0.461 ± .058b
Evenness (J)	0.136	0.364 ± .406b	0.584 ± .048a	0.312± 0.42b	0.285 ± .035b
Richness (s)	1.7	5.0 ± .29 b	8.3 ± .54 a	6.1 ± .40 b	5.5 ± .45 b

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* L.S.D. = Least Significant Difference with α = .05.

** Means followed by the same letter are not significantly different at α = .05, Duncan's Multiple Range Test.

After summer mowing the community showed similar changes to those on summer burned plots ($H' = 0.937$, $J' = 0.505$, s = 6.8).

5.4.1.2 Dominance-Diversity Curves

Diversity indices are a convenient way to reduce large masses of data to single numbers but in so doing we lose a great deal of information about the community (Green,1979). Thus these indicies should not be used alone but with other methods to present results in a meaningful fashion. An alternative way to represent community diversity is by dominance-diversity curves (Whittaker, 1965). When the aerial production of each species in a community is plotted against its rank among the species in the community a dominance-diversity curve is produced (Figure 5-3). For most plant communities these curves have a sigmoid shape with a few (in this case one) dominant species at the top, a plateau consisting of a number of species of intermediate importance (eg. Mentha arvensis, Lycopus asper, Teucrium occidentale and Urtica dioica) and a sloping end consisting of rare species (eg. Scutellaria galericulata). When the mean biomass data is so plotted for each treatment (Figure 5-3) a number of changes in the plant community after the different burning treatments can be seen. The first of these is a change in the distance from the dominant to the plateau. This increased after spring burning P. austalis biomass increased) but after summer burning decreased (P. australis biomass decreased; substorey biomass increased). The second is the reordering of species on the plateau. For example after summer burning Cirsium arvense increased but T. occidentale declined. It is interesting to note that after spring burning there is almost no such

reordering. The next observation is that new species may appear on the plateau (eg. <u>Atriplex</u> <u>patula</u> and <u>Sonchus</u> after summer burning). These may either move from the lower tail of the community (eg. <u>Atriplex</u>) or become newly established in the community (eg. <u>Sonchus</u> <u>arvensis</u>). A final observation is that new species may be added to the tail (eg. <u>Ep-ilobium</u> <u>glandulosum</u> after summer burning). There is little difference in the shape of the curve after spring and fall burning just as there is little change in the diversity characteristics for plots burned at these times. There is however a slight increase in the plateau length after fall burning due to high production by <u>A</u>. <u>patula</u>. The curve for summer burned plots is different from the control in that both the plateau length and the overall length of the curve is increased. This corresponds to increased evenness and species number after this treatment. Plateau species increasing in biomass are <u>A</u>. <u>patula</u>, <u>C</u>. <u>arvense</u> and <u>S</u>. <u>arvensis</u>. In conjunction with these increases the decline in <u>P</u>. <u>aus-tralis</u> biomass increased evenness.

Grime (1973) noted that increased diversity in plant communities often results from moderate levels of management induced stresses but if these are too severe diversity declines and only highly tolerant species survive. Increased diversity was reported by van der Valk and Davis (1976) after a marsh drawdown. Auclair et al. (1973) indicated that disturbances such as fire can increase species diversity in marsh meadow communites. My study shows that fire is a management tool which increases diversity in this emergent community but only if applied during the growing season of the dominant.

Figure 5-3. Dominance-diversity curves for after four treatments, prepared after Whittaker (1965). Symbols represent species, indicating their mean biomass (on the ordinate) against the species number in the sequence from the most to least productive (on the abscissa). In each curve the highest point represents the most productive species (species # 1 in the sequence) and the lowest point the least productive species in the community.

Species codes are:

A - Atriplex patula

C - Cirsium arvense

E - Epilobium glandulosum

L - Lycopus asper

M - Mentha arvensis

P - P. australis

Sc - Scutellaria galericulata

So - Sonchus arvensis

St - Stachys palustris

T - Teucrium occidentale

U - Urtica dioica
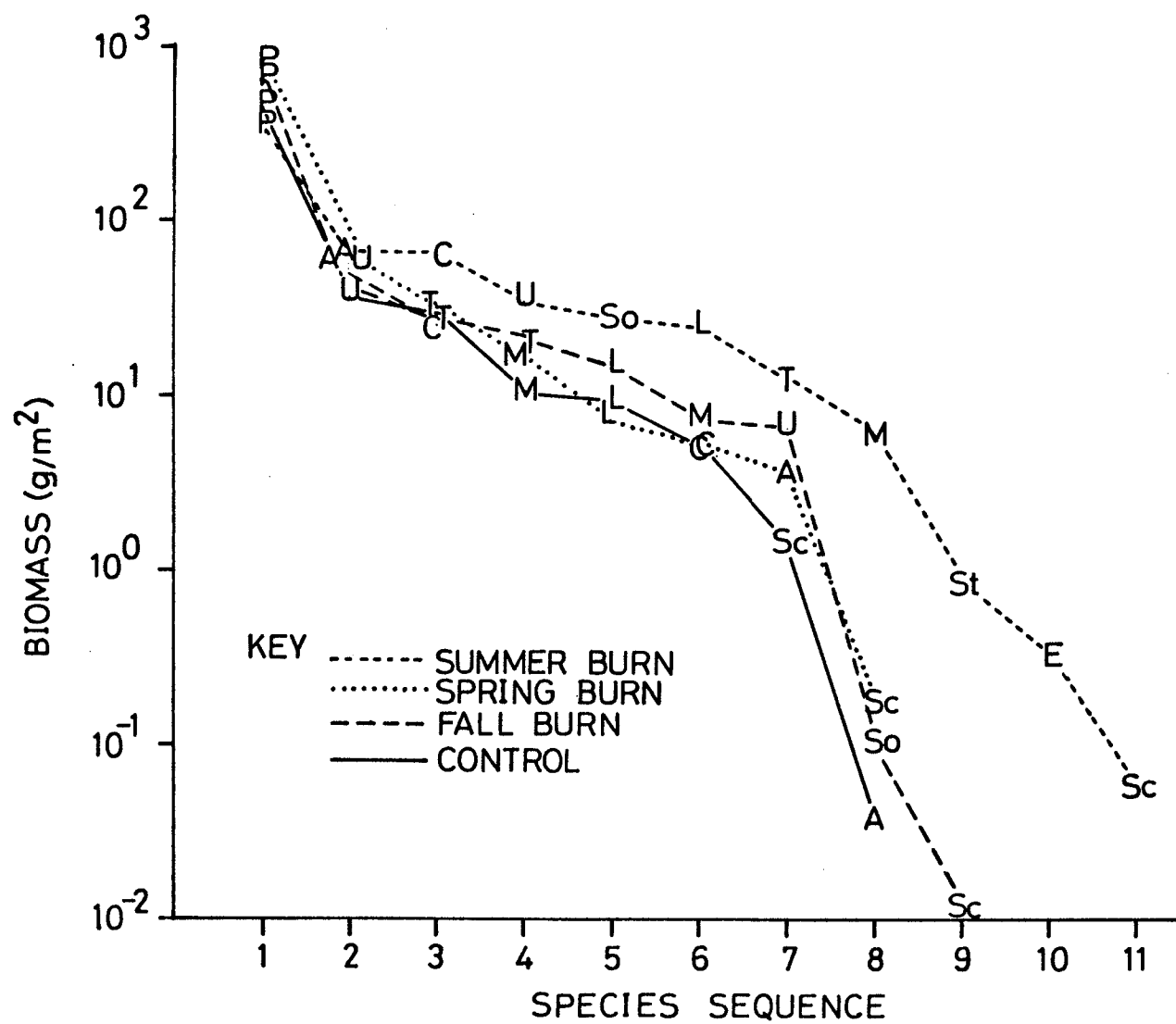
5.4.2   Community Structure

5.4.2.1   Distribution of Biomass between Canopy and Understorey

There was a significant increase in the combined aerial biomass of substorey species on summer burned plots but not on spring and fall burned plots (Table 5-3). After summer and fall burning the combined biomass of 'disturbance' species increased but not after spring burning (Table 5-4). After spring burning there was a significant increase in the combined biomass of 'native' species, no change after summer burning and a decline after fall burning (Table 5-4). Changes in substorey biomass were related to changes in P. australis biomass (Chapter 3). After summer burning where P. australis biomass declined substorey biomass increased the most. In contrast, after spring burning there was the greatest increase in P. australis biomass and the smallest increase in substorey biomass. Only after summer burning was there a significant change in community structure (i.e. distribution of biomass among both substorey and P. australis). This is reflected in the percentage of the total biomass as P. australis (Table 5-3) which significantly declined on summer burned plots. Although substorey biomass increased (not statistically significant with this sample size) to some extent after spring and fall burning, P. australis biomass increased as well, so that there was no net change in the relative contribution of the dominant to community biomass. Total community production increased after spring and fall burning (Table 5-3) reflecting increased P. australis biomass but total production after summer burning was not different from that of the controls. This was because the increase in substorey biomass compensated for the decline in that of P. australis.

P. australis dominates this community and accounted for 91 % of the of the community biomass in 1979. The production of the substorey appears to be limited by accumulation of P. australis litter (Chapter 1). Haslam (1971) emphasized the importance of the litter component in preventing the establishment of seedlings by potential invading species. Auclair et al. (1973) noted that marsh meadow communities were more diverse where litter accumulations had been reduced by fire.

Grime (1973) outlined several characteristics of highly competitive species including tall stature, a high relative growth rate, a growth form that allows rapid spread by structures like perennial rhizomes and the ability to accumulate large amounts of litter. P. australis posesses all these attributes. Burning at any time removes the litter mat. Summer burning results in reduced height and a thinner canopy and may also reduce the rate of vegetative spread by rhizome growth. Fall and spring burning do not appear to thin the P. australis canopy, although the increases in biomass after spring burning were more consistent. After spring burning the denser canopy prevents the invasion by disturbance species, i.e. the competitive ablity of the dominant is enhanced rather than reduced.

5.4.3 Community Composition

5.4.3.1 Similarity Indicies

The 1979 preburn substorey species compositions of the sets of four plots assigned the four different experimental treatments resembled the controls as shown by the similarity index matrix (Figure 5-4a) for that year, calculated from stem densities of individual substorey species.

Table 5-3   Categorized Aerial Biomass for the Community, 1980.

Characteristic	L.S.D. *	TREATMENT MEAN **			
		Control	Summer	Fall	Spring
Substorey Biomass	047.1	090.3 $\pm$ 12.4b	236.5 $\pm$ 25.9a	126.0 $\pm$ 27.4b	119.3 $\pm$ 13.4b
Phragmites Biomass	154.8	472.8 $\pm$ 61.8b	326.8 $\pm$ 32.6b	659.3 $\pm$ 58.3a	806.7 $\pm$ 82.0a
Total Biomass	151.4	563.2 $\pm$ 64.9b	563.3 $\pm$ 47.6b	785.4 $\pm$ 47.6a	926.0 $\pm$ 76.0a
% Biomass Phragmites	8.1	82.0 $\pm$ 2.9a	57.8 $\pm$ 4.8b	83.2 $\pm$ 3.9a	85.7 $\pm$ 2.3a

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* L.S.D. = Least Significant Difference with α = .05.

