

**First-year Regrowth of Three Marsh Plant Communities  
After Fall and Spring Fires  
in the Delta Marsh, Manitoba.**

by

Jason Andrew Greenall

A thesis presented to the University of Manitoba in partial fulfillment of the requirements  
for the Master of Science degree in the Faculty of Graduate Studies

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AFTER FALL AND SPRING FIRES IN THE DELTA MARSH, MANITOBA

BY

JASON ANDREW GREENALL

**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

This study examined the effects of fall (1990) and spring (1991) burns on neighbouring marsh plant communities dominated by *Typha x glauca*, *Phragmites australis*, or *Scolochloa festucacea* in the Delta Marsh, Manitoba. The focus was on plant regrowth in the first post-burn season.

Two study plots 25 m x 25 m were laid out in areas where *Typha*, *Phragmites*, or *Scolochloa* had previously been dominant in fall-burned, spring-burned and unburned sites. Within these plots, subplots were randomly selected and the regrowth, in terms of shoot height, density, flowering, and aboveground biomass of the dominant species was monitored. The composition and aboveground biomass of the understorey was also monitored. In all plots, the position of the water table was determined and soil samples collected for moisture, organic, conductivity and pH measurements. Temperature and humidity were recorded from May to August in fall-burned and unburned *Phragmites* stands.

In *Typha* communities, regrowth began earliest in plots that had been burned, but by the end of the season unburned plots produced the tallest shoots. Mean shoot density was significantly higher in fall-burned plots (108 shoots·m<sup>-2</sup>) than in other plots, which had densities of approximately 55 shoots·m<sup>-2</sup>. Aboveground biomass of *Typha* was lowest after fall burning, intermediate in spring burned plots and highest in unburned plots. Mean biomass of *Typha* shoots was 6.5 g·shoot<sup>-1</sup> in fall-burned plots, compared with 13 to 16 g·shoot<sup>-1</sup> in the other plots. Understorey species were sparse in *Typha* study plots, and were a small component of the total community biomass. Significant differences in water levels were observed between burn treatments.

In *Phragmites* communities, regrowth also began earlier in burned plots than in unburned plots. Mean shoot density in fall-burned plots (126 and 139 shoots·m<sup>-2</sup>) was significantly higher than in unburned plots with 50 shoots·m<sup>-2</sup>, or in spring-burned plots

with 80 shoots $\cdot$ m<sup>-2</sup>. Aboveground biomass was also higher after both fall and spring burns than in unburned plots. Fall-burned plots had lower species richness and understorey biomass than either spring-burned or unburned plots. Both fall-burned and spring-burned *Phragmites* communities exhibited increased production over unburned areas. Significant differences in water levels, both within and between burn treatments, appeared to affect a number of regrowth parameters in this community.

In *Scolochloa* communities, there were no significant differences between burn treatments because there was significant variability within the fall-burned treatment for all measured vegetation parameters. However, *Scolochloa* shoot density was higher in spring-burned plots than in fall-burned plots, which tended to have shoot densities similar to unburned plots, but produced smaller shoots. Spring-burned plots had higher mean aboveground biomass (860 g $\cdot$ m<sup>-2</sup>) than unburned plots with 750 g $\cdot$ m<sup>-2</sup>. Mean biomass in fall-burned plots ranged from 300 to 815 g $\cdot$ m<sup>-2</sup>. Both fall and spring burning led to increases in the mean species richness and aboveground biomass of understorey species. High soil conductivity in fall-burned plots appeared to affect the vegetation, with poor performance of *Scolochloa* and high abundance *Atriplex patula*.

Vegetation regrowth in the three communities did not occur in a consistent or predictable manner.

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# CHAPTER 1

## INTRODUCTION AND LITERATURE REVIEW

On October 13-14, 1990 and April 12-14, 1991, accidental fires occurred in two areas of the Delta Marsh. The burned sites were separated by the Assiniboine River Diversion, a distance of approximately 400 m. Each fire burned approximately 250 hectares, and encompassed a number of marsh plant communities, dominated by *Typha x glauca* Godr., *Phragmites australis* (Cav.) Trin., or *Scolochloa festucacea* (Willd.) Link<sup>1</sup>. The timing of the burns provided an opportunity to examine first-year regrowth of these plant communities after two different burn treatments, and compare them with unburned sites. Most research into the effects of fire on wetland plant communities has focused upon only one plant community, or examines only one season of burning. The advantage of this study was the opportunity to simultaneously study the regrowth in three different plant communities after both fall and spring burns in a natural experiment (Diamond 1986).

The objective of this study was to determine the effects of fall and spring burning on regrowth of plant communities dominated by *Typha glauca*, *Phragmites australis*, or *Scolochloa festucacea* in the first post-fire growing season. The remainder of Chapter 1 is a review of the literature pertaining to the three plant communities and to the effects of fire on them. Chapter 2 describes the study site, Delta Marsh, and the burned areas being examined. The methods used for monitoring regrowth follow in Chapter 3. Chapter 4 presents the results of the study, and in Chapter 5 these are discussed and compared with other research.

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<sup>1</sup> Nomenclature follows Scoggan (1978). See Appendix 1 for complete nomenclature of plants encountered.

## **1.1 HISTORY OF FIRE IN PRAIRIE WETLANDS**

Historical evidence indicates that fire was once a common occurrence across the prairies. Ward (1968) cites accounts from the 1800's which describe fires stretching for hundreds of miles across the Red River plains, while Kantrud (1986) lists a number of accounts which specifically mention fires burning through prairie wetlands. Lightning is often responsible for starting wildfires (Wright and Bailey 1982; Thompson and Shay 1989; Kirkman and Sharitz 1994), as are humans. Aboriginal peoples once set fires intentionally both as signals and to improve success of bison hunting (Ward 1968). The arrival of European settlers in North America generally led to an era of fire suppression in many habitats (Wright and Bailey 1982).

The importance of fire as a disturbance which has shaped the natural vegetation of North America was recognized early in this century (Vogl 1967). Since that time, many researchers have examined the effects of prescribed burning on wetland vegetation for management purposes. Early studies were largely qualitative in nature, aimed at improving wildlife habitat by suppressing growth of dominant species (Vogl 1967, Schlichtemeier 1967, Ward 1968). Recently, researchers have also become interested in the effects of fire on community composition (Thompson and Shay 1989, Schmalzer et al. 1991, Cowie et al. 1992, Kirkman and Sharitz 1994), due in part to a desire to increase or maintain diversity in wetland habitats (Kirkman and Sharitz 1994). As well, there is an interest in examining how alterations in wetland disturbance regimes may affect vegetation (Mallik and Wein 1986, Turner 1987). However, despite increased interest in wetland communities as a whole, emphasis has remained on dominant wetland species because of the influence they have on other species, both before and after fire.

## 1.2 ECOLOGY OF THE DOMINANT SPECIES

Plants in prairie wetlands are positioned along a water depth gradient indicative of their tolerances to flooding (Kantrud et al. 1989). The dominant species in the three plant communities studied, *Typha glauca*, *Phragmites australis* and *Scolochloa festucacea*, are no exception. *Typha glauca* can survive in up to 100 cm of standing water (Waters and Shay 1990), but can also perform well in drawdown sites (Shay and Shay 1986). *Phragmites australis* can withstand prolonged flooding to a depth of 50 cm and drawdown to a depth of 100 cm (Shay and Shay 1986). While *Scolochloa festucacea* shares similar water depth tolerances to those of *P. australis*, it generally requires a seasonal drawdown to survive. Stands of *S. festucacea* are killed when continuously flooded from May to October (Neckles et al. 1985). Because each of these species is capable of growing under drawdown conditions, it appears that flooding episodes have determined the locations of each plant community by selectively killing species not adapted to particular water depths. Thus *T. glauca* and *P. australis* are generally found at lower elevations than *S. festucacea* because these sites would have undergone deeper and more prolonged flooding than *S. festucacea* could tolerate at some time in the past.

Each of the three species are herbaceous perennials which spread by rhizomes (Scoggan 1978). The rhizomes have a number of buds which may elongate to produce aboveground shoots. The largest buds are found at the apex of the rhizome, and may chemically suppress elongation of smaller lateral buds through apical dominance (Thompson 1982). Bud size determines basal diameter of shoots, which is in turn positively correlated with shoot height (van der Toorn and Mook 1982; Haslam 1970). Apical buds are therefore capable of producing larger shoots than lateral buds.

Once established, these species grow vegetatively and form monodominant stands, capable of suppressing invasion by other species and eliminating other species already

present (van der Valk and Davis 1980). They exhibit characteristics which make them excellent competitors, such as large storage organs, a height advantage over other species in the community, the ability to spread laterally both above and below ground, high growth rate, and the ability to respond rapidly to stress and disturbance (Grime 1979). The combined effects of these characteristics allows a high rate of resource acquisition in crowded and productive vegetation, and rapid adjustment to changes in the growing environment. These species are therefore able to outcompete the other species found in their understorey. The process by which this competition occurs is described by Keddy (1989) as competitive dominance, whereby one species suppresses another through exploitation and/or interference competition. First, the dominant species is able to lower the resources available to the subordinate, while using the resources it has exploited to produce more growth, further lowering resources available to the subordinate species. Second, the dominant species can interfere with subordinates, leaving more resources available to the dominant to increase its interference over them.

Among the most important features that the dominant plant species in this study possess is their ability to produce large amounts of biomass. Below ground level, the high density of rhizomes produced by the dominant species interferes with the establishment of other species, and allows the dominant species to exploit resources at the expense of other species. Above ground level, high productivity allows greater exploitation of light by shading the understorey species. Furthermore, the slow decomposition of this biomass, typical of wet environments, results in large buildups of plant litter and standing dead material, which may persist for several years before being decomposed. In *Phragmites australis* communities, the mass of dead plant material may be greater than the mass of living canes (Thompson and Shay 1985). Eventually, the buildup of plant material can also have shading and crowding effects on the dominant species themselves, as they must expend larger amounts of stored reserves in spring before shoots can emerge from the litter and begin to undergo photosynthesis (Graneli 1989).

Accumulations of dead plant material by the dominant marsh species significantly reduce understorey species richness and abundance (Thompson and Shay 1989). Litter buildups may inhibit seedling establishment in several ways (van der Valk 1986). Mats of plant litter may be so thick that they prevent seeds from reaching the soil surface after their dispersal. If seeds do reach the surface, they may be inhibited from germinating. Many seeds require intense light, or fluctuations in temperature to germinate, both of which are reduced by the shade the plant litter produces. If seeds successfully germinate, shade may inhibit seedling growth sufficiently to cause their death. Allelopathy has also been mentioned as a possible factor in the inhibition of seed germination in wetlands, through a release of compounds found in dead plant material. McNaughton (1968) reported an allelopathic effect using *Typha latifolia* L. leaf extracts, but these results could not be duplicated by other researchers (Grace 1983).

### **1.3 THE ROLE OF DISTURBANCE IN WETLANDS**

#### **Fluctuating water levels**

In prairie wetlands, periodic disturbance is an important process in renewing species and habitat diversity by reducing the dominance of a small number of species (van der Valk 1981). The most important type of natural disturbance in these systems is fluctuating water levels. Cycles of flooding and drawdown normally occur every 5 to 20 years (van der Valk and Davis 1980) as a result of unstable precipitation patterns (Adams 1988). Prolonged flooding may kill all emergent vegetation, and the subsequent drawdown provides an opportunity for seed germination on exposed mudflats (van der Valk 1981). Species colonizing mudflats may include the former dominants, as well as a number of ruderal species adapted to exploiting disturbed environments. Ruderals are generally annuals or short-lived perennials which complete their reproductive cycles rapidly

before being eliminated by another change in the growing environment (Grime 1979). A return to normal water levels will eliminate species which are unable to tolerate the new growing conditions, and over time, a number of highly competitive species become dominant, eliminating other species through modifications to their environment (van der Valk and Davis 1980). A period of prolonged flooding is then required to renew this cycle of vegetation change.

## **Fire**

In some respects, fire is analogous to a period of flooding followed by drawdown, in that both may kill off vegetation and expose the soil surface, providing a substrate and suitable conditions for seed germination. However, while prolonged flooding may result in the elimination of entire plant communities, fire rarely does. Kantrud (1986) states that little change in marsh community composition occurs when perennials with meristems at or below ground level are burned in the dormant season. Even summer burning is unable to eradicate all species (Thompson and Shay 1989). Regrowth of surviving species and invasion by new species after fire is, therefore, more difficult to predict than the colonization after flooding and drawdown (Smith and Kadlec 1985b).

### **1.4 EFFECTS OF FIRE ON WETLAND PLANT COMMUNITIES**

Differences in vegetation regrowth between spring and fall burns are due not only to the direct effects of burning, but also to the indirect effects that result from the complex interactions of fire with the environment. The direct effects of burning are the combustion of fuel and the production of heat and ash. Thompson and Shay (1985) reported temperatures of 250 to 500 °C at the soil surface when burning *Phragmites australis*. However, Wright and Bailey (1982) state that for the type of fuels found in marshes, temperatures below the soil surface generally do not exceed 80°C, do not rise appreciably

beyond a depth of 10 mm, and do not persist for more than two to four minutes. Under these conditions, temperatures should have little effect on soil organic matter, microbial populations, or buried seeds (Wright and Bailey 1982). It thus seems unlikely that high temperatures are responsible for all burn effects.

There are many potential indirect effects attributable to environmental changes that may play a role in vegetation regrowth following fire. Most of these changes may be traced back to the removal of plant material by fire. Burning removes the insulating layer of plant litter on the soil surface (van der Valk 1986). This is especially important in the fall. While litter has insulation value, it also causes snow to accumulate, which helps to prevent frost damage to rhizomes. Thompson and Shay (1985) found that fall-burned stands of *P. australis* accumulated one third as much snow as unburned stands, making fall-burned stands susceptible to earlier and deeper ground frosts. In contrast, spring-burned and unburned stands are insulated by plant litter and deeper snow cover, which protects them from frost damage. Spring fires remove the insulating layer of plant litter, but by that time temperatures are often mild enough that frost damage to rhizomes is unlikely.

The effects of litter removal on soil temperature continue to be important in the early part of the growing season. The soil surface in burned areas warms more rapidly than in unburned areas because it is not being shaded by plant litter, and because fire leaves behind a blackened surface (Smith 1973). The dark surface absorbs more radiant solar energy than unburned areas covered with reflective plant material, resulting in higher soil and water temperatures in early spring (Diirro 1982). In early spring, fall-burned sites may be warmer than spring-burned sites because the reduced accumulations of snow melt faster and expose the soil surface earlier to the warming effects of the sun.

Litter removal and its influence on microclimate may play an important role in determining the water levels found within different treatments, especially fall burns. Reduced snow accumulation after fall burns leads to decreased spring runoff (Kantrud et

al. 1989). Spring-burned sites may accumulate as much snow as unburned areas, but they are influenced by environmental changes brought about by burning such as more rapid warming of the soil surface.

Combustion of aboveground biomass can have several effects on soil properties, and in turn, on the vegetation growing after fire. Fire essentially consumes organic matter, usually a slow process of litter decomposition (Wright and Bailey 1982). Fire results in the deposition of partially burned plant material and ash on the soil surface. Partially burned plant material may be incorporated into the soil after fire, resulting in increased soil organic matter (Schmalzer and Hinkle 1992). Alternatively, decreases in soil organic matter have been observed after burning due to increased rates of biological activity by soil fauna (Wright and Bailey 1982). The ash contains a number of basic cations (Ca, Mg and K), and anions (phosphates, sulphates, oxides and carbonates) left behind after organic molecules are oxidized. These ions may be available for immediate uptake by plants, or incorporation into the soil. If incorporated into the soil, the additional ions increase soil electrical conductivity (Schmalzer and Hinkle 1992). Basic cations found in the ash generally increase soil pH after burning (Schmalzer and Hinkle 1992). Rivard and Woodard (1989) found that addition of *Typha latifolia* ash increased the pH of leaf extract solutions by 2-3 pH units.

Removal of plant litter is a key factor in the vegetation changes which occur after burning. Burning provides understory species with the opportunity to become established in previously unsuitable sites (van der Valk 1986). Removal of litter exposes the soil surface to bright sunlight, so that at the beginning of the first post-fire growing season, soils warm more rapidly and provide favourable conditions for seed bank germination, resulting in increased species diversity (Thompson and Shay 1989). The increased light intensity can also have profound effects on the dominant marsh species. Thompson and Shay (1985) state that tillering of these species increases with light intensity at the soil

surface, resulting in higher shoot densities. Thus, litter removal by fire may be able to stimulate growth of a more diverse and productive habitat.

Experiments dealing with the effects of fire on marsh vegetation have been conducted in many areas. Mallik and Wein (1986) studied seasonal burning and flooding treatments in a brackish New Brunswick marsh. Smith and Kadlec (1985a,b,c) examined various effects of burning in a Great Salt Lake marsh. The effects of burning on *Phragmites australis* have been documented in the U. K. (Cowie et al. 1992) and in the Netherlands (van der Toorn and Mook 1982, Mook and van der Toorn 1982). Turner (1987, 1988) performed a burn study in a *Spartina alterniflora* Loisel. marsh in Georgia. Fall burning of *Spartina bakeri* Merr. and *Juncus roemerianus* Scheele marshes in Florida was studied intensively (Schmalzer et al. 1991, Schmalzer and Hinkle 1992, 1993). However, many of these studies were performed where climate, salinity, hydrology, and species composition differed from the prairies, making comparison with prairie marshes difficult. The number of burn studies in prairie wetlands is small, but will be the focus where possible of the following review of the effects of fire on wetland vegetation.

Fire is often used in an attempt to reduce density of *Typha* spp., with results varying from ineffective to very successful (Kantrud 1986). Mallik and Wein (1986) found that *Typha* spp. cover, shoot density, height, and basal diameter all increased following spring, summer, and autumn burns in areas flooded to a 50 cm depth, but decreased following similar fires in drained areas. Ball (1990) reported that winter burning followed by spring flooding of *Typha* spp. in Ontario resulted in reduced shoot density and shoot height, as well as a complete lack of flowering shoots. Where burning and flooding left no dead standing shoots above the water, oxygen could not reach the rhizomes via the air spaces in leaves, and rhizomes were killed. If, however, even a small part of a plant remained above water, sufficient oxygen could reach the rhizomes to allow some shoots to emerge and grow.

Burning of *Phragmites australis* stands in spring and summer by Ward (1968) reduced its cover, increased its quality as waterfowl habitat, and removed invading shrubs from the dry parts of the marsh. Schlichtemeier (1967) removed large amounts of litter from *P. australis* stands in Nebraska with a winter burn. He claimed an 85% reduction in density, but it is unclear if dead standing canes were included in the density counts of unburned stands. van der Toorn and Mook (1982) studied the effects of spring burning on *P. australis* stands in the Netherlands. Death of apical buds on rhizomes due to fire or frost damage released subsidiary buds from apical dominance, leading to increased shoot density and decreased shoot size. These findings were similar to those reported by Cowie et al. (1992) after spring burning of a *P. australis* marsh in the U. K.

Thompson and Shay (1985, 1989) experimented with burns of *P. australis* in spring, summer and fall. They found that shoot densities increased greatly following all fires. Compared with controls, aboveground biomass was higher after spring and fall burns, but lower after a summer burn. In all burn treatments, mean shoot biomass was less than on the controls, due to the high shoot densities. Sampling over several years revealed that spring, summer, and fall burns all affected community productivity for as long as four years (Shay et al. 1987).

In contrast to the use of fire to suppress *Typha* and *Phragmites* communities, burning of *Scolochloa festucacea* stands is often used to increase production for haying. Fall burning led to increased production of *S. festucacea* in North Dakota (Smith 1973). Diiro (1982) reported that fall burning resulted in significant increases in shoot density and aboveground biomass, and that spring burning led to increases in shoot height and shoot density, compared with unburned controls. However, these increases in *S. festucacea* yield after fire were dependent upon spring flooding (Neckles et al. 1985).

The effects of fire on marsh plant communities vary from study to study. Vogl (1969) commented that marsh burning could have the desired effect of killing invading

shrubs in wetlands, but could also produce undesirable effects by allowing invasion of *Urtica dioica* and other weedy species. Mallik and Wein (1986) reported no change in species richness after any combinations of draining or flooding with seasonal burning treatments in a New Brunswick *Typha* marsh, although species composition changed somewhat in burned areas. Thompson and Shay (1989) reported increases in abundance of ruderal species such as *Sonchus arvensis*, *Atriplex patula*, and *Cirsium arvense* after burning stands of *P. australis* at Delta Marsh. Abundance of non-ruderal species (*Mentha arvensis*, *Teucrium occidentale* and *Urtica dioica*) increased after spring burning, but not after fall burning. Despite these changes, species richness and diversity were unchanged after fall and spring burning (Thompson and Shay 1989). These results differed from those of Cowie et al. (1992), who found increased species richness and diversity in a burned *Phragmites* marsh in the U. K.

Much of the variability in results between different burn studies is due to the different growing conditions found in each experiment (Kantrud 1986). Studies comparing fall and spring burn treatments in a prairie marsh are uncommon in the literature, and none have focused upon regrowth in three plant communities in the first season after a fall and spring burn. In some cases, the effects of seasonal burning were examined in only one plant community (Mallik and Wein 1986, Thompson and Shay 1985, 1989, Diiro 1982). Other studies examined the effects of only one season of burning on a plant community (Cowie et al. 1992, Ball 1990, van der Toorn and Mook 1982, Mook and van der Toorn 1982). In addition, differences in species composition, timing of the burn, and environmental conditions between studies may all have different effects on post-fire regrowth. Comparisons between studies which vary in this manner make it difficult to predict burn effects if the prevailing conditions are not the same. Thus, the value of this research is the information provided by the combination of different burn treatments and plant communities studied simultaneously in one setting.

## **CHAPTER 2 STUDY SITES**

The Delta Marsh is an approximately 15000 hectare freshwater wetland complex located adjacent to Lake Manitoba in south-central Manitoba (Shay et al. 1987). The marsh consists of a series of shallow bays of open water connected by narrow channels (Figure 2.1.1). Marsh plant communities surround the open water in zones, roughly based upon water depth.

### **2.1 PHYSICAL SETTING**

#### **Geology**

The Delta Marsh area is underlain by a sequence of Devonian, Silurian, and Ordovician bedrock (Last 1984). This bedrock is overlain by Quaternary sediments up to 100 m thick. These sediments are of glacial, fluvial, and lacustrine origin and have been strongly influenced by glacial Lake Agassiz. Teller and Last (1981) summarize the glacial and post-glacial history of Lake Manitoba. The area currently covered by Lake Manitoba's South Basin was covered with ice until approximately 12000 years before present (BP). When the glaciers retreated, the area was covered by the meltwater of Lake Agassiz. From 4500 to 2000 years BP the Assiniboine River diverted its flow into the western end of the lake. The river carried alluvial sediment which formed a sandy delta, subsequently redistributed by wave action to form the barrier ridge along the south shore of the lake.

Sproule (1972) described the post-glacial history of Delta Marsh using sediment cores. The macrofossils and pollen he found revealed that marsh conditions have existed in the area for approximately 2400 years, although fluctuations in pollen composition

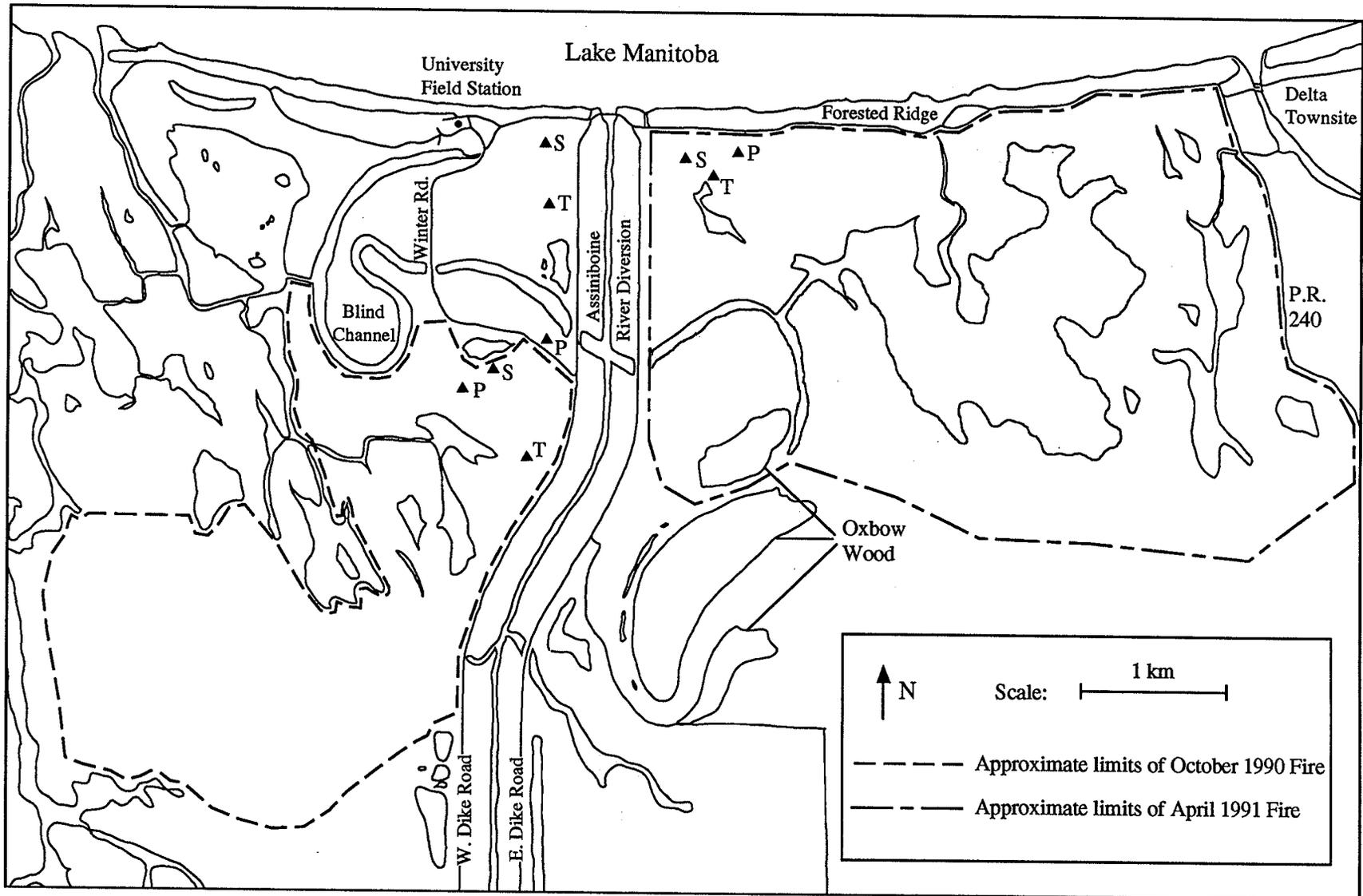


Figure 2.1.1. Location of burned areas and study sites in the Delta Marsh, Manitoba. T=*Typha glauca* study sites; P=*Phragmites australis* study sites; S=*Scolochloa festucacea* study sites.

indicated that changing water levels have resulted in alternating periods where either upland or wetland vegetation dominated the area.

## **Geography**

The barrier ridge separating Delta Marsh from Lake Manitoba has several breeches which allow direct exchange of water between lake and marsh (Last 1984). It is the proximity of the marsh and lake, as well as these connections, which tie the water regime of the marsh to that of the lake and cause a strong correlation between marsh and lake water levels (de Geus 1987).

Last (1984) outlines the hydrology of Lake Manitoba and its drainage basin. Lake Manitoba has a surface area of 4706 km<sup>2</sup>, making it the third largest lake in Manitoba. It has a maximum depth of 6.3 m and a mean depth of 4.5 m. The drainage basin of Lake Manitoba covers an area of over 80000 km<sup>2</sup>. The lake's main inflows are the Assiniboine River Diversion and the Whitemud River at the south end, and Lake Winnipegosis at the north end. The Fairford River, at the northern end of the lake, is the sole outflow. A control structure built at this outflow regulates the discharge from Lake Manitoba to maintain lake levels between 247.3 and 247.9 m above sea level.

## **Soils**

Soils of the Delta Marsh have been classified broadly as undifferentiated muck and peat soils (Ehrlich et al. 1957). Currently, soils are poorly developed Regosols, owing to their immaturity. Parent material is lacustrine or alluvial in origin, ranging in texture from sandy loam to silty clay. Near the dune ridge, larger amounts of sand are often found where high lake levels once allowed water to flow over the ridge, carrying sand with it (Sproule 1972). Prominent rust-coloured mottles in the soil profiles indicate anaerobic conditions during all or part of the year as a result of being saturated with water. Organic

matter is accumulating at the soil surface due to the high rates of production and the low rates of decomposition found under anaerobic conditions. Over time, these conditions will result in the formation of Gleysolic and Humic Gleysolic soils (Agriculture Canada Expert Committee on Soil Survey 1987).

## Climate

The climate of the Delta Marsh area is classed as cool to mild continental (Weir 1960). The area receives an average of 120 frost-free days. Temperature measurements from 1967-1990 at the Delta meteorological station average -18.1 °C in January, 19.2 °C in July, and 1.9 °C annually (Environment Canada 1993). Precipitation averages 515 mm per year, 74% of which falls as rain between April and October. Evaporation exceeds precipitation throughout the summer months.

## Vegetation

The vegetation of the Delta Marsh was described by Love and Love (1954). They stated that the marsh was made up of mostly *Phragmites australis*, broken up only by open water and patches of *Scolochloa festucacea*. *Scirpus* spp. and *Typha latifolia* were found in small amounts along the edges of open water. They stated that *Typha angustifolia* was absent from that part of North America.

