

EFFECTS OF FIRE ON
PHRAGMITES AUSTRALIS (CAV.) TRIN. EX STEUDEL
AND ASSOCIATED SPECIES AT DELTA MARSH MANITOBA

BY

DONALD JAMES THOMPSON

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

© 1982

Permission has been granted to the LIBRARY OF THE UNIVER-
SITY OF MANITOBA to lend or sell copies of this thesis, to
the NATIONAL LIBRARY OF CANADA to microfilm this
thesis and to lend or sell copies of the film, and UNIVERSITY
MICROFILMS to publish an abstract of this thesis.

The author reserves other publication rights, and neither the
thesis nor extensive extracts from it may be printed or other-
wise reproduced without the author's written permission.

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 initially lower TNC level at the beginning 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 due to increased production by C. arvense and due to the establishment of Sonchus arvensis and Atriplex patula which produced considerable biomass.

CONTENTS

ABSTRACT	ii
LIST OF TABLES	ix
LIST OF FIGURES	xiii
ACKNOWLEDGEMENTS	xvii
INTRODUCTION	xix

Chapter

page

I.	THE SPECIES COMPOSITION AND PRODUCTION OF A MARSH COMMUNITY . .	1
	INTRODUCTION	1
	METHODS	2
	RESULTS	4
	<u>P. australis</u>	4
	Substorey	6
	Relationship between <u>P. australis</u> and Substorey	6
	DISCUSSION	9
	<u>Phragmites australis</u>	9
	Substorey	11
	Relationship between <u>P. australis</u> and Substorey	11
	SUMMARY	13
	REFERENCES	13
II.	INFLUENCE OF SUMMER MOWING AND BURNING ON STAND REGENERATION .	18
	INTRODUCTION	18
	METHODS	19
	RESULTS	22
	Environmental Changes	22
	Physical Characteristics	22
	Chemical Characteristics	22
	Reed Regrowth	35
	Shoot Biomass, Density and Morphology	35
	Shoot Mineral Contents	35
	Rhizome Reserves	35
	Substorey Regrowth	42
	Seedlings	42
	Regrowth from Rhizomes	42
	DISCUSSION	46
	Environmental Changes	46
	Physical Characteristics	46

Chemical Characteristics	47
Reed Regrowth	50
Shoot Biomass, Density and Morphology	50
Shoot Mineral Content	51
Rhizome Reserves	51
Substorey Regrowth	52
Seedlings	52
Regrowth from Rhizomes	52
CONCLUSIONS	53
REFERENCES	54

III. POSTFIRE PERFORMANCE OF PHRAGMITES AUSTRALIS 58

INTRODUCTION	58
METHODS	59
Site Preparation	59
Firing Techniques	61
Shoot Density and Biomass	61
Shoot Morphology	62
Below-ground Standing Crop	62
DATA ANALYSIS	64
RESULTS AND DISCUSSION	65
Shoot Biomass	65
Total Shoot Biomass	65
Flowering vs Vegetative Shoot Biomass	66
Shoot Density	74
Total Density	74
Percent flowering	77
Flowering density	77
Vegetative Density	83
Mean Weight per Stem	83
Overall mean Stem Weight	83
Flowering and Vegetative Stem Weight	84
Shoot Morphology	89
Flowering Shoots	89
Vegetative Shoots	92
General Discussion of Shoot Origins	96
Growth form of <u>Phragmites</u>	96
Summer Burning	97
Spring Burning	98
Fall Burning	98
Shoot Aggregations and Shoot Origins	99
Below-ground Biomass	99
CONCLUSIONS	103
REFERENCES	104

IV. EFFECTS OF FIRE ON PHRAGMITES RHIZOME RESERVES 109

INTRODUCTION	109
METHODS	110
Sampling Schedule	110
Sample Preparation	111
Carbohydrate Assay	111
RESULTS	111

New Rhizomes	111
Old Rhizomes	113
DISCUSSION	115
TNC Levels- Autumn 1979	115
TNC Levels- 1980 Growing Season	115
CONCLUSIONS	117
REFERENCES	118