** Means followed by the same letter are not significantly different at α = .05, Duncan's Multiple Range Test.

Table 5-4

Categorized Understorey Biomass, 1980. Means with Standard Errors. ***

TREATMENT MEAN

Characteristic	Control	Summer	Fall	Spring
Disturbance species *				
	13.9 ± 9.1	148.4 ± 21.8	77.8 ± 29.3	9.0 ± 2.9
Native species **				
	89.7 ± 11.1b	77.8 ± 10.6b	48.6 ± 8.6c	110.3 ± 13.3a

----

* includes Atriplex, Cirsium, Epilobium and Sonchus.

** includes Lycopus, Mentha, Scutellaria, Stachys, Teucrium, and Urtica.

*** means followed by the same letter are not significantly different at α = .05, according to Duncan's Multiple Range Test. Disturbance species biomass was not compared using analysis of variance because values from different treatments have unequal variance.

Figure 5-4. Sorensen's similarity indicies comparings substorey

species compositions of sets of plots assigned different

treatments.

1979 values were calculated using stem densities of the

various substorey species.

1980 values were calculated using biomasses of the various

substorey species.

SIMILARITY INDICIES

1979

	SPRING	FALL	SUMMER
CONTROL	·548	·581	·764
SUMMER	·618	·536	
FALL	·475		

1980

	SPRING	FALL	SUMMER
CONTROL	·530	·322	·279
SUMMER	·326	·467	
FALL	·334		

The sets of plots assigned summer burning, fall burning and spring burn-
ing were consecutively less floristically similar to the controls in
1979. The pattern changed dramatically in 1980 as shown in the similar-
ity matrix for that year (Figure 5-4b) calculated from substorey species
biomasses. Summer burned plots, formerly most similar to the controls,
were now least similar to the controls. Spring burned plots, which were
least similar to the controls before burning were now most similar.
Fall burned plots became somewhat less similar to the controls than pri-
or to burning.

Stresses put on plant communities often favor the invasion of spec-
ies which are highly tolerant of those stresses (Grime,1973). Clearly
summer burning and summer mowing in conjunction with a drawdown were se-
vere stresses which allowed invasion by weeds. Haslam (1972) stated
that summer burning or mowing reduced reeds and allowed increased growth
by weeds. In contrast she noted that spring burning can be used to fa-
vor P. australis over its competitors but that if this treatment were
discontinued invasion by weeds was likely in drier stands. Invasion of
reed stands by shrubs or trees such as alders and willows was also sug-
gested as common where reedbeds had been abandoned. Auclair et al.
(1973) suggested that fire is one of the major factors preventing the
invasion of wet meadows by trees. One of the main values of fire in
marshes is that it kills invading trees (Ward,1948 and Ward,1968) It is
also possible that a summer fire could enhance the invasion by forest
through removing litter and allowing the germination of tree seedlings
within the stand. This did not occur in the stand studied because it
was not adjacent to forest but located in the middle of the marsh.

5.4.4 Species Biomasses

5.4.4.1 Summer Burning

The change in the similarity of control and summer burned plots was greater than after any other burning treatment and was mainly due to considerable production of biomass by Atriplex patula and Sonchus arvensis (Table 5-5), which were not present before burning, as well as to a dramatic increase in the biomass of Cirsium arvense in 1980. These changes occurred to differing degrees along the soil moisture gradient (Table 5-6). A. patula was not present in the first (driest) row after summer burning. Its biomass was high in the second and third rows and declined in the last (wettest) row. S. arvensis was most productive in the drier (first and second) rows but declined dramatically in the third and fourth (wetter) rows. C. arvense similarily was more abundant in the drier plots and less productive in wetter plots. The biomasses of other species were extremely variable but several trends appear in overall means. After summer burning the biomasses of Teucrium occidentale and Mentha arvensis were depressed but that of Lycopus asper increased.

5.4.4.2 Summer Mowing

Species compositions were very similar in 1980 on plots which had been mowed or burned the previous summer (Table 5-5), but some differences occurred in their biomasses. The biomasses of A. patula and L. asper were less after burning than mowing but that of C. arvense was greater. The similar changes in species composition after these two treatments were probably in response to the weakening of the reed canopy and removal of litter, but the differences in A. patula and C. arvense

biomass may be due to the different responses of their seeds to the heat of the fire. As suggested in Chapter 2 fire may enhance germination of A. patula seeds but it may kill much smaller thistle seeds. Also the rhizome regrowth of thistle in the fall of 1979 was more after mowing than burning (Chapter 2) and this may have allowed a greater accumulation of reserves before frost and contributed as well to increased thistle biomass in 1980.

5.4.4.3 Fall Burning

Reduced similarity between fall burned and control plots was due to considerable production by A. patula which was especially high in the second row of plots where the P. australis canopy was thinned the most by this treatment. Other changes were similar to those after summer burning but occurred to a lesser degree. C. arvense and L. asper increased in biomass but M. arvensis and Teucrium decreased. One difference was that S. arvensis never produced significant biomass after this treatment. This species is biennial and thus seedlings established in 1980 could not reach appreciable size until the next year.

5.4.4.4 Spring Burning

After spring burning few new species were introduced but the biomasses of those present before burning (M. arvensis, T. occidentale and U. dioica) increased (Table 5-5). These species reacted similarily to P. australis in this respect; M. arvensis increased by 62%, T. occidentale by 16% and U. dioica by 45% after this treatment.

Table 5-5. Mean biomasses of substorey species (g/m^2).

TREATMENT

SPECIES	SUMMER BURN	SUMMER MOW	CONTROL	FALL BURN	SPRING BURN
Atriplex patula	67.1	23.7	0.1	51.8	3.7
Cirsium arvense	63.1	86.1	5.1	26.2	5.3
Epilobium glandulosum	0.4	0.1	0.0	0.0	0.0
Lycopus asper	24.4	7.1	8.9	14.5	7.3
Mentha arvensis	5.8	7.8	10.3	6.5	16.7
Scutellaria galericulata	0.1	3.6	0.0	0.1	0.0
Sonchus arvensis	28.2	51.9	0.0	0.1	0.0
Stachys palustris	0.9	0.0	0.0	0.0	0.0
Teucrium occidentale	12.7	8.9	28.5	20.6	33.3
Urtica dioica	34.0	19.0	36.4	6.4	52.7

Table 5-6. PERFORMANCE OF THREE SPECIES ON CONTROL AND SUMMER BURIED PLOTS*

SOIL MOISTURE LEVEL

(A) BIOMASS		1	2	3	4
Atriplex patula	Su. Burn	-	114.2 ± 22.6	122.7 ± 33.8	31.6 ± 27.6
	Control	-	0.2 ± 0.1	-	-
Cirsium arvense	Su. Burn	148.2 ± 15.8	64.4 ± 34.1	20.9 ± 3.3	19.4 ± 4.7
	Control	0.6 ± 0.5	17.7 ± 10.8	1.9 ± 1.8	-
Sonchus arvensis	Su. Burn	43.0 ± 17.9	55.8 ± 1.0	12.3 ± 5.2	2.0 ± 0.8
	Control	-	-	-	-

(B) DENSITY		1	2	3	4
Atriplex patula	Su. Burn	-	114.3 ± 22.0	153.7 ± 70.5	9.3 ± 6.2
	Control	-	2.7 ± 1.8	-	-
Cirsium arvense	Su. Burn	38.7 ± 3.5	18.3 ± 7.4	9.8 ± 1.9	10.3 ± 2.9
	Control	0.5 ± 0.5	2.7 ± 0.7	0.5 ± 0.5	-
Sonchus arvensis	Su. Burn	9.5 ± 3.3	13.3 ± 0.9	2.7 ± 1.0	6.5 ± 4.5
	Control	-	-	-	-

* VALUES ARE MEANS ± STANDARD ERRORS.

A. patula, C. arvense and S. arvensis are very
stress tolerant species in that they are able to survive as agricultural
weeds. These species would be expected to increase if the community
were subjected to further burning or mowing. Ward (1942) reported that
after only three summers of mowing, P. australis was replaced by a mixed
sedge, grass and S. arvensis community. S. arvensis and C. arvense form
almost stable communities in the marsh in association with such plants
as Carex atherodes, Hordeum jubatum and Scolochloa festucacea. Harris
and Marshall (1963) reported that a Typha stand drawndown for two sea-
sons developed a mixed community consisting of emergents, mud flat
weeds, and upland weeds such as C. arvense and S. arvensis. Annuals
like Bidens cernua became abundant in a drawndown marsh studied by van
der Valk and Davis (1978). In the last two mentioned studies the inva-
sion species died off with rising water levels. It is hypothesized that
the changes observed after summer burning in my study will not be last-
ing unless water levels remain low.

5.4.5   Sources of Regrowth

5.4.5.1   Seedlings

Numerous seed of perennials such as S. arvensis and U. dioica ger-
minated in the fall of 1979 following summer burning or mowing (Chapter
2). Lower densities of Cirsium, Lycopus, Mentha, and Teucrium seedlings
were also developed at this time. Survivorship of Cirsium and S. arven-
sis seedling rosettes appeared to be high through the winter of 1979 as
there were dramatic increases in both their densities and biomasses in
1980. A large proportion of the shoots of these species flowered in

1980 indicating that they were not young of the year. S. arvensis was

not present in these plots before burning and C. arvense initial densi-

ties were too low to account for the dramatic increase in their abun-

dance in 1980.   Seedlings of U. dioica appeared to have low survival

during the winter of 1979 as most of the shoots sampled in 1980 were

large mature shoots. L. asper and T. occidentale did not produce appre-

ciable seedling densities in the fall of 1979 (Chapter 2) so that most

of the smaller shoots of these species in 1980 were seedlings which ger-

minated this year as indicated by the presence of cotyledons and lack of

developed rhizomes.   Overwinter survival of seedlings from 1979 was

therefore also low.   In 1980 high seedling densities of T. occidentale

$(57.4 \pm 7.8$ sdl./m^2) and L.   asper $(64.4 \pm 22.7$ sdl./m^2) occurred

only on the wettest summer burned plot and not after other treatments.

It may be that these species have very specific light or temperature re-

quirements for germination that were met only under these conditions

(i.e. bared soil and thinned P. australis canopy).   Thompson (1969) re-

ported that Lycopus europaeus L.   has an absolute requirement for light

and fluctuating temperatures in order to germinate.   No information is

available regarding T. occidentale germination requirements but it may

require light.   After summer burning L. asper and T. occidentale see-

dlings made a significant contribution to the biomasses of these species

in 1980 because of their very high densities.   Seedlings of Epilobium

glandulosum were not recorded in 1979 probably due to their very low

densities.   The mature shoots of this species appeared only on summer

burned plots in 1980. Seedling densities of perennials were very low on

fall or spring burned plots in 1980.   A few rosettes of C. arvense and

S. arvense were noted after both treatments but did not account for appreciable biomass. No seedlings of any perennial species was recorded on control plots in 1980. It may be that these perennials become established from seed only when the litter layer is removed by burning or some other disturbance.