Walker (1965) examined the vegetation changes which occurred as a result of falling water levels from 1959 to 1961. The colonizing vegetation formed either a zoned or a mosaic pattern that was determined by water levels and soil salinity. By 1961, *Scolochloa festucacea* was the dominant species in most drawn down sites. *Phragmites australis* had also formed extensive stands by that time.

By the 1980's, de Geus (1987) reported a considerable change in the vegetation composition of Delta Marsh. Regulation of marsh water levels beginning in 1961 resulted

in an overall change from a *Phragmites*-dominated marsh to a *Typha*-dominated marsh. This change has occurred in conjunction with the appearance of the hybrid cattail, *Typha x glauca*, in the marsh. This species is capable of expanding aggressively, from seed or by vegetative reproduction, over wider ranges of water depths than either of the two parental species *T. latifolia* and *T. angustifolia* (Waters and Shay 1992). *T. glauca* now makes up the majority of cattail stands in Delta Marsh (Waters and Shay 1990), and was the only species of cattail encountered in this study.

### **Recent history**

Historically, water levels in the Delta Marsh have fluctuated over a range greater than 2.2 m (de Geus 1987). These fluctuations were responsible for perpetuating a cycle of vegetation change. During prolonged periods of high water, as occurred in the 1950's, emergent macrophytes died back because their water depth tolerance was exceeded. When water levels receded in the early 1960's, exposed mudflats and areas of shallow water became the sites of seedbank release. Eventually, emergent macrophytes became the dominant species through shading and crowding effects. Normally, a period of flooding would eliminate the dominant species and allow recolonization when water receded. Alternating periods of flooding and drawdown thus served to maintain the marsh ecosystem in a highly productive state by causing a cycle of vegetation change. However, since 1961, the regulation of water levels in Lake Manitoba has altered the marsh ecosystem. Water levels are now held within a range of 0.6 m (de Geus 1987), insufficient for a cycle of dynamic vegetation change to occur. Because water levels have not exceeded the tolerance of emergent macrophytes for the last thirty years, there has been no substantial dieback of vegetation. As a result, stands of macrophytes have continuously invaded shallow marsh shores. The marsh is becoming filled with vegetation at the expense of open water. An increase in the width of the terrestrial vegetation along the dune ridge

(Kenkel 1986) and invasion of trees along the southern end of the marsh are further evidence of drying out in the marsh.

## 2.2 STUDY SITE DESCRIPTIONS

### The October 1990 burn

The first accidental fire began in late afternoon on 13 October, and died down in the early morning hours of 14 October, although it continued to smolder for several more days (R. Mead 1993, pers. comm.). The fire encompassed an area of roughly 250 hectares. It is speculated that a discarded cigarette from a vehicle driving on West Dike Road was responsible for starting the fire. The burn moved west, from the West Dike Road into the marsh, and north, from the boundary of Field Station property toward the winter road and Blind Channel (Figure 2.1.1). The weather was warmer than normal at the time of the fire, with a high of 16 °C on 13 October, and an overnight low of -0.5 °C (Goldsborough 1991). Initially, winds were westerly (19 km/h at 1600 hrs), but eventually shifted, first to southerly (9.5 km/h at 2000 hrs), then to northeasterly (5.5 km/h at 2200 hrs), then back to westerly (11 km/h at 0400 hrs). The fire alternately burned with and against the wind throughout the evening. Relative humidity ranged from a low of 26% at 1600 hrs on 13 October to a high of 94% at 0600 hrs on 14 October. There was a trace of precipitation (0.4 mm) on 13 October.

The dryness of plant litter and standing dead material in the marsh at the time of the fire resulted in an almost complete removal of dead vegetation. With the exception of a few charred shoots of *T. glauca*, all plant material was burned to the soil surface. The surface was blackened, but it did not appear that the fire burned the upper organic portion of the soil.

## **The April 1991 burn**

The second accidental fire began on the afternoon of 12 April, and continued until early morning on 14 April (R. Mead 1993, pers. comm.), again covering approximately 250 hectares. A cottage owner burning garbage is believed responsible for starting the fire. The burn moved west, from Provincial Road 240 near the Delta townsite, to the East Dike Road, and south, from the forested ridge along the lake to Oxbow Woods and the Blind Channel (Figure 2.1.1). Air temperatures ranged from highs of 7.5 °C and 13.0 °C on 12 and 13 April respectively, to an overnight low of -5.0 °C (Goldsborough 1992). Initially, winds were westerly (19 km/h at 1600 hrs), but shifted first to southerly (9.5 km/h at 2000 hrs), then to northeasterly (5.5 km/h at 2200 hrs). The fire was thus burning with the wind throughout the evening. Relative humidity was 73% at 1600 hrs on 12 April when the fire began, and ranged from a low of 27% to a high of 100% over the next two days. Rainfall of 6 mm fell on 14 April.

The wetter conditions found in the marsh immediately after spring thaw left small patches of unburned standing vegetation throughout the burned area, presumably where the dead plant debris was too wet to ignite as the fire moved past. More debris remained unburned on the surface of the soil than in the fall burn. It appeared that in these places, water levels were above the soil surface at the time of the fire. Later, when water levels dropped below the surface this debris was left behind as evidence of the wet conditions at the time of the fire.

## **The unburned sites**

Plant communities which had not been burned were sampled from a location north of the Winter Road and west of the West Dike Road (Figure 2.1.1). Sampling sites from the two burn treatments and the unburned control were thus separated by no more than 2 km.

Unburned sites contained an abundance of dead plant material. Dead *Typha glauca* shoots were up to 1 m high in places. In *Phragmites* communities, previous years' canes stood as high as 2 m, and litter from understorey species was approximately 0.5 m deep. *Scolochloa festucacea* formed dense tangled mats of plant litter 0.5 m high, or laid flat 0.15m thick on the soil surface.

## CHAPTER 3 METHODS

### 3.1 SITE SELECTION

Study sites were chosen in early May to allow vegetation sampling to begin as early as possible in the growing season. A preliminary survey showed that the dominant plant species of each plant community could be recognized either by the debris which remained after the fire, by the litter and standing dead in unburned areas, or by the new shoots which had begun to emerge. Study sites within chosen plant communities were selected based upon an adequate stand area to permit the establishment of study plots, their apparently uniform topography, and similarity of water levels.

### 3.2 SAMPLING DESIGN

Three plant communities were chosen for study, each dominated by either *Typha glauca*, *Phragmites australis*, or *Scolochloa festucacea*. These three species have different tolerances to water depth and flooding regime (Squires and van der Valk 1992) and thus show little overlap in their distribution. It was therefore relatively easy to choose sites that contained monodominant stands of the desired species. Study sites were selected in fall-burned and spring-burned areas, as well as an unburned area acting as a control.

Two study plots, each 25 m x 25 m, were staked out in each burn treatment and plant community (Figure 3.2.1). Plots were divided into 5 m x 5 m subplots, producing five 'columns' with five subplots in each. Subplots were numbered using a coordinate system, with the origin in the northeast corner of the plot. Ten subplots were used to sample vegetation using a stratified random design, where two subplots were selected randomly from each of the five columns of the study plot. Each of the ten chosen subplots

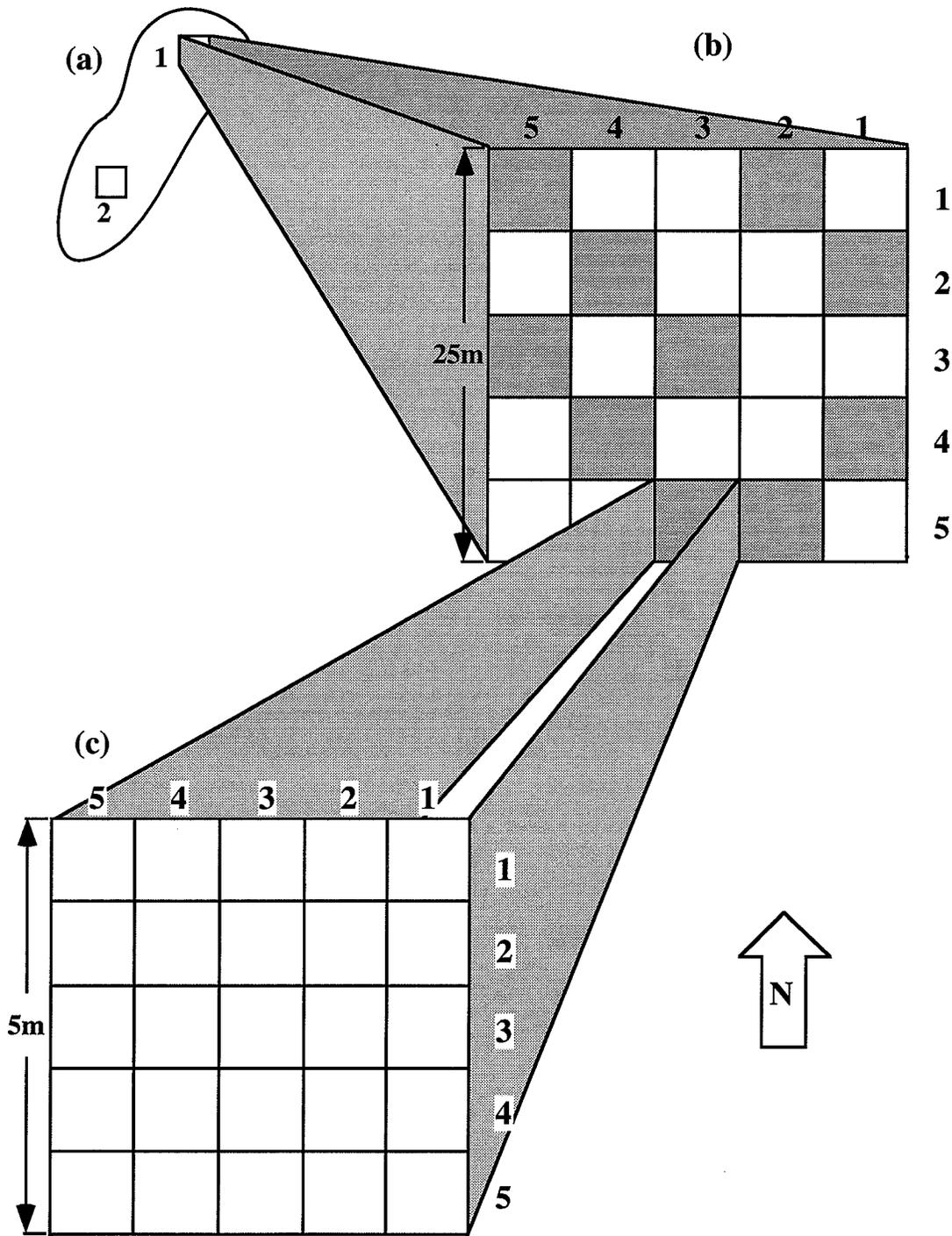


Figure 3.2.1. Layout of sample plots. (a) Replicate study plots, located within each plant community and burn treatment. (b) Detail of a 25 m x 25 m study plot, divided into 5 m x 5 m subplots. Subplots were numbered beginning in the northeast corner. Shading represents one possible combination of randomly selected subplots used for sampling. (c) Detail of a subplot, divided into a grid of 25 squares. Numbering in subplots was identical to that in the study plots.

were divided into 25 1 m x 1 m squares, again numbered with a coordinate system. Depending upon the sample size used (Section 3.3 defines sample sizes and quadrat sizes used), a number of squares were randomly selected for quadrat sampling (for sample size  $n=10$ , one square was chosen per subplot; for  $n=40$ , four squares were chosen). Quadrats were then positioned at the southwest corner of each square. After plots were established and shoot density was sampled within them in May, they were not entered until end-of-season sampling was performed, to prevent trampling effects. As plots were being laid out, four points were selected at random distances (up to 15 m) from each other outside the plots, and their positions marked with a stake. The five shoots of the dominant species which emerged closest to each stake were tagged, and their height was measured periodically throughout the season.

Preliminary sampling was undertaken to determine optimum sample sizes. Using the mean and standard deviation of the preliminary samples, the minimum sample size necessary to produce 95% confidence in the results was calculated (Eckblad 1991). Different quadrat sizes were also used during preliminary sampling to choose the quadrat size which could be used most rapidly, but would not result in excessive sample variability. The size and density of the plants in each community played an important role in the ultimate choice. *Typha glauca* and *Phragmites australis*, as well as their understorey species, were larger and less dense than *Scolochloa festucacea* and its understorey species. Larger quadrats could be used in *Typha* and *Phragmites* communities to reduce sample variability, without greatly increasing sampling time. In *Scolochloa* communities, the high densities of plants meant that a smaller quadrat was necessary for expedience, but larger sample sizes were used to prevent excessive variability.

In fall-burned *Scolochloa* communities, it became evident early in the growing season during shoot density and height sampling that there was significant variability in regrowth between plots F1 and F2. Consequently, a third study plot (F3) was established

in mid-June, with the hope that the variability within the fall-burned treatment could be reduced by using an additional plot.

### **3.3 VEGETATION PARAMETERS**

Vegetation sampling occurred throughout the spring and summer of 1991 (sampling dates are in Appendix 2). Sampling began in May and ended in September to allow study of regrowth over the full season.

#### **Shoot height**

At each study plot, the height of tagged shoots was measured during weekly visits from late May until July. When growth of these shoots slowed in late July, measurements were made after a two week interval, then again after three and a half weeks. Initial sample sizes were 20 shoots per study plot. However, any shoots that died during the season were excluded from all calculations.

Shoot height of *P. australis* and *S. festucacea* was measured from ground level to the tip of the newest, unfurled leaf. Shoot height of *T. glauca* was measured to the tallest point of the shoot, either the longest leaf or the tip of the male inflorescence. Heights were measured to the nearest 0.5 cm.

#### **Shoot density**

The shoot density of the dominant species in each community was sampled at the beginning and end of the 1991 growing season. Following the layout of study plots in May, shoot densities were first sampled from mid-May to early June. The time span was due in part to the different dates when the shoots in each burn treatment began to emerge. Shoot density was sampled again at the end of the growing season in August and

September when flowering and vegetative shoots could be reported separately. In *Typha* and *Phragmites* communities, four quadrats, 0.25 m<sup>2</sup> (0.5 x 0.5 m) in size, were sampled per subplot for a total of n=40 per plot. In *Scolochloa* communities, five quadrats, each 0.0625 m<sup>2</sup> (0.25 x 0.25 m) in size, were sampled per subplot for a total of n=50 per plot. Shoot densities were reported on a shoots•m<sup>-2</sup> basis.

Because of an oversight at the time of sampling, flowering and vegetative shoots were not counted separately in unburned *Phragmites* plots. In order for comparisons of these variables to be made between the three treatments, *P. australis* shoot densities were reported from quadrats sampled for biomass (outlined below). The sample size and quadrat size differed from those given above. One 0.5 m<sup>2</sup> (0.71 x 0.71 m) quadrat was sampled from each subplot, for a total of 10 per plot.

### **Aboveground biomass**

At the end of the growing season, aboveground biomass was harvested from the three plant communities. In each quadrat sampled, all aboveground biomass produced in the 1991 season was clipped at ground level and placed in labeled paper bags. Separate bags were used for flowering and vegetative shoots of the dominant species, as well as for each understorey species. The bags were dried at 90°C for up to four days, until constant mass was reached.

The aboveground biomass of *Scolochloa* communities was harvested first, from 29 July to 2 August. In these communities, three 0.0625 m<sup>2</sup> (0.25 x 0.25 m) quadrats were harvested in each subplot, for a total of 30 per plot. The *Phragmites* communities were sampled from 12 to 20 August, and the *Typha* communities were sampled on 21 and 22 August. In both cases, one 0.5 m<sup>2</sup> (0.71 x 0.71 m) quadrat was harvested from each subplot, for a total of 10 per plot. Biomass was reported on a g•m<sup>-2</sup> basis.

### 3.4 ENVIRONMENTAL VARIABLES

#### Weather

Weather conditions before, during and after each of the two fires were compiled from University Field Station annual reports (Goldsborough 1991, 1992). Comparisons with long term means (Environment Canada 1993) were made where appropriate. Weather conditions within a fall-burned stand of *Phragmites australis* were compared with a nearby unburned stand by placing a hygrothermograph with Stevenson screen in each stand. Temperature and relative humidity were monitored there from 5 June to 15 August.

#### Soil analysis

Soil samples were collected from 9 to 25 July 1991. Ten randomly selected samples were collected from each plot. All samples were collected from the 0-20 cm depth, bagged, and stored at 4 °C until analyzed. Laboratory analysis included measurements of soil moisture, soil organic matter, electrical conductivity, and pH.

#### Moisture

A known mass of wet soil was placed in a beaker and oven-dried at 105 °C for 48 hours. The mass of dry soil was found, and used to calculate soil moisture as a percentage of dry mass (McRae 1988) as follows:

$$\% \text{ soil moisture} = \frac{\text{mass of wet soil (g)} - \text{mass of dry soil (g)}}{\text{mass of dry soil (g)}} \times 100\%$$

#### Organic matter

Soil organic matter was determined using the loss on ignition method (McRae 1988). Oven-dried soils were ground with a mortar and pestle and passed through a 2 mm

sieve. Samples of known mass were placed in ceramic crucibles and fired in a muffle furnace at 400 °C for 24 hours. After cooling, the mass of fired soil was found and used to calculate the soil organic matter as a percentage of dry mass as follows:

$$\% \text{ organic matter} = \frac{\text{mass of pre-fired soil (g)} - \text{mass of fired soil (g)}}{\text{mass of pre-fired soil}} \times 100\%$$

### **Conductivity and pH**

Measurements made using a saturation extract, or paste, have the advantage of more closely resembling field conditions, but the difficulty in mixing pastes to the same consistency is a serious drawback. Hogg and Henry (1984) found high correlations (>0.9) between electrical conductivity measurements using saturation and dilution extracts, and as the latter gives more precise and reproducible results, the dilution extract method was used.

Dilution extracts were prepared using a 1:5 soil to water ratio. Ten grams of dry, ground soil and 50 ml of distilled water were placed in 125 ml Erlenmeyer flasks and placed on a mechanical shaker for 90 minutes. The mixtures were then vacuum filtered using a Buchner funnel and Whatman Number 1 filter paper. Soil particles were discarded, and filtrate was retained for measurement. Electrical conductivity of the filtrate solution was measured using an Analytical Instrument Science™ Conductance/TDS Meter with a Radiometer™ CDC 104 platinum electrode. Using the same filtrate, soil pH was measured using a Fisher™ pH probe, Model 229.

### **Water Levels**

When the vegetation was sampled in 1991, water levels differed noticeably, either within or between treatments, in a number of plant communities. Thus, in 1992, measurements of water levels were made in each subplot where vegetation sampling had occurred the previous summer. Although these data were collected the year after the vegetation was sampled, comparisons of water levels within and between treatments could

still be made using the position of the water table as an indication of a site's relative elevation.

Since the water table in the marsh is directly related to the fluctuations in Lake Manitoba (de Geus 1987), all water level data for a given community had to be collected on a single day to allow accurate comparisons between measurements. Prior to actually taking the measurements, all subplots to be measured in a given community were visited on the same day (14 July for *Typha*, 15 July for *Phragmites*, and 16 July for *Scolochloa* communities, respectively). If the water table was below the soil surface, a small pit was dug to a depth where water began to fill the hole (if standing water was found, this was unnecessary). After a lag of at least three days to allow the water in the pits to equilibrate with the water table, the subplots were revisited (17 July for *Typha*, 20 July for *Phragmites*, and 21 July for *Scolochloa* communities, respectively). The depth of standing water (above the soil surface) was recorded as positive, while the distance from the soil surface to the surface of the water in a hole was recorded as negative. Measurements were made to the nearest 0.5 cm.

### **3.5 DATA PRESENTATION AND ANALYSIS**

Graphical presentation of most data used Tukey boxplots (Emerson and Strenio 1983). The advantage of boxplots over bar graphs is their ability to present the spread of all data points rather than just the sample mean and standard deviation. By presenting all data, the effect of any outliers in the data can be easily noted and interpreted. Outliers and extreme outliers are calculated by the computer and displayed as circles or stars, respectively, on the boxplot. If bar graphs and error bars are used, outlying points are not displayed, and in fact, can skew the results sufficiently to misrepresent the overall trend.

Boxplots also have the advantage of displaying shaded 95% confidence intervals of the mean, allowing some interpretation of statistical significance directly from the figure.

Analysis of variance was used to compare the results obtained from the two burns and the unburned control. Because of the hierarchical structure of the data (i.e. quadrats within subplots, subplots within columns, columns within plots, plots within burn treatments), it was necessary to use nested analysis of variance (Zar 1987). This test could determine whether data differed significantly between treatments and/or within treatments. The Data Desk<sup>®</sup> statistical package was used to perform these tests.

When more than one quadrat was sampled in each subplot, the values from the quadrats in each subplot were averaged to produce one value from each subplot for the analysis of variance (for instance, where  $n=40$  for shoot density sampling in *Typha* communities, four quadrats were sampled in each of the ten subplots. The four quadrats were pooled into one mean value, providing a sample of 10 density values per study plot rather than the original forty). If all quadrats were used in the analysis, the variation between individual quadrats may have been sufficiently large so as to affect significance testing at the treatment or plot level. Tukey boxplots of the data in these cases also used pooled values rather than the original data, so that easier interpretation of analysis of variance results could be obtained.

## CHAPTER 4 RESULTS

### 4.1 ENVIRONMENTAL VARIABLES

#### Weather Conditions

In the period leading up to each fire, the monthly precipitation and mean monthly temperature closely resembled the long-term means collected at the University Field Station (Figure 4.1.1). From January to September 1990, precipitation was near the 24-year average. Despite above average rainfall in June, the growing season (May to September 1990) received only 90% of normal precipitation. Mean monthly temperatures were close to normal throughout the growing season, but were slightly above average in August and September. From October 1990 to April 1991, when the second fire occurred, precipitation was slightly below average, although precipitation in March and April was slightly above average (Figure 4.1.1). Mean monthly temperatures were well above average from February to April resulting in an early spring thaw. Most of the snow had melted prior to the April fire.

The 1991 growing season was both warmer and wetter than normal (Figure 4.1.1). Above normal monthly temperatures were recorded from February to September. Precipitation was above normal from March to July. The 97 mm of rain which fell on 27 June was itself more than the 24-year average for the whole month. Precipitation from April through August was 142% of normal.

Table 4.1.1 summarizes the data collected from the hygrothermographs located in fall-burned and unburned areas of the marsh. Because only one hygrothermograph was placed in each of these treatments, these data have not been statistically analyzed. Temperatures were higher in the fall-burned site than in the unburned site, with the most

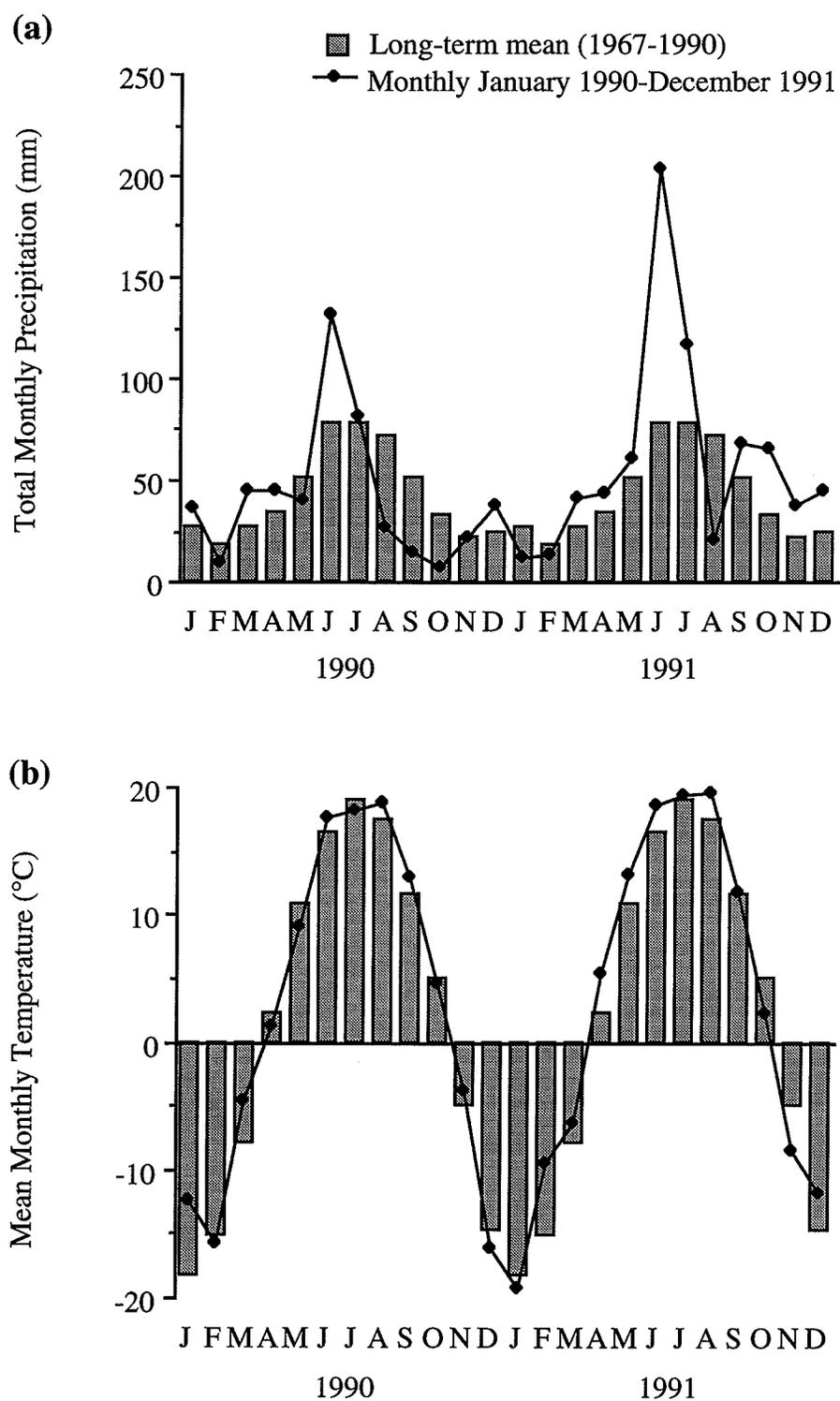


Figure 4.1.1. Mean monthly precipitation and temperature from 1967 - 1990 (shaded bars) and during 1990 and 1991 (line). (a) Total monthly precipitation (mm). (b) Mean monthly temperature (°C).

extreme difference, 1.8 °C, being between mean daily minimum temperatures. Mean daily maximum temperatures differed by only 0.6 °C between sites. Relative humidity was higher in the unburned site than the fall-burned site. Very little difference was found in maximum daily relative humidities between sites, but minimum daily relative humidity had an average difference of 4.9%.

Table 4.1.1. Summary of data collected from hygrothermographs placed in *Phragmites australis* stands from 5 June to 15 August 1991. Values are means of measurements collected each day. Mean daily temperature and relative humidity were calculated by averaging daily minima and maxima.

	Fall-burned	Unburned
Temperature (°C)		
Maximum	23.9	23.6
Minimum	12.4	10.6
Daily mean	18.2	17.1
Relative Humidity (%)		
Maximum	88.1	89.0
Minimum	51.7	56.6
Daily mean	69.9	72.8

## Water Levels and Soils

### *Typha* communities

Water levels differed significantly ( $p=0.0013$ ) between treatments (Table 4.1.2, Figure 4.1.2). Fall-burned plots were driest, with the water table approximately 8 cm lower than spring-burned plots and 16 cm lower than unburned plots.

Table 4.1.2. Water levels of *Typha glauca* study plots in July 1992. Negative values are the distance to water table below the soil surface; positive values are the depth of standing water above the surface. Values are means and standard errors (n=10).

Treatment	Plot	Water level (cm)
Fall-burned	F1	-6.0 ± 1.1
	F2	-6.7 ± 0.6
Spring-burned	S1	2.4 ± 1.2
	S2	0.8 ± 1.1
Unburned	U1	12.3 ± 1.9
	U2	10.2 ± 0.9
PTreatment		0.0013
PPlot		0.6227

Soil parameters measured in *Typha* communities were generally similar (Table 4.1.3, Figure 4.1.3). Wide variability of soil moisture measurements resulted in no statistically significant differences, although samples from spring-burned plots tended to have the highest soil moisture. Mean soil organic matter was between 40 and 50% in all plots, and did not differ significantly. Soil samples from spring-burned plots had significantly lower conductivities than soil samples from fall-burned plots ( $p=0.0163$ ). Conductivities in unburned plots varied widely, with those in plot U2 ranging from 1.6 to 10.3  $\text{mS}\cdot\text{cm}^{-1}$ , but the mean conductivities of the two unburned plots fell into an intermediate position between the two burned sites. The pH of soil dilution extracts tended to be slightly basic, although samples from plot F1 had pH as low as 6.83. Burned plots had lower soil pH than unburned plots, but only the variability in soil pH between plots F1 and F2 was significant ( $p=0.0043$ ).