V. THE EFFECTS OF FIRE ON A MARSH PLANT COMMUNITY 120

INTRODUCTION	120
STUDY SITE	122
METHODS	124
1979 Season	124
1980 Season	124
Data Analysis	125
RESULTS AND DISCUSSION	126
Diversity	126
Diversity Indices	126
Dominance-Diversity Curves	130
Community Structure	133
Distribution of Biomass between Canopy and Understorey	133
Community Composition	134
Similarity Indices	134
Species Biomasses	139
Summer Burning	139
Summer Mowing	139
Fall Burning	140
Spring Burning	140
Sources of Regrowth	143
Seedlings	143
Regrowth of Substorey from Rhizomes	147
CONCLUSIONS	150
REFERENCES	150

VI. CONCLUSIONS 155

Appendix

	<u>page</u>
A. EFFECTS OF DROUGHT ON THE GROWTH OF <u>PHRAGMITES AUSTRALIS</u>	158
INTRODUCTION	158
METHODS	160
RESULTS	160
Reed Performance	160
Community Structure	160
DISCUSSION	165
Reed Performance	165
Community Structure	167
REFERENCES	168

B.	EFFECTS OF FLOODING AND BURNING ON <u>PHRAGMITES AUSTRALIS</u> . . .	170
	INTRODUCTION	170
	METHODS	172
	RESULTS	173
	Water Levels	173
	Reed Growth Above Dieoff Levels	173
	Reed Growth Below Dieoff Levels	173
	DISCUSSION	177
	CONCLUSIONS	182
	References	182
C.	REED GROWTH AFTER SUMMER BURNING WITH OPTIMAL WATER LEVELS .	184
	Introduction	184
	MATERIALS AND METHODS	185
	RESULTS AND DISCUSSION	186
	Canopy Development	186
	Final Harvest	187
	Height	187
	Basal Diameter	191
	Leaf Number	192
	Biomass	192
	Density	197
	Mean Shoot Weight	198
	CONCLUSIONS	198
	REFERENCES	199

LIST OF TABLES

Table 1-1. Correlations between <u>P. australis</u> characteristics, preliminary sampling 1979.	5
Table 1-2. Frequencies of substorey species, preliminary sampling 1979.	7
Table 2-1. Treatment means for soil chemical characteristics, after summer burning 1979.	26
Table 2-2. Analysis of variance for extractable soil phosphate, after summer burning and on controls 1979.	28
Table 2-3. Analysis of variance for extractable soil nitrate, after summer burning and on controls 1979.	30
Table 2-4. Analysis of variance for extractable soil potassium, after summer burning and on controls 1979.	31
Table 2-5. Analysis of variance for soil conductivity, after summer burning and on controls 1979.	34
Table 2-6. <u>P. australis</u> regrowth after summer burning and summer mowing, fall 1979.	36
Table 2-7. Analyses of variance for <u>P. australis</u> regrowth, fall 1979.	37

Table 2-8. Analyses of variance for <u>P. australis</u> shoot phosphorus and potassium, fall 1979.	38
Table 2-9. Mineral contents of <u>P. australis</u> regrowth shoots after summer burning and mowing, fall 1979.	39
Table 2-10. Analyses of variance <u>P. australis</u> rhizome carbohydrate levels after three treatments, Nov 1 1979.	40
Table 2-11. Mean % nonstructural carbohydrates of <u>P. australis</u> rhizomes after three treatments, Nov 1 1979.	41
Table 2-12. Seedling frequencies and densities following summer burning and summer mowing, fall 1979.	43
Table 2-13. Percent change in densities of substorey species after summer burning and mowing, from initial to regrowth.	44
Table 2-14. Density of substorey regrowth from rhizomes following summer burning and mowing, fall 1979.	45
Table 2-15. Nutrient content of ash.	48
Table 3-1. Analysis of variance for <u>P. australis</u> biomass, 1980.	68
Table 3-2. Phenological development of <u>P. australis</u> shoots after four treatments, 1980.	69
Table 3-3. Compartmentalized <u>P. australis</u> biomass, August 15 1980.	71
Table 3-4. Analysis of variance for total <u>P. australis</u> density, 1980.	75