Pederson (1979) working in the east part of Delta marsh found that the seedbanks of a P. australis stand contained considerable numbers of the seeds of these species, except for U. dioica and T. occidentale. which did not appear. van der Valk (1981) typed these species as perennials which establish themselves in drawdown years. My study suggests that they will not establish themselves in P. australis stands unless the litter layer is removed and the canopy thinned, so that van der Valk's prediction should be qualified.

Atriplex patula seeds germinated in both 1979 and 1980 on summer burned plots. After fall burning some germination of this species occurred on plots where the P. australis canopy had been thinned. This species seemed to be a good indicator of the competitive vigor of P. australis. A. patula did not appear to an appreciable extent on spring burned plots (Tables 5-5 and 5-7). It could be that the denser P. australis canopy after this treatment moderated soil temperatures favoring germination. Seedlings of A. patula were not observed on the control plots in the preburn sampling but a small number of thin-stemmed seedlings were found in 1980 on one of the control plots which had low P. australis density and little litter accumulation. In both 1979 and 1980 there was no germination of A. patula seeds in the driest row of plots after any treatment. If these seeds are water dispersed it may be that

seeds were never transported to this seldom inundated part of the stand. Walker (1965) mentions this species as common in drier P. australis and Scolochloa festucacea stands where openings in the litter mat occur, and as common on exposed mudflats after drawdowns. She also found that seeds of this species were numerous in the sediments. Pederson (1979) reported high numbers of seeds of this annual in the seed bank of a P. australis stand, but he found even higher numbers of Chenopodium rubrum L. seeds. Ward (1968) mentioned high densities of C. rubrum seedlings after summer burning in the east part of the marsh but did not report A. patula as being important. I found no C. rubrum seedlings in 1979 or 1980 in the stand under study. This, along with the absence of T. occidentale and U. dioica seeds in the stand studied by Pederson (1979,) suggests that there is a great deal of variability between the seed banks of P. australis stands located in different parts of Delta Marsh.

Noticeable changes occurred in the composition of this marsh community due to establishment of seedlings when litter was removed by burning, especially summer burning. This is similar to of Lloyd (1972) who found changes in the species composition of an upland grassland community following burning. In contrast Millar (1973) reported little change in the species composition of several wetland communities following fire. The fires in the sites he studied were mostly set during the fall when the plants had senesced, and not after summer burning when I found the most dramatic changes. All the species with noticeable seedling densities were classified by van der Valk (1981) as wetland species which establish themselves during drawdowns. If the burning treatments were applied in a flooded stand a different expression of the seed bank would be manifest.

5.4.5.2 Regrowth of Substorey from Rhizomes

Burning treatments were not severe enough to damage rhizomes or rootstalks of plants in this community. Hoffpauir (1961) recorded little change in soil temperature during a marsh fire in Louisiana. I found temperatures ranging from $149\,^{\circ}$ C to $482\,^{\circ}$ C at the soil surface during fires but it is unlikely that there would be appreciable penetration into the soil owing to the short duration of the heat pulse and the poor thermal conduction of peaty soils. All species in this community were either hemicryptophytes or cryptophytes without aerial perennating organs and thus would receive lasting damage only if the peat were very dry and actually burned. At Delta,Ward (1942) reported that in very dry years peat fires could be initiated and thus eliminated P. australis.

After summer burning,densities and biomasses of T. occidentale and M. arvensis were reduced (Tables 5-7 and 5-5). Regrowth of these species in the fall of 1979 may have exhausted either rootstalk growing points or depleted energy reserves so that 1980 regrowth was poor. In contrast, densities of U. dioica and L. asper increased in 1980 on summer burned plots. L. asper (unlike M. arvensis and T. occidentale) has a well developed tuber which probably contains considerable storage reserves that could be used in the formation of new shoots after damage by fire or frost. U. dioica stems on summer burned plots appeared thinner and shorter (although this was not quantified) than on the controls. This species responded similarily to P. australis in that summer burning resulted in higher densities of shorter thin stemmed shoots.

Table 5-7. Mean densities of substorey species. (shoots/m^2).

TREATMENT

SPECIES	SUMMER BURN	SUMMER MOW	CONTROL	FALL BURN	SPRING BURN
Atriplex patula	152.2	34.2	0.1	149.9	15.4
Cirsium arvense	19.2	41.4	0.8	7.1	3.9
Epilobium glandulosum	0.5	0.1	0.0	0.0	0.0
Lycopus asper	10.0	5.6	6.2	10.2	7.8
Mentha arvensis	5.0	6.9	6.7	5.5	7.9
Scutellaria galericulata	0.2	4.8	1.2	0.1	0.5
Sonchus arvensis	16.0	15.9	0.0	0.6	0.0
Stachys palustris	0.8	0.0	0.0	0.0	0.0
Teucrium occidentale	9.5	28.3	17.8	20.2	20.2
Urtica dioica	18.4	18.1	6.7	4.1	18.3

The stem density of C. arvense was greater on summer mowed than summer burned plots (Table 5-7). This may be related to more vigorous fall regrowth seen on mowed plots in the fall of 1979. Unlike summer burning, mowing did not lead to lower densities of M. arvensis and T. occidentale. Probably the more vigorous fall regrowth of these species after burning in 1979 depleted the number of dormant buds which could produce next year's crop of shoots. Unlike thistle these species do not have vigorous rhizome systems that can produce an almost limitless number of new shoots if damaged.

After fall burning most of the 'native' substorey species were reduced in biomass if not in density (Tables 5-5 and 5-7). There was reduced accumulation of snow on fall burned plots during the winter of 1979. This together with the removal of litter may have increased the speed with and the depth to which frost penetrated into the soil and thus caused some mortality of overwintering buds of these species. Another reason for this decline was the heavy degree of infection of these species, especially M. arvensis with dodder (Cuscuta) which developed only to any appreciable extent on fall burned plots.

Increased biomass of U. dioica after spring burning corresponded to increased stem density (Tables 5-5 and 5-7). To a lesser degree this was also true of L. asper, M. arvensis and T. occidentale. It is possible that a flush of nutrients, similar to that described in Chapter 2 after summer burning, enhanced the growth of these plants so that more vigorous individual stems were produced.

5.5 CONCLUSIONS

This study showed that prescribed burning caused some short term changes in the dynamics of this plant community, and that the magnitude of these changes varied according to season of burning. The changes were the greatest after summer burning where the competitive vigor of the dominant Phragmites australis had been reduced. This reduction was only appreciable after summer burning or mowing. In contrast, almost no change in substorey composition or production occurred after spring burning which increased P. australis biomass. Fall burning had intermediate effects, the production of the dominant increased somewhat but there were some changes in species composition. Species diversity increased on summer burned and mowed plots but not on spring or fall burned plots.

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Chapter VI

CONCLUSIONS

It has been shown in this thesis that fire does have measureable effects on both the dominant, Phragmites australis, and the substorey species of this emergent plant community.

Controlled burning is feasible at the three times studied. In established stands the large quantity of standing dead canes makes it possible for fires to burn in the summer in spite of the high moisture content of the living shoots. Wind speed is a critical factor when burning at this time, as under a minimum speed fires will die out. Other factors such as fuel loading, the orientation of the dead canes and fuel moisture content also appear to influence fire behaviour. Fire behaviour in this community requires further study as it is necessary to develop some sort of predictable model in order to carry out controlled buring and achieve the desired results. Another aspect that deserves study is how soon after a particular burning treatment burning can be reapplied (i.e. how much fuel must accumulate before a fire will run on a previously burned plot).

Burning in different seasons had differing effects on the dominant, P. australis. Considering such performance characteristics as aerial standing crop and flowering shoot density, spring burning led to enhanced performance but summer burning depressed its performance. Both burning and mowing during the growing season of reed led to a decline in

rhizome reserves that was not restored until late in the subsequent growing season. These treatments also depleted the store of primary growing points on the rhizomes so that growth in the subsequent season was depressed. The best time to apply control measures in the summer needs to be discovered. A further study could investigate burning at different times throughout the summer. Spring burning has management potential where it is desirable to enhance the performance of sparse reed stands. Fall burning has intermediate effects, in that in spite of an increase in aerial standing crop flowering stem density declined. Fall burning has the disadvantage of resulting in the loss of snow cover in the winter. On the other hand, in combination with overwinter or early spring flooding it may cause partial dieoffs of reed (Appendix B).

Burning at the different times also had differing effects on the species composition and the performance of substorey species. After spring burning, performance of the substorey species present before burning was enhanced and no new species became established. After summer burning and mowing two species, Atriplex patula and Sonchus arvensis, became established in the community and the performance of Cirsium arvense was much enhanced. In contrast the performance of Mentha arvensis and Teucrium occidentale was depressed. Fall burning had intermediate effects in that the performance of M. arvensis and T. occidentale were depressed but the performance of Cirsium arvense was enhanced and Atriplex patula became established.

The effects of burning in combination with water level management has promise in the control of reed growth. In appendix B partial dieoffs as a result of fall burning followed by early spring flooding are

described. It appears that water level changes between seasons has appreciable effects on reed growth, even without burning. Comparison of reed performance on control plots between 1979 and 1980 suggest that lowering water levels depresses the perfomance of P. *australis* (appendix A). These data indicate that much of the difference in production seen in the 1980 field season after spring burning may be because fire overcomes a partial dormancy mechanism which was induced in reed due to the drought present that spring. This observation is supported by the results of a greenhouse experiment (appendix C) which showed a greater disparity in production between summer burned and control samples.

Appendix A

EFFECTS OF DROUGHT ON THE GROWTH OF PHRAGMITES AUSTRALIS

A.1   INTRODUCTION

The prairies of North America experience a continental climate with extreme fluctuations in temperature and precipitation. Delta marsh lies on the western edge of the sub-humid moisture region in Manitoba (Weir, 1960) with a mean annual precipitation of 52.1 cm.   In this region evapotranspiration exceeds precipitation (Dillon, 1966) so that by late summer plants are usually suffering moisture debt. Lake Manitoba levels have historically fluctuated on an approximately 11-15 year cycle with periods of high water alternating with low water (Walker, 1965).   Delta marsh is open to water from the lake and during high water periods flooding may cause extensive dieoffs in emergent marsh vegetation. Walker (1965) described the colonization of areas exposed after the recession of flood water.   In prairie marshes Van der Valk and Davis (1978) tied cycling in marsh vegetation types to such moisture cycles.

Changes in Lake Manitoba levels have been less extreme since the installation of a dam at Fairford on the north outlet in 1961, but minor fluctuations in lake and marsh water levels still occur.   In 1979 marsh levels rose due to high late winter precipitation and a rapid thaw which caused widespread flooding throughout Manitoba.   In contrast in 1980 snowfall was low and no preciptation was recieved from April to mid August and lake and marsh levels declined significantly.