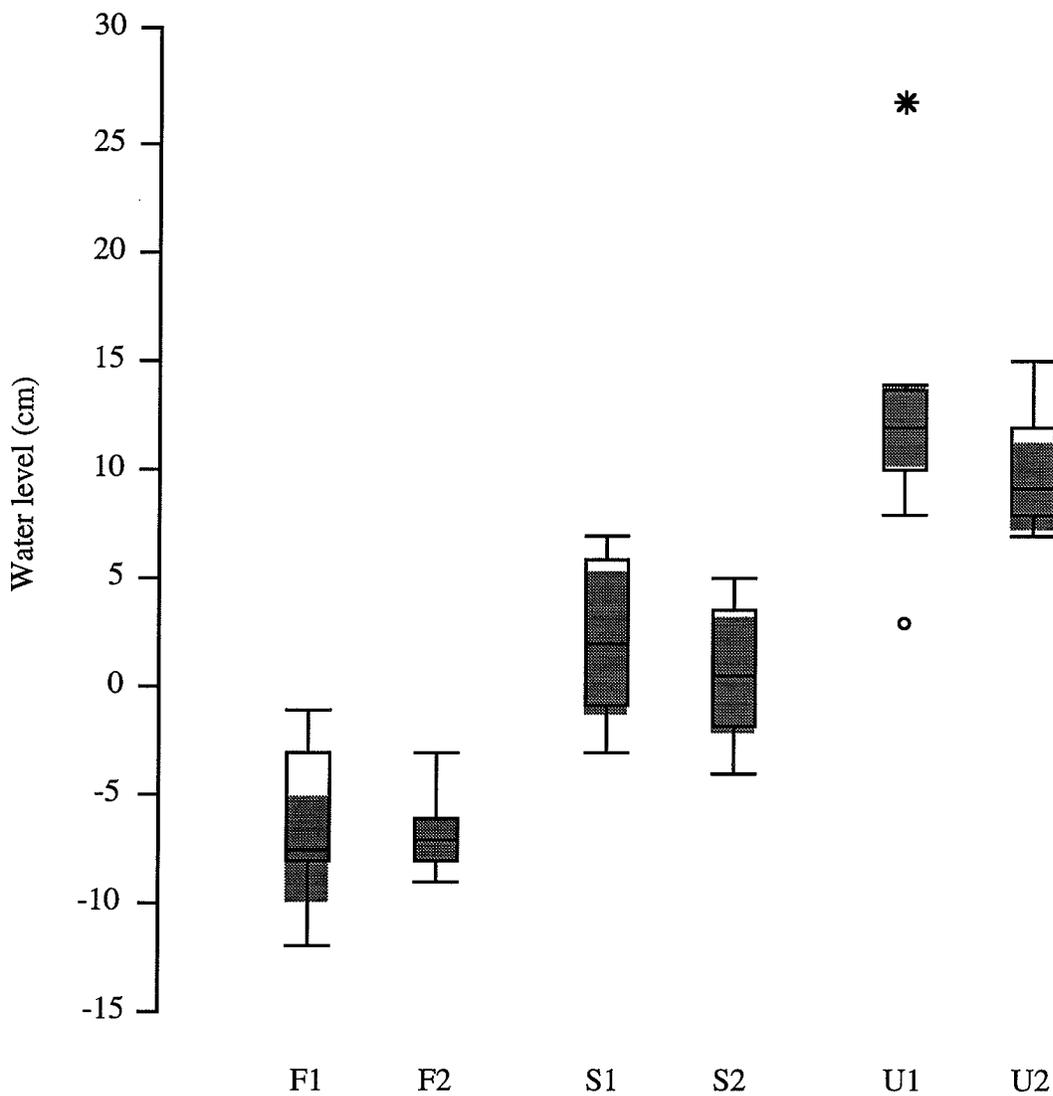


Figure 4.1.2. Water levels of *Typha* study plots, measured 17 July 1992. Values greater than 0 cm represent water above the substrate surface; values less than 0 cm represent depth below the surface to the water table (n=10 measurements per study plot, corresponding with the 10 subplots where vegetation sampling occurred in 1991) (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

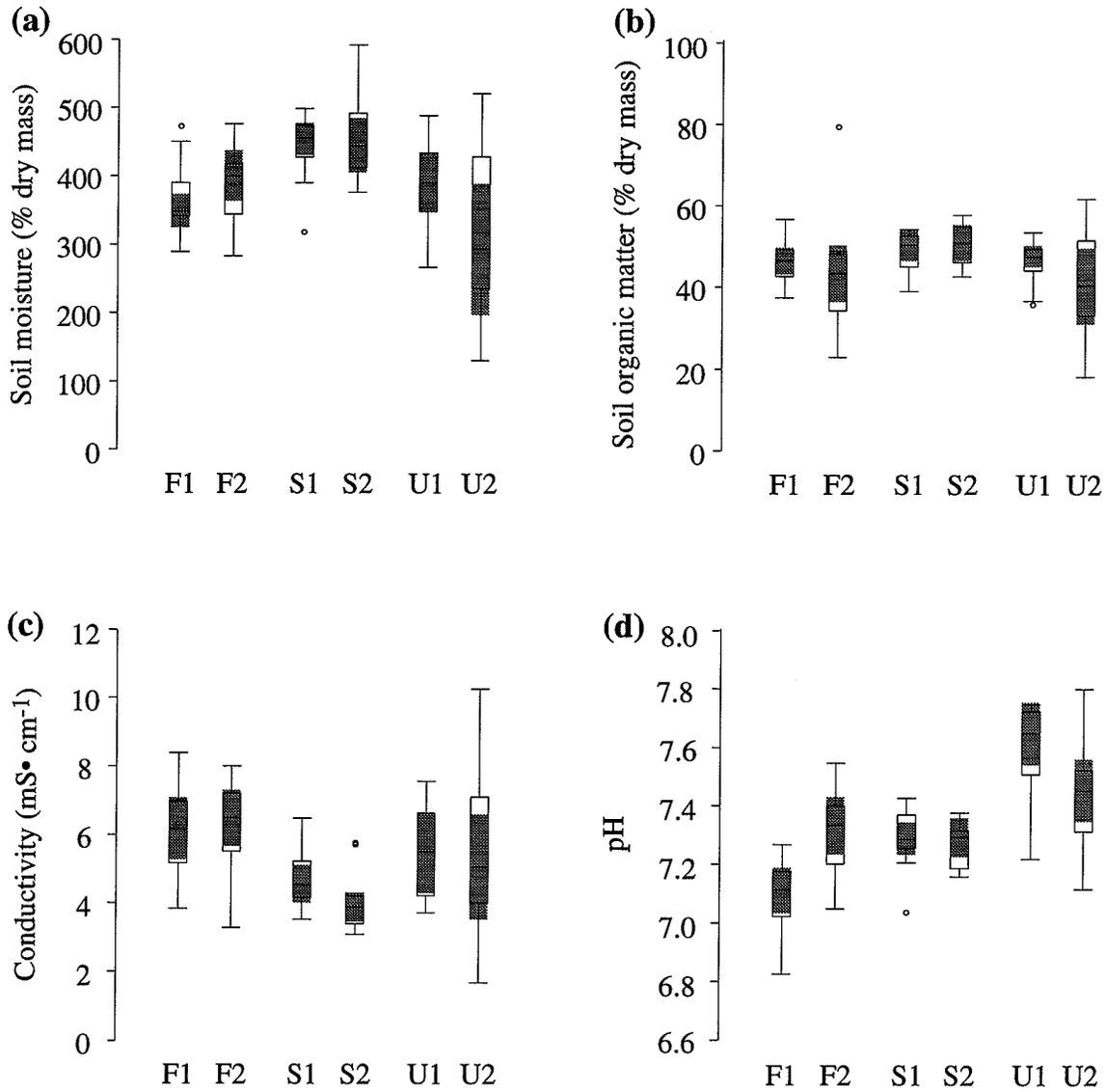


Figure 4.1.3. Soil characteristics in *Typha* study plots, July 1991 (n=10 samples per study plot). (a) Moisture, and (b) Organic matter, both measured as a percentage of dry mass. (c) Electrical conductivity, and (d) pH, both of 1:5 soil to water dilution extracts (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

Table 4.1.3. Soil characteristics of *Typha* communities, measured from soil samples collected in July 1991. Values are means  $\pm$  standard errors (n=10).

Treatment	Plot	Soil moisture (% dry weight)	Organic matter (%)	Conductivity (mS $\cdot$ cm $^{-1}$ )	pH
Fall-burned	F1	372 $\pm$ 18	46.5 $\pm$ 1.8	6.05 $\pm$ 0.47	7.14 $\pm$ 0.04
	F2	388 $\pm$ 19	43.9 $\pm$ 4.8	6.21 $\pm$ 0.49	7.30 $\pm$ 0.05
Spring-burned	S1	442 $\pm$ 17	49.0 $\pm$ 1.7	4.72 $\pm$ 0.29	7.29 $\pm$ 0.03
	S2	457 $\pm$ 21	50.7 $\pm$ 1.8	4.09 $\pm$ 0.30	7.27 $\pm$ 0.03
Unburned	U1	388 $\pm$ 76	46.4 $\pm$ 1.8	5.57 $\pm$ 0.45	7.60 $\pm$ 0.05
	U2	324 $\pm$ 42	41.0 $\pm$ 4.6	5.54 $\pm$ 0.85	7.43 $\pm$ 0.07
P <sub>Treatment</sub>		0.0856	0.1726	0.0163	0.1223
P <sub>Plot</sub>		0.3156	0.5797	0.8454	0.0043

### *Phragmites* communities

Water levels differed markedly between burn treatments (Table 4.1.4, Figure 4.1.4). Fall-burned plots were wettest, with the water table averaging 2.5 cm below the surface. This differed significantly from unburned plots (p=0.0064), where the water table averaged 50 cm below the surface. There was little variation within either the fall-burned or unburned treatments, but plots in the spring-burned treatment varied significantly (p=0.0322). Plot S1 had a range of water levels of 55 cm, with some of the lowest water levels encountered. Plot S2 had some of the deepest water measured in any *Phragmites* plot, so that the mean water level was 13 cm higher there than in plot S1.

Table 4.1.4. Water levels of *Phragmites australis* study plots in July 1992. Negative values are the distance to water table below the soil surface. Values are means  $\pm$  standard errors (n=10).

Treatment	Plot	Water level (cm)
Fall-burned	F1	-2.5 $\pm$ 0.7
	F2	-2.8 $\pm$ 1.1
Spring-burned	S1	-38.0 $\pm$ 6.2
	S2	-25.2 $\pm$ 4.9
Unburned	U1	-49.7 $\pm$ 1.3
	U2	-51.6 $\pm$ 1.0
PTreatment		0.0064
PPlot		0.0322

Soil factors in *Phragmites* communities were characterized by significant differences between fall-burned and unburned treatments, with intermediate and widely variable values in spring-burned plots (Table 4.1.5, Figure 4.1.5). Soil moisture was significantly higher ( $p=0.0081$ ) in fall-burned plots, at 280-320% dry weight, than in either spring-burned plots (160-200% dry weight) or unburned plots (120% dry weight). Soil organic content was significantly higher in fall-burned plots ( $p=0.0040$ ) than in other plots by 15-20%. Mean conductivities were significantly higher ( $p=0.0004$ ) in soil samples from fall-burned plots than those from other plots. Mean conductivity of fall-burned plots was approximately eight times greater than in unburned plots and four times greater than in spring-burned plots. Burned plots had ranges of conductivity of roughly  $4 \text{ mS}\cdot\text{cm}^{-1}$ , while little variation was found in unburned plots. The pH of soil dilution extracts was significantly lower in fall-burned plots than plots in other treatments ( $p=0.0106$ ). Mean soil pH differed by approximately 1 unit between the slightly acidic extracts from fall-burned plots and the slightly basic extracts from spring-burned and unburned plots.

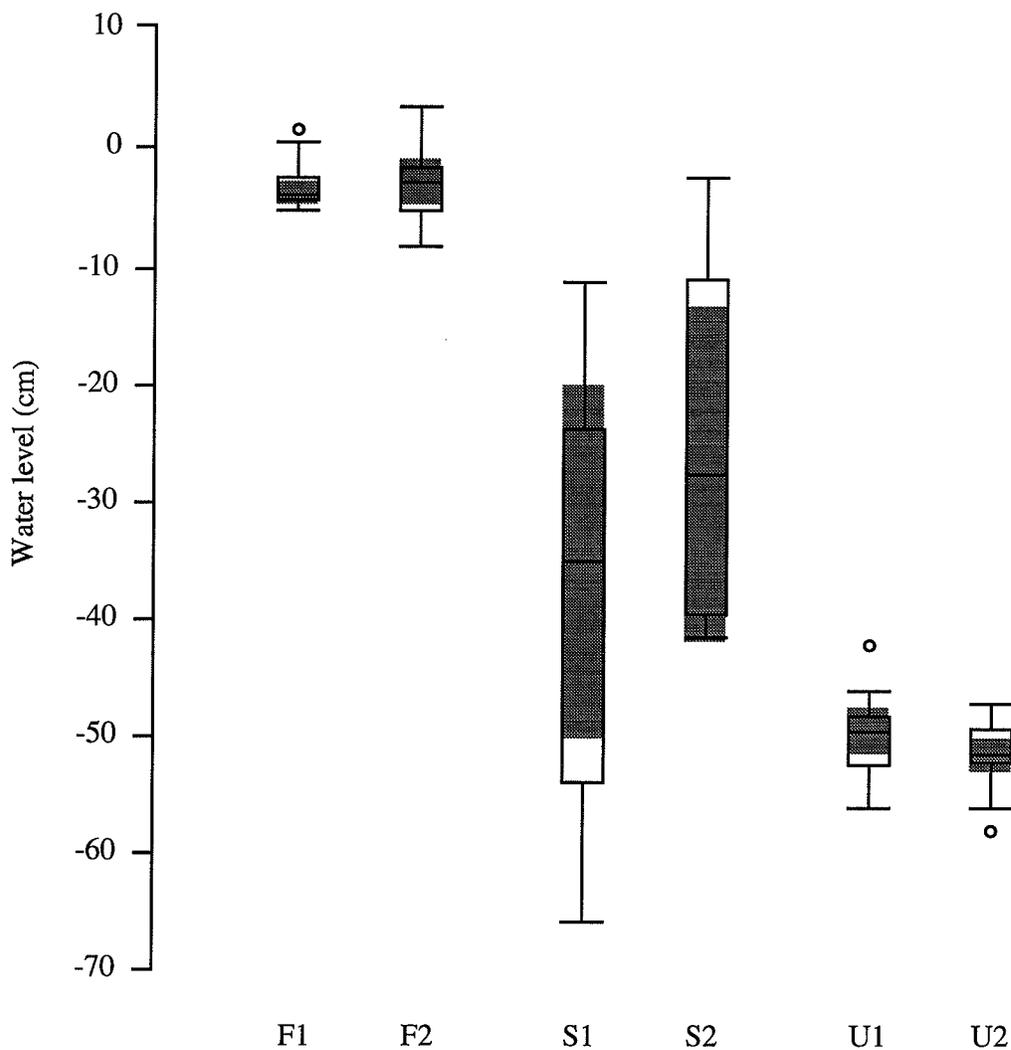


Figure 4.1.4. Water levels in *Phragmites* study plots, 20 July 1992. Values greater than 0 cm represent depth of standing water above the substrate surface; values less than 0 cm represent depth below the surface to the water table (n=10 measurements per study plot, corresponding with the 10 subplots where vegetation sampling occurred in 1991) (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

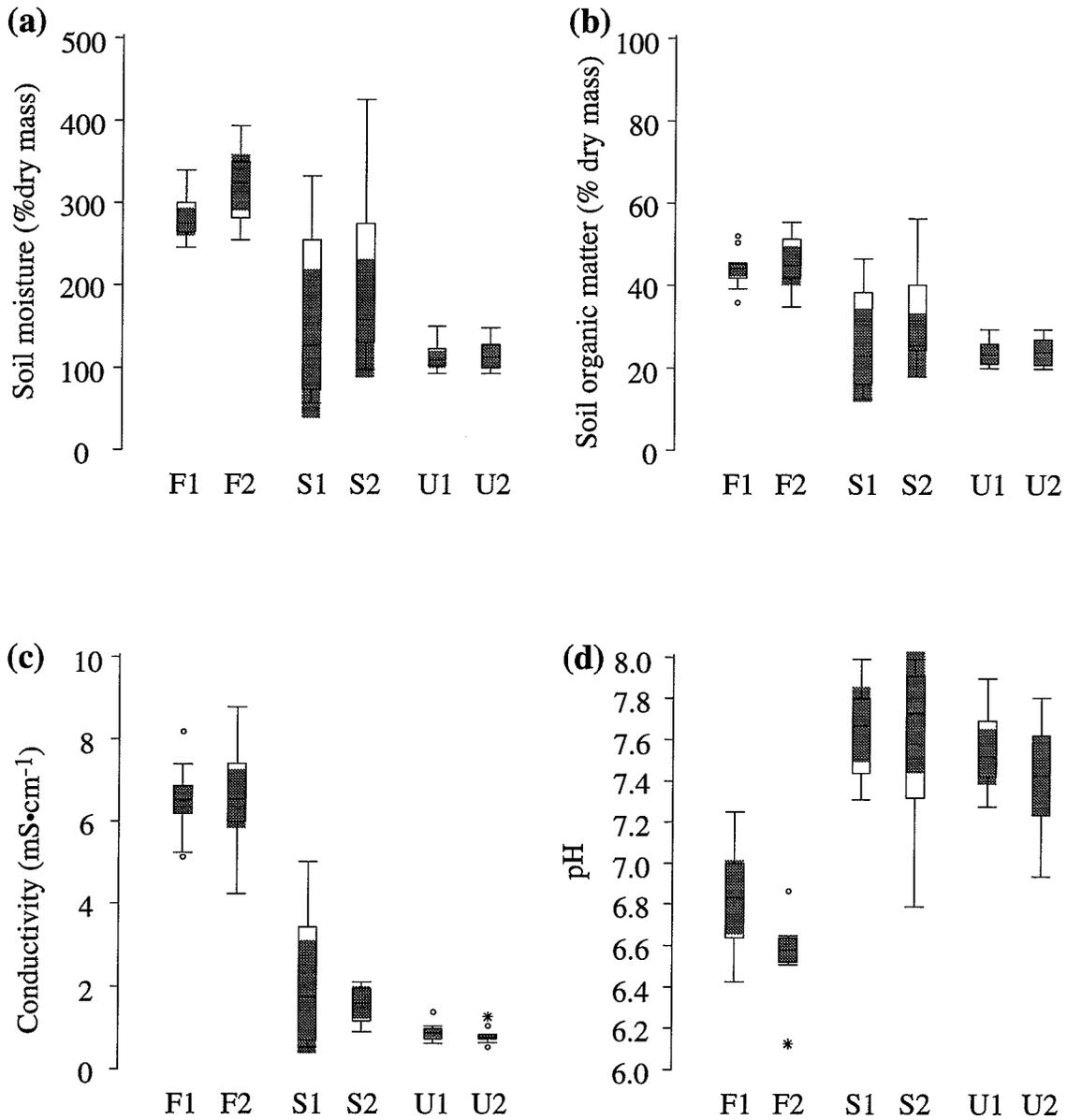


Figure 4.1.5. Soil characteristics in *Phragmites* study plots, July 1991 (n=10 samples per study plot). (a) Moisture, and (b) Organic matter, both measured as a percentage of dry mass. (c) Electrical conductivity, and (d) pH, both of 1:5 soil to water dilution extracts (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

Table 4.1.5. Soil characteristics of *Phragmites* communities, measured from soil samples collected in July 1991. Values are means  $\pm$  standard errors (n=10).

Treatment	Plot	Soil moisture (% dry weight)	Organic matter (%)	Conductivity (mS $\cdot$ cm $^{-1}$ )	pH
Fall-burned	F1	282 $\pm$ 9	44.1 $\pm$ 1.5	6.52 $\pm$ 0.28	6.83 $\pm$ 0.08
	F2	319 $\pm$ 15	45.9 $\pm$ 2.1	6.68 $\pm$ 0.44	6.56 $\pm$ 0.06
Spring-burned	S1	164 $\pm$ 35	26.9 $\pm$ 4.1	2.14 $\pm$ 0.51	7.64 $\pm$ 0.08
	S2	204 $\pm$ 33	31.6 $\pm$ 4.1	1.53 $\pm$ 0.15	7.58 $\pm$ 0.14
Unburned	U1	116 $\pm$ 6	23.7 $\pm$ 1.0	0.88 $\pm$ 0.07	7.57 $\pm$ 0.06
	U2	116 $\pm$ 6	24.1 $\pm$ 1.1	0.81 $\pm$ 0.06	7.41 $\pm$ 0.09
P <sub>Treatment</sub>		0.0081	0.0040	0.0004	0.0106
P <sub>Plot</sub>		0.3718	0.6274	0.5438	0.1077

### *Scolochloa* communities

Unlike the other plant communities examined, *Scolochloa* communities did not exhibit significant differences in water levels between treatments (Table 4.1.6). Mean water levels were lowest in spring-burned plots, highest in unburned plots and intermediate, but variable, in fall-burned plots (Figure 4.1.6). Only 30 cm separated the most extreme measurements in all plots, while mean water levels of the wettest plot (U1) and the driest plot (S2) differed by only 15 cm. Variability of water levels within both the fall-burned and unburned treatments was significant ( $p=0.0004$ ).

In *Scolochloa* communities, only soil pH differed significantly between treatments ( $p=0.0029$ ), with samples from fall-burned plots having pH approximately 0.5 units lower than those in unburned plots, and with spring-burned plots falling into an intermediate range. The remaining soil parameters varied significantly within treatments, rather than between treatments (Table 4.1.7, Figure 4.1.7), although the trends were toward fall-

burned plots having higher soil moisture, soil organic matter, and conductivity than plots in other treatments. A range of soil moisture measurements from 66% to 396% of dry mass within the fall-burned plots was highly significant ( $p < 0.0001$ ). Extremes in conductivity of 5.0-7.5  $\text{mS}\cdot\text{cm}^{-1}$  were measured in extracts from fall-burned and unburned plots, but it was the differences in conductivity between plots S1 and S2 that were significant ( $p = 0.0055$ ).

Table 4.1.6. Water levels of *Scolochloa festucacea* study plots in July 1992. Negative values are the distance to water table below the soil surface; positive values are the depth of standing water above the surface. Values are means  $\pm$  standard errors ( $n = 10$ ).

Treatment	Plot	Water level (cm)
Fall-burned	F1	-15.1 $\pm$ 0.6
	F2	-16.1 $\pm$ 0.4
	F3	-19.9 $\pm$ 1.3
Spring-burned	S1	-22.3 $\pm$ 1.4
	S2	-24.2 $\pm$ 1.5
Unburned	U1	-9.2 $\pm$ 1.7
	U2	-16.0 $\pm$ 1.4
P <sub>Treatment</sub>		0.0619
P <sub>Plot</sub>		0.0004

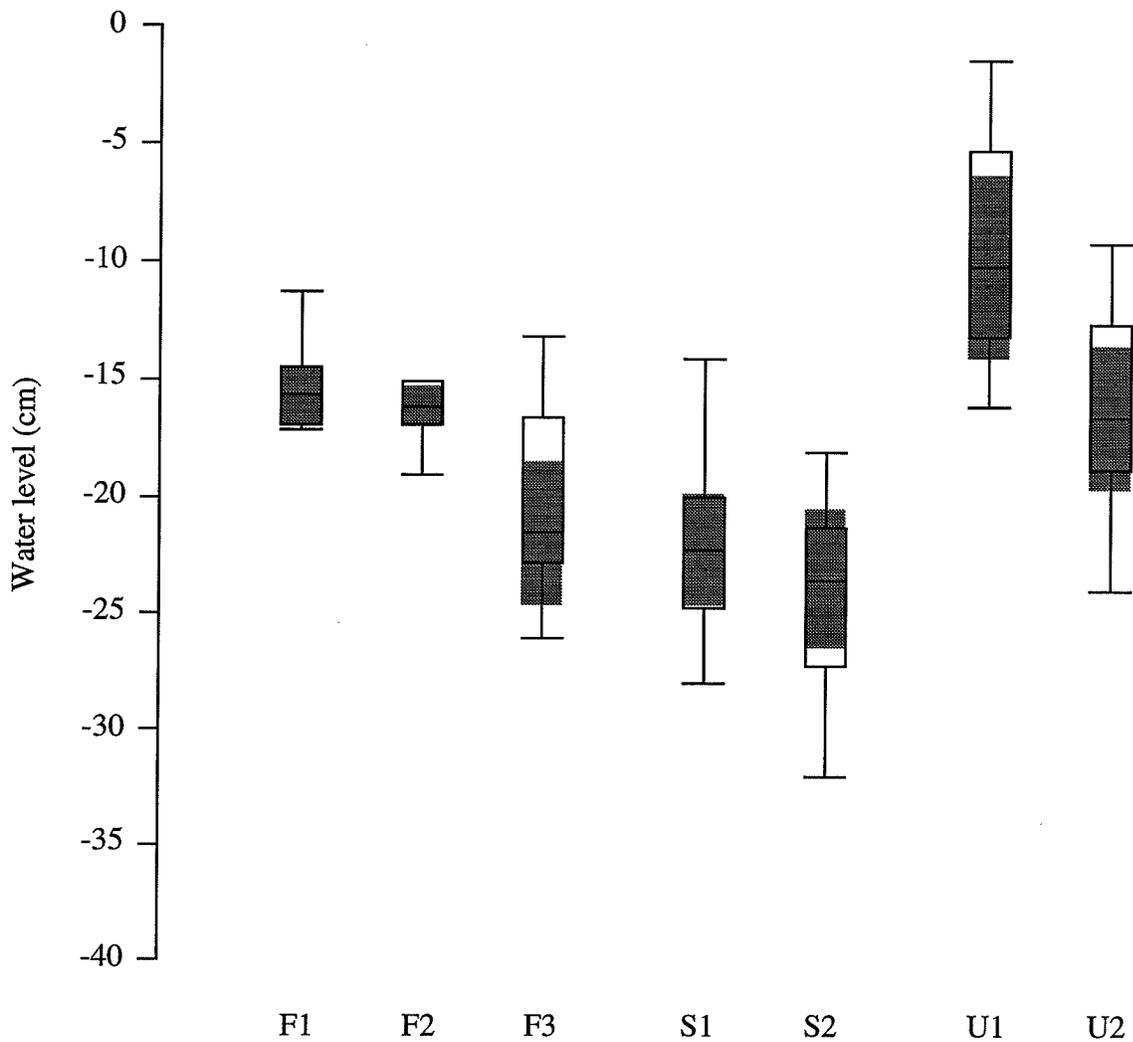


Figure 4.1.6. Water levels in *Scolochloa* study plots, 21 July 1992. Values less than 0 cm represent depth below the surface to the water table (n=10 measurements per study plot, corresponding with the 10 subplots where vegetation sampling occurred in 1991) (F1, F2 and F3 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

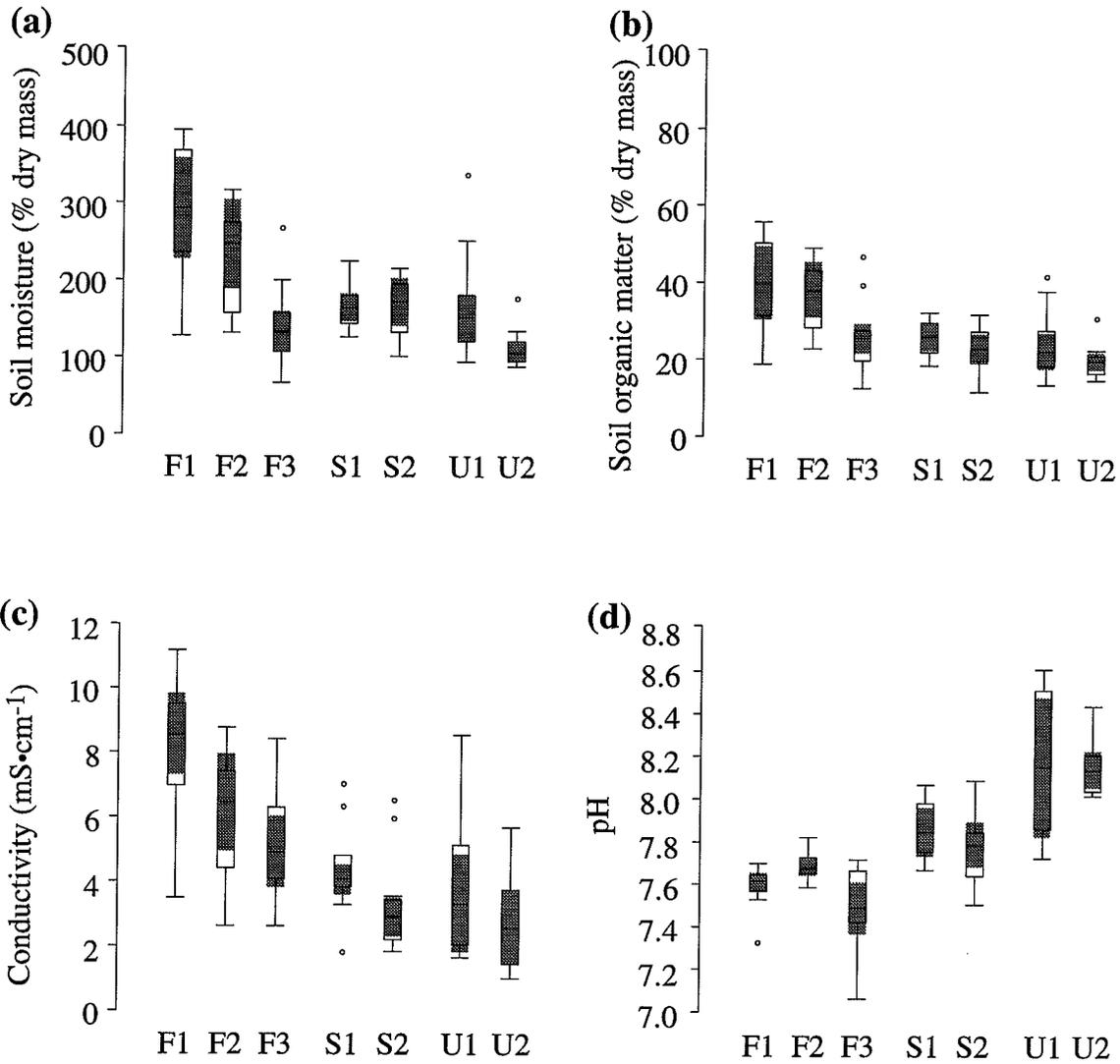


Figure 4.1.7. Soil characteristics in *Scolochloa* study plots, July 1991 (n=10 samples per study plot). (a) Moisture, and (b) Organic matter, both measured as a percentage of dry mass. (c) Electrical conductivity, and (d) pH, both of 1:5 soil to water dilution extracts (F1, F2 and F3 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

Table 4.1.7. Soil characteristics of *Scolochloa* communities, measured from soil samples collected in July 1991. Values are means  $\pm$  standard errors (n=10).