Table 3-5. Analysis of variance for percent of <u>P. australis</u> shoots flowering, 1980.	79
Table 3-6. Analysis of variance for <u>P. australis</u> flowering shoot density, 1980.	82
Table 3-7. Analysis of variance for <u>P. australis</u> vegetative shoot density, 1980.	85
Table 3-8. Analysis of variance for <u>P. australis</u> mean shoot weight.	86
Table 3-9. <u>P. australis</u> flowering shoot morphology, August 1-10 1980.	91
Table 3-10. <u>P. australis</u> vegetative and flowering shoot morphology after four treatments, Sept. 1 1980.	94
Table 4-1. <u>P. australis</u> , percent total nonstructural carbohydrates (TNC) throughout the 1980 growing season after four treatments.	114
Table 5-1. Analyses of variance for diversity characteristics of the plant community, August 1-10 1980.	127
Table 5-2. Mean diversity characteristics for the plant community following four treatments, August 1-10 1980.	129
Table 5-3. Categorized community biomass, August 1-10 1980.	135
Table 5-4. Categorized understorey biomass, August 1-10 1980.	136
Table 5-5. Mean biomasses of individual substorey species after four treatments, August 1-10 1980.	141

- Table 5-6. Performance of three species at different moisture levels 142
on control and summer-burned plots, August 1-10 1980.
- Table 5-7. Mean densities of individual substorey species after four 148
treatments, August 1-10 1980.
- Table 6-1. Analyses of variance for P. australis characteristics, com- 162
paring controls in 1979 with 1980.
- Table 6-2. Mean P. australis characteristics on controls in 1979 and 163
1980.
- Table 6-3. Analyses of variance for community characteristics on con- 164
trols in 1979 and 1980.
- Table 7-1. Frequency, density and aerial biomass of P. australis on 176
burned, mowed and control plots, fall 1979.
- Table 8-1. Compartmentalized P. australis biomass, greenhouse experi- 195
ment 1979.
- Table 8-2. Mean shoot weights of P. australis, greenhouse experiment 196
1979.

LIST OF FIGURES

- Figure 1-1. Site preparation, summer 1979. 3
- Figure 1-2. Relationship between dry weight of substorey species and that of P. australis litter. 8
- Figure 2-1. Study site showing location of burned and mowed areas, fall 1979. 20
- Figure 2-2. Air temperatures recorded on a burned and a control plot for three days following burning. 23
- Figure 2-3. Soil temperatures recorded on a burned and a control plot for three days following burning. 24
- Figure 2-4a. Solar radiation recorded on a burned and a control plot for a three day period following burning. 25
- Figure 2-4b. Relative humidity recorded on a burned and a control plot for a three day period following burning. 25
- Figure 2-5. Interactions in analyses of variance for exchangeable phosphorus and nitrate. 29
- Figure 2-6. Treatment by depth interaction for extractable soil potassium, fall 1979. 33
- Figure 3-1. Study site spring 1980. 60

Figure 3-2.	Sampling design for the sampling of <u>P. australis</u> aerial biomass and density, 1980.	63
Figure 3-3.	Seasonal trends for <u>P. australis</u> aerial biomass, 1980.	67
Figure 3-4.	Aerial biomass of <u>P. australis</u> sampled August 15, 1980 and divided according to flowering and vegetative shoots.	70
Figure 3-5.	Biomass of <u>P. australis</u> inflorescences produced after four treatments, August 1 1980.	72
Figure 3-6.	Seasonal trends for <u>P. australis</u> total shoot density, 1980.	73
Figure 3-7.	Seasonal trends for percent of <u>P. australis</u> flowering, 1980.	76
Figure 3-8.	Seasonal trends for <u>P. australis</u> flowering shoot density, 1980.	81
Figure 3-9	Seasonal trends for <u>P. australis</u> mean shoot weight, 1980.	87
Figure 3-10.	Mean weight per shoot for flowering and vegetative shoots, August 15 1980.	88
Figure 3-11.	Frequency distribution for height of <u>P. australis</u> flowering shoots, August 1 1980.	90
Figure 3-12.	Weight per <u>P. australis</u> inflorescence, August 1 1980.	93
Figure 3-13.	Diagrammatic representation of <u>P. australis</u> shoot origins September of 1980 after four treatments.	95