Several marsh emergents have been shown to fluctuate widely between years in biomass and density in response to changing water levels. Leiffers (1980) found that water level and salinity changes could account for large seasonal changes in the density and production of Scirpus maritimus var. paludosus (Neils.) Kuk.. A decline in moisture levels between years resulted in reduced density and biomass of Scolochloa festucacea (Wild.) Link. (Smith,1973). Van der Valk and Davis (1978) reported a dramatic decline in the total production of a marsh community with falling water levels. The density and biomass of reed, Phragmites australis (Cav.) Trin., has also been shown to fluctuate widely between years in the same sites with declining moisture (Haslam,1969; Dykyjova and Hradecka,1973). According to Haslam (1970) reed performs best in a given habitat when subjected to a stable moisture regime and when this mositure regime fluctuates between seasons its performance declines. P. australis is known to require large amounts of water for transpiration to the extent that diurnal fluctuations in Delta marsh water tables have been tied to transpiration by large reed stands (Philips, 1976). According to Haslam (1970) reed produces more numerous and taller shoots when innundated by shallow water and standing water can also minimize damage to emerging shoots by spring frost. As indicated in Chapter 1 water levels have an important effect on several other aspects of reed performance if flooded and dry parts of the same stand are compared.

As a part of this study of the effects of fire on reed the same stand was sampled 1979 (flooded) and 1980 (drawndown). Comparison of reed performance between years on the control plots offer valuable insight into the effects of lowered water levels on reed performance.

A.2 METHODS

The sampling of reed in 1979 and 1980 is described in detail in Chapters 1 and 3 respectively. Reed biomass, total, flowering and vegetative shoot density and mean stem weight were compared on the control plots between 1970 and 1980 using analysis of variance. In addition combined substorey biomass, total community biomass, and the percentage of the total as reed were similarily compared.

A.3 RESULTS

A.3.1 Reed Performance

Between 1979 and 1980 biomass and density declined significantly (Table 6-1). The relationship between density and biomass was much stronger in the drought year (1980), $r = .908$ than in the wetter year (1979), $r = .680$ (Figure 6-1). For any given density there was much less spread in the biomass. Flowering and non flowering density declined to approximately the same degree with drier conditions so that the percentage of shoots flowering did not change between years. In contrast to the other variables, mean stem weight increased with the drought (Table 6-2).

A.3.2 Community Structure

Total community biomass declined from 1979 to 1980 (Table 6-2). The percentage of biomass as reed declined greatly because, in conjunction with a decline in reed biomass, there was an increase in substorey biomass.

Figure 6-1. Relelationship between P. australis biomass and density on

control plots in 1979 (n=80) and 1980 (n=48).   The 1980

data consists of data collected on July 15, Aug 1, Aug 15

and Sept 1 from control plots.
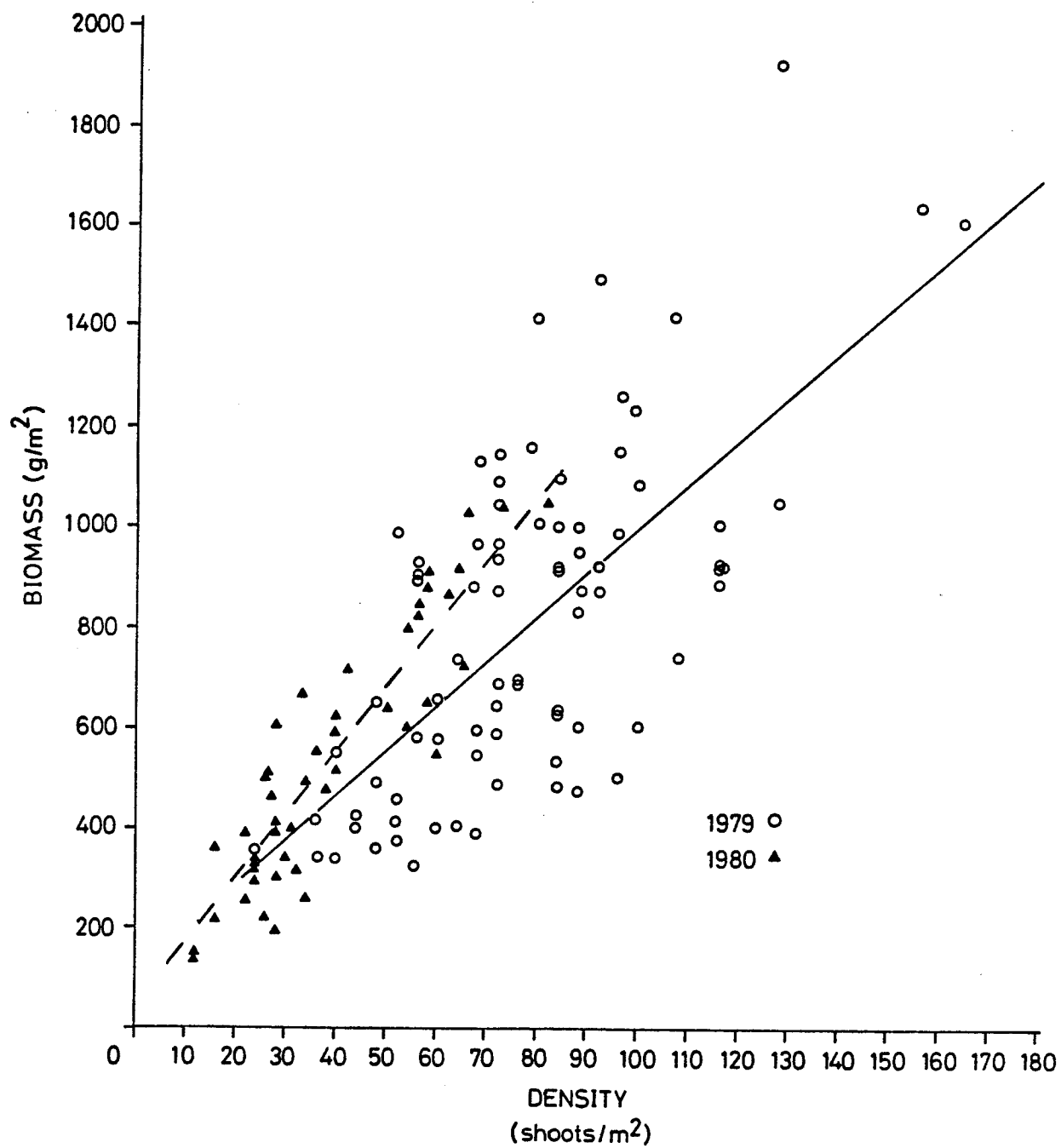
Table 6-1. Analyses of variance for P. australis 1979 vs. 1980.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
		BIOMASS			
YEAR	1	702,500	702,500	19.02	.0003
BLOCK	3	654,243	218,081	5.90	.0047
YxB	3	204,450	68,150	1.83	.1716
ERROR	20	738,805	36,940		
TOTAL	27	2,300,000			
		DENSITY			
YEAR	1	10,120	10,120	46.85	.0001
BLOCK	3	1,030	343	1.59	.2235
YxB	3	2,023	674	3.12	.0489
ERROR	20	4,320	216		
TOTAL	27	17,492			
		WEIGHT PER STEM			
YEAR	1	63	63	7.63	.0120
BLOCK	3	111	37	4.48	.0146
YxB	20	31	10	1.26	.3140
ERROR	20	165	8		
TOTAL	27	369			
		# FLOWERING			
YEAR	1	1,683	1,683	17.62	.0004
BLOCK	3	3,043	1,014	10.62	.0002
YxB	3	1,463	488	5.11	.0087
ERROR	20	1,919	96		
TOTAL	27	8,099			
		# VEGETATIVE			
YEAR	1	3,549	3,549	18.64	.0003
BLOCK	3	1,555	518	2.72	.0714
YxB	3	2,271	757	3.98	.0225
ERROR	20	3,807	190		
TOTAL	27	11,183			

Table 6-2 Mean P. australis Characteristics on Controls in
          1979 and 1980.

- -
- -

	MEAN VALUES* 1979 vs 1980	
CHARACTERISTIC	1979	1980
BIOMASS	793.0 ± 143.8	404.0 ± 121.9
DENSITY	71.8 ± 5.0	33.3 ± 8.6
WEIGHT PER STEM	11.2 ± 1.7	13.3 ± 3.5
% FLOWERING	47.4 ± 12.8	53.0 ± 10.3
# FLOWERING	33.8 ± 10.0	18.8 ± 6.2
# VEGETATIVE	38.0 ± 11.5	15.3 ± 5.1
SUBSTOREY BIOMASS	49.8 ± 19.2	90.3 ± 27.3
TOTAL BIOMASS	842.8 ± 141.7	494.4 ± 119.7
% TOTAL AS PHRAGMITES	93.3 ± 3.6	79.3 ± 7.0

        * mean± 95% confidence intervals

Table 6-3. Analyses of variance for community characteristics 1979 vs. 1980.

SOURCE OF VARIATION	D.F.	SUM SQUARES	MEAN SQUARE	F calc.	Pr > F
		SUBSTOREY BIOMASS			
YEAR	1	11,252	11,252	7.92	.0107
BLOCK	3	9,411	3,137	2.21	.1187
YxB	3	1,699	566	0.40	.7555
ERROR	20	28,415	1,421		
TOTAL	27	50,778			
		TOTAL BIOMASS			
YEAR	1	535,937	535,937	14.32	.0012
BLOCK	3	647,946	215,982	5.74	.0053
YxB	3	216,509	72,170	1.92	.1595
ERROR	20	753,201	37,660		
TOTAL	27	2,153,594			
		% TOTAL AS PHRAGMITES			
YEAR	1	8.7	8.7	12.08	.0024
BLOCK	3	4.3	1.4	1.99	.1482
YxB	20	0.2	0.1	0.11	.9543
ERROR	20	14.4	0.7		
TOTAL	27	27.6			

A.4 DISCUSSION

A.4.1 Reed Performance

The decline in shoot density between 1979 and 1980 with drying supports Haslam's (1970b) observation that a good water supply increases bud formation and thus shoot density. In 1979 when water levels were higher, shoot density was greater than in 1980, the drier year. It is interesting to note that less of a decline occurred in the moistest control plot between years.

Ondok (1970a) studied in detail the relationship between density and biomass in reed. He concluded that much of the large variation in biomass was due to aggregation of shoots into clumps so that either very large or many quadrats must be sampled to get an accurate estimate of production. Concerning the relationship between density and biomass he found that in a drier part of the same stand there was a stronger relationship (r = .82) than in a wetter part (r = .50). In my study the correlation between density and biomass was higher in the drier than wetter year, apparently reed limits its biomass in response to drought by reducing its density. The spread of biomass about a given density is due to variation in the average size of stems. The lesser spread in the dry year is due to much less variable stem size, so that not only is density decreased but the origins of shoots which develop is less varied. Mean stem weight increased from the wet to dry year and this is reflected in the steeper slope for the regression line for the drier year. This contrasts with Haslam's (1970) statement that height declines in response to drought. The height of the quadrats' tallest shoots did not change between 1979 and 1980 but these shoots are only the upper extreme

of the population. Mean shoot height for the population probably increased because few of the smaller shoots which are axillary in origin developed in 1980, and the population was then mostly the tall shoots arising from terminal buds. Gorham and Bernard (1978) pointed out the importance of shoots being of axillary or rhizomatous origin, in their contribution to production in _Carex_ species. In chapter 3 it was hypothesized that terminal buds have apical dominance over laterals. Differences between 1979 and 1980 suggest that the degree of apical dominance is greater in a more severe (drier) conditions than in less severe (moister) conditions. If terminal buds are more likely to produce inflorescences than laterals then it would be expected that with a drawdown there would be an increase in the percentage of shoots flowering. This was not the case, (Table 6-3) flowering density decreased as much as non flowering density between the wet and the drier year. Haslam (1971) suggested that a greater proportion of shoots flower in more favorable growth conditions. It may be that this applies to shoots arising from terminal buds as well as those arising from laterals. It appeared that in the drier year only the very largest shoots produced inflorescences. Because larger inflorescences are produced on larger shoots it may be that inspite of a decline in flowering stem density the total yeilds of inflorescences declined only slightly.