Treatment	Plot	Soil moisture (% dry weight)	Organic matter (%)	Conductivity (mS $\cdot$ cm <sup>-1</sup> )	pH
Fall-burned	F1	286 $\pm$ 31	39.3 $\pm$ 4.1	8.14 $\pm$ 0.72	7.59 $\pm$ 0.03
	F2	224 $\pm$ 22	36.1 $\pm$ 2.9	5.99 $\pm$ 0.67	7.69 $\pm$ 0.02
	F3	141 $\pm$ 19	26.1 $\pm$ 3.4	5.17 $\pm$ 0.55	7.50 $\pm$ 0.06
Spring-burned	S1	165 $\pm$ 9	25.6 $\pm$ 1.6	4.40 $\pm$ 0.47	7.86 $\pm$ 0.05
	S2	164 $\pm$ 13	22.5 $\pm$ 2.1	3.35 $\pm$ 0.51	7.77 $\pm$ 0.05
Unburned	U1	169 $\pm$ 24	24.7 $\pm$ 2.9	3.99 $\pm$ 0.78	8.18 $\pm$ 0.11
	U2	113 $\pm$ 9	20.0 $\pm$ 1.5	2.75 $\pm$ 0.49	8.16 $\pm$ 0.04
P <sub>Treatment</sub>		0.3790	0.1314	0.0925	0.0029
P <sub>Plot</sub>		<0.0001	0.0110	0.0055	0.1830

## 4.2 VEGETATION PARAMETERS

### *Typha* communities

#### Overview

In *Typha* communities, regrowth began earliest after burning, but prolonged growth in unburned plots eventually produced the tallest *Typha glauca* shoots. Shoot density was significantly higher after fall burning than in the other treatments. The aboveground biomass of *Typha glauca* was lower after fall burning than in unburned stands; production in spring burned plots was variable, but tended to be lower than in unburned plots. Fall-burned plots, and to a lesser extent spring-burned plots, produced

shoots that were significantly smaller, in terms of shoot height and biomass, than unburned plots. Little understorey growth was found in any study plots. Understorey species were encountered only in the burned plots, but they made up a small component of the total community biomass. Neither fall burning nor spring burning significantly increased the proportion of understorey biomass in these communities.

### **Growth characteristics of *Typha glauca***

Emergence of *Typha glauca* shoots in the 1991 growing season began earliest in fall-burned sites, and were observed as early as 29 April. Figure 4.2.1 shows the mean height of tagged shoots in 1991. Differences between treatments were significant on 4 June, and again from 16 July until the end of sampling (Table 4.2.1). Shoots in burned plots ceased growth by mid-July, while those in unburned plots continued to grow throughout July and August, and eventually grew tallest. Flowering was first observed on 11 June in burned sites, but not until 20 June in plot U1 and 4 July in plot U2.

In May, *Typha glauca* mean shoot density of 100 shoots $\cdot$ m<sup>-2</sup> in fall-burned plots was significantly higher ( $p=0.0075$ ) than in either spring-burned or unburned plots, which had densities of 40-60 shoots $\cdot$ m<sup>-2</sup> (Table 4.2.2, Figure 4.2.2). Total *T. glauca* shoot density in August remained significantly higher ( $p=0.0011$ ) in fall-burned plots, with densities of 108 shoots $\cdot$ m<sup>-2</sup>, than in other plots, which all had densities of approximately 55 shoots $\cdot$ m<sup>-2</sup>. Vegetative shoot density exhibited a similar trend, with significantly higher numbers of shoots in the fall-burned treatment ( $p=0.0013$ ). Mean flowering shoot density was similar in all plots, with 2-4 flowering shoots $\cdot$ m<sup>-2</sup>, except in plot S1, with 16 shoots $\cdot$ m<sup>-2</sup>. Variability of flowering shoot density within the spring-burn was significant ( $p=0.0001$ ). Flowering shoots made up between 2 and 8% of all shoots, except in plot S1, where 26% of the shoots flowered. This higher proportion resulted in the only difference

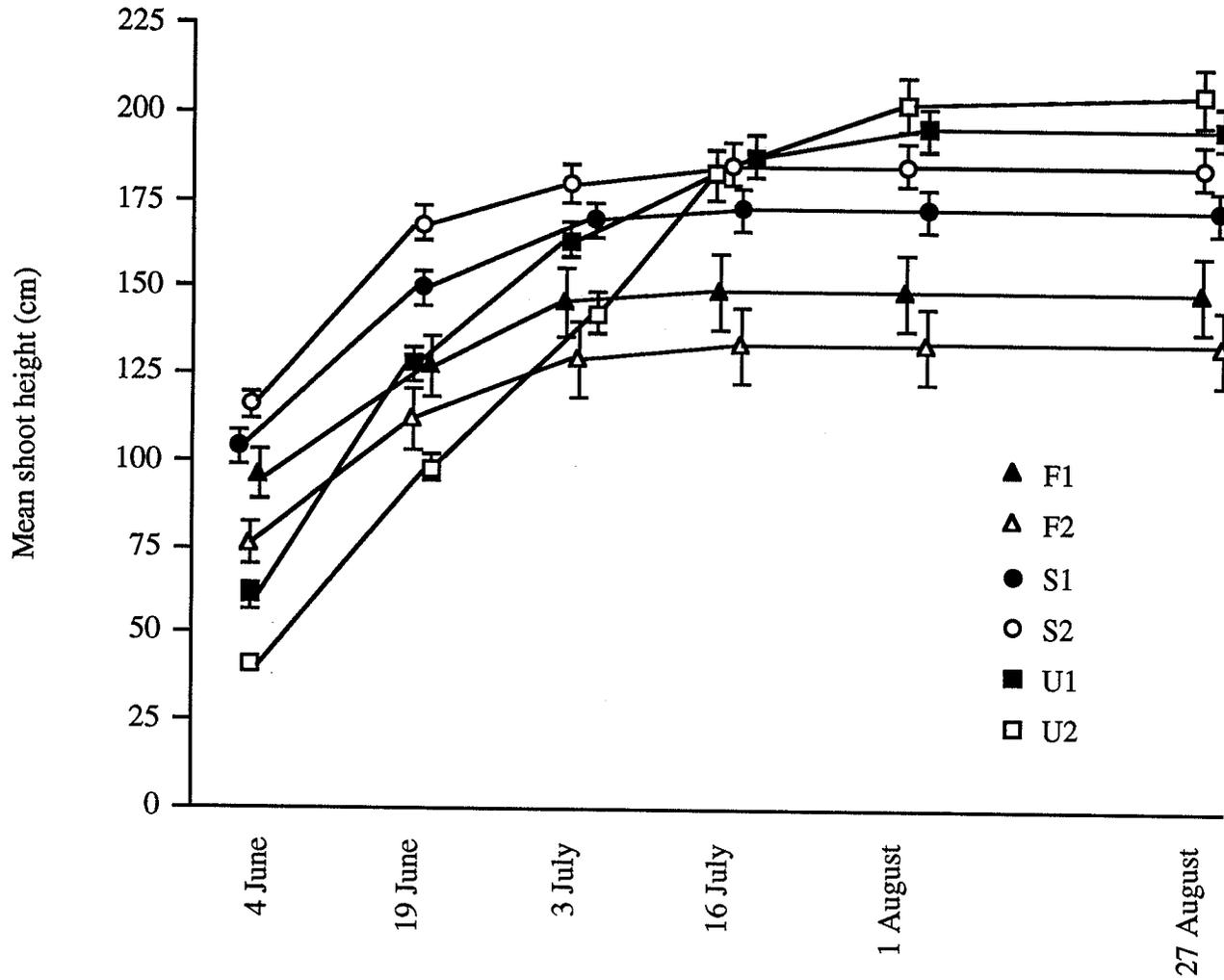


Figure 4.2.1. Mean height ( $\pm 1$  SE) of *Typha glauca* shoots sampled repeatedly throughout the 1991 growing season. Initial sample size was 20 shoots per study plot, or 120 total; mortality reduced the sample size to a total of 113 shoots. Several sampling dates were omitted for clarity of the figure.

Table 4.2.1. Mean height in cm ( $\pm$  1SE) of tagged *Typha glauca* shoots measured repeatedly throughout the 1991 growing season. Initial sample size was n=20 shoots per plot, or 120 total. Sample size was reduced by shoot mortality to 113 shoots. P-values  $\leq$  0.05 indicate significant differences between treatments (Treatment) and/or within treatments (Plot) at each sampling date. Dashes denote plots where shoot heights were not measured on a particular sampling date, and the subsequent lack of significance testing.

Treatment	Fall-burned		Spring-burned		Unburned		p values	
	F1	F2	S1	S2	U1	U2	Treatment	Plot
Sampling date:								
24 May	63 $\pm$ 5	38 $\pm$ 4	51 $\pm$ 4	51 $\pm$ 2	-	-	-	-
4 June	96 $\pm$ 7	76 $\pm$ 6	104 $\pm$ 5	116 $\pm$ 4	61 $\pm$ 4	38 $\pm$ 2	0.0457	0.0111
10 June	112 $\pm$ 8	92 $\pm$ 7	128 $\pm$ 6	147 $\pm$ 5	93 $\pm$ 5	65 $\pm$ 3	0.0824	0.0063
19 June	127 $\pm$ 9	112 $\pm$ 9	150 $\pm$ 5	168 $\pm$ 5	128 $\pm$ 5	98 $\pm$ 4	0.1058	0.0339
25 June	135 $\pm$ 9	120 $\pm$ 9	158 $\pm$ 5	174 $\pm$ 5	144 $\pm$ 5	119 $\pm$ 4	0.1117	0.0732
3 July	146 $\pm$ 10	129 $\pm$ 11	170 $\pm$ 5	180 $\pm$ 5	164 $\pm$ 5	143 $\pm$ 6	0.1179	0.1395
10 July	148 $\pm$ 10	133 $\pm$ 11	172 $\pm$ 5	184 $\pm$ 5	178 $\pm$ 6	167 $\pm$ 6	0.0620	0.3405
16 July	149 $\pm$ 11	134 $\pm$ 11	173 $\pm$ 6	186 $\pm$ 6	188 $\pm$ 6	183 $\pm$ 7	0.0390	0.4019
1 August	149 $\pm$ 11	134 $\pm$ 11	173 $\pm$ 6	186 $\pm$ 6	196 $\pm$ 6	203 $\pm$ 8	0.0173	0.5280
27 August	149 $\pm$ 11	134 $\pm$ 11	173 $\pm$ 6	186 $\pm$ 6	197 $\pm$ 6	206 $\pm$ 8	0.0169	0.5129

Table 4.2.2. Summary of *Typha glauca* growth variables (mean  $\pm$  1SE). Shoot density was sampled in May and again in August (n=40 quadrats, each 0.25 m<sup>2</sup>). August samples were partitioned into vegetative and flowering shoots, summed to give totals. Mean biomass per shoot was obtained for each quadrat by dividing aboveground biomass in the quadrat by the number of shoots present. Biomass sample size was n=10 quadrats, each 0.5 m<sup>2</sup>. P-values  $\leq$  0.05 indicate significant differences between treatments (Treatment) and/or within treatments (Plot) for each variable.

Treatment	Fall-burned		Spring-burned		Unburned		p values	
	F1	F2	S1	S2	U1	U2	Treatment	Plot
Shoot density (shoots·m <sup>-2</sup> )								
May	97 $\pm$ 5	99 $\pm$ 4	60 $\pm$ 3	56 $\pm$ 2	52 $\pm$ 4	37 $\pm$ 3	0.0075	0.3663
August								
Total	108 $\pm$ 4	108 $\pm$ 4	60 $\pm$ 2	53 $\pm$ 2	53 $\pm$ 2	59 $\pm$ 2	0.0011	0.6060
Vegetative shoots	106 $\pm$ 4	103 $\pm$ 5	44 $\pm$ 2	50 $\pm$ 2	48 $\pm$ 2	56 $\pm$ 2	0.0013	0.5784
Flowering shoots	2 $\pm$ 1	4 $\pm$ 1	16 $\pm$ 2	3 $\pm$ 1	4 $\pm$ 1	3 $\pm$ 1	0.4803	0.0001
Aboveground biomass (g·m <sup>-2</sup> )								
Total	630 $\pm$ 25	611 $\pm$ 53	974 $\pm$ 78	618 $\pm$ 59	847 $\pm$ 77	980 $\pm$ 61	0.3067	0.0082
Vegetative shoots	584 $\pm$ 25	491 $\pm$ 38	594 $\pm$ 72	516 $\pm$ 44	737 $\pm$ 59	895 $\pm$ 57	0.0694	0.1249
Flowering shoots	46 $\pm$ 18	120 $\pm$ 59	380 $\pm$ 70	101 $\pm$ 58	110 $\pm$ 60	84 $\pm$ 20	0.4406	0.0143
Mean biomass per shoot (g)								
Total	6.1 $\pm$ 0.3	6.6 $\pm$ 1.1	14.9 $\pm$ 0.7	12.7 $\pm$ 1.1	16.2 $\pm$ 0.7	15.5 $\pm$ 0.6	0.0047	0.2905
Vegetative shoots	5.8 $\pm$ 0.4	5.5 $\pm$ 0.5	11.5 $\pm$ 0.8	11.6 $\pm$ 1.0	15.5 $\pm$ 0.7	14.9 $\pm$ 0.6	0.0001	0.9061
Flowering shoots *	22.5 $\pm$ 4.1	20.7 $\pm$ 2.0	26.7 $\pm$ 0.9	27.9 $\pm$ 2.2	34.3 $\pm$ 12.8	26.5 $\pm$ 2.0	0.2408	0.6285

\* Where no flowering shoots were present in a quadrat, sample size was reduced to n=6 in plot F1, n=8 in plot F2, n=9 in plot S1, n=5 in plot S2, n=4 in plot U1, and n=8 in plot U2.

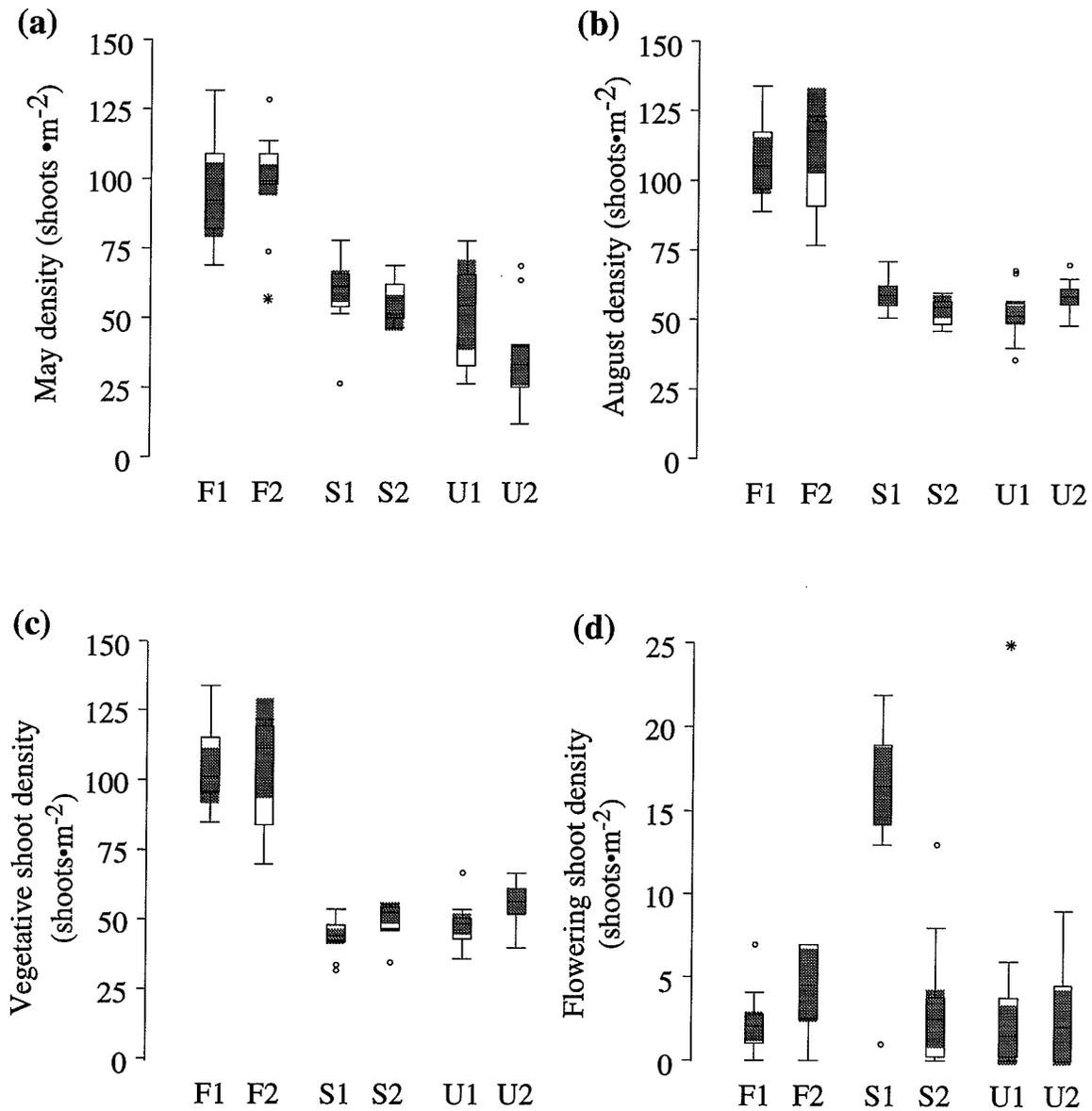


Figure 4.2.2. Density of *Typha glauca* (n=40 quadrats per plot). (a) May 1991. (b) August 1991. (c) Vegetative shoots in August sample. (d) Flowering shoots in August sample (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

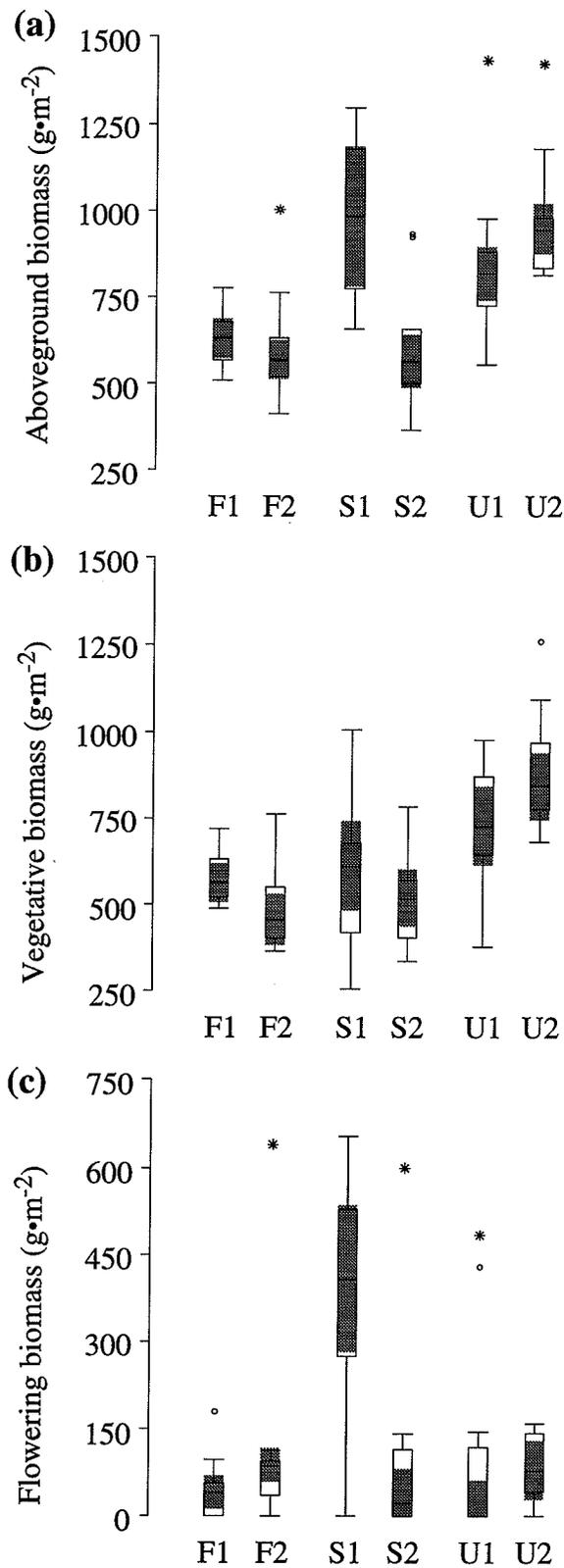


Figure 4.2.3. Aboveground biomass of *Typha glauca* in August 1991 (n=10 samples per study plot). (a) *T. glauca* shoots. (b) Vegetative shoots. (c) Flowering shoots (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

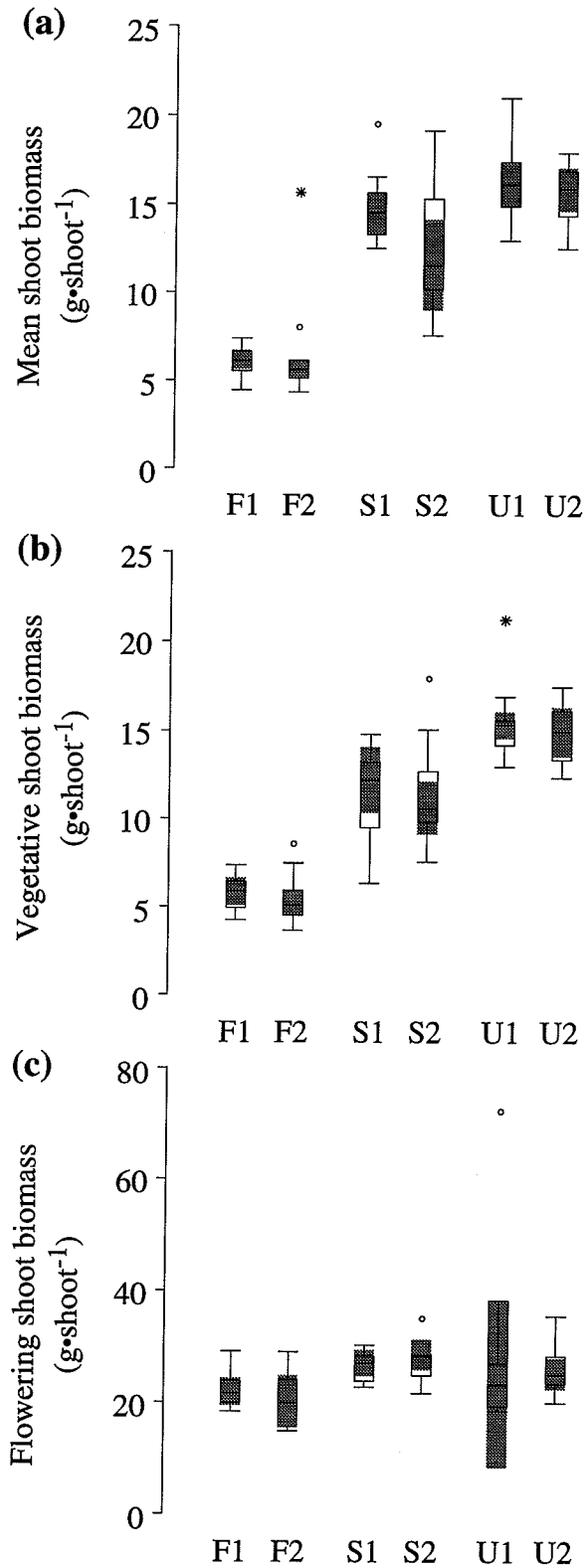


Figure 4.2.4. Mean shoot aboveground biomass of *Typha glauca* in August 1991 (n=10 samples per study plot). (a) All *T. glauca* shoots. (b) Vegetative shoots. (c) Flowering shoots. Sample sizes were reduced where no flowering shoots were sampled (Details in Table 4.2.2) (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

in the trends between vegetative and total shoot densities, with plot S1 having a lower vegetative shoot density than plot S2, but a higher total shoot density.

Although the aboveground biomass of *T. glauca* tended to be higher in unburned plots than in fall-burned plots, there was no significant difference between treatments (Table 4.2.2, Figure 4.2.3), due to the significant variability within the spring-burned treatment ( $p=0.0082$ ). The significant difference in flowering shoot biomass within the spring-burned treatment ( $p=0.0143$ ) was responsible for the overall variability. Flowering shoot biomass was relatively similar in all plots except for plot S1, where it was between three and eight times higher. Flowering shoot biomass made up 39% of the *T. glauca* biomass in plot S1, compared with between 7 and 20% in the other plots. The aboveground biomass of *T. glauca* vegetative shoots was between 150 and 300  $\text{g}\cdot\text{m}^{-2}$  higher in the unburned plots than in any of the burned plots, but this difference could be considered only marginally significant ( $p=0.697$ ).

The mean biomass of *T. glauca* shoots was significantly lower ( $p=0.0047$ ) in fall-burned plots, ranging from 6.1 to 6.6  $\text{g}\cdot\text{shoot}^{-1}$ , than in the other treatments, where mean shoot biomass ranged from 12.7 to 16.2  $\text{g}\cdot\text{shoot}^{-1}$  (Table 4.2.2, Figure 4.2.4). The overall trend was influenced strongly by the significantly lower mean biomass of vegetative shoots in fall-burned plots than in other treatments ( $p=0.0001$ ). Mean biomass of flowering shoots was similar in all plots, although the absence of flowering shoots in some quadrats reduced sample sizes to as low as four in plot U1, making it difficult to determine the actual trend.

### ***Typha* community characteristics**

The *T. glauca* communities studied contained few other species, and where other species were encountered, they were in small quantities (Figure 4.2.5). In five of the six plots, no other species produced more than  $1.0 \text{ g}\cdot\text{m}^{-2}$  of aboveground biomass (Table 4.2.3). In these plots understory species contributed only 0.3% to the aboveground biomass of the community. The plants in these plots were either annuals, such as *Atriplex patula* and *Rumex maritimus*, or new seedlings of herbaceous perennials, such as *Sonchus arvensis* and *Cirsium arvense*. A patch of *P. australis* occurred adjacent to plot U2, and was encountered in two of the ten biomass quadrats, resulting in a mean biomass of  $24.7 \text{ g}\cdot\text{m}^{-2}$ , and accounting for 2.5% of the plot biomass. Aboveground biomass of understory species did not exhibit any significant differences, and because understory species contributed so little to the total biomass, there was no significant difference in understory biomass as a percentage of the total.

The small amount of understory biomass present in the study plots resulted in little difference between the trends for total biomass of *Typha* communities (Figure 4.2.5) and biomass of *T. glauca* alone (Figure 4.2.3). Total community biomass differed significantly between spring-burned plots ( $p=0.0065$ ) for the same reasons outlined previously.

The dominance of *T. glauca* in all plots is illustrated clearly in Table 4.2.4. The total number of species in a single quadrat ranged from a low of one in plot U1 (only *T. glauca* was encountered) to a high of only six in plot S2. The most species encountered in any quadrat was five, in plot S2. The mean number of species per quadrat ranged from one to two.

Table 4.2.3. Aboveground biomass ( $\text{g}\cdot\text{m}^{-2}$ ) of species found in *Typha* communities. Values denoted by "Tr" indicate trace amounts (mean biomass  $\leq 0.1 \text{ g}\cdot\text{m}^{-2}$ ). Values are means  $\pm$  standard errors (n=10).