- Figure 3-14. Maps of shoot origins within representative quadrats from 100
variously treated plots, August 1 1980.
- Figure 3-15. Mean below-ground biomass of P. australis collected Sep- 101
tember 15 1980 from different treatments.
- Figure 3-16. Mean density of P. australis buds excavated in September 102
from different treatments.
- Figure 4-1. Mean total nonstructural carbohydrate (TNC) content of 112
rhizomes collected from the different treatments throughtout
the 1980 growing season.
- Figure 5-1. Location of study site. 123
- Figure 5-2. Shannon and Weaver diversity indicies and species numbers 128
after different treatments, 1980.
- Figure 5-3. Dominance-diversity curves for the plant community after 132
the four treatments, 1980.
- Figure 5-4. Sorensen's similarity indicies comparing the 1979 (pre- 137
burn) and 1980 (post-burn) understorey species compostions
of differently treated sets of plots.
- Figure 6-1. Relationship between P. australis aerial biomass and den- 161
sity on control plots in 1979 and 1980.
- Figure 7-1. Dieoff front on the burned and flooded plot in June of 174
1979.

Figure 7-2. Height and leaf area of marked shoots from above dieoff 175 levels on fall burned, mowed and control plots in June of 1979.

Figure 7-3. P. australis / Scolochloa festucacea interface on a plot 179 which was mowed in the fall of 1980 and flooded in the spring of 1979.

Figure 7-4. P. australis / Typha glauca interface on an area burned in 180 the fall of 1978 and flooded in the spring of 1979.

Figure 7-5. Mowed, burned and control plots burned in the fall of 1978 181 and flooded in the spring of 1979, showing P. australis dieoff and Typha seedlings.

Figure 8-1. Height of marked P. australis shoots from burned and con- 188 trol plots, greenhouse experiment.

Figure 8-2. Leaf area of marked P. australis shoots from burned and 189 control plots, greenhouse experiment.

Figure 8-3. Frequency distribution for height of all P. australis 190 shoots at final harvest, greenhouse experiment.

Figure 8-4. Frequency distributions for P. australis shoot basal diam- 194 eter and leaf number at final harvest, greenhouse experiment.

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.

I would also like to thank Dr. R. Jones, marsh manager, for the loan of fire-fighting equipment. Also thanks go to the Portage Country Club for the use of their land and dock.

The advice and support of the staff and students in the Botany and Zoology Departments was very valuable. Especially I would like to thank Dr. V.J. Lieffers, for his friendship and help in designing and carrying out this project, and Mr. C. Day, who offered a great deal of encouragement while writing this thesis. Lastly, I would like to thank my relatives for continued help throughout this thesis, especially Ron Drysdale, Don and Mary Popien, and Tom Thompson who helped me with different parts of the fieldwork and provided encouragement throughout.

Research funds for this study included a University of Manitoba grant to Dr. Shay and support for the 1979 and 1980 field seasons from the Delta Waterfowl Research Station. Contributors to the Waterfowl Station research funds included, the Canadian National Sportsmen's Fund, the North American Wildlife Foundation and the Government of Manitoba. The Natural Sciences and Engineering Research Council of Canada provided a scholarship during the last two years of this thesis.

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 precipitation 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 occurred 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.