These data suggests that reed adapts to drought by reducing its density. In Chapter 4 its was shown that extent of decline in rhizome reserves during the spring growth period is greater with increased shoot density. Philips (1976) tied transpiration to shoot density, water use being less with lower density. Furthermore canopy development is limit-

ed to larger terminal stems. This ensures that sexual reproduction is maintained at almost a constant level, and because shoot height is tied to the competitive ability of the plant, prevents to some extent the increased success of competitors in response to reduced density. The net result of this response is that water use is more conservative, rhizome reserves are maintained, seed production is maintained, and the growth of competitors is still influenced by reed.

A.4.2 Community Structure

There was a significant increase in substorey biomass with falling water levels between 1979 and 1980. This would be expected if the reed canopy were thinned, reducing light interception, and if the substorey species were better adapted to a drier moisture regime than the dominant. Two upland species, Cirsium arvense (L.) Scop. and Urtica dioica, L. were observed to increase in density and biomass in response to the drier conditions. This was a similar trend to that noticed by Harris and Marshall (1963) who found that during a drawdown of a Typha stand a mixed community including such upland weeds as Cirsium arvense and Sonchus arvensis L. developed in response to drying and reduced performance by the dominant. Scirpus maritimus (Neils.) Kuk. stands showed similar trends during drawdowns, the density and dominant was much reduced and the aerial cover of competitors increased significantly (Leiffers, 1980).

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Appendix B

EFFECTS OF FLOODING AND BURNING ON PHRAGMITES AUSTRALIS

B.1 INTRODUCTION

Several authors have documented dieoffs of marsh emergents as a result of excessive water levels. McDonald (1955) reported dieoffs of a number of emergents including cattail, Typha angustifolia L. and Typha latifolia L., bullrushes, Scripus acutus Muhl. Scirpus fluviatilus (Torr.) Gray and Scirpus validus Vahl., a sedge, Carex stricta Lam. and reed, Phragmites australis (Cav.) Trin. in response to winter flooding. Harris and Marshall (1963) reported dieoffs of Scirpus validus, Eleocharis palustris (L.) R. and S., Typha latifolia and Typha glauca Godr., Carex atherodes Spreng., C. lacustris Willd. and C. pseudo-cyperus L. occurred after several years of flooding with over 40 cm of water. Millar (1972) reported dieoffs of Polygonum coccineum Muhl., Carex atherodes, Scolochloa festucacea (Willd.) Link., and Eleocharis palustris after either extreme flooding for one year or lesser flooding for two years. Leiffers (1980) noted the death of roots of Scirpus maritimus L. var. paludosus (Neils.) with excessive water levels and high summer temperatures. Walker (1965) reported that extensive areas of emergent vegetation were killed by flooding in the Delta Marsh in the early 1960's, including Phragmites australis. Van der Toorn (1972) reported that reed density declined with flooding up to a depth of 1m.

MacDonald (1965) suggested that dieoffs of _Typha latifolia_ in a Lake Erie marsh were due to a lack of oxygen as a result of the submergence of the dormant shoots throughout the winter. Millar (1972) reported that greater than normal water levels at the start of the growing season can cause partial dieoffs of shallow water species but that overwinter flooding is required to produce total dieoffs in the spring.

Several authors have reported dieoffs of emergents in response to lesser water levels when their standing dead aerial stems have been removed before spring flooding. Smith (1973) described dieoffs of _Scirpus acutus_ which occurred when standing dead stems were removed from over the ice by bulldozer and its replacement in the subsequent growing season by _Scolochloa festucacea_. Leiffers (1980) reported localized dieoffs of _Scirpus maritimus_ in areas where standing dead stems had been flattened by algal debris or cut off by muskrats and the stand was innundated throughout the winter and spring. _Phragmites australis_ has been described as more suseptible to winter or spring flooding when its dead aerial stems have been removed. Rudescu et. al. (1972) reported that flooding the stubble of mowed reed stands overwinter reduces bud formation and the density of the next season's crop. Haslam (1972) recommended that when reed is being propagated from rhizome portions dead aerial stems should be left on,when planting in the spring. When transplanting reed rhizomes to study the effects of water levels on its growth Yamasaki and Tange (1981) included the attached aerial stems.

This appendix will describe partial dieoffs of reed in response to flooding observed at various sites in the Delta Marsh where the standing dead canes had been removed the previous fall by mowing or burning.

B.2   METHODS

At one study site two 30m by 10m experimental plots had been out-
lined by mowing a 10m wide strip around their perimeter in late October
of 1978.   One sampling transect was located in each of these plots and
reed stems (current year's growth only) were clipped, counted and oven
dried to constant weight at 80 $^\circ$ C from a number of 1m^2 quadrats.   One
plot was burned in late October and the other left as an untreated con-
trol.

In the spring of 1979 the stand was flooded with rising marsh lev-
els and dieoffs of reed were observed on the mowed and burned areas.
Dieoffs occurred abruptly beyond a certain water level, while growth was
relatively uneffected at lesser water levels.   There was a narrow trans-
itional area where sporadic dense clumps of stunted stems were produced.
Water levels were measured on the burned and mowed plots at random in-
tervals along the dieoff front in early June 1979.   Reed density was
sampled in June on the areas elevated above the dieoff level in mowed,
burned, and control areas.   The development of the reed canopy was fol-
lowed throughout June on these areas by measuring the height and leaf
area of marked shoots.   In late August 1979 reed biomass and density was
sampled from 1m^2 quadrats, located adjacent to the quadrats sampled in
the fall of the previous year.

Additional observations were made at another site which had been
burned in the fall of 1978 and flooded in the spring of 1979.   Water
levels were measured along the dieoff front at this site at the same
time as measurments were made at the main study site.

B.3 RESULTS

B.3.1 Water Levels

Dieoffs occurred at similar water depths on mowed and burned areas at the main study site, water depths on June 14 averaged 11.6 cm on the burned area and 12.9 cm on the mowed area.   In contrast no dieoffs of reed were observed at water depth up to 40 cm on the control plot.   At the other study site water levels along the dieoff front averaged 18.2 cm on June 14 (Figure 7-1).

B.3.2 Reed Growth Above Dieoff Levels

The mean height of shoots sampled from the control area was greater than that of shoots sampled from mowed or burned areas (Figure 7-2a). The leaf area of marked shoots from the three treatment was similar throughout June (Figure 7-2b). Shoot density (on June 15) was higher on (mean = 68 shoots/m^2) and mowed areas (mean = 71 shoots/m^2) than on the control area (mean = 46 shoots/m^2) all sampled at similar elevations.

B.3.3 Reed Growth Below Dieoff Levels

Reed performance in 1978 (before treatments) was very similar on the control (biomass = 429 g/m^2 and density = 53 shts/m^2 .) and on the to be burned plot (biomass = 427 g/m^2 and density = 55 shts/m^2) as shown in the fall sampling. Pre-treatment means were far from being siginficantly different according to the Student's T-test.

All the quadrats sampled in the fall of 1978 were located in the dieoff area in 1979.

Figure 7-1. Dieoff front on the burned and flooded plot in June of 1979. No growth on area below dieoff front (foreground) healthy growth above dieoff front (background).

Figure 7-2a. Height of marked shoots above dieoff front throughout
June on a burned, mowed and control plot (n=24).

Figure 7-2b. Leaf area of marked shoots above dieoff front throughout
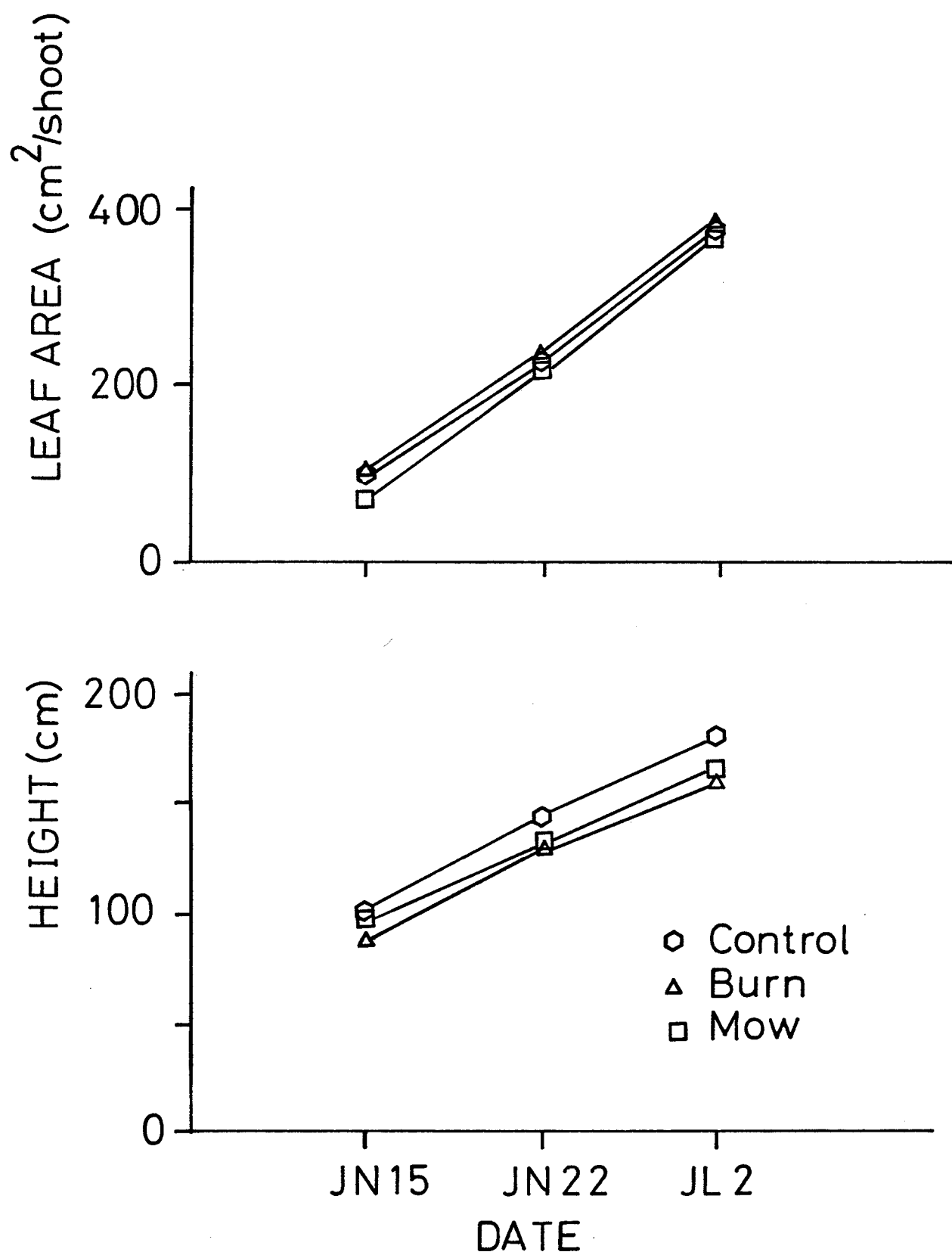June on a burned, mowed and control plot (n=24).