Treatment Species	Fall-burned		Spring-burned		Unburned	
	F1	F2	S1	S2	U1	U2
<i>Typha x glauca</i>	630.4 $\pm$ 25.4	611.0 $\pm$ 52.9	974.0 $\pm$ 77.8	617.7 $\pm$ 58.7	847.3 $\pm$ 76.7	979.6 $\pm$ 60.5
Understorey species:						
<i>Phragmites australis</i>	0	0	0	0	0	24.7 $\pm$ 17.6
<i>Sonchus arvensis</i>	Tr	Tr	Tr	Tr	0	0
<i>Cirsium arvense</i>	Tr	0	Tr	0.9 $\pm$ 0.7	0	0
<i>Atriplex patula</i>	Tr	0	0	1.0 $\pm$ 0.5	0	0
<i>Rumex maritimus</i>	0	0	0	Tr	0	0
Unidentified species	Tr	Tr	0	Tr	0	0
Total understorey biomass *	0.2 $\pm$ 0.2	0.04 $\pm$ 0.03	0.1 $\pm$ 0.1	2.0 $\pm$ 1.2	0	24.7 $\pm$ 17.6
Total community biomass **	630.6 $\pm$ 25.4	611.1 $\pm$ 52.8	974.2 $\pm$ 77.8	619.7 $\pm$ 58.4	847.3 $\pm$ 76.7	1004.3 $\pm$ 55.6
% Understorey ***	<0.1%	<0.1%	<0.1%	0.3	0.0	2.5

\*  $P_{\text{Treatment}} = 0.4919$ ;  $p_{\text{Plot}} = 0.1116$

\*\*  $P_{\text{Treatment}} = 0.2974$ ;  $p_{\text{Plot}} = 0.0065$

\*\*\*  $P_{\text{Treatment}} = 0.5131$ ;  $p_{\text{Plot}} = 0.1023$

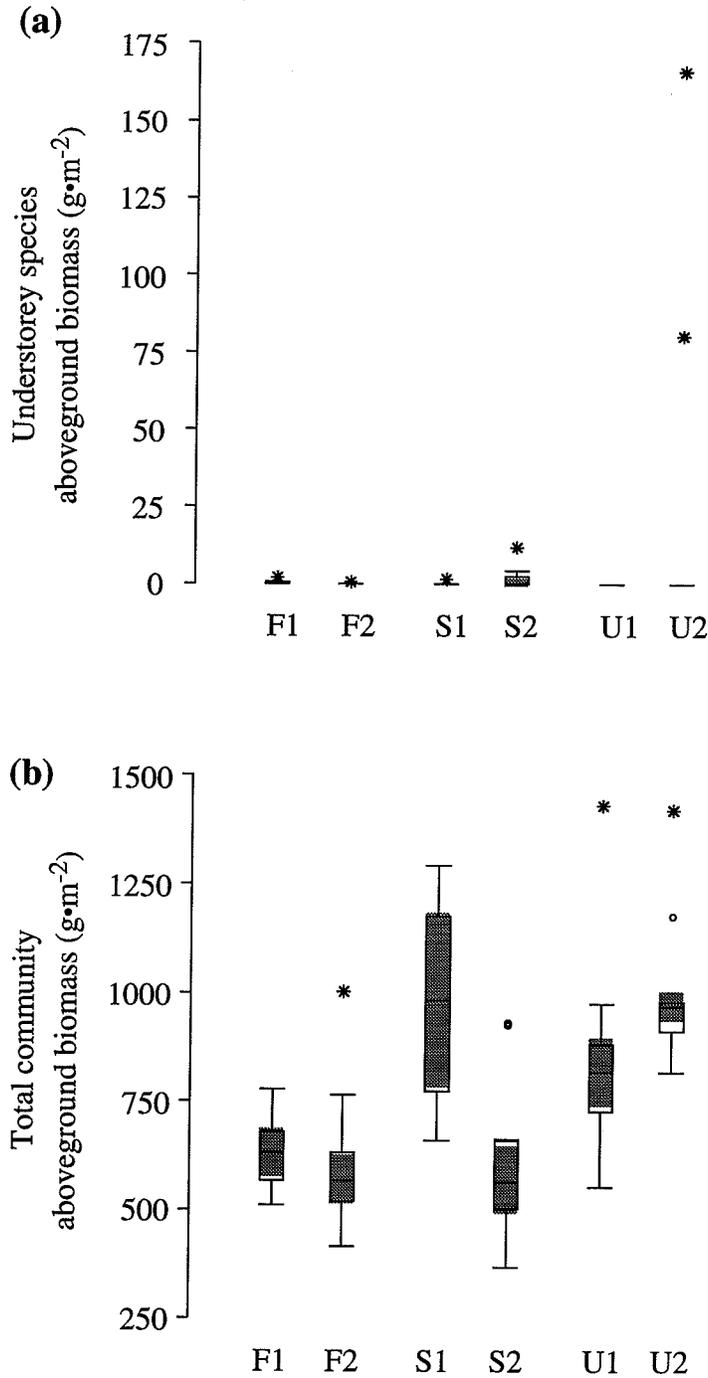


Figure 4.2.5. Aboveground biomass of *Typha* communities, August 1991 (n=10 samples per study plot). (a) Understorey species. (b) *Typha glauca* plus understorey biomass (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

Table 4.2.4. Summary of species richness of *Typha* communities in August 1991. Species richness is reported as the total number of species encountered in all quadrats, as well as the maximum, minimum and mean number of species per quadrat (n=10 quadrats, area 0.5 m<sup>2</sup>).

Treatment	Plot	Number of species per quadrat:			
		Total	Max	Min	Mean
Fall-burned	F1	5	3	1	1.4 ± 0.2
	F2	3	2	1	1.2 ± 0.1
Spring-burned	S1	3	3	1	1.2 ± 0.2
	S2	6	5	1	2.0 ± 0.4
Unburned	U1	1	1	1	1.0
	U2	2	2	1	1.2 ± 0.1

## ***Phragmites* communities**

### **Overview**

In *Phragmites* communities, regrowth began earlier in burned plots than in unburned plots. Shoot density and aboveground biomass were higher after both fall and spring burns than in unburned plots. Fall-burned plots had lower species richness and understorey biomass than either spring-burned or unburned plots, which were relatively similar in these regards. Both fall-burned and spring-burned *Phragmites* communities had higher aboveground biomass than unburned areas.

### Growth characteristics of *Phragmites australis*

*P. australis* shoot emergence in the 1991 growing season began earliest in fall-burned sites when buds were observed at or just above the soil surface on 29 April, but were not yet visible in other treatments. By 3 June, mean heights of shoots measured in unburned plots were similar to those in burned plots. After 3 June, shoots in plot U1 grew most rapidly, while shoots in plot U2 grew at a pace similar to those in burned plots (Figure 4.2.6). Differences in mean height were not significant between treatments (Table 4.2.5). Flowering was observed in fall-burned sites on 25 June, followed by spring-burned sites on 4 July and unburned sites on 10 July.

In May, the density of *Phragmites australis* shoots in fall-burned and spring-burned plots were double those of the unburned plots (Table 4.2.6, Figure 4.2.7). However, significant variability within the two burns ( $p=0.0027$ ) masked the increased densities in those treatments so that there was no significant difference ( $p=0.0653$ ). By August, the mean density of *P. australis* shoots had increased to 126 and 139 shoots $\cdot$ m<sup>-2</sup> in fall-burned plots, significantly higher ( $p=0.0019$ ) than in unburned plots, with mean densities of around 50 shoots $\cdot$ m<sup>-2</sup>, or in spring-burned plots, with 80 shoots $\cdot$ m<sup>-2</sup>. The mean density of vegetative shoots exhibited a similar, significant trend ( $p=0.0082$ ). Mean flowering shoot density was 20-30 shoots $\cdot$ m<sup>-2</sup> higher in fall-burned plots than in unburned plots, while the variability of flowering shoot densities in the spring-burned plots was significant ( $p=0.0008$ ). Flowering shoots made up 16% of the shoots in plot S1 and 39% of the shoots in plot S2. These percentages represented the extremes from all plots (35% and 29% flowering shoots in plots F1 and F2; 25% and 24% flowering shoots in plots U1 and U2, respectively).

The mean aboveground biomass of *P. australis* was higher in fall-burned plots (791 and 734 g $\cdot$ m<sup>-2</sup>) than in unburned plots (402 and 423 g $\cdot$ m<sup>-2</sup>). However, this increase was

Table 4.2.5. Mean height in cm ( $\pm$  1SE) of tagged *Phragmites australis* shoots measured repeatedly throughout the 1991 growing season. Initial sample size was n=20 shoots per plot, or 120 total. Sample size was reduced by shoot mortality to 106 shoots. P-values  $\leq$  0.05 indicate significant differences between treatments (Treatment) and/or within treatments (Plot) at each sampling date. Dashes denote plots where shoot heights were not measured on a particular sampling date, and the subsequent lack of significance testing.

Treatment	Fall-burned		Spring-burned		Unburned		p values	
	F1	F2	S1	S2	U1	U2	Treatment	Plot
Sampling date								
24 May	-	-	66 $\pm$ 2	64 $\pm$ 2	-	-	-	-
3 June	89 $\pm$ 6	80 $\pm$ 7	110 $\pm$ 3	113 $\pm$ 3	114 $\pm$ 4	93 $\pm$ 3	0.1324	0.0520
10 June	111 $\pm$ 5	106 $\pm$ 7	131 $\pm$ 3	133 $\pm$ 3	146 $\pm$ 3	116 $\pm$ 4	0.2352	0.0199
19 June	133 $\pm$ 5	130 $\pm$ 8	150 $\pm$ 4	153 $\pm$ 3	173 $\pm$ 4	138 $\pm$ 5	0.2783	0.0192
25 June	146 $\pm$ 5	140 $\pm$ 8	154 $\pm$ 4	159 $\pm$ 4	185 $\pm$ 5	147 $\pm$ 5	0.3861	0.0155
4 July	150 $\pm$ 5	149 $\pm$ 9	159 $\pm$ 5	164 $\pm$ 3	195 $\pm$ 5	155 $\pm$ 6	0.3534	0.0356
10 July	158 $\pm$ 6	151 $\pm$ 10	161 $\pm$ 4	168 $\pm$ 3	192 $\pm$ 10	161 $\pm$ 8	0.3164	0.1913
16 July	158 $\pm$ 6	153 $\pm$ 10	161 $\pm$ 4	172 $\pm$ 2	203 $\pm$ 5	161 $\pm$ 9	0.3707	0.0605
2 August	162 $\pm$ 7	152 $\pm$ 10	162 $\pm$ 4	175 $\pm$ 2	207 $\pm$ 5	166 $\pm$ 9	0.3344	0.0619
27 August	162 $\pm$ 7	152 $\pm$ 10	162 $\pm$ 4	173 $\pm$ 2	208 $\pm$ 5	165 $\pm$ 9	0.3371	0.0548

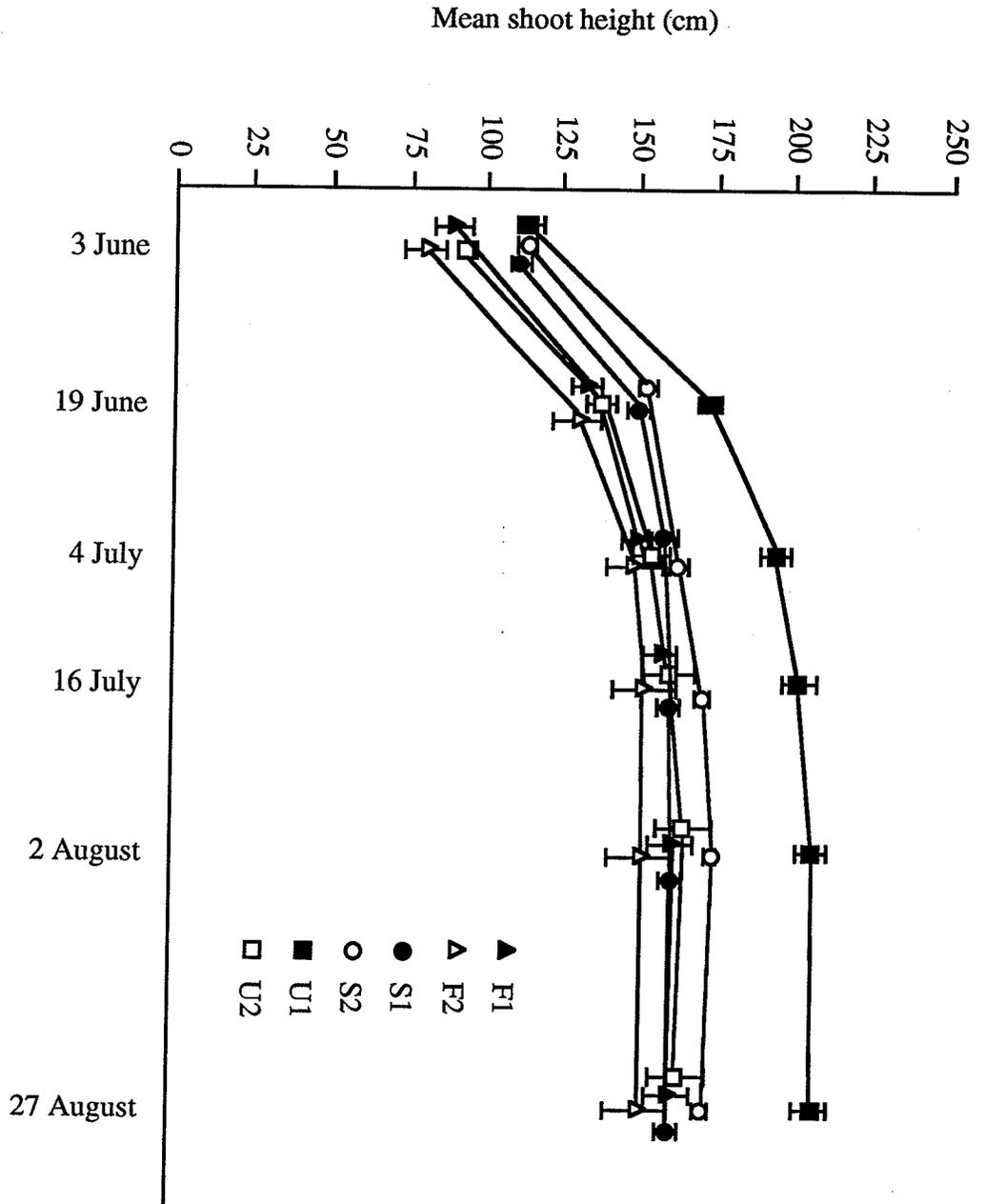


Figure 4.2.6. Mean height ( $\pm 1$  SE) of *Phragmites australis* shoots sampled repeatedly throughout the 1991 growing season. Initial sample size was 20 shoots per study plot, or 120 total; mortality reduced the sample size to a total of 106 shoots. Several sampling dates were omitted for clarity of the figure.

Table 4.2.6. Summary of *Phragmites australis* growth variables (mean  $\pm$  1SE). Shoot density was sampled in May (n=40 quadrats, each 0.25 m<sup>2</sup>) and again in August (n=10 quadrats, each 0.5 m<sup>2</sup>). August samples were partitioned into vegetative and flowering shoots, summed to give totals. Mean biomass per shoot was obtained for each quadrat by dividing aboveground biomass in the quadrat by the number of shoots present. Sample size was n=10 quadrats, 0.5 m<sup>2</sup>. P-values  $\leq$  0.05 indicate significant differences between treatments (Treatment) and/or within treatments (Plot) for each variable.

Treatment	Fall-burned		Spring-burned		Unburned		p values	
	F1	F2	S1	S2	U1	U2	Treatment	Plot
Shoot density (shoots·m <sup>-2</sup> )								
May	100 $\pm$ 5	80 $\pm$ 4	80 $\pm$ 4	104 $\pm$ 5	45 $\pm$ 3	49 $\pm$ 3	0.0027	0.0653
August								
Total	139 $\pm$ 9	126 $\pm$ 7	77 $\pm$ 6	81 $\pm$ 6	53 $\pm$ 5	47 $\pm$ 3	0.0019	0.5747
Vegetative shoots	90 $\pm$ 7	89 $\pm$ 7	64 $\pm$ 6	49 $\pm$ 6	40 $\pm$ 6	36 $\pm$ 3	0.0082	0.4574
Flowering shoots	49 $\pm$ 5	37 $\pm$ 4	13 $\pm$ 4	31 $\pm$ 7	13 $\pm$ 2	11 $\pm$ 2	0.0938	0.0008
Aboveground biomass (g·m <sup>-2</sup> )								
Total	791 $\pm$ 53	734 $\pm$ 65	588 $\pm$ 63	785 $\pm$ 125	402 $\pm$ 30	423 $\pm$ 24	0.0503	0.1363
Vegetative shoots *	374 $\pm$ 31	323 $\pm$ 29	428 $\pm$ 35	394 $\pm$ 31	316 $\pm$ 59	257 $\pm$ 32	0.0523	0.6496
Flowering shoots *	395 $\pm$ 41	349 $\pm$ 65	155 $\pm$ 64	304 $\pm$ 162	123 $\pm$ 43	145 $\pm$ 27	0.0141	0.8654
Mean biomass per shoot (g)								
Total	5.7 $\pm$ 0.3	5.8 $\pm$ 0.4	7.7 $\pm$ 0.6	9.4 $\pm$ 1.0	7.7 $\pm$ 0.3	9.1 $\pm$ 0.5	0.0933	0.0389
Vegetative shoots *	4.2 $\pm$ 0.2	4.0 $\pm$ 0.4	7.6 $\pm$ 1.0	7.0 $\pm$ 0.8	6.6 $\pm$ 0.3	8.9 $\pm$ 1.1	0.0835	0.1863
Flowering shoots **	7.9 $\pm$ 0.4	9.2 $\pm$ 1.0	10.2 $\pm$ 0.9	10.6 $\pm$ 0.8	10.0 $\pm$ 0.2	12.5 $\pm$ 0.8	0.2329	0.1236

\* In several biomass samples, distinctions between vegetative and flowering shoots were not made, and only a total biomass could be reported. Sample sizes were reduced to n=7 in plot F1, n=6 in plot F2, n=7 in plot S1, n=5 in plot S2, n=5 in plot U1, and n=4 in plot U2.

\*\* Where no flowering shoots were present in a quadrat, sample size was further reduced to n=6 in plot S1 and n=4 in plot U1.

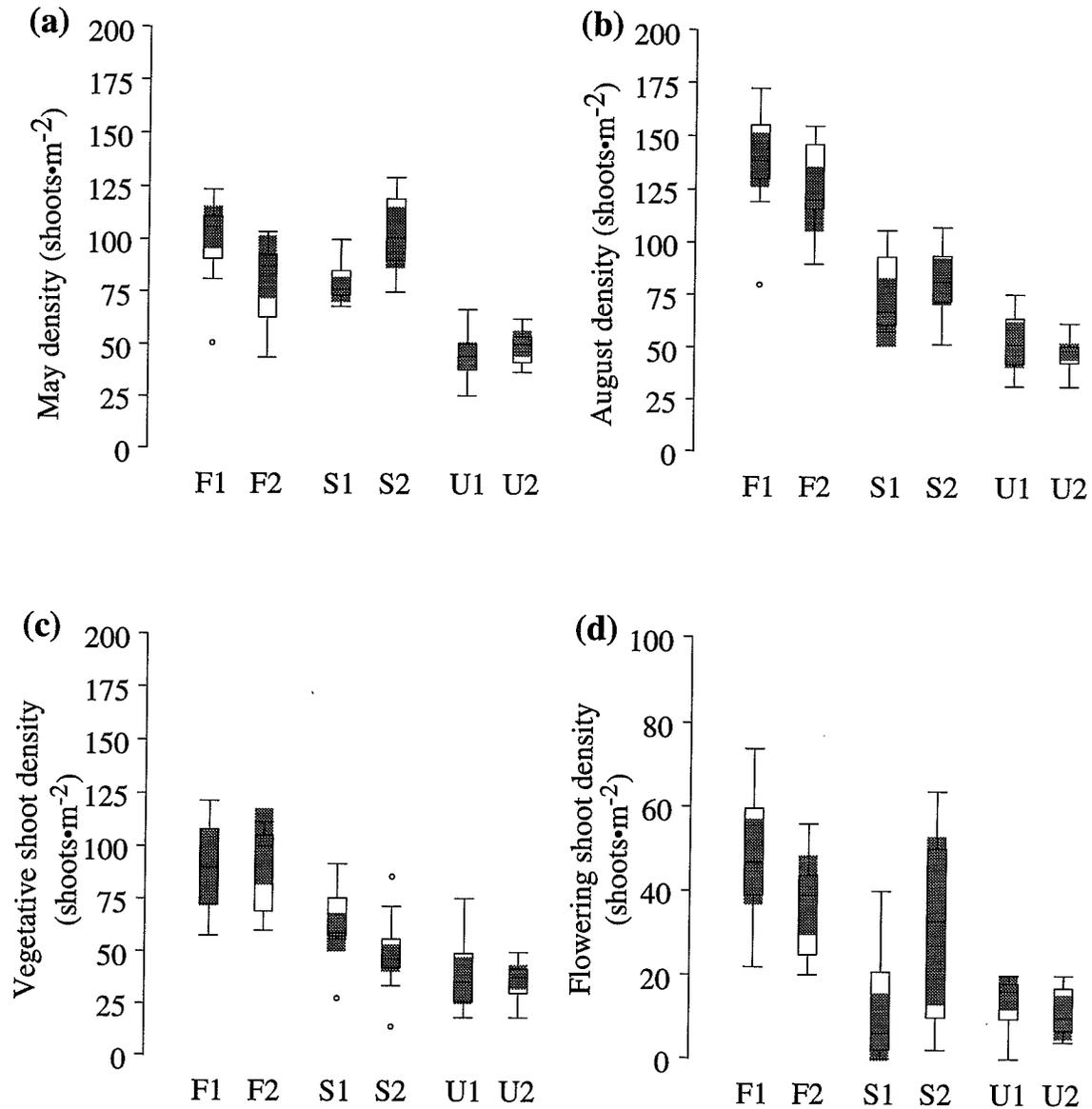


Figure 4.2.7. Density of *Phragmites australis*. (a) May 1991 (n=40 quadrats). (b) August 1991 (n=10 quadrats). (c) Vegetative shoot component in August sample. (d) Flowering shoot component in August sample (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

only marginally significant ( $p=0.0503$ ), due to the variability between the spring-burned plots, which produced 588 and 785  $\text{g}\cdot\text{m}^{-2}$  of aboveground biomass, respectively. Spring-burned plots had the highest mean vegetative biomass, followed closely by fall-burned plots. These increases after burning were marginally significant ( $p=0.0523$ ). Flowering shoot biomass of 395 and 349  $\text{g}\cdot\text{m}^{-2}$  in fall-burned plots was significantly higher ( $p=0.0141$ ) than in unburned plots, which produced 123 and 145  $\text{g}\cdot\text{m}^{-2}$  of flowering shoot biomass, respectively. The small number of flowering shoot samples, especially in spring-burned plots did not obscure the overall trend.

The mean biomass of *P. australis* shoots was lowest in fall-burned plots, while shoots in spring-burned and unburned plots were of similar size (Table 4.2.6, Figure 4.2.9). Variability within the spring-burned and unburned treatments was significant ( $p=0.0389$ ) and appeared to obscure the trend exhibited by shoots in fall-burned treatment, where both vegetative and flowering shoots decreased in size. Reduced sample sizes (as low as  $n=4$ ) may have prevented these trends from being significant.

### ***Phragmites* community characteristics**

The understorey of the three treatments differed greatly in both species composition and abundance (Table 4.2.7).. Fall-burned plots had a sparse understorey, as evidenced by the presence of quadrats containing no species other than *P. australis* (Table 4.2.8). The species richness of spring-burned plots was similar to unburned plots, but the understorey varied greatly within the spring-burned plots, from dense, metre-high patches of *Cirsium arvense*, *Sonchus arvensis*, and *Urtica dioica*, to patches without understorey species. Several species were more abundant in spring-burned plots than anywhere else, notably *Cirsium arvense*. The large amount of *C. arvense* biomass accounted for 79 and 87% of understorey biomass in plots S1 and S2, respectively. Unburned plots had an understorey

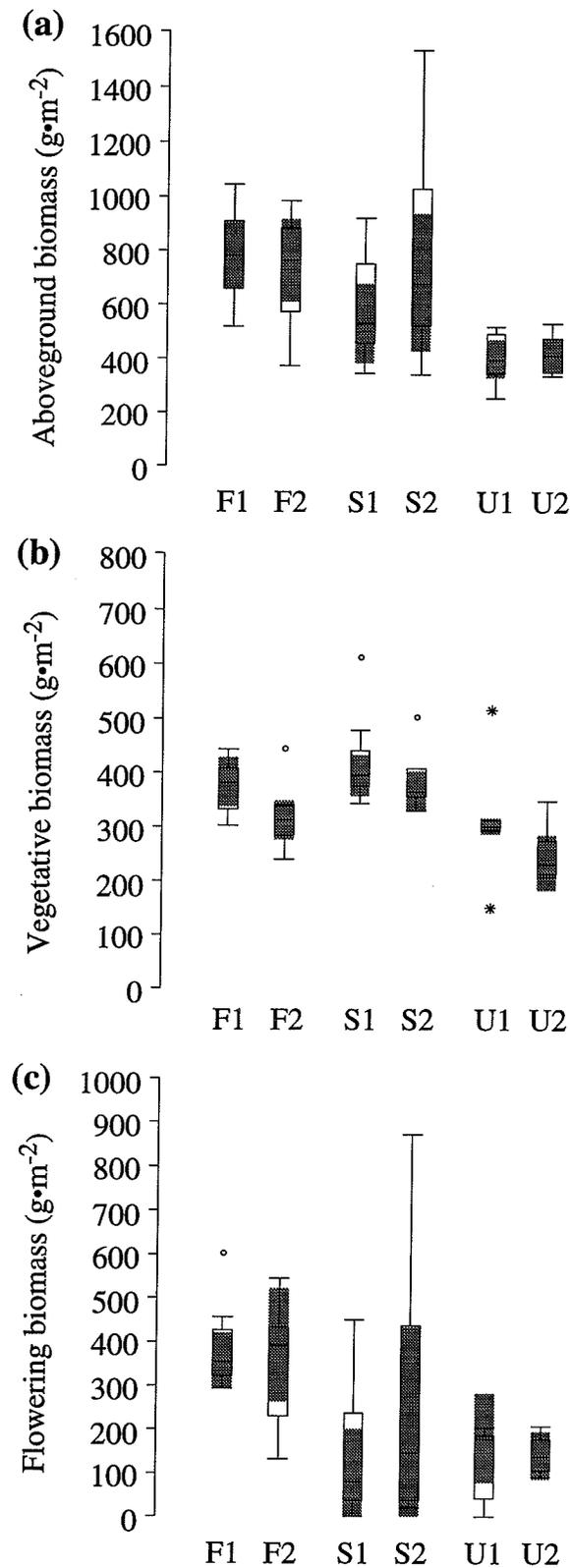


Figure 4.2.8. Aboveground biomass of *Phragmites australis* in August 1991 (n=10 samples per study plot). (a) All *P. australis* shoots. (b) Vegetative shoots. (c) Flowering shoots (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

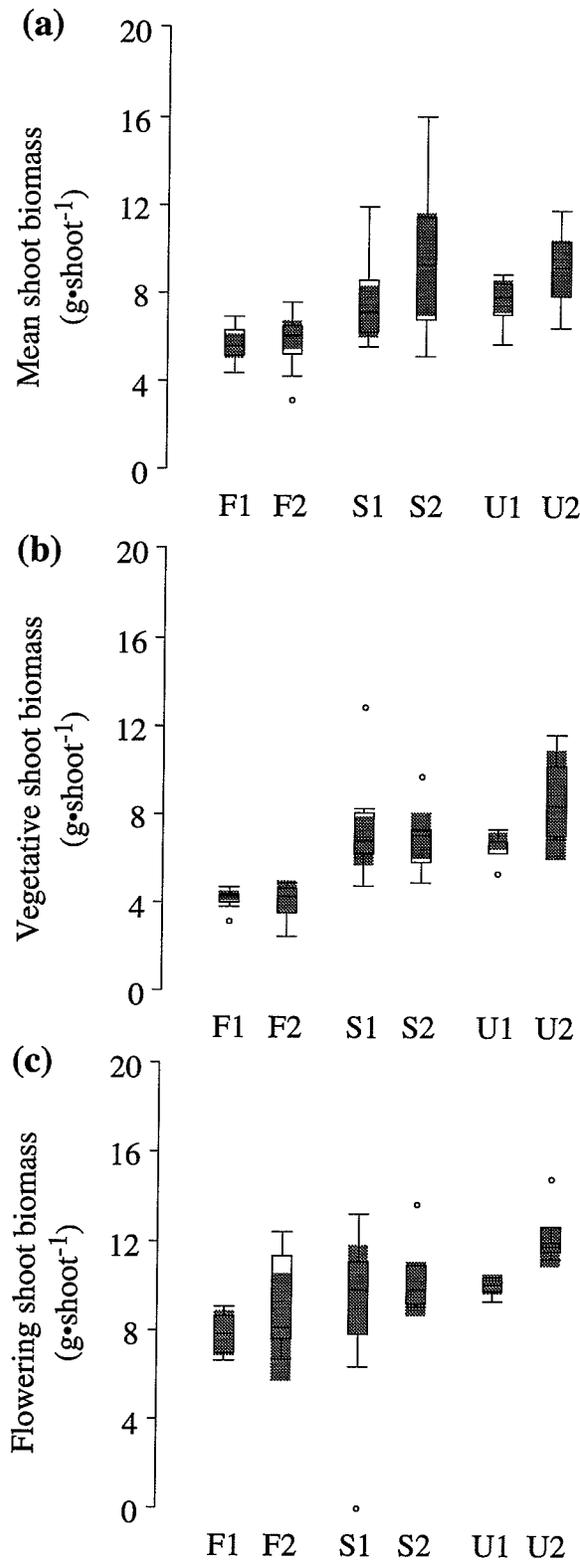


Figure 4.2.9. Mean shoot aboveground biomass of *Phragmites australis* in August 1991 (n=10 samples per study plot). (a) All *P. australis* shoots. (b) Vegetative shoots. (c) Flowering shoots. Sample sizes were reduced where no flowering shoots were sampled (Details in Table 4.2.6) (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

Table 4.2.7. Aboveground biomass ( $\text{g}\cdot\text{m}^{-2}$ ) of species found in *Phragmites* communities. Values denoted by "Tr" indicate trace amounts (mean biomass  $\leq 0.1 \text{ g}\cdot\text{m}^{-2}$ ). Values are means and standard errors (n=10).