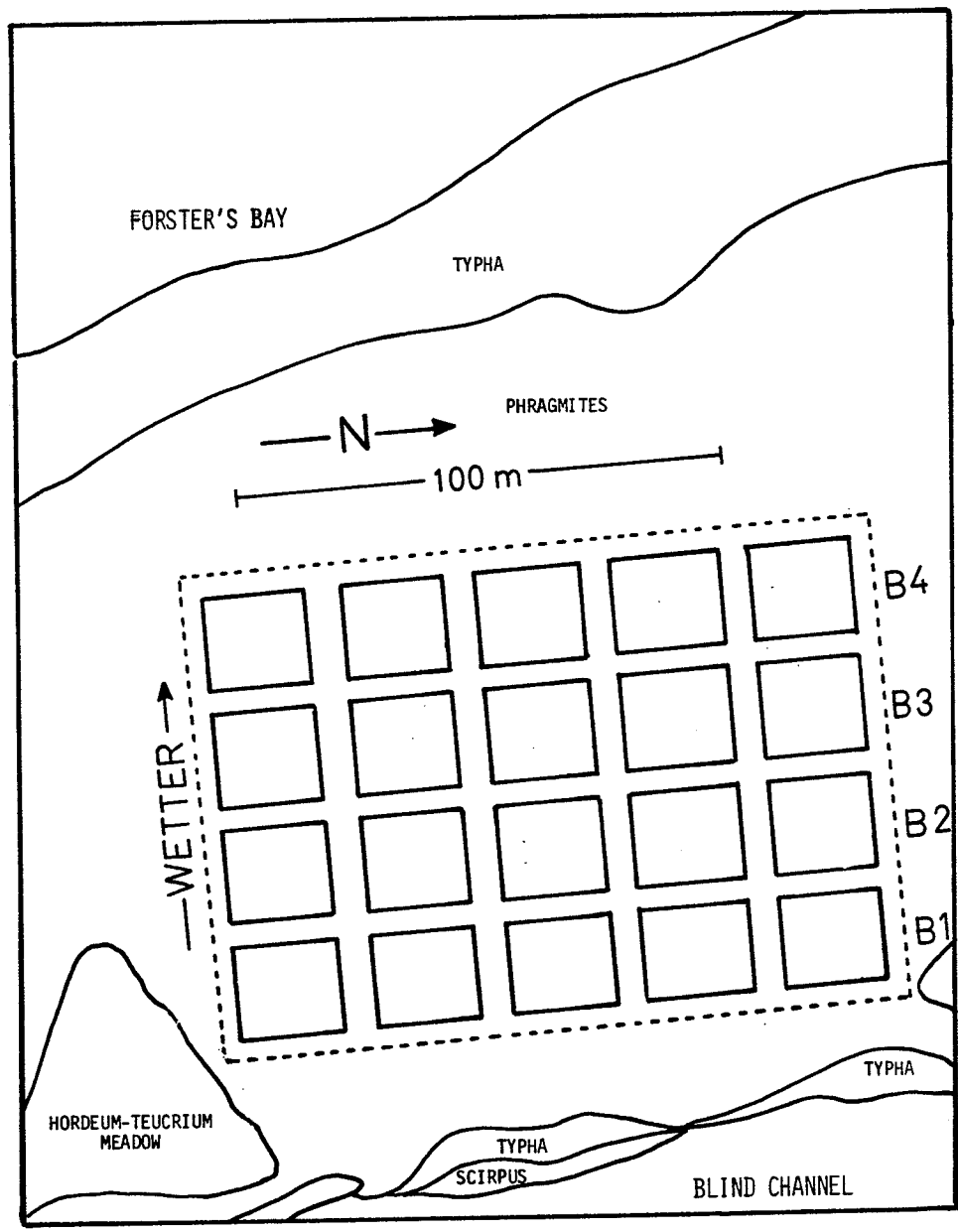
(1) Formerly named Phragmites communis Trin. Taxonomic change according to Clayton (1968).

1.2 METHODS

In late July 1979 part of one dense P. australis stand was divided into a grid of twenty, 400 m² 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 m² (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).

(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.



1.3 RESULTS

1.3.1 P. australis

Mean biomass for the stand was 812 ± 38.4 g/m², which was less than the mass of its litter (984 ± 32.8 g/m²). Mean biomass differed significantly ($\alpha = .01$) 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 ($\alpha = .05$) between water levels, declining from the first (driest) row of plots to the last (wettest) row.

Mean shoot density was 78.3 ± 2.9 shoots/m². There was a consistent trend where density increased with increasing moisture ($\alpha = .01$). Flowering density averaged 31.2 ± 2.4 shoots/m², and varied significantly between moisture levels ($\alpha = .001$). 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 ± 2.4 cm and varied significantly between water levels ($\alpha = .0001$), due to a dramatic reduction in shoot height in row two. The mean number of leaves for these shoots was 13.9 ± 0.1 which did not vary significantly across water levels.

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

There were significant correlations between several of the P. australis characteristics measured (Table 1-1).

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

<u>Characteristics</u>	<u>Correlation (r)</u>	<u>Significance level</u>
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/m², which varied between moisture levels ($\alpha = .01$). 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/m² and a density of 19.5 \pm 2.2 shoots/m². The density of this species varied across the water level gradient ($\alpha = .0001$). 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 ($r = -.252, \alpha = .05$) but was not significantly related to its biomass. There was a stronger relationship between substorey biomass and the weight of P. australis litter ($r = -.548, \alpha = .0001$).