Table 7-1. Reed characteristics after three treatments, 1979.

TREATMENT

CHARACTERISTIC	CONTROL	BURN	MOW
Frequency (%)	100	25	35
Density (shts/m sq.)	75.5	7.4	12.4
Biomass (g/m sq.)	673.3	22.7	7.7

There was a dramatic decline in the frequency, density and biomass of reed (Table 7-1) on the burned and mowed areas in comparison with the controls. Where reed shoots did emerge from dieoff areas along the transects they were very stunted an occurred only in isolated patches.

B.4   DISCUSSION

Dieoffs occurred where aerial stems had been removed in the previous fall by burning or mowing were flooded by more than 20 cm in the spring. Reed shoots emerged in a healty condition where standing dead canes remained. Similar reed dieoffs were observed where standing dead canes had been flattened the previous fall or winter by all terrain vehicles so that they did not project above the water surface. In dieoff areas there was a total failure of reed rhizomes to initiate growth in the spring and the below ground organs were blackened and flaccid when dug up in early September. These symptoms were similar to those described by Klotzli (1971) in reed beds infected by 'reed death'. Similar symptoms have also been reported for Scirpus maritimus root death (Leiffers,1980) and for Spartina dieoffs in British salt marshes (Goodman et al.,1961). It is hypothesized that the standing dead stems of P. australis serve as channels for the diffusion of oxygen through the water to the rhizome system and that this is especially important in the early spring when there are no living stems to serve this function. It was shown in Chapter 4 that there is a rapid mobilization of rhizome reserves at this time in an unflooded stand. Such a mobilization would require considerable energy an in anaerobic conditions rhizome tips may be either unable to provide sufficient energy to initiate growth by

anaerobic respiration, or toxic levels of alcohol could develop due to anaerobic respiration and cause rhizome death.

After both burning and mowing density increased and stem height declined above the dieoff level. The trends found above the dieoff level in density and height were similar to those found in 1980 after fall burning when no flooding occurred.

Biomass and density declined in the dieoff areas. There was some colonization of dieoff areas by legeharme (long runners) produced from healthy stems at the edge of the dieoff front at both sites where die-offs were observed.

There were some changes in community composition observed on dieoff areas. Where Scolochloa festucacea intermixed with P. australis, reed died off due to mowing and flooding but the growth of S. festucacea was uneffected (Figure 7-3). At another site, where reed died off adjacent Typha glauca growth was unaffected (Figure 7-4). At the main study site on the burned area a dense stand of Typha seedlings germinated in June and with falling water levels in August became established (Figure 7-5). Dieoff areas which had also developed dense growth of Lemna minor. No germination of Typha was observed on the mowed dieoff areas (Figure 4). Sifton (1959) found that Typha latifolia L. germination was very low without light and was enhanced by low oxygen concentrations. Bedish (1967) found in a greenhouse experiment that germination of T. glauca was much greater when the soil surface was flooded with one to six inches of water. On the mowed areas, the cut up litter covered the soil surface and this would effectively intercept light, thus preventing the germination of cattail seeds.

Figure 7-3. Scolochloa/Phragmites interface on a plot which had been

mowed the fall of 1978 and flooded in the early spring of

1979.

Uneffected reed growth on unmowed area (left).

Dieoff of reed where the standing canes had been mowed in

fall 1978.

Healthy Scolochloa growth on mowed area at elevation where

P. australis was killed off (background).

Figure 7-4. Phragmites/Typha interface on an area burned in the fall

of 1978 and flooded in the spring of 1979.

Uneffected Typha growth and killed reed (foreground).

Healthy reed growth where water levels were less than the

critical value (background).

Figure 7-5. Mowed, burned and control areas below dieoff front.

Mowed area (foreground) with dieoff of reed and no Typha

seedlings.

Burned area (between posts) with dieoff of reed but a dense

stand of Typha seedlings.

Control area (background) with uneffected reed growth at

similar elevation to that at which dieoffs occured on

burned and mowed areas.

B.5 CONCLUSIONS

Dieoffs of reed occurred where standing dead stems had been removed by burning or mowing in the fall of 1978 and the stand was flooded with stagnant water to a depth in excess of 20 cm in the subsequent spring. At shallower water depths reed growth was not deleteriously effected where mowing or burning had been carried out. This has great promise as a marsh management technique in that these conditions could be duplicated in order to create openings in dense reed stands. It appears that different marsh emergents such as Carex atherodes, Scolochloa festucacea and Typha glauca have greater resistence to spring flooding when their standing dead stems have been removed, and that this could be used to manipulate marsh cover types. Mowing and burning of reed standing dead followed by flooding had similar effects on reed growth but after burning the dieoffs were colonized by Typha seedlings whereas on the mowed areas no such colonization occurred. This gives the marsh manager another option in the manipulation of marsh vegetation by this technique.

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Appendix C

REED GROWTH AFTER SUMMER BURNING WITH OPTIMAL WATER LEVELS

C.1   INTRODUCTION

Throughout this thesis the importance of water levels in determining reed performance has been constantly stressed. In appendix A changess in reed growth due to a drawdown between 1979 and 1980 were described and in appendix B the combined effects of flooding and burning on reed growth following fall burning (at a different site) were discussed.

The question arises as to what the effects of burning would be on reed would be if water levels were conducive to optimal growth. Haslam (1970) defined optimal water levels for _Phragmites australis_ (Cav.) Trin. as where there was some standing water throughout the growing season.   Similarily Smith (1973) noted that _Scolochloa festucacea_ (Willd.) Link. had highest production and flowered most abundantly where there was some ponding of water, at least in the spring.

To evaluate reed perfomance in the growth season following summer burning under favorable water levels blocks of dormant reed were excavated in the winter and grown under   a constant water level in a greenhouse. Several authors have grown _P. australis_ in culture in order to study various aspects of its biology.   Szczepanska (1971) studied reed growth in competition with other wetland emergents and in 1971 investigated the course of development of its belowground organs in a

greenhouse experiment. Szczepanski (1969) studied the relationship between aerial and belowground production in culture. Szczpanska and Szczepanski were co-authors of two papers: one studying the effects of soil fertiltiy on reed performance (1976a) and the other studying the relationship between density and production (1976b). Van der Toorn (1972) investigated the effects of nutrient availability on reed yield by fertilizing reed seedlings grown in containers to different levels. All these culture studies used reed seedlings as experimental material. This paper presents one of the first attempts to grow field treated reed, sampled from established stands, under controlled conditions.

C.2 MATERIALS AND METHODS

Two clumps of reed were excavated from each of two control and two summer burned plots on November 11, 1979. The number of samples was low due to the difficulty involved in digging, transporting, and storing the samples. The samples were cubes of soil 25 by 25 cm in surface dimensions and were dug to a depth of 30 cm around the clump of stems nearest to a randomly chosen point. Standing dead canes were cut at a height of 20 cm to facilitate transport and the samples were stored in a cold room at 4° C until the commencement of the experiment.

In the experiment the clumps of reed were placed in wooden boxes 25 by 25 cm in length and width and 35 cm in depth which were lined with clear 5 mil polyethylene and their surfaces were adjusted to the same level by adding a mixture of two parts loam to one part peat and one part fine sand. Growth was initiated in a growth chamber held at 20° C for a 16 hour day and at 10° C for a 8 hour night. After three weeks

the shoots were too large to continue unhampered growth and so were moved to a greenhouse where they were maintained at a similar tempera-ture regime and under natural light supplemented with florescent light supplied for a 16 hour day.

At the time of emergence six shoots were tagged in each container and their height to the topmost unfolded leaf, their leaf number and the maximum length and width of each leaf recorded approximately weekly. Leaf measurements were used to estimate leaf area for each shoot based on the formula $A = LW/ 1.71$ (Walker and Waygood, 1968). At the conclu-sion of the experiment (day 57) all shoots were clipped at ground level, counted and measured (height to topmost leaf, leaf number, and basal di-ameter) before oven drying at 80 deg. C. to constant weight. Inflores-cences, leaves and stems were weighed separately from each container. The belowground organs were washed clear of soil and divided into three categories, (new rhizomes, new roots, and old roots and rhizomes) for oven drying at 80° C. The biomass and density recorded for each clump were multiplied by an appropriate conversion factor to estimate a yeild per square meter. Field data collected in 1979 indicated that there are approximately eight of these clumps of shoots per square meter.

C.3   RESULTS AND DISCUSSION

C.3.1   Canopy Development

Shoots from the controls were taller throughout the experiment than those from the summer burned samples (Figure 8-1). The height of con-trol shoots began to level off later than for the summer burned samples. The growth potential of reed shoots is related to their origin in the

rhizome system (as discussed in Chapter 3). Shoots of terminal origin have greater growth potential than those of axillary origin and thus elongate for a longer period before levelling off. Most of the shoots emerging on the burned samples were of axillary origin and thus their growth potential was less.

Leaf area per shoot was greater for control than summer burned samples (Figure 8-2). The increase in leaf area with time was more sigmoid for control than summer burned samples. Leaf area and biomass are highly related (Mochnaka-Lawacz, 1980). The greater leaf area for control shoots is related to the larger size of individual leaves rather than to increased leaf number (see below). Leaf area is an indicator of the photosynthetic potential and per shoot control shoots are probably able to produce assimilate at a higher rate. This could explain somewhat the more rapid increase in height seen for control shoots.

C.3.2   Final Harvest

C.3.2.1   Height

Mean height, for all shoots which developed by the end of the experiment, was much greater for the controls (Figure 8-3a) than for the burn samples (Figure 8-3b). Summer burned samples did not produce any shoots over 175 cm in height but the controls procuced many. Shoot height was more evenly divided among size classes for the controls than for the summer burned samples for which most of the shoots were between 100 and 150 cm tall.