Treatment Species	Fall-burned		Spring-burned		Unburned	
	F1	F2	S1	S2	U1	U2
<i>Phragmites australis</i>	791.2 $\pm$ 52.7	733.7 $\pm$ 63.0	588.1 $\pm$ 63.4	785.4 $\pm$ 124.5	402.4 $\pm$ 30.3	423.4 $\pm$ 24.2
Understorey species:						
<i>Cirsium arvense</i>	0	0.7 $\pm$ 0.4	266.8 $\pm$ 58.5	169.9 $\pm$ 39.3	105.4 $\pm$ 20.9	139.4 $\pm$ 19.4
<i>Sonchus arvensis</i>	0	1.1 $\pm$ 0.6	7.5 $\pm$ 4.2	1.1 $\pm$ 1.1	71.4 $\pm$ 11.9	13.9 $\pm$ 8.9
<i>Teucrium occidentale</i>	0	0	5.4 $\pm$ 1.2	7.4 $\pm$ 2.9	8.2 $\pm$ 2.0	19.9 $\pm$ 4.0
<i>Urtica dioica</i>	0	0	4.3 $\pm$ 2.3	7.5 $\pm$ 7.2	8.2 $\pm$ 4.1	8.7 $\pm$ 3.7
<i>Stachys palustris</i>	0	0	0.3 $\pm$ 0.3	24.0 $\pm$ 6.1	1.2 $\pm$ 0.6	0
<i>Chenopodium rubrum</i>	0.2 $\pm$ 0.2	3.6 $\pm$ 2.5	0.6 $\pm$ 0.6	0	0	0
<i>Mentha arvensis</i>	0	0.8 $\pm$ 0.7	0	3.2 $\pm$ 1.2	Tr	0
<i>Lycopus asper</i>	0.9 $\pm$ 0.9	0	0	0.3 $\pm$ 0.2	1.3 $\pm$ 0.7	0
<i>Typha x glauca</i>	33.6 $\pm$ 9.8	92.4 $\pm$ 35.0	0	0	0	0
<i>Carex atherodes</i>	0	0	9.2 $\pm$ 6.5	0	0	5.7 $\pm$ 3.9
<i>Cuscuta gronovii</i>	0	0	2.0 $\pm$ 1.8	0.7 $\pm$ 0.5	0	0
<i>Impatiens capensis</i>	0	0	1.2 $\pm$ 0.5	0.9 $\pm$ 0.9	0	0
<i>Spartina pectinata</i>	0	0	0	0	46.7 $\pm$ 22.7	0
<i>Scolochloa festucacea</i>	0	0	0	0	11.0 $\pm$ 9.8	0

cont'd....

Table 4.2.7 cont'd

Treatment Species	Fall-burned		Spring-burned		Unburned	
	F1	F2	S1	S2	U1	U2
<i>Solidago</i> sp.	0	0	8.6 ± 8.6	0	0	0
<i>Convolvulus sepium</i>	0	0	2.1 ± 2.1	0	0	0
<i>Rumex maritimus</i>	0	1.3 ± 0.6	0	0	0	0
<i>Carex</i> sp.	0	1.3 ± 0.7	0	0	0	0
Unidentified species	0	2.3 ± 1.8	0	0	0	0
Total understorey biomass *	34.7 ± 9.9	103.5 ± 33.7	307.9 ± 64.0	215.0 ± 38.5	253.5 ± 32.5	187.5 ± 20.5
Total community biomass **	825.9 ± 53.1	837.2 ± 68.2	896.1 ± 29.4	1000.4 ± 98.8	655.9 ± 40.7	610.9 ± 27.6
% Understorey ***	3.3 ± 1.0	11.9 ± 3.8	34.2 ± 6.5	25.1 ± 5.5	37.9 ± 4.1	30.5 ± 2.9

\*  $P_{\text{Treatment}} = 0.0747$ ;  $P_{\text{Plot}} = 0.1109$

\*\*  $P_{\text{Treatment}} = 0.0149$ ;  $P_{\text{Plot}} = 0.5087$

\*\*\*  $P_{\text{Treatment}} = 0.0378$ ;  $P_{\text{Plot}} = 0.2011$

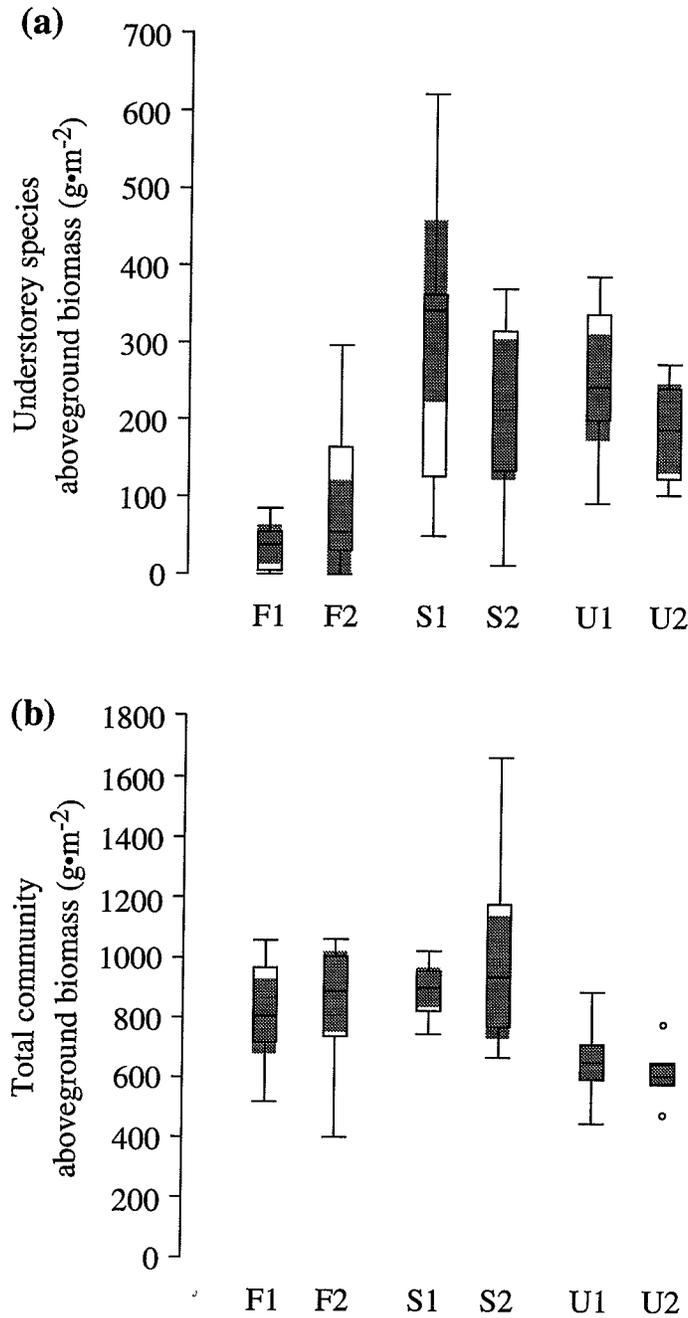


Figure 4.2.10. Aboveground biomass of *Phragmites* communities in August 1991 (n=10 samples per study plot). (a) Understorey species. (b) *Phragmites australis* plus understorey biomass (F1 and F2 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

similar to spring-burned plots. *C. arvense* was the most abundant species in the understorey, accounting for 42 and 74% of the understorey in plots U1 and U2, respectively. *Teucrium occidentale*, one of several Labiateae species, was common in the unburned plots, along with *Scolochloa festucacea* and *Spartina pectinata*.

Fall-burned plots produced little understorey biomass compared with either spring-burned or unburned plots, but this difference was not significant (Table 4.2.7). Spring-burned plots were highly variable (Figure 4.2.10), with plot S1 having a range of approximately 600 g•m<sup>-2</sup>. Understorey biomass as a percentage of total community biomass was significantly lower (p=0.0378) in fall-burned plots than in either spring-burned or unburned plots, which had similar percentages. Plots in both fall-burned and spring-burned treatments had significantly higher community biomass than unburned plots (p=0.0149).

Table 4.2.8. Summary of species richness of *Phragmites* communities in August 1991. Species richness is reported as the total number of species encountered in all quadrats, as well as the maximum, minimum and mean number of species per quadrat (n=10 quadrats, area 0.5 m<sup>2</sup>).

Treatment	Plot	Number of species per quadrat:			
		Total	Max	Min	Mean
Fall-burned	F1	4	3	1	1.9 ± 0.2
	F2	9	6	1	3.8 ± 0.5
Spring-burned	S1	12	7	3	5.1 ± 0.4
	S2	10	7	3	4.8 ± 0.4
Unburned	U1	10	9	5	6.2 ± 0.4
	U2	6	5	3	4.1 ± 0.2

## ***Scolochloa* communities**

### **Overview**

In *Scolochloa* communities, significant variability within the fall-burned treatment was observed for all measured vegetation parameters except for shoot height, resulting in no significant differences between burn treatments. However, the general trend was toward increased shoot density and aboveground biomass of *Scolochloa festuacea* in spring-burned plots. Fall-burned plots tended to have shoot densities similar to unburned plots, but produced smaller shoots and less aboveground biomass. Both fall and spring burning led to increases in the mean species richness and aboveground biomass of understorey species, and consequently to higher proportions of the community consisting of understorey species. However, fall burning did not result in increased community productivity when compared with unburned plots.

### **Growth characteristics of *Scolochloa festuacea***

Emergence of *Scolochloa festuacea* shoots began earliest in fall-burned sites. On 29 April, shoots were observed at the two-leaf stage in fall-burned sites, but were just emerging from the surface in spring-burned sites, and had not yet emerged in unburned sites. However by 24 May, when shoots were tagged and measured for the first time at each site, shoots at fall-burned sites were smallest, and remained so for the entire growing season (Table 4.2.9, Figure 4.2.11). Shoots were significantly smaller in fall-burned plots on all sampling dates except 10 July. High shoot mortality reduced sample sizes by 25% by the end of season. Flowering of *S. festuacea* did not occur in any study plots, and was a rare event throughout the marsh in 1991. As a result, any mention of *S. festuacea* shoots hereafter refers to vegetative shoots only.

Table 4.2.9. Mean height in cm ( $\pm$  1SE) of tagged *Scolochloa festucacea* shoots measured repeatedly throughout the 1991 growing season. Initial sample size was n=20 shoots per plot, or 120 total. Sample size was reduced by shoot mortality to 88 shoots. P-values  $\leq$  0.05 indicate significant differences between treatments (Treatment) and/or within treatments (Plot) at each sampling date.

Treatment	Fall-burned		Spring-burned		Unburned		p values	
	F1	F2	S1	S2	U1	U2	Treatment	Plot
Sampling date								
24 May	20 $\pm$ 1	19 $\pm$ 1	31 $\pm$ 2	33 $\pm$ 2	30 $\pm$ 3	27 $\pm$ 3	0.0024	0.9051
4 June	30 $\pm$ 2	29 $\pm$ 2	53 $\pm$ 2	58 $\pm$ 2	41 $\pm$ 3	47 $\pm$ 4	0.0057	0.6488
10 June	33 $\pm$ 2	40 $\pm$ 2	66 $\pm$ 4	67 $\pm$ 2	46 $\pm$ 4	54 $\pm$ 3	0.0130	0.4580
19 June	40 $\pm$ 3	50 $\pm$ 4	73 $\pm$ 4	78 $\pm$ 3	59 $\pm$ 4	74 $\pm$ 4	0.0379	0.0974
26 June	48 $\pm$ 3	56 $\pm$ 4	80 $\pm$ 4	73 $\pm$ 4	71 $\pm$ 4	82 $\pm$ 5	0.0346	0.1966
4 July	51 $\pm$ 3	59 $\pm$ 3	88 $\pm$ 4	85 $\pm$ 3	76 $\pm$ 5	89 $\pm$ 5	0.0235	0.2766
10 July	57 $\pm$ 3	68 $\pm$ 4	87 $\pm$ 3	87 $\pm$ 3	76 $\pm$ 4	93 $\pm$ 3	0.0621	0.0910
16 July	56 $\pm$ 4	65 $\pm$ 3	86 $\pm$ 4	92 $\pm$ 3	81 $\pm$ 5	91 $\pm$ 3	0.0296	0.2644
2 August	58 $\pm$ 4	63 $\pm$ 3	91 $\pm$ 4	91 $\pm$ 3	84 $\pm$ 4	91 $\pm$ 3	0.0061	0.5883
27 August	54 $\pm$ 3	67 $\pm$ 4	90 $\pm$ 4	92 $\pm$ 4	81 $\pm$ 4	90 $\pm$ 4	0.0323	0.1769

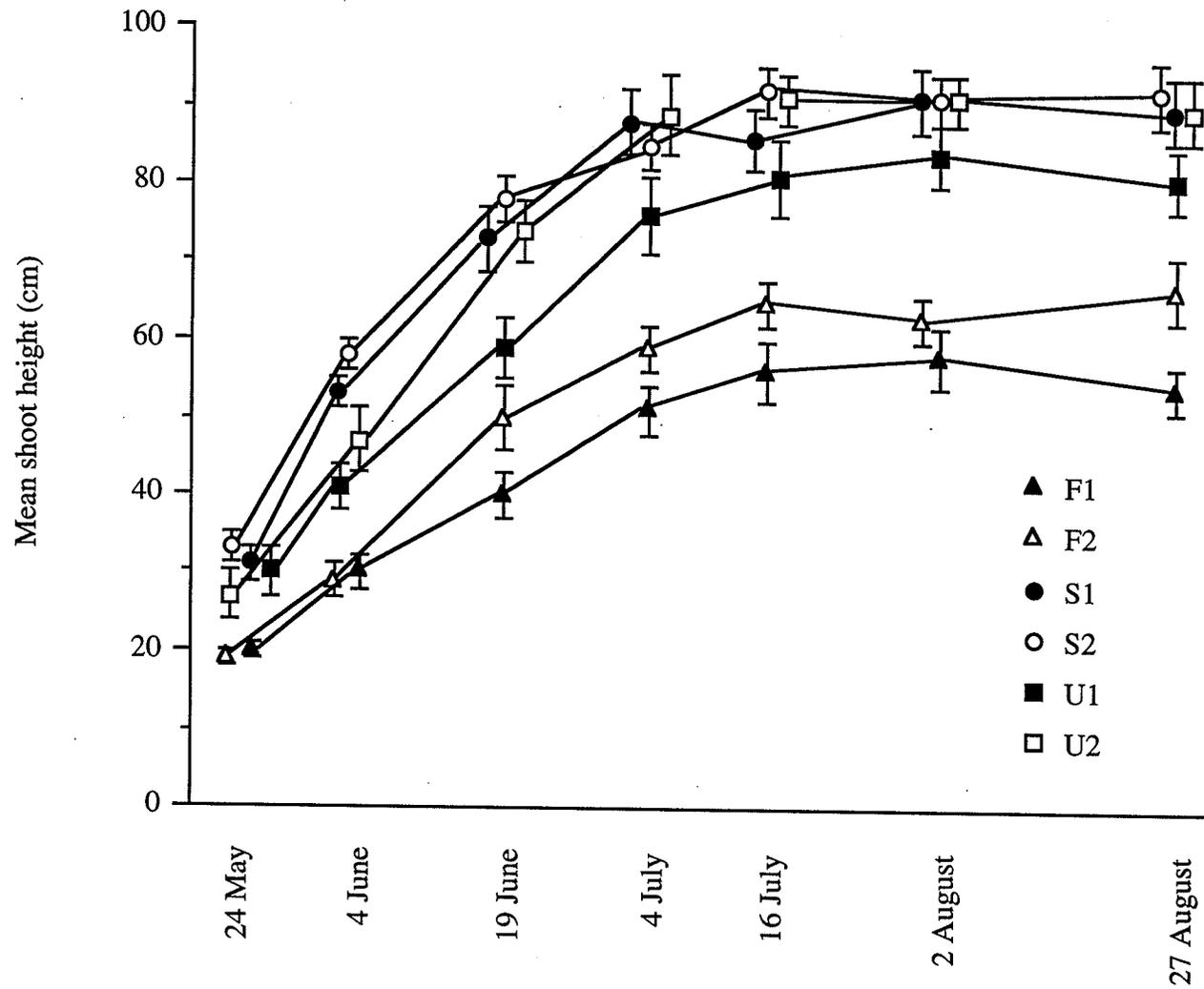


Figure 4.2.11. Mean height ( $\pm 1$  SE) of *Scolochloa festucacea* shoots sampled repeatedly throughout the 1991 growing season. Initial sample size was 20 shoots per study plot, or 120 total; mortality reduced the sample size to a total of 98 shoots. Several sampling dates were omitted for clarity of the figure.

Table 4.2.10. Summary of *Scolochloa festucacea* growth variables (mean  $\pm$  1SE). Shoot density was sampled in May and again in August (n=50 quadrats, each 0.0625 m<sup>2</sup>). August samples did not contain any flowering shoots, so data represent vegetative shoots only. Mean biomass per shoot was obtained for each quadrat by dividing aboveground biomass in the quadrat by the number of shoots present. Biomass sample size was n=30 quadrats, each 0.0625 m<sup>2</sup>. P-values  $\leq$  0.05 indicate significant differences between treatments (Treatment) and/or within treatments (Plot) for each variable.

Treatment	Fall-burned			Spring-burned		Unburned		p values	
	F1	F2	F3	S1	S2	U1	U2	Treatment	Plot
Shoot density (shoots•m <sup>-2</sup> )									
May	611 $\pm$ 28	967 $\pm$ 32	N/A	794 $\pm$ 27	840 $\pm$ 38	773 $\pm$ 32	782 $\pm$ 31	0.9630	< 0.0001
August	587 $\pm$ 28	739 $\pm$ 24	607 $\pm$ 26	684 $\pm$ 28	685 $\pm$ 25	612 $\pm$ 27	611 $\pm$ 32	0.5192	0.0116
Aboveground biomass (g•m <sup>-2</sup> )									
Vegetative shoots	298 $\pm$ 30	815 $\pm$ 44	515 $\pm$ 40	872 $\pm$ 61	856 $\pm$ 39	747 $\pm$ 52	761 $\pm$ 50	0.2523	< 0.0001
Mean biomass per shoot (g)									
Vegetative shoots	0.51 $\pm$ 0.05	1.12 $\pm$ 0.05	0.84 $\pm$ 0.03	1.32 $\pm$ 0.06	1.28 $\pm$ 0.07	1.19 $\pm$ 0.04	1.33 $\pm$ 0.05	0.1031	< 0.0001

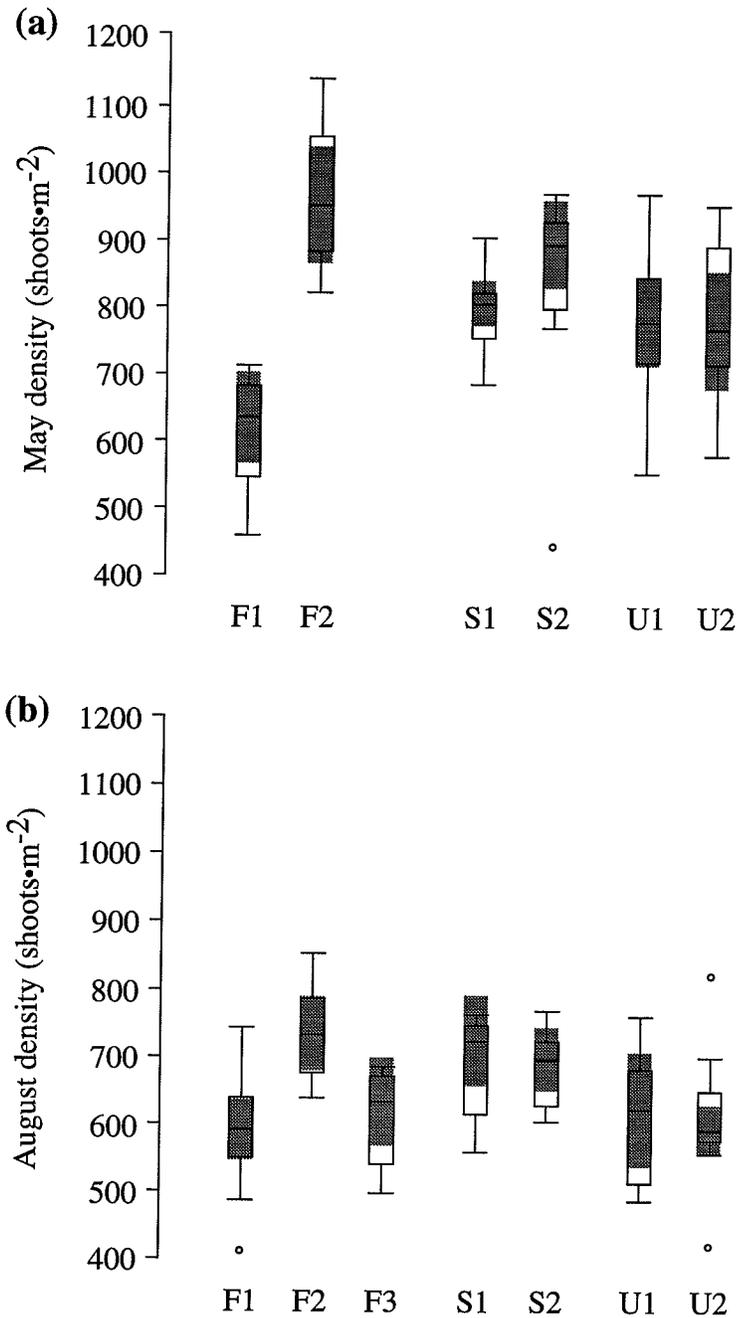


Figure 4.2.12. Density of *Scolochloa festucacea* (n=50 quadrats). (a) May 1991. (b) August 1991 (F1, F2 and F3 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

In May 1991, densities of *Scolochloa festucacea* shoots in plots burned that spring were similar to unburned plots (Table 4.2.10, Figure 4.2.12). Plots F1 and F2 had the lowest and highest mean densities of all plots, at 611 shoots·m<sup>-2</sup> and 967 shoots·m<sup>-2</sup>, respectively, resulting in a significant within-treatment difference ( $p < 0.0001$ ). In August, mean shoot densities of 684 and 685 shoots·m<sup>-2</sup> in spring-burned plots were higher than densities of 612 and 611 shoots·m<sup>-2</sup> in unburned plots, but not significantly so. There was a significant difference within the fall-burned treatment ( $p = 0.0116$ ), following the pattern established in May. Plot F2 had the highest shoot density (739 shoots·m<sup>-2</sup>), while densities of plots F1 (587 shoots·m<sup>-2</sup>) and F3 (607 shoots·m<sup>-2</sup>) were similar to those in other treatments.

The aboveground biomass of *S. festucacea* shoots was highest in the spring-burned plots, at 860 g·m<sup>-2</sup>, followed closely by unburned plots at 750 g·m<sup>-2</sup> (Table 4.2.10, Figure 4.2.13). Plots F1 and F3 had the lowest biomass, but the significant variability between those two plots and plot F2 ( $p < 0.0001$ ) precluded any significant difference between burn treatments.

The mean biomass of *Scolochloa festucacea* vegetative shoots was not significantly different between spring-burned and unburned plots (Table 4.2.10, Figure 4.2.13). Plots F1 and F3 contained smaller shoots than plots in other treatments. Plot F2 again differed significantly from other plots within the fall-burned treatment ( $p < 0.0001$ ).

### ***Scolochloa* community characteristics**

The burn treatments each had a distinctly different understorey (Table 4.2.11). Although *Atriplex patula* was present in all plots, it made up only 11-13% of the understorey biomass of unburned plots. This contrasted with the understorey of fall-burned plots, which contained 99-100% *A. patula*. Spring-burned plots had 46% and 65%

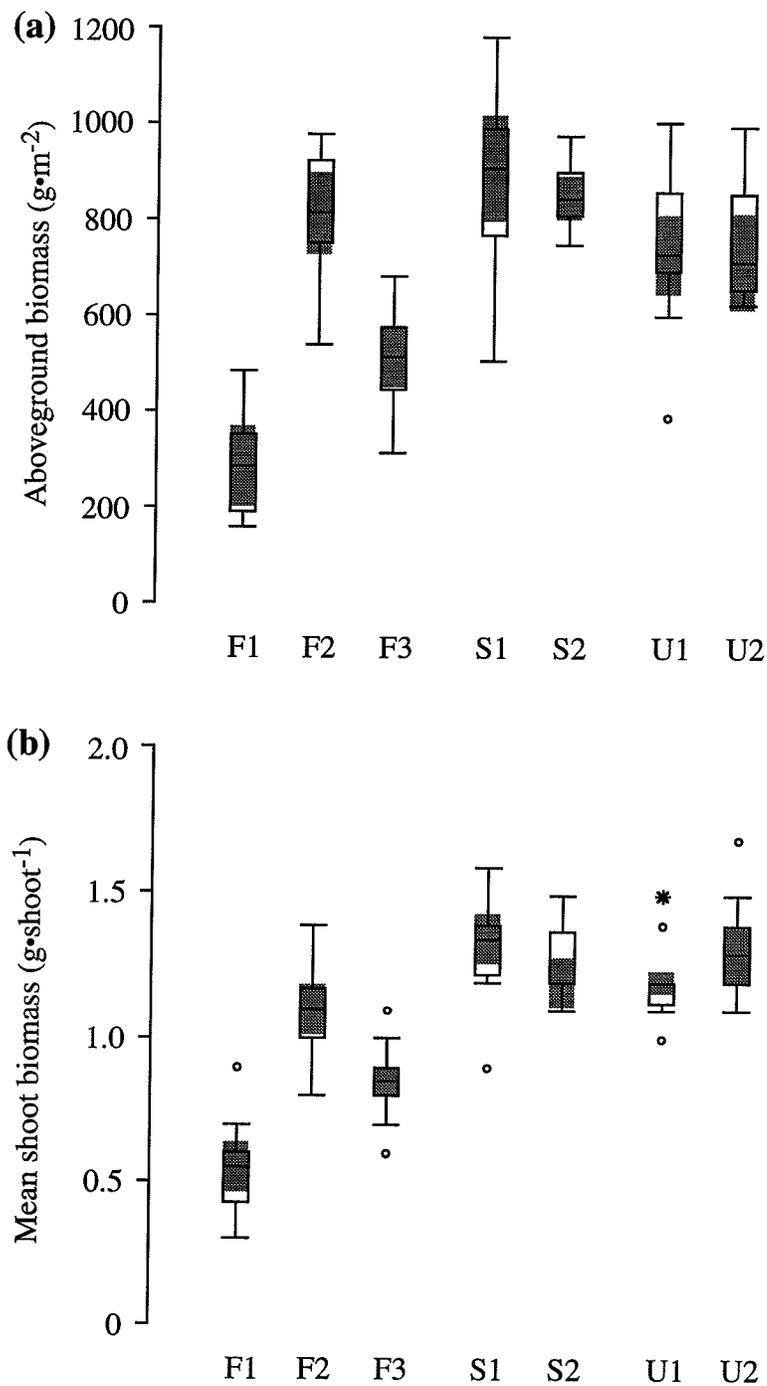


Figure 4.2.13. (a) Aboveground biomass, and (b) Mean shoot biomass of *Scolochloa festucaeae* in August 1991 (n=30 samples per study plot) (F1, F2 and F3 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

Table 4.2.11. Aboveground biomass ( $\text{g}\cdot\text{m}^{-2}$ ) of species found in *Scolochloa* communities. Values denoted by "Tr" indicate trace amounts (mean biomass  $\leq 0.1 \text{ g}\cdot\text{m}^{-2}$ ). Values are means  $\pm$  standard errors (n=30).