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

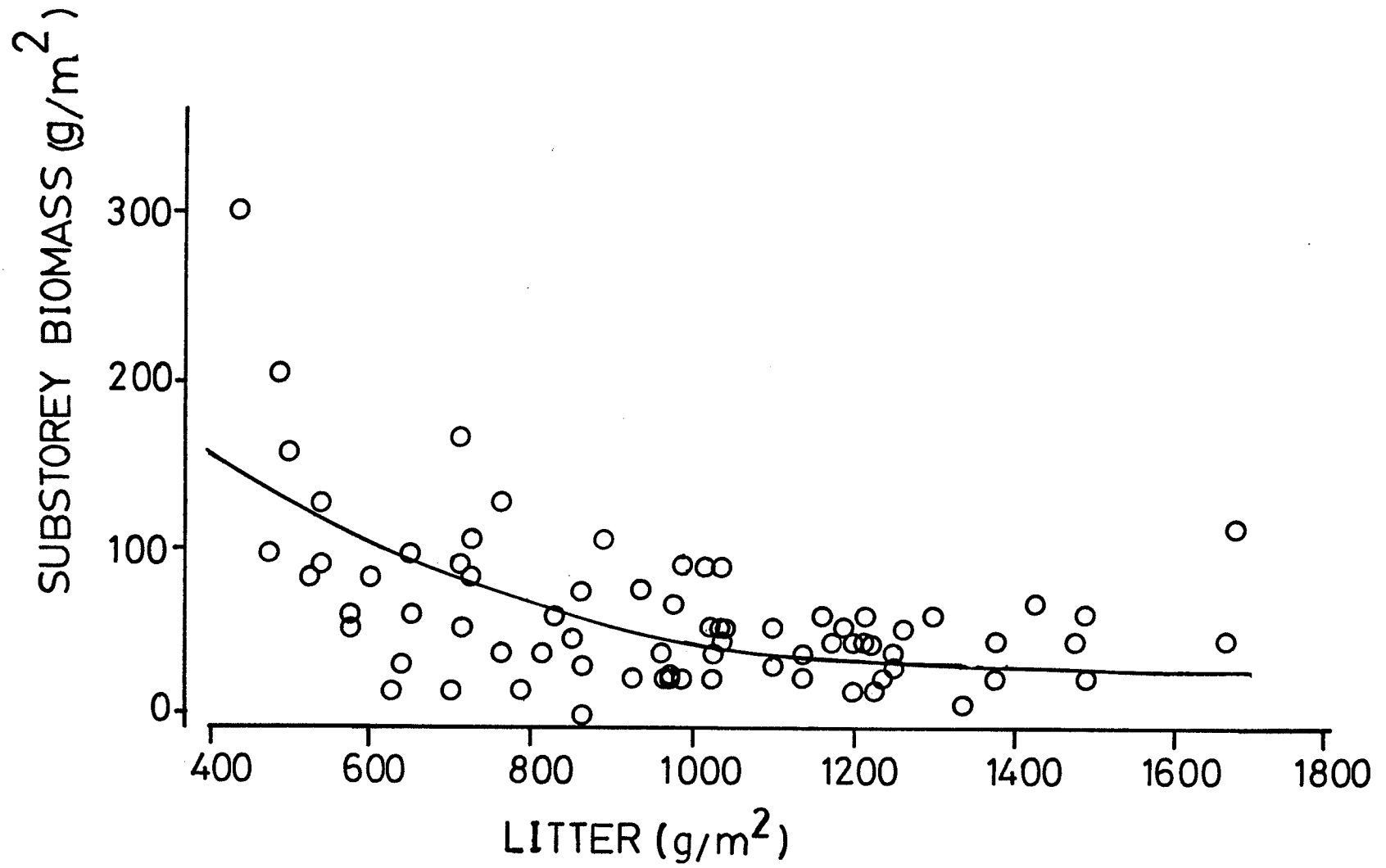
MOISTURE LEVEL

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

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

* 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 Kowalczewski 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 peninsula 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 ($r = .329, \alpha = .05$). 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.