Figure 8-1. Height of marked P.   _australis_ shoots (n=24),   greenhouse
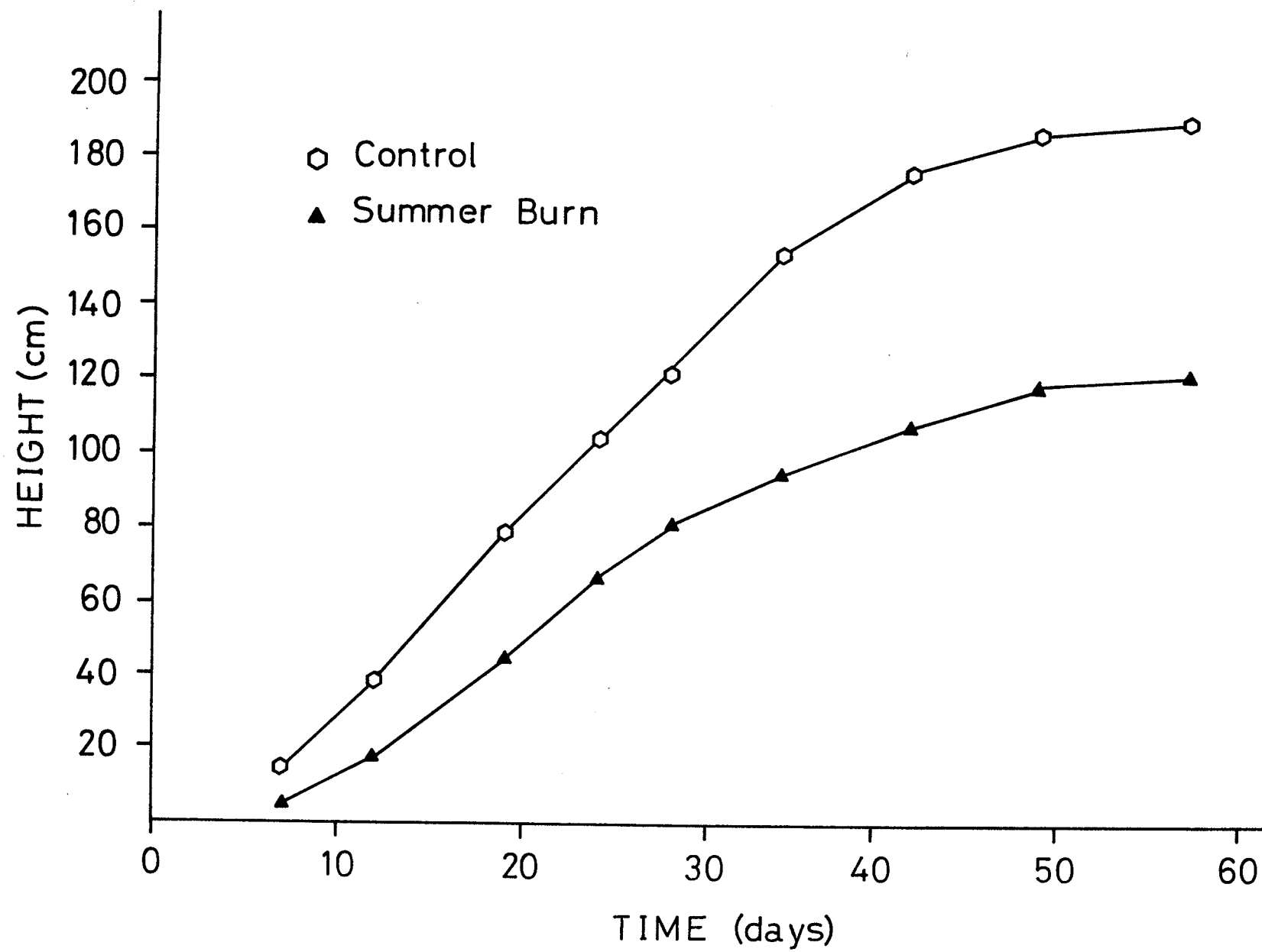
   experiment.

Figure 8-2. Leaf area of marked P. australis shoots (n=24), greenhouse
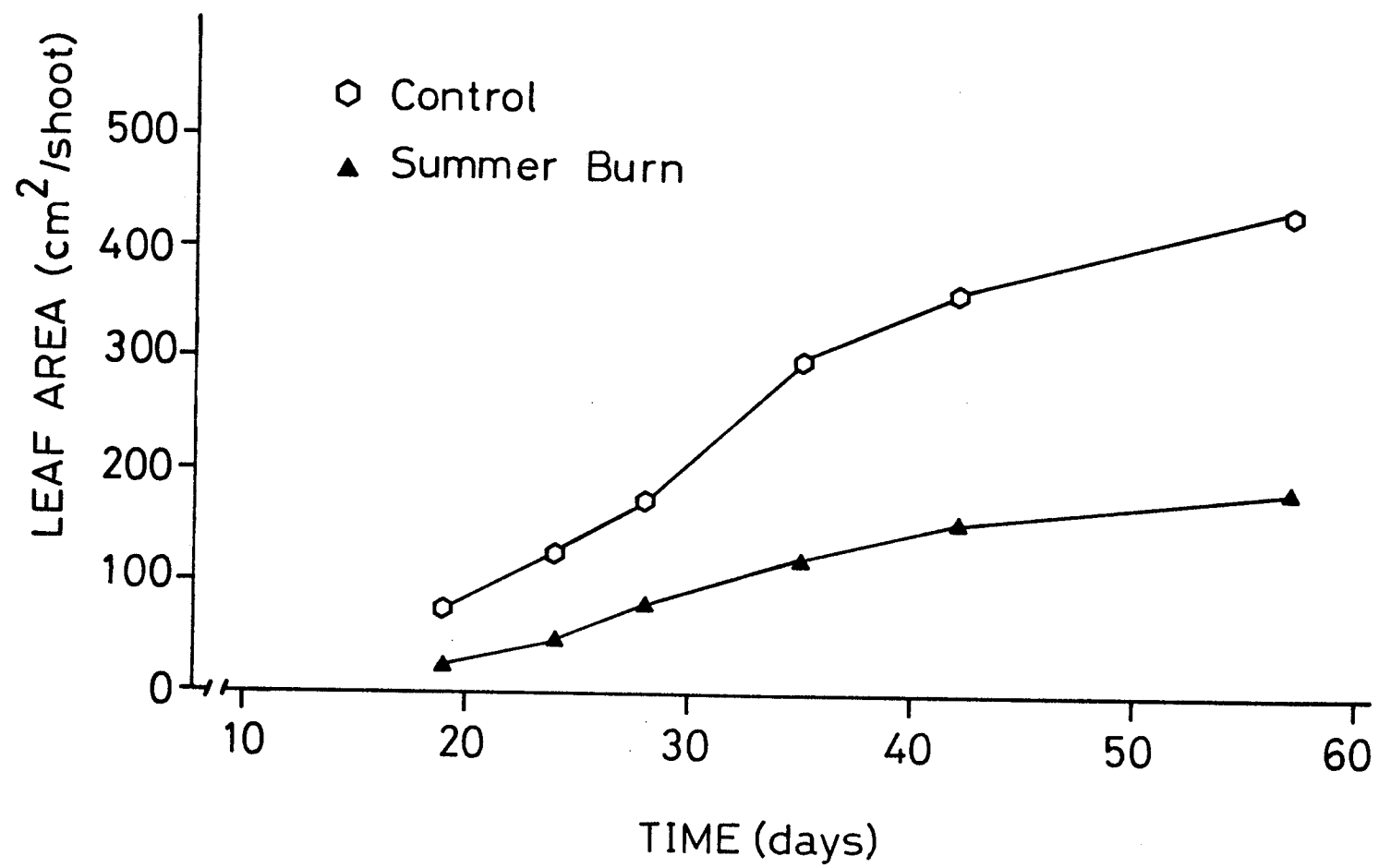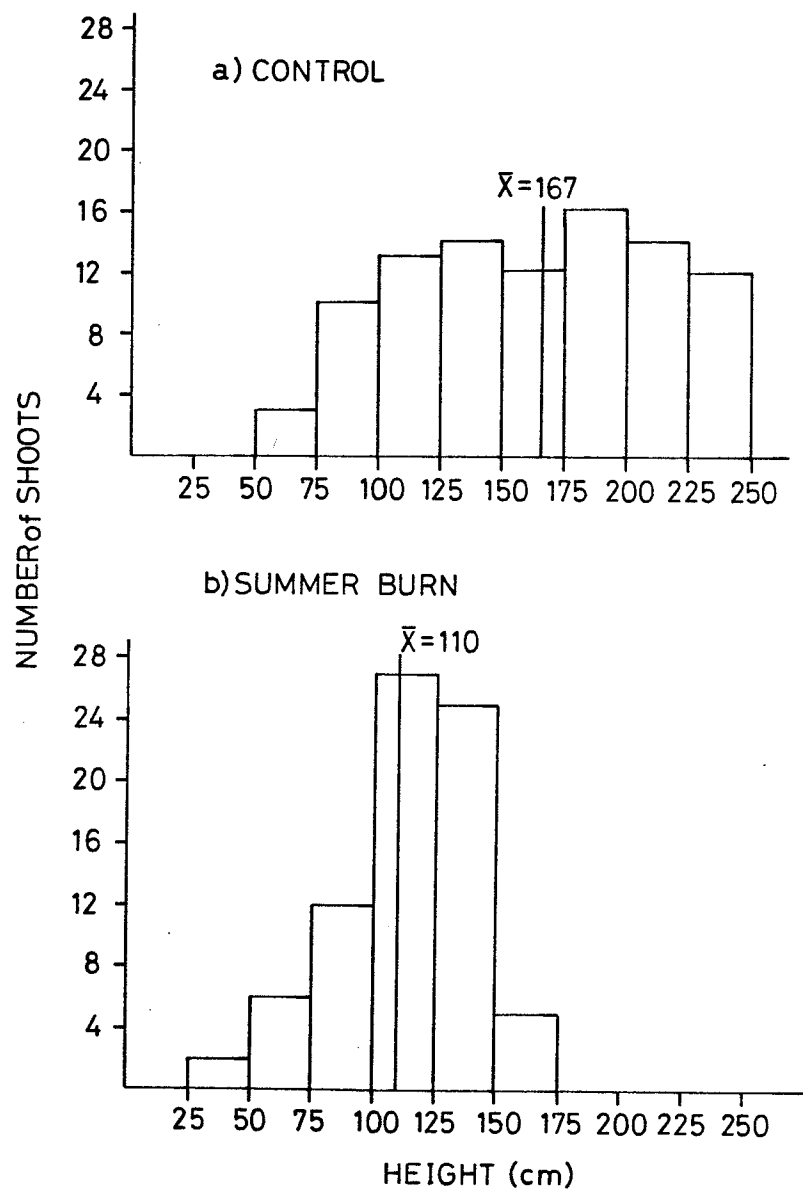
experiment.

Figure 8-3. Frequency distribution for height of all shoots at the

final harvest, greenhouse experiment.

The tallest shoots in the controls were almost always flowering shoots but no flowering shoots were produced by the summer burned samples. For both the burned and control samples a number of shoots sprouted midway through the experiment but did not exceed 25-75 cm by its termination. The mean height of harvested shoots from controls was somewhat lower than that of the marked shoots, because the first shoots to emerge from the controls were used but there were two distinct cohorts of shoots produced. In contrast all the shoots emerged from the burned samples at the same time and the height of marked shoots closely resembled that for the larger population. These height frequency distributions are more revealling than those drawn from field data collected in 1980 because the contribution of both flowering and nonflowering shoots are represented to the appropriate degree. Thus the overall performance of the plant is more clearly shown. Shorter shoots emerging later in the season after both treatments were termed 'summer' shoots by Haslam (1970). They originate from the large terminal buds which normally remain dormant until the following growing season but under certain conditions develop in the season of their formation.