Treatment Species	Fall-burned			Spring-burned		Unburned	
	F1	F2	F3	S1	S2	U1	U2
<i>Scolochloa festucacea</i>	297.7 $\pm$ 30.0	814.7 $\pm$ 44.2	515.0 $\pm$ 39.8	871.7 $\pm$ 61.4	856.1 $\pm$ 38.6	747.0 $\pm$ 52.4	760.7 $\pm$ 50.1
Understorey species:							
<i>Atriplex patula</i>	146.9 $\pm$ 15.9	62.8 $\pm$ 6.0	139.8 $\pm$ 14.1	26.9 $\pm$ 7.2	28.1 $\pm$ 8.4	0.8 $\pm$ 0.4	4.1 $\pm$ 1.3
<i>Sonchus arvensis</i>	0	0.3 $\pm$ 0.3	0	0.9 $\pm$ 0.5	15.5 $\pm$ 6.7	6.3 $\pm$ 2.3	25.9 $\pm$ 6.8
<i>Teucrium occidentale</i>	0	0.5 $\pm$ 0.5	1.3 $\pm$ 0.6	12.1 $\pm$ 3.5	10.2 $\pm$ 2.7	0	1.0 $\pm$ 0.5
<i>Cirsium arvense</i>	0	0	0	1.3 $\pm$ 0.8	6.6 $\pm$ 5.3	Tr	0
<i>Mentha arvensis</i>	0	0	0	0	0.4 $\pm$ 0.2	0	0
Total understorey biomass *	146.9 $\pm$ 15.9	63.5 $\pm$ 5.9	141.1 $\pm$ 13.9	41.1 $\pm$ 7.3	60.7 $\pm$ 10.7	7.2 $\pm$ 2.3	30.9 $\pm$ 6.5
Total community biomass **	444.6 $\pm$ 30.6	878.2 $\pm$ 41.6	656.1 $\pm$ 32.6	912.8 $\pm$ 58.2	916.9 $\pm$ 34.3	754.2 $\pm$ 52.5	791.6 $\pm$ 50.4
% Understorey ***	34.6 $\pm$ 3.2	8.2 $\pm$ 1.0	23.3 $\pm$ 2.5	5.8 $\pm$ 1.1	7.2 $\pm$ 1.4	1.2 $\pm$ 0.4	4.0 $\pm$ 0.8

\*  $p_{\text{Treatment}} = 0.0764$ ;  $p_{\text{Plot}} = 0.0003$

\*\*  $p_{\text{Treatment}} = 0.2997$ ;  $p_{\text{Plot}} = 0.0001$

\*\*\*  $p_{\text{Treatment}} = 0.1651$ ;  $p_{\text{Plot}} < 0.0001$

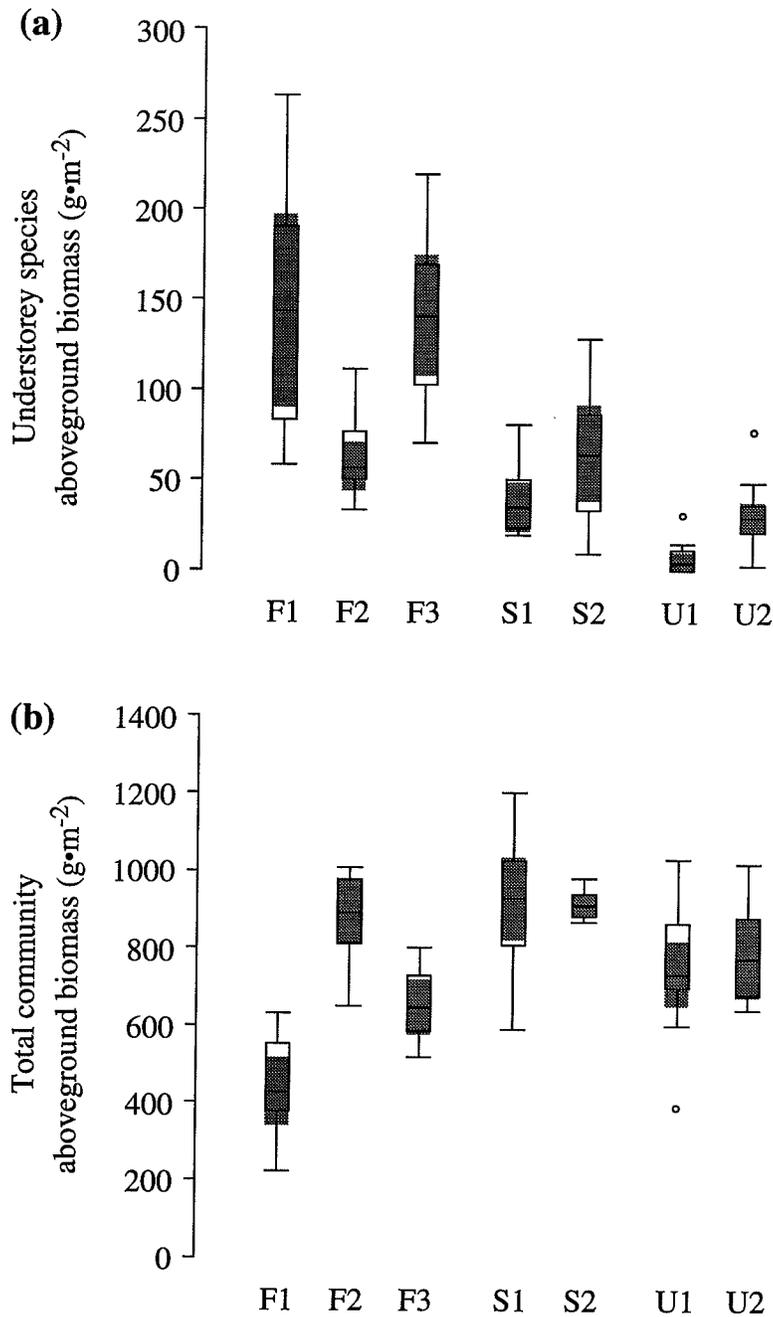


Figure 4.2.14. Aboveground biomass of *Scolochloa* communities in August 1991 (n=30 samples per study plot). (a) Understorey species. (b) *Scolochloa festucaceae* plus understorey biomass (F1, F2 and F3 = fall-burned plots; S1 and S2 = spring-burned plots; U1 and U2 = unburned plots). For an explanation of boxplots, refer to Section 3.5.

*A. patula* biomass in the understorey, but had the highest species richness (Table 4.2.12), and the most even distribution of biomass among those species. Unlike burned plots, *Sonchus arvensis* was the most common understorey species in unburned plots.

Trends in the amount of biomass produced by the understorey species (Figure 4.2.14) were the inverse of trends in the amount of *S. festuacea* biomass (Figure 4.2.13), with the least understorey biomass produced in plots with the most *S. festuacea* biomass. Fall-burned plots had the most understorey biomass, but the variability between them was significant ( $p=0.0003$ ). Despite having the most abundant understorey, plots F1 and F3 still had the lowest total community biomass of all plots (Table 4.2.11).

Table 4.2.12. Summary of species richness of *Scolochloa* communities in August 1991. Species richness is reported as the total number of species encountered in all quadrats, as well as the maximum, minimum and mean number of species per quadrat ( $n=30$  quadrats, area  $0.0625 \text{ m}^2$ ).

Treatment	Plot	Number of species per quadrat:			
		Total	Max	Min	Mean
Fall-burned	F1	2	2	1	$1.97 \pm 0.03$
	F2	4	3	1	$2.03 \pm 0.06$
	F3	3	3	2	$2.17 \pm 0.07$
Spring-burned	S1	6	5	1	$2.70 \pm 0.10$
	S2	6	4	1	$2.90 \pm 0.10$
Unburned	U1	4	3	1	$1.50 \pm 0.10$
	U2	4	4	1	$2.03 \pm 0.10$

## CHAPTER 5 DISCUSSION

Differences in vegetation regrowth between fall-burned, spring-burned, and unburned areas are due not only to the direct effects of burning, but also to the indirect effects that result from the complex interactions between fire and the environment. These potential effects were outlined in Chapter 1. Direct damage to living plant tissues occurs only if they are consumed by the fire, or harmed by the heat the fire produces. However, since the plants in the burned communities were all herbaceous, and both fires occurred when the marsh plant communities were dormant for the winter, any potential heat damage to living tissues was limited to the propagules of species in the seed bank, or to the buds and rhizomes of perennial species. Damage or mortality of plant tissues beneath the soil surface was unlikely, since the high temperatures produced by fire are short-lived and do not extend to appreciable soil depths (Wright and Bailey 1982). The only living plant tissue above ground level would have been the buds of the dominant species, which protrude from the soil in fall in preparation for growth the following spring. They remain covered by litter throughout the winter. In burned areas, these buds survived and produced shoots, despite evidence of charring. Thus, the survival of buds and rhizomes near the soil surface suggested that there was little damage or death of vegetation that could be attributed directly to the burns. Instead, differences in vegetation regrowth after fall or spring burning must have been largely the result of changes in the growing environment.

This natural experiment (Diamond 1986) involved the selection of control sites (unburned) and burned sites that appeared to be similar in all respects, other than the burns. It had all the advantages and disadvantages discussed by Diamond (1986). An experiment such as this is a realistic examination of the results of large, natural fires. It is unlikely that such fires could be duplicated on the same spatial scale by a tightly controlled field

experiment. However, its main drawbacks are the inability to control variables or match sites, since the fires were not planned and data were not collected prior to the burns.

Study sites were chosen as soon as most of the snow had melted in early spring, to allow examination of regrowth as soon as it commenced. At the time of site selection, water levels appeared similar for each community and were, in fact, one of the primary considerations for choosing study site locations. Unfortunately, when the ground thawed and regrowth was well underway, it became apparent that there were a number of differences in water levels and soil variables.

For several reasons, differences in the environmental variables measured in this study should not necessarily be attributed to burning. First, when comparing water levels in the burned and unburned sites, it must be remembered that all the burn sites were small components of the large Delta Marsh complex. The influences of water levels of Lake Manitoba and of the surrounding marsh, far outweigh the effects a fall burn could have on the water table if it led to reduced snow accumulation and subsequent spring runoff. In addition, water level measurements were made the year after vegetation was sampled, in part to examine whether topography varied in study plots. Even after a short time, any burn-related effects on the position of the water table would have disappeared due to the overriding importance of lake levels in marsh hydrology.

Similarly, soil sampling was performed nine months after the fall fire and three months after the spring fire, too late to detect the immediate, short-term changes in soil properties that typically occur after marsh fires (Schmalzer and Hinkle 1992). Soils may also have been less likely to exhibit differences as a result of burning than those in terrestrial systems. Where standing water was present, ash and partially burned material entered the water column rather than being deposited directly onto the soil surface. This appears to decrease the effects of fire on soil properties. Thompson (1982) found no significant increases in soil nitrate or phosphate in flooded portions of burned *Phragmites*

*australis* plots, and hypothesized that these ions were removed in sheet runoff when water levels declined.

It is evident that a number of significant differences in water levels and soil variables were not attributable to fire-related effects, but were probably the result of site differences. Hence, these environmental variables are considered to influence post-fire vegetation regrowth independently of burning treatments. Significant differences in environmental variables will be mentioned in the discussion of vegetation regrowth where it appears that they may have had an influence upon the vegetation.

## **5.1 ENVIRONMENTAL VARIABLES**

### **Weather Conditions**

The weather before each fire influenced vegetation regrowth indirectly because temperature and precipitation affect the moisture content of the plant litter that is burned. In the three weeks preceding the October 1990 fire, only 0.6 mm of rain was recorded (Goldsborough 1991), producing ideal conditions for a fire. In addition, the burn occurred in what is usually the driest period of the year in the marsh. Water levels in Delta Marsh typically fluctuate on a seasonal basis, with high levels in spring after snow melt, and low levels in fall due to evaporation and evapotranspiration exceeding precipitation through the summer (de Geus 1987). The October 1990 fire was, therefore, able to consume virtually all the accumulated plant litter. In contrast, the fire in April 1991 occurred at a time of year when the marsh is normally wettest. Temperatures were unseasonably warm in March and April 1991, so that most of the snow in the marsh had melted, although the ground was still frozen. Precipitation was also above normal for that time. As a result, the litter was saturated and the spring burn left some partially burned plant debris across most of the soil

surface. Patches of standing dead plant material also remained unburned, particularly in slight depressions.

Following the fires, several events illustrated the continued importance of weather on regrowth. In the fall burn, less snow accumulation led to earlier snow melt and soil exposure. The darkened soil surface warmed more rapidly and shoots emerged earlier than in other treatments. Normally, early regrowth would be an advantage for fall-burned sites, but frost and snow in early May retarded regrowth substantially. The spring-burned and unburned sites were less affected because the plants there had not emerged prior to the frost. For the remainder of the growing season, temperatures were slightly warmer than average, which usually would have resulted in drier than normal conditions. However, 1991 was a wet summer, with precipitation 42% above normal between April and August. This high precipitation affected the water regime of the marsh, particularly after a storm on June 26 dropped 97 mm of rain. Water levels increased noticeably after that date and remained high for several weeks, at a time when they are normally decreasing.

Comparing the data from hygrothermographs in fall-burned and unburned stands of *P. australis*, it is evident that burning resulted in consistently higher temperatures and lower relative humidities. The insulating effect of plant litter prevented unburned stands from reaching temperatures as high as where litter was removed during fall burning. Lower relative humidity in the fall-burned stand may have been due to its openness. The shelter provided by plant litter and dead standing shoots in the unburned stand resulted in decreased air circulation compared with the fall-burned stand, where the lack of dead plant material resulted in increased ventilation. Water vapour in the fall-burned stand could thus be dispersed by wind, resulting in lower relative humidity.

## Water Levels and Soils

Table 5.1.1 summarizes the data from environmental variables sampled by comparing the characteristics in each burn treatment directly with characteristics in the unburned treatment.

### *Typha* communities

Although water levels in burned *Typha* plots were significantly lower than in unburned plots, this does not necessarily mean that growth responses in burned sites were confounded by differing water levels. Mean water levels in unburned plots were about 20 cm higher than in fall-burned plots and 10 cm higher than in spring-burned plots. In cases where standing water was not present, the water table was within 10 cm of the surface, a depth where marsh soils generally remain saturated (Neill 1990a). High soil moisture values in all plots confirm that differences in water levels were not sufficient to reduce soil moisture and create non-saturated soil conditions in any study plots. Studies of *Typha* spp. growth responses to a water level gradient by Grace and Wetzel (1982) and by Waters and Shay (1990, 1992) found differences in growth parameters as water depths increased, but usually over a greater range of water depths than those reported here. In addition, their studies were performed at greater water depths than those found in this study, making direct comparisons of water depth effects difficult.

Soil variables in burned plots did not exhibit any trends that could be attributed to burn effects. It is unlikely that decreased pH in burned plots could be a remnant burning effect, since soil pH generally increases after fire (Wright and Bailey 1982). Schmalzer and Hinkle (1992) found that soil pH in *Juncus* and *Spartina* marshes increased immediately after burning, but returned to normal levels in less than one month. The delay between the fires and collection of soil samples in this study (nine months after the fall burn

Table 5.1.1. Summary of environmental variables sampled in the first regrowth season after fall and spring burns, and in unburned marsh plant communities. Variables were described as higher, lower, or not differing from controls after burning ('H' and 'L' signify variable was significantly higher/lower than in unburned treatment; 'h' and 'l' signify variable tended to be higher/lower than in unburned treatment, but not significantly so; '≈' signifies no difference between the treatments. Significant variability within a treatment is denoted by an asterisk (\*).

	Fall-burned treatment vs. Unburned treatment			Spring-burned treatment vs. Unburned treatment		
	<i>Typha</i>	<i>Phragmites</i>	<i>Scolochloa</i>	<i>Typha</i>	<i>Phragmites</i>	<i>Scolochloa</i>
Position of water table	L	H	l*	L	H*	l
Soil moisture	≈	H	h*	h	h	≈
Soil organic matter	≈	H	h*	≈	≈	≈
Soil conductivity	≈	H	l*	≈	h	≈*
Soil pH	l	L	l*	l	≈	d

and three months after the spring burn, respectively) also suggests that soils would not be exhibiting any burn effects. Sites probably differed prior to burning.

### ***Phragmites* communities**

An examination of environmental variables in *Phragmites* communities reveals that differences in soil parameters appeared to be related to differences in water levels, rather than the result of burning effects. For all variables, fall-burned and unburned plots represented the extremes. Fall-burned plots had the highest water levels, soil moisture, soil organic matter and conductivity, as well as lowest soil pH. With the exception of increased soil conductivity, which may be expected after fire (Schmalzer and Hinkle 1992), these trends could not be explained within the context of burning effects. Environmental variables in spring-burned plots all ranged widely and appeared to be related to water levels. Water levels were affected by the slightly sloping topography and sandier soils in slightly elevated areas.

### ***Scolochloa* communities**

Soil pH was the only variable to differ significantly between the *Scolochloa* communities, but as was the case in *Typha* communities, a decrease in pH after fire was not expected or explicable. Fall-burned plots also had significant within-treatment variability in water levels, soil moisture, soil organic matter, and conductivity. Conductivity of plots F1 and F2 was high enough to have been responsible for a number of the significant within-treatment differences in vegetation regrowth (to be discussed later).

## 5.2 EFFECTS OF FIRE ON VEGETATION REGROWTH

Table 5.2.1 summarizes the effects of fall and spring burning on vegetation in the first regrowth season by comparing the vegetation characteristics in each burn treatment with characteristics in the unburned treatment.

### *Typha* communities

#### Growth characteristics of *Typha glauca*

Fall burning resulted in increased *Typha glauca* shoot density, and decreased aboveground biomass. This resulted in shoots that were smaller than in unburned plots, in both mean biomass and mean height. Since flowering shoots did not differ in number or size from unburned plots, these differences were due to the increased production of small vegetative shoots. Spring burned plots exhibited an initial increase in *T. glauca* shoot density compared with unburned plots, but by August, they no longer differed. Shoots in unburned sites emerged noticeably later in the season and May density sampling underestimated their number. Slight decreases in vegetative shoot size (height and mean biomass per shoot) following the spring burn resulted in lower vegetative biomass compared with unburned plots.

Significant decreases in shoot height after both burns did not correspond with the results of Mallik and Wein (1986), who found that spring burning led to a significant decrease in *T. glauca* shoot height under drained conditions, but to a significant increase in shoot height under flooded conditions (50 cm standing water) in a New Brunswick marsh; fall burning did not result in a change in shoot height from controls in either flooding condition. However, Ball (1990) reported a reduction in *Typha* spp. shoot height after early spring burning in southwestern Ontario.

Table 5.2.1. Summary of vegetation characteristics sampled in the first regrowth season after fall and spring burns, and in unburned marsh plant communities. Variables were described as increasing, decreasing, or not differing from controls after burning ('I' and 'D' signify significant increases/decreases compared with unburned treatment; 'i' and 'd' indicate a the variable tended to increase/decrease, but not significantly so; '≈' signifies no difference between the burned and unburned treatments. Significant variability within a treatment is denoted by an asterisk (\*).

	Fall-burned treatment vs. Unburned treatment			Spring-burned treatment vs. Unburned treatment		
	<i>Typha</i>	<i>Phragmites</i>	<i>Scolochloa</i>	<i>Typha</i>	<i>Phragmites</i>	<i>Scolochloa</i>
Shoot height	D	d	D	D	d	≈
Shoot density (May)	I	I	≈*	i	I	i
Shoot density (August)						
Total	I	I	-	≈	i	-
Vegetative shoot	I	I	≈*	≈	i	i
Flowering shoots	≈	i	-	i*	i*	-
Aboveground biomass						
Total	d	I	-	d*	i	-
Vegetative shoots	d	i	d*	d	I	i
Flowering shoots	≈	I	-	i*	i	-
Mean biomass per shoot						
Total	D	d	-	d	≈	-
Vegetative shoots	D	d	d*	D	≈	≈
Flowering shoots	≈	d	-	≈	≈	-
Biomass of understorey species	≈	d	i*	≈	≈	i
Percentage understorey biomass	≈	D	i*	≈	≈	i
Toal community biomass	≈	I	d*	≈	I	i
Mean species richness	≈	d	i	≈	≈	I

Shoot densities in spring-burned and unburned treatments were somewhat higher than the mean density of 40 shoots•m<sup>-2</sup> reported for Delta Marsh sites by Shay and Shay (1986), but were within the typical *T. glauca* density range of 45 to 79 shoots•m<sup>-2</sup> reported under drawdown conditions by van der Valk and Davis (1980) in an Iowa marsh. Given the similarity of water depths between the Iowa site and the sites in this study, it appears that increased shoot density in fall-burned plots can be attributed to the effects of fall burning rather than to water level differences. In contrast, Mallik and Wein (1986) found no change in mean shoot density of 10 to 15 shoots•m<sup>-2</sup>, after fall or spring fires in a New Brunswick marsh, but their conditions differed from those in the present study.

The variability of *T. glauca* flowering shoot density within spring-burned plots is not readily explicable. It is possible that the plots contained clones which differed genetically with respect to the number of flowering shoots they were capable of producing. Alternatively, van der Valk and Davis (1980) suggested that high *T. glauca* flowering shoot densities one year led to lower flowering shoot densities the next year, so that perhaps plot S1 was simply not on the same cycle as other plots, and this trend was independent of any burn treatment.

The increase in *T. glauca* shoot density after fall burning may represent a response by a clonal species to disturbance, where production of a large number of new vegetative shoots ensures the colonization of space created by fire. This response may have been triggered by apical bud damage by fire, or later by frost. Subsequent release of dormant buds on rhizomes from apical dominance resulted in an increase in the number of shoots emerging in spring. Since spring-burned stands did not undergo similar increases in shoot density, their apical dominance presumably persisted.

Given that both fall-burned and spring-burned stands of *T. glauca* began growing earlier in spring than unburned stands, it is surprising that they did not produce more

aboveground biomass during their extended growing season. However, there are a number of reasons why aboveground biomass production might be limited after burning. First, it has been speculated that since rhizomes contain a limited amount of reserves, each shoot in a dense stand receives a smaller allocation of reserves and therefore cannot grow as large as shoots in less dense stands (Thompson 1982). This overlooks the ability of the shoots to produce photosynthate for additional growth beyond the reserves provided in the rhizome. Another possibility is that an extended growing season cannot overcome the limits placed upon shoot size by the size of the bud it originates from. Haslam (1970) stated that in *Phragmites australis*, bud size limits eventual shoot size. In fall-burned plots, it is likely that the lateral buds which developed and emerged were smaller than average, and thus produce smaller than average shoots. These shoots had the photosynthetic potential to grow larger, but their small basal diameters may have made it impossible for them to support themselves if they grew larger. When these shoots reached their maximum size, photosynthate would have been directed to the rhizomes for storage for the remainder of the season. In contrast, shoots in unburned stands, which originated from larger buds, continued growing until they reached a larger size, and thus had less time to direct photosynthate to rhizomes for storage. It is possible that rhizome biomass increased after burning compared with rhizomes in unburned stands, but belowground biomass was not measured. Finally, the dense shoot population may be competing for limited resources such as light, nutrients, or space. This intraspecific competition may be limiting the overall production of the stand.

### ***Typha* community characteristics**

There were no understorey species in unburned stands of *Typha glauca*. In contrast, fall and spring burning resulted in increased species richness compared with unburned plots. Species richness also increased after burning a *Typha* marsh in New Brunswick, although not significantly (Mallik and Wein 1986). Understorey species in burned plots of this study did not greatly alter community structure, as they contributed

0.3% or less to the total biomass. However, their presence was an indication of the change in growing conditions as a result of the fires. Understorey species in the burned plots were either annuals (*Atriplex patula* and *Rumex maritimus*), or seedlings of short-lived herbaceous perennials (*Sonchus arvensis* and *Cirsium arvense*), and were all shade-intolerant drawdown species, with long-lived propagules capable of surviving in the seed bank (van der Valk 1981). While unburned plots may have contained the same propagules, germination was inhibited by high water levels and shading of the surface by plant litter. Thompson and Shay (1989) found that these species were incapable of establishing within existing vegetation and required disturbance to provide an opportunity for colonization. In this study, litter removal through burning allowed more light to reach the soil surface. Along with drawdown conditions present in burned plots, this stimulated germination of ruderal species in much the same way that flooding followed by drawdown does naturally.

Above-normal precipitation in the summer of 1991 contributed to the scarcity of understorey species in *Typha* communities. Prior to the heavy rainfall in June, water levels in burned plots had fallen below the surface from higher levels in early spring. After the heavy rains, however, standing water was again present for several weeks, preventing colonization by understorey species. By the time water levels receded, the growth of *T. glauca* had shaded the soil surface and reduced opportunities for germination that burning had provided. The contributions of understorey biomass was so small that the total aboveground biomass produced in each community was virtually identical to that for *T. glauca* alone.

## ***Phragmites* communities**

### **Growth characteristics of *Phragmites australis***

The regrowth of *Phragmites australis* after fall and spring fires exhibited a number of similarities. Both fall-burned and spring-burned treatments had an immediate increase in shoot density in May, which persisted for the remainder of the growing season. In both burn treatments, this was due to increases in both vegetative and flowering shoot densities. Thompson and Shay (1985) reported similar increases in vegetative shoot densities after burning, but they found that flowering increased after spring burning and decreased after fall burning. This study found that flowering shoots increased after both fall and spring burning, with highest densities in fall-burned plots. The percentage of shoots which flower in a stand is a good performance characteristic, since under optimum conditions, small shoots may flower in addition to large shoots (Haslam 1971). In this study, flowering shoots made up an average of 35% of the total in plot F1, 29% in plot F2, 15% in plot S1, 38% in plot S2, 28% in plot U1, and 24% in plot U2, suggesting that growing conditions after burning were ideal for regrowth and subsequent flowering of shoots. Thompson and Shay (1989) found that in fall and spring burns both decreased the percentage of flowering shoots, and Cowie et al. (1992) found significant increases in percent flowering shoots after spring burning in an English reed bed. Increases in *P. australis* aboveground biomass after both fall and spring burns were similar to trends reported by Thompson (1982). Mook and van der Toorn (1982) also reported significant increases in aboveground biomass after spring burning.

A key difference in *P. australis* regrowth between the two burns was that shoot size (mean biomass and mean height) decreased in fall-burned plots, compared with unburned controls, but remained similar between spring-burned and unburned plots. The decrease in shoot size after fall burning was largely due to the abundance of small vegetative shoots

branching from the base of large, early-emerging (often flowering) shoots, or originating from dead stem bases. This clustered pattern of shoots was also observed by Thompson (1982), who contrasted them with the solitary shoots arising from terminal buds in unburned controls. Decreased shoot size is also due to the restriction of shoot size by bud size. Haslam (1970) stated that the size of buds on the rhizomes of *P. australis* determines the eventual shoot height, with small axillary buds unable to produce shoots as large as those originating from larger, apical buds.

Most of the small vegetative shoots emerged after density sampling occurred in spring, as evidenced by the 40 shoots·m<sup>-2</sup> increase in shoot density observed in fall-burned plots between May and August. The emergence of these shoots in mid-season had a substantial effect on the overall size of the *P. australis* populations in fall-burned plots, resulting in lower mean biomass per shoot than in other plots. This decrease in biomass was not reflected in measurements of shoot height, however, because shoots were tagged for sampling prior to development of the small side shoots, and did not account for their appearance in the population. Furthermore, the tagged shoots adjacent to fall-burned plots contained a higher proportion of flowering shoots than the stand as a whole. Since flowering shoots are generally larger than vegetative shoots (Haslam 1970), these samples represented an overestimate of shoot height for these plots.

There are two possible explanations for the development of shoots in mid-season following a fall burn. According to Haslam (1969), mid-season increases in shoot density are the result of a second round of shoot emergence from buds formed during that growing season, after the early emergence of overwintering buds. Damage to apical buds due to burning or frost provides a stimulus for the formation of additional buds in spring. A different mechanism for density increases was advanced by van der Toorn and Mook (1982) and by Thompson and Shay (1985), who argued that litter removal by fire stimulates new shoot production. They stated that increased light intensity at the soil

surface could promote tillering, presumably of dormant, overwintering buds on rhizomes, resulting in new shoot emergence in mid-season. It is important to attempt to understand these two possible mechanisms for inducing mid-season increases in *P. australis* shoot density, because there was a different response in the two burn treatments. If damage to buds or rhizomes was responsible, then it implies that fall burning did sufficient damage (heat or frost) to rhizomes to cause an increase in density, while spring burning did not. If increased light intensity was responsible for density increases, it indicates that increases were stimulated prior to the spring fire. After the spring fire, growing conditions in the two burn treatments were similar, except for some additional debris left on the soil surface in the spring burn. In the present study, early emerging buds showed some evidence of scorching but still reached maturity, suggesting that apical bud mortality due to fire was minimal. There was also no evidence of frost damage to emerging shoots in spring. However, the possibility of the first mechanism being correct should not be totally discounted, since scorching of buds, rather than bud mortality, may have been sufficient "damage" to induce the production of new buds as suggested by Haslam.

Shoot densities in plots S1, U1 and U2 showed little change between May and August, while the shoot density in plot S2 decreased from 104 to 81 shoots·m<sup>-2</sup>. This decrease did not appear to be simply the result of shoot mortality, since all shoots that had clearly been produced during the season, living or dead at the time of sampling, were included in August sampling. Furthermore, shoot mortality representing a 20% loss was not observed during regular visits to the stand throughout the summer. Thompson and Shay (1985) also found no evidence of mid-season shoot mortality in their study, reporting that shoot density increased in all treatments between June 1 and June 15, then remained relatively steady for the remainder of the season. It is possible that this decrease is an anomaly resulting from the use of different quadrat and sample sizes in the May and August sampling periods, for the reasons outlined in Chapter 3. The reduction from forty to ten

quadrats in August could have resulted in the shoot density in plot S2 being underestimated.

In contrast with the results of fall and spring burns, Shay et al. (1987) found that a summer burn substantially reduced the aboveground biomass of *P. australis*. They found that it was four years before shoot density, aboveground biomass, and mean shoot biomass approached that of control plots. Summer burning modified the regrowth of *P. australis* to a greater extent than either fall or spring burning, and appeared to be a better alternative if the objective of burning was to retard the growth of *P. australis*.

### ***Phragmites* community characteristics**

As with *Typha* communities, unburned *Phragmites* communities were not invaded by additional understorey species during the 1991 growing season. The understorey of unburned plots consisted exclusively of rhizomatous perennial species, with no evidence that any had germinated during that growing season. Shade from *P. australis* and other species, as well as accumulated plant litter on the surface, can inhibit germination of seeds which require intense light and fluctuating temperatures (Thompson and Shay 1989). Given these conditions, perennials can only become established in gaps in the litter, then spread vegetatively.