C.3.2.2   Basal Diameter

As for height the mean basal diameter of control shoots was much greater than that of treated samples. In the controls (Figure 8-4a) the frequency distribution for basal diameter was skewed to the right (the most numerous size class being between 6 and 7 mm) but for the treated shoots(Figure 8-4b) the distribution was skewed to the left with the most numerous size class between 3 and 4 mm. The upper size classes

(6-8 mm) contained a few shoots which developed midway through the grow-

ing season in both treatments, and were very broad in basal diameter.

The potential height of shoots is related to the diameter of the buds

from which they arise. Larger shoots in the controls arise from over-

wintering buds are thicker than lateral buds and thus can develop into

taller shoots. The very thickest shoots were the same 'summer' shoots

which did not develop fully by the completion of the experiment.

C.3.2.3 Leaf Number

The number of leaves per shoot was slightly higher for burned than

for control samples. The most numerous size class for the burned sam-

ples was for shoots with 16 to 20 leaves (Figure 8-4d) but for the con-

trols was for shoots with 12 to 16 leaves (Figure 8-4c). The shoots

with low numbers of leaves were 'summer' shoots which did not reach full

development by the end of the experiment. Leaf number was slightly

greater for shoots from the burned samples because most of the larger

control shoots flowered and the flag leaf is seldomly beyond the 14th

formed. In contrast vegetative shoots are indeterminate in growth and

may produce up to 24 leaves. Beyond the approximately the 14th leaf the

size of leaves produced by vegetative shoots declines markedly, so that

further leaves do not add appreciably to either leaf area or biomass.

C.3.2.4 Biomass

The biomass of leaves, stems and inflorescences was higher for the con-

trol than for the burned samples (Table 8-1). There were no inflores-

cences produced by the burned samples. The total aerial biomass for the

burned samples was approximately one half that of the controls. The biomass of summer burned samples was similar to the peak biomass reached after this treatement in the field in 1980 (Chapter 3). In contrast the aerial biomass of the controls exceeded that recorded in the field for control plots in the field in 1980 (during a drought year) but was close to that produced in the field in 1979 (during the wetter year). This suggests that if it had not been for the spring drought the disparity in biomass between summer burned and control plots would be greater than observed in the field in 1980. The belowground biomass (for new roots, new rhizomes and old biomass) was also higher for the controls than for summer burned samples. Similar to aerial production belowground production was greater than observed in the field in 1980 for the controls, but was similar for greenhouse and field grown reed after summer burning. The difference in old belowground biomass is interesting in that it may indicate reduced belowground production by reed in the fall of the year of burning. After summer burning shoot senescence did not occur normally and there was likely less investment in belowground production for that reason. Visual comparison of reed rhizome systems sampled in 1979 (wet year) and from the greenhouse experiment (with optimal mosisture) with those produced on control plots in 1980 (during the drought) suggested developmental differences. The horizontal rhizomes in the drought year were very short (their internodes not elongating) and almost immediately turned up to form overwintering tillers. In contrast, in wetter conditions, horizontal rhizomes were much larger and for this reason belowground production was greater.

Figure 8-4a. Frequency distribution for basal diameter of all shoots
          from controls, greenhouse experiment.

Figure 8-4b. Frequency distribution for basal diameter of all shoots
          from summer burned samples, greenhouse experiment.

Figure 8-4c. Frequency distribution for leaf number of all shoots from
          controls, greenhouse experiment.

Figure 8-4d. Frequency distribution for leaf number of all shoots from
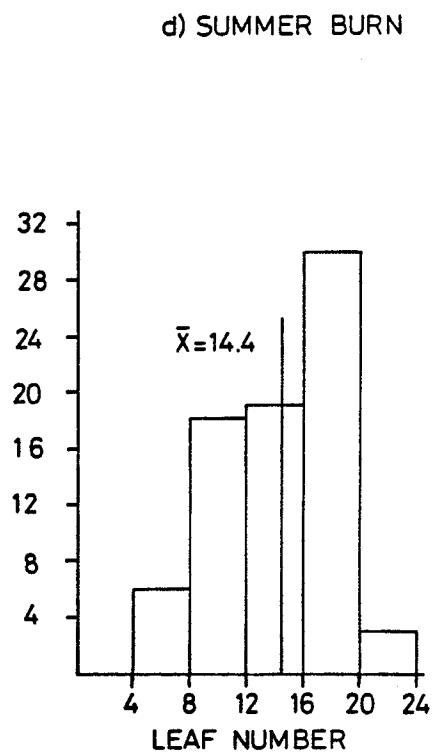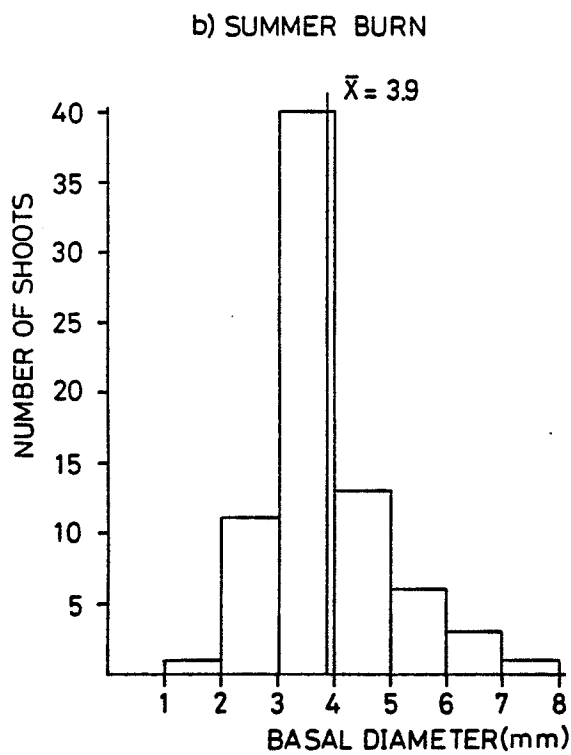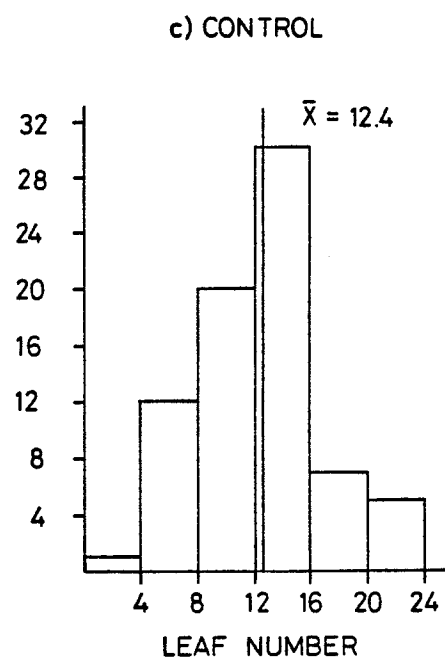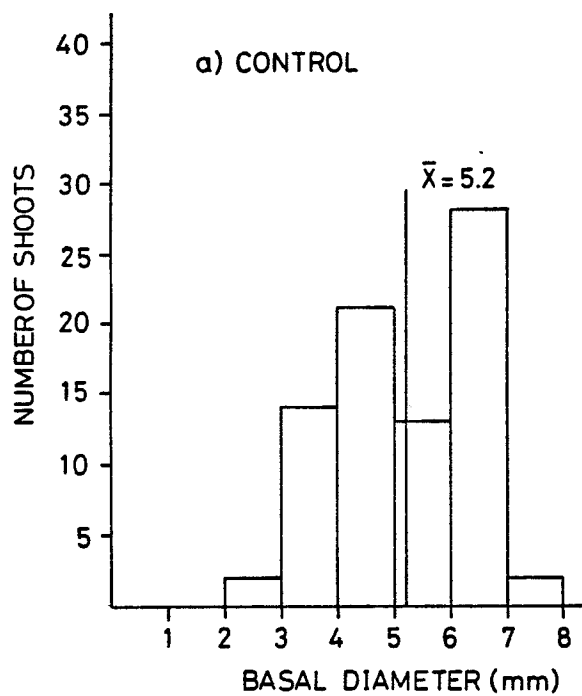   summer burned samples, greenhouse experiment.

a) CONTROL

$\bar{X} = 5.2$

b) SUMMER BURN

$\bar{X} = 3.9$

c) CONTROL

$\bar{X} = 12.4$

d) SUMMER BURN

$\bar{X} = 14.4$

Table 8-1. <u>Phragmites</u> biomass harvested from greenhouse experiment.

	PLANT PART	BURN	CONTROL
Aerial Biomass	Leaf	149.6	251.2
	Stems	265.6	570.4
	Inflorescences	-	13.6
	Total	415.2	835.2
Belowground	New Roots	112.8	139.2
	New rhizomes	104.0	246.4
	Old Biomass	1125.6	1409.4
	Total	1342.4	1876.0

Table 8-2. Mean shoot weights, greenhouse experiment.

CHARACTERISTIC

PART	BURN	CONTROL
Wt./Stem	1.70	3.65
Wt./Leaf	0.07	0.13
Total Wt./Shoot	2.66	5.35

The ratio of belowground production to aerial production also differed between treatments being greater for burned samples (3.24) than for controls (2.25). The greater ratio for the burned plots may represent an adaptive response to the disturbance in the plant's seasonal growth pattern. More energy is probably invested in the production of larger growing points for the next season's growth than in the production of aerial stems for in the post-fire growth season. It is interesting to note that the ratio of subterranean to aerial biomass in the controls was very similar to that found by Szczepanski (1969) for reed grown in culture. He found a ratio of approximately 2.0 over a wide range of aerial and belowground biomasses. It appears that a conversion factor of 2:1 may give an adequate estimate for belowground biomass from aerial biomass of natural reed stands if growth conditions are optimal.

C.3.2.5 Density

Shoot density was approximately equal for summer burned and control samples with a mean of 160 per m^2 for controls and a mean of 156 per m^2 for the burned. This density for the summer burned plots is only slightly less than observed in the field after this treatment in 1980, but for the controls is much greater than reached in the field in 1980. This is in fact very close to the postemergent density reached in the field after spring burning in 1980. The relationship between litter removal and reed density was discussed in Chapter 3, as being one of the possible reasons for increased density after burning. It was necessary to remove a large portion of the litter from the control samples in the course of this experiment, and this together with a better moisture re-

gime than observed in the field in 1980 may account for high contol density.

C.3.2.6 Mean Shoot Weight

Mean shoot weight was greater for the controls than for the burned samples (Table 8-2). Both mean leaf and stem weight was less for burned shoots. Mean shoots weight for the burned samples was similar to that reached on the summer burned plots in the field in 1980. For the controls however, mean stem weight approximated closely that reached after spring burning in the field in 1980 (Chapter 3). Both leaves and stems were much lighter in the summer burned shoots than for the controls and this reflects their leaf area and height and diameter respectively.

C.4 CONCLUSIONS

This experiment showed that the performance of reed would be reduced in the season following summer burning even if water levels were conducive to optimal performance. After summer burning shoot height, basal diameter, leaf area, aerial and subterranean biomass were reduced in comparison with the controls. The biomass of control samples were similar to that observed in the field in 1979 (a wet year) but greater than observed in the field in 1980 (a dry year). Several reed characteristics resembled more closely the performance seen on spring-burned plots in 1980. This was because shoots were produced from most of the avaiable growing points.

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