The two burn treatments allowed the germination of a number of annual species. *Rumex maritimus* and *Chenopodium rubrum* were found in fall-burned plots, while *Impatiens capensis*, *Cuscuta gronovii*, and *Chenopodium rubrum* were found in spring-burned plots. In addition, seedlings of *Cirsium arvense* and *Sonchus arvensis* appeared after fall burning and in some samples after spring burning. The small amount of biomass produced by *Cirsium arvense* and *Sonchus arvensis* in fall-burned plots reflected the fact that this was their first year of growth. Thompson (1982) found that as biennials, their seedlings produced a rosette form the first season, and were able to reach full size and

flower the following year. Disturbance by fire opened up the canopy and allowed invasion early in the growing season by species that could not colonize unburned sites. But, by late June, rapid growth of *P. australis* in burned sites produced dense shade at the soil surface. Growth of shade-intolerant seedlings was greatly reduced, resulting in their small stature and inability to mature and reproduce.

There were 14 species encountered during biomass sampling in spring-burned *Phragmites* plots, compared with 11 in unburned plots, and 10 in fall-burned plots. These findings differed from those of Thompson and Shay (1989), who reported increased species richness after summer burning, but no difference in species richness between fall-burned or spring-burned treatments and unburned controls. However, Cowie et al. (1992) found a consistent, though not significant, increase in species richness and diversity after spring burning and flooding of reed beds in the U.K., and Gryseels (1989) reported increased species richness after winter cutting of *P. australis* marshes in Belgium.

Fall-burned plots produced a sparse understorey, with some quadrats devoid of any species, and others with species in low abundance. Understorey biomass would have been almost nil after fall burning were it not for the presence of *Typha glauca*. The *T. glauca* shoots did not flower and were small in comparison with their normal size. They were on the fringe of a larger stand of *T. glauca* adjacent to the *P. australis* study plots. The selection of these study plots resulted from the difficulty in finding stands of *P. australis* free from the other dominant species and large enough to sample. Community composition appeared to be affected by the significantly higher water levels in fall-burned plots than in other treatments. High water levels resulted in soils being saturated for most of the growing season, and submerged after heavy June rains. Germination of species which require drawdown conditions would have been impossible during this time, and species already growing may also have been set back by this inundation. The scarcity or absence of a number of species common in slightly drier parts of the marsh, notably *Cirsium*

*arvense*, *Sonchus arvensis*, *Teucrium occidentale*, *Stachys palustris*, *Lycopus asper* and *Urtica dioica*, is an indication that soils were too wet to support understorey species typical of other sites.

The understorey of spring-burned and unburned plots was similar in terms of species composition, the amount of biomass produced and the proportion of the total stand biomass composed of understorey species. In the spring-burned treatment, sites chosen for sampling contained an unavoidable water level gradient which may have played a part in the variability of the understorey found there. Understorey species abundance was low where plots were driest, increased as water levels rose, then decreased again where water levels reached the soil surface. In plot S2, the three quadrats with highest water levels also had the lowest understorey biomass. Notably, these three quadrats also had high *P. australis* density and biomass, so that understorey species growth may also have been suppressed by shading and crowding effects exerted by the dominant species. However, the effect of spring burning on understorey species abundance clearly varied based upon water levels, given the observable change in understorey species abundance as one moved along the water level gradient.

Unburned study plots were drier than those in other treatments, with the water table an average of 50 cm below the soil surface. Although soils were moist, they were not saturated, and standing water was not observed in unburned plots at any time during the study. Unburned study plots were surrounded by an upland meadow, dominated by species such as *Scolochloa festucacea*, *Spartina pectinata*, *Cirsium arvense*, *Sonchus arvensis*, and *Urtica dioica*. These species encroached upon the unburned study plots and made up a larger share of the overall biomass than might otherwise have been expected. Thompson (1982), for example, found that understorey species made up only 18% of all biomass in the unburned plots, but in the present study, understorey biomass made up over 30% of the total. The dryness of the unburned plots, and the vegetation data derived from

them, may therefore provide a somewhat distorted picture of a typical *Phragmites australis* community.

Community composition of each plot may also have been affected by differences in the species which had the opportunity to invade each treatment. Apart from established perennials, species with the potential to invade an opening in a marsh plant community must either have viable propagules in the seed bank, or if propagules are short-lived, be established near the opening and release seeds at an opportune time (van der Valk 1981). The seed bank of *Phragmites* communities contained only 13 species in a study performed at Delta (van der Valk 1981), some of which were different from the species encountered in the present study. If seed banks, or the species surrounding the study plots which could disperse seeds, were different in each burn treatment (a possibility, since treatments were spatially separated), this could have been responsible for some differences in the community composition.

Although the total biomass of *Phragmites* communities increased after both fall and spring burning, the community composition of the two burn treatments differed greatly. The small amount of understorey biomass in the fall-burned plots, when combined with the large amount of *P. australis* biomass, exceeded the amount of biomass in the unburned treatment. Spring-burned plots had a combination of moderate amounts of understorey biomass and *P. australis* biomass that resulted in the highest total biomass of any treatment. Thompson (1982) found that both fall and spring burning resulted in significant increases in total aboveground biomass, due in both cases to increased production of *P. australis* but not of understorey species.

## ***Scolochloa* communities**

### **Growth characteristics of *Scolochloa festucacea***

Observations on 29 April indicated, as with the other plant communities studied, that *Scolochloa festucacea* shoot emergence was most advanced in the fall-burned treatment, followed by the spring-burned treatment. These observations are consistent with those of Diiro (1982), who reported significantly taller *S. festucacea* shoots after fall burning compared with spring-burned, mowed, or unburned sites. He attributed the rapid growth to earlier substrate thawing and to increased surface temperatures. In this study, the spring burn did not remove all the litter, so that the substrate surface was subject to less extreme temperatures early in the growing season than in the fall burn, but was still noticeably advanced compared with unburned plots.

The rapid early season growth observed in the fall burn in late April was short lived, as shoots in fall-burned plots were surpassed in height by those in other treatments by 24 May. There are several possible reasons for this change. First, there was the snowfall on 30 April and cold temperatures from 30 April to 5 May. Frost appeared to have serious effects on *Scolochloa festucacea*, unlike *Typha glauca* or *Phragmites australis*. Observations after the snow melted indicated some frost damage, with the most severe effects in the fall-burned treatment. With no litter to insulate the delicate young shoots, many were either killed, or lost a number of early leaves as a result of the frost. There was also the possible effect of plot water levels on shoot height. Unburned plots had the highest water levels and the tallest shoots sampled. Similarly, Diiro (1982) found that *S. festucacea* shoots grew tallest where water levels were highest. However, shoot heights in spring-burned and fall-burned plots differed significantly, despite having similar water levels, suggesting that other factors also influenced shoot height.

Perhaps the most important factor affecting growth of *S. festucacea* in fall-burned plots was high soil salinity. Electrical conductivity of soils in plots F1 and F2, where shoot height measurements occurred, were the highest of any plots sampled. Neckles et al. (1985) stated that *S. festucacea* grows best in soils ranging in conductivity from 2.5 to 7.5  $\text{mS}\cdot\text{cm}^{-1}$ , while in this study, conductivities of soil dilution extracts were as high as 11.1  $\text{mS}\cdot\text{cm}^{-1}$  in plot F1 and 8.9  $\text{mS}\cdot\text{cm}^{-1}$  in plot F2. Most areas of these plots had low shoot density and aboveground biomass, and contained *S. festucacea* shoots which were noticeably stunted.

The lack of significant differences between burn treatments in *S. festucacea* shoot density, aboveground biomass, or mean shoot biomass was due to significant differences within the fall-burned treatment for all these characteristics. Variability in early season shoot density and height measurements between plots F1 and F2 prompted the establishment of a third study plot (F3) in mid-June. It was hoped that some variability between plots could be eliminated by using an additional study plot. However, the results from plot F3 tended to be intermediate between those in plots F1 and F2 in most respects, and did not reduce the variability of the growth parameters studied. The reasons for such large within-treatment variability are not easily discernible. I initially assumed that differences in vegetation were due to the higher soil salinity found in plot F1 than in plot F2. However, plot F3 had the least saline soil conditions of the three fall-burned plots, while exhibiting *S. festucacea* regrowth characteristics intermediate to the extremes of the other fall-burned plots.

The similarity of shoot density, aboveground biomass, and mean shoot biomass in spring-burned and unburned plots was somewhat surprising given the differences in their visual appearance. Spring-burned stands appeared to be denser and more robust, because of the regular distribution of shoots over the area. In unburned stands, mats of plant litter

required additional energy expenditure for shoots to grow into gaps. Shoots were weaker and had a patchy distribution.

All plots had lower *S. festucacea* shoot densities in August than in May. In fall-burned plots, shoot mortality may have been due to high soil salinity, or the lingering effects of the late frost on the earliest emerging shoots. Shoots in unburned plots had weak stems incapable of supporting themselves, which would have been susceptible to breakage and mortality when standing plant litter from previous years shifted, or was stepped upon. This was a concern because unburned plots appeared to be areas of heavy deer traffic. Spring-burned plots contained the most robust shoots, and at the relatively high densities found there, competition and shading may have been the most important factors contributing to shoot mortality.

Diuro (1982) reported *S. festucacea* shoot densities in unburned marshes of 280 and 140 shoots $\cdot$ m<sup>-2</sup> in two consecutive growing seasons. Fall-burned stands showed significant increases in density to 690 and 540 shoots $\cdot$ m<sup>-2</sup> in the same seasons. Density of spring-burned stands also increased to between 410 and 690 shoots $\cdot$ m<sup>-2</sup> one year (increasing with lateness of burning in May), and to 330 shoots $\cdot$ m<sup>-2</sup> the next. These densities were less than most of those found in the present study, but indicate that burning normally leads to increased shoot density in the absence of confounding factors such as soil salinity.

No flowering shoots were found in any of the plots in this study, although flowering shoots were observed elsewhere in the marsh. *S. festucacea* requires flooding from spring thaw until early June to initiate flowering (Neckles 1984). I observed some small areas in unburned and fall-burned plots which contained standing water in early spring, as well as after heavy rains in June, but continuous flooding over that time period did not occur and flowering was not initiated.

Mortality of tagged shoots was approximately 25%. Shoots were more susceptible to damage from repeated handling than those in other plant communities because of their smaller size. Trampling by deer was also evident. van der Toorn and Mook (1984) stated that repeated handling led to increased mortality of *Phragmites australis* shoots. This only appeared to be a problem in *S. festucacea* in this study.

### ***Scolochloa* community characteristics**

Burning created sites for other species to invade which were not available in unburned areas covered with thick litter. Litter accumulations in unburned stands of *S. festucacea* consist of patches where dead stems either fall over and lie flat on the soil surface, or become lodged and remain standing. The small amount of understorey biomass in unburned *Scolochloa* communities indicates how inhospitable these stands are to other species. The increased abundance of *Atriplex patula* after burning, as well as the increased species richness of spring-burned treatments, reflects the improved conditions provided in burned sites. Neill (1994) found that in stands of *S. festucacea* flooded until June, understorey species were virtually absent, while drawdown stands had up to 50% understorey biomass. Low water levels in all plots in this study suggest that other factors must have also contributed to the low biomass of understorey species in all but the fall-burned plots.

The species composition of *Scolochloa* plots in this study were similar to those of Neill (1990b). However, in the most directly comparable plots of his study, the aboveground biomass of understorey species averaged  $145 \text{ g}\cdot\text{m}^{-2}$ , while biomass of *S. festucacea* averaged  $374 \text{ g}\cdot\text{m}^{-2}$ . *Scolochloa* was thus less dominant than in all plots in this study, except for plot F1. However, plot F1 contained only *Atriplex patula* in its understorey, while Neill reported six species in the understorey, two of which were more abundant than *A. patula*. Other plots in the fall-burned treatment of this study had slightly higher species richness, but *A. patula* was still the dominant understorey species.

In fall-burned plots, *A. patula* germinated at high densities in May and June, and produced a virtual carpet throughout the entire treatment. Neill (1990b) states that high densities of *A. patula* seedlings are common on bare exposed mud, and that these seedlings may actually inhibit germination of other species by completely colonizing the surface. The high soil salinity found in fall-burned plots was undoubtedly an important factor affecting community composition. *Atriplex patula*, *Sonchus arvensis* and *Teucrium occidentale*, understory species found in fall-burned plots, are some of the most salt-tolerant plants found in prairie wetlands. They grow in soils with conductivities as high as 76.4, 20.8, and 9.1 mS·cm<sup>-1</sup>, respectively (Kantrud et al. 1989). In comparison, *Cirsium arvense* and *Mentha arvensis*, the understory species found in other treatments but not in fall-burned plots, have only been observed growing where conductivities were 5.0 mS·cm<sup>-1</sup> (Kantrud et al. 1989).

Spring burning stimulated the development of understory species when compared with controls. The most abundant understory species after spring burning was *A. patula*, but in lesser amounts than after fall burning. Instead, spring-burned plots contained a larger number of species, all in relatively small amounts. Partially burned plant material found on the soil surface in spring-burned stands prevented seed germination to the same extent as in fall-burned stands. As well, the vigorous growth of *S. festucacea* in spring-burned plots could have resulted in shading effects that the stunted growth of *S. festucacea* in fall-burned plots did not produce.

In unburned stands, less than 5% of the total biomass in the community was made up of understory species, in sharp contrast to the 28% understory biomass reported by Neill (1990b). Changes due to fire in this study were therefore able to reduce the competitive dominance of *S. festucacea*. In spring-burned plots, the result of burning was a more productive and diverse community. In fall-burned plots, high soil salinity appears to have interfered with the potential for similar vegetation change.

### 5.3 SUMMARY

This study examined the effects of fire on plant communities dominated by *Typha glauca*, *Phragmites australis*, and *Scolochloa festucacea* after fall and spring burns. The focus was on regrowth during the first post-fire season. The performance of the three dominant species and of understorey species in burned sites was compared with unburned controls. Similarities and differences are summarized in Table 5.2.1.

The majority of regrowth variables in spring-burned communities were similar to unburned sites. This suggests that spring burning did not appreciably affect these plant communities. In contrast, fall-burned communities exhibited either increases or decreases in regrowth variables relative to unburned communities. Fall burning produced more marked changes in the environment and on plant regrowth than spring burning.

Post-fire regrowth of *Typha glauca* and *Phragmites australis* exhibited a number of similarities. Both species had higher densities after fall burning than in their respective unburned controls, resulting from increases in the density of vegetative shoots. Although not of the same magnitude, spring burning also tended to result in increased shoot density. Accompanying increased shoot density in all cases were decreases in shoot size, in terms of mean shoot height and biomass

Season of burn did not result in consistent differences in production of aboveground biomass in these plant communities. Both burns resulted in decreased biomass in *Typha*, but increased aboveground biomass in *Phragmites*. *Scolochloa* biomass decreased after fall burning and increased after spring burning.

Characteristics of the understorey in the three communities also produced few consistent differences. Burning had little or no effect on *Typha* communities. The

understorey of spring-burned *Phragmites* communities exhibited little change in species composition and biomass compared with the unburned controls. But, in fall-burned *Phragmites* communities, species richness and understorey biomass both decreased. In *Scolochloa* communities, both burns resulted in increased species richness and understorey biomass.

Most researchers have tended to examine the effects seasonal burning on only one plant community at a time. It is difficult to compare such studies, since conditions vary and growth conditions change from one year to another. This natural experiment took advantage of the opportunity to examine three neighbouring plant communities each burned in both the fall and spring fires.

Despite the fortuitous opportunity to study vegetation regrowth afforded by the two accidental fires, there were a number of drawbacks in this study. First, there was no pre-burn sampling. With no information about the study sites prior to sampling in 1991, it was impossible to say whether significant differences in abiotic variables during the regrowth period were due to pre-burn differences, or to burning effects. Where variables such as soil salinity appeared to influence vegetation regrowth, it became difficult to attribute vegetation change to burning effects alone. The lack of pre-burn data also led to difficulties in choosing similar study sites. Thus, when a range of regrowth characteristics was found within a burn treatment, it was impossible to say whether it was due to burning or some other factor. Although such problems complicate the interpretation of results, they do not invalidate the value of this study. This study demonstrated that burning a number of marsh plant communities in the fall and spring could induce a range of growth responses. If prescribed burning is to be used for management purposes in prairie marshes, the manager should be aware that the results of seasonal burning on different plant communities may not be easily predictable.

This study also showed that one fall or spring burn has little effect on the three dominant species, *Typha glauca*, *Phragmites australis* and *Scolochloa festucacea*. Since the goals of marsh management practices are often to rejuvenate the habitat and promote greater use by wildlife through either decreased vegetation cover, increased amounts of open water, or increased species diversity, a prescribed fall or spring burn of the type studied here would be ineffective.

There are several avenues that could be followed in future research. Earlier studies of *Phragmites* show that summer burns have greater potential for achieving the above-stated management objectives than fall or spring burns, but whether the same applies to *Typha* and *Scolochloa* should be investigated. Field experiments with planned spring, summer and fall burns followed by flooding could indicate whether this combination is more effective as a management tool than either technique alone. Furthermore, investigations using repeated annual burns could provide useful data regarding their long-term effects on marsh plant communities.

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## APPENDIX 1

### VASCULAR PLANTS FOUND IN THIS STUDY

Nomenclature follows Scoggan (1978).

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*Atriplex patula* L.  
*Carex atherodes* Spreng.  
*Carex* sp.  
*Chenopodium rubrum* L.  
*Cirsium arvense* (L.) Scop.  
*Convolvulus sepium* L. var. *sepium*  
*Cuscuta gronovii* Willd.  
*Hordeum jubatum* L.  
*Impatiens capensis* Meerb.  
*Lycopus asper* Greene  
*Mentha arvensis* L. var. *villosa* (Benth.) Stewart  
*Phragmites australis* (Cav.) Trin.  
*Rumex maritimus* L. var. *fueginus* (Phil.) Dusén  
*Scolochloa festucacea* (Willd.) Link  
*Solidago canadensis* L. var. *canadensis*  
*Sonchus arvensis* L. var. *glabrescens* Guenth., Grab., & Wimm.  
*Spartina pectinata* Link f. *pectinata*  
*Stachys palustris* L. var. *pilosa* (Nutt.) Fern.  
*Teucrium occidentale* Gray  
*Typha x glauca* Godr.  
*Urtica dioica* L. ssp. *gracilis* (Ait.) Selander

## APPENDIX 2 SAMPLING TIMETABLE

Abbreviations used: first letter-dominant species (T=*Typha glauca*, P=*Phragmites australis*, S=*Scolochloa festucacea*); second letter-treatment (F=fall-burned, S=spring-burned, U=unburned); number (1, 2, or 3)-plot number.

### 1991

29 April	Inspected burned areas. Identified potential study sites.
8 May	Set up plots SF1, SS1, and SU1. Performed preliminary sampling of shoot density in these plots.
15 May	Set up plots SF2, SS2, and SU2. Sampled shoot density in these plots. Tagged and measured individual shoots at these plots.
23-24 May	Set up all plots in <i>Typha</i> and <i>Phragmites</i> communities. Sampled shoot density in plots TF1, TF2, PF1, PF2, SF1, SS1, and SU1. Tagged and/or measured individual shoots at all plots except PU1 and PU2 (which were yet to emerge).
3-5 June	Set up new PF1 and PF2 plots (other plots were atypical of this community and burn condition). Sampled shoot density in all <i>Phragmites</i> plots, as well as plots TS1, TS2, TU1, and TU2. Measured all tagged shoots.
10-11 June	Measured all tagged shoots.
19-20 June	Set up plot SF3. Measured all tagged shoots.
25-26 June	Measured all tagged shoots.
3-5 July	Measured all tagged shoots.
9-12 July	Measured all tagged shoots. Collected soil samples from plots TF1, TF2, SS1, SS2, SU1, and SU2.
16-19 July	Measured all tagged shoots. Collected soil samples from plots TS1, TS2, PU1, PU2, SF1, and SF2.

- 22-25 July Measured all tagged shoots. Collected soil samples from plots TU1, TU2, PF1, PF2, PS1, PS2, and SF3.
- 29 July-2 August Collected aboveground biomass from all *Scolochloa* plots. Measured all tagged shoots.
- 6-9 August Sampled shoot density and recorded species presence/absence in all *Scolochloa* plots.
- 12-15 August Collected aboveground biomass from all *Phragmites* plots.
- 19-22 August Continued collection of aboveground biomass from all *Phragmites* plots. Collected aboveground biomass from all *Typha* plots.
- 26-27 August Measured all tagged shoots.
- 29-31 August Sampled shoot density and recorded species presence/absence in all *Phragmites* plots. Sampled shoot density and recorded species presence/absence in plots TS1, TS2, TU1, and TU2.
- 5 September Sampled shoot density and recorded species presence/absence in plots TF1 and TF2.

## 1992

- 14-17 July Excavated holes for water depth measurements in all plots. Measured water depths in all *Typha* plots (17 July only).
- 20-21 July Measured water depths in all *Phragmites* plots (20 July) and all *Scolochloa* plots (21 July).

Table A1. Results of soil analyses performed in the three plant communities.

<i>Typha</i>					<i>Phragmites</i>					<i>Scolochloa</i>				
Plot	Soil moisture (% dry mass)	Organic matter (% dry mass)	Conductivity (mS*cm-1)	pH	Plot	Soil moisture (% dry mass)	Organic matter (% dry mass)	Conductivity (mS*cm-1)	pH	Plot	Soil moisture (% dry mass)	Organic matter (% dry mass)	Conductivity (mS*cm-1)	pH
F1	386	49.8	3.87	7.07	F1	294	44.5	6.90	7.00	F1	224	31.0	8.23	7.56
	393	47.9	7.44	6.83		266	42.1	6.22	7.02		387	50.4	8.88	7.33
	351	46.6	5.10	7.09		247	36.1	6.85	7.00		289	32.8	6.61	7.64
	347	46.1	6.93	7.14		340	52.2	7.38	6.71		354	50.0	8.16	7.70
	342	39.3	5.43	7.27		302	45.4	6.67	6.43		396	55.8	9.19	7.53
	346	46.6	5.73	7.27		250	39.3	6.40	6.86		297	41.6	10.13	7.66
	290	37.7	6.62	7.19		266	41.8	5.15	6.62		135	21.7	5.86	7.59
	451	56.8	8.39	6.93		303	50.7	6.21	6.59		127	18.8	9.63	7.65
	335	41.9	3.96	7.15		271	43.8	5.26	6.81		374	52.5	3.50	7.61
	473	52.5	6.99	7.01		283	45.3	8.19	7.25		272	37.9	11.17	7.62
F2	282	33.4	7.15	7.34	F2	354	47.8	6.62	6.52	F2	132	22.8	3.06	7.72
	328	32.6	4.20	7.55		314	45.0	5.95	6.51		135	24.0	2.62	7.77
	477	79.6	8.02	7.35		257	35.0	4.25	6.61		259	42.1	6.50	7.66
	447	48.8	5.96	7.42		257	39.0	5.57	6.62		279	43.4	7.52	7.65
	373	38.1	3.31	7.48		336	44.9	7.68	6.12		289	45.2	5.82	7.68
	415	42.4	6.49	7.19		372	54.1	8.63	6.65		317	49.1	8.78	7.63
	401	44.8	7.22	7.05		394	52.9	8.81	6.65		244	38.2	6.41	7.68
	419	49.2	7.88	7.07		290	41.8	6.58	6.53		191	29.7	7.14	7.59
	401	47.2	5.41	7.33		340	55.6	6.23	6.87		146	28.2	3.96	7.73
	334	23.0	6.49	7.25		279	42.7	6.52	6.55		248	38.0	8.12	7.82
S1	444	42.4	4.26	7.42	S1	54	14.8	0.62	7.31	F3	128	25.6	3.91	7.71
	442	52.2	4.86	7.04		78	17.2	0.70	7.88		100	18.5	3.09	7.72
	499	53.2	5.53	7.29		213	36.8	3.31	7.39		146	27.3	6.49	7.06
	466	48.5	3.52	7.43		331	46.7	5.05	7.33		134	25.5	4.74	7.52
	475	51.0	4.18	7.21		330	40.3	3.50	7.60		201	39.4	6.69	7.42
	474	54.2	4.19	7.39		53	12.4	0.54	7.78		268	46.9	8.42	7.43
	424	50.2	5.31	7.29		266	39.1	3.53	7.59		132	24.2	4.79	7.39
	319	39.3	3.74	7.31		67	15.6	0.69	7.81		162	27.6	5.81	7.62
	490	54.5	6.50	7.26		145	29.0	1.86	7.75		70	12.5	5.08	7.46
	391	44.2	5.10	7.26		106	17.2	1.64	7.99		66	13.0	2.63	7.68
								0.00						
S2	484	55.6	5.71	7.22	S2	235	30.8	2.02	7.62	S1	126	18.5	4.10	8.01
	376	42.7	5.80	7.16		114	17.7	1.00	7.92		144	18.8	4.03	7.89
	496	54.5	4.04	7.18		135	24.3	1.14	7.76		161	28.0	3.82	7.90
	592	51.4	3.61	7.31		158	25.2	1.89	7.99		168	24.4	7.04	7.68
	416	43.6	3.33	7.28		131	25.6	1.17	7.89		225	31.1	3.31	7.80

cont'd....

Table A1. Results of soil analyses performed in the three plant communities (cont'd).

<i>Typha</i>					<i>Phragmites</i>					<i>Scolochloa</i>							
Plot	Soil moisture (% dry mass)	Organic matter (% dry mass)	Conductivity (mS·cm-1)	pH	Plot	Soil moisture (% dry mass)	Organic matter (% dry mass)	Conductivity (mS·cm-1)	pH	Plot	Soil moisture (% dry mass)	Organic matter (% dry mass)	Conductivity (mS·cm-1)	pH			
S2	389	46.9	3.10	7.18	S2	96	19.5	0.88	7.92	S1	146	21.6	4.83	7.67			
	519	56.8	4.31	7.37		290	43.4	2.11	7.22		140	23.7	1.80	8.05			
	412	58.0	3.77	7.32		161	25.5	1.33	7.71		170	27.5	6.34	7.79			
	421	46.2	3.23	7.32		426	56.3	1.84	6.79		184	30.2	4.78	7.75			
	468	50.9	4.00	7.38		289	47.4	1.95	6.96		184	32.2	3.96	8.07			
U1	278	36.1	4.01	7.74	U1	110	23.6	0.85	7.28	S2	128	19.7	2.13	8.09			
	338	48.1	4.08	7.66		151	29.5	1.05	7.41		198	24.3	5.97	7.51			
	437	47.7	6.62	7.64		110	20.3	0.96	7.90		151	20.3	2.46	7.94			
	381	47.8	5.99	7.68		104	21.1	0.60	7.54		216	31.8	1.83	7.70			
	267	36.8	3.71	7.75		144	26.4	1.36	7.78		108	12.9	3.55	7.59			
	384	46.7	4.79	7.74		105	21.3	0.82	7.70		188	25.4	6.54	7.62			
	397	43.6	4.98	7.42		124	25.2	0.95	7.68		102	11.7	3.08	7.78			
	482	51.8	6.63	7.47		92	19.7	0.69	7.50		190	28.1	2.73	7.80			
	489	53.7	7.55	7.22		122	26.5	0.87	7.39		203	29.0	3.09	7.84			
	430	50.0	7.29	7.63		103	23.3	0.68	7.47		157	21.5	2.14	7.85			
	U2	446	56.8	4.84		7.39	U2	150	29.5		0.78	7.18	U1	161	26.0	2.24	8.28
228		32.9	2.72	7.8	120	26.3		0.79	6.94	337	41.9	8.56		7.79			
521		62.1	10.29	7.12	127	25.7		0.76	7.41	168	21.1	4.03		8.03			
264		35.0	5.30	7.14	130	27.7		1.03	7.76	252	38.1	7.50		7.73			
297		40.2	4.85	7.44	96	20.3		0.64	7.43	185	28.3	5.51		7.83			
382		48.5	5.50	7.47	105	20.8		1.26	7.81	109	13.7	3.82		7.96			
503		53.0	7.63	7.54	92	19.6		0.71	7.46	122	17.9	2.00		8.56			
131		17.8	1.66	7.66	107	22.2		0.75	7.68	121	20.0	2.83		8.41			
181		22.8	3.76	7.48	136	27.6		0.83	7.43	144	23.7	1.79		8.61			
291		40.9	8.85	7.29	93	21.6		0.54	6.98	92	16.7	1.62		8.55			
												U2		97	15.6	0.99	8.32
														87	16.4	2.96	8.15
														116	21.1	3.55	8.16
										122	21.3		3.81	8.08			
										176	30.9		5.70	8.03			
										116	21.3		4.16	8.02			
										97	17.6		1.08	8.13			
										135	22.5		1.72	8.23			
										92	18.5		2.20	8.03			
										93	14.7		1.35	8.44			

Table A2. Results of water level and vegetation sampling in *Typha* communities.

Plot	Water level (cm)	Shoot Density (shoots·m <sup>-2</sup> ):				<i>Typha glauca</i> biomass (g·m <sup>-2</sup> ):			Mean biomass per shoot (g):		
		May	August (Total)	Vegetative shoots	Flowering shoots	Total	Vegetative shoots	Flowering shoots	Overall	Vegetative shoots	Flowering shoots
F1	-3	87	101	98	3	513	513	0	5.8	5.8	-
	-1	83	89	85	4	639	639	0	6.5	6.5	-
	-3	81	96	95	1	689	689	0	7.2	7.2	-
	-2	98	90	88	2	779	720	59	6.7	6.3	29.4
	-8	82	118	116	2	551	551	0	7.4	7.4	-
	-8	69	109	102	7	585	488	96	6.2	5.4	24.1
	-7	112	134	134	0	627	579	48	5.1	4.7	23.8
	-8	123	127	126	1	564	524	40	4.4	4.2	19.9
	-8	132	116	114	2	659	619	40	6.2	6	19.9
	-12	100	102	101	1	701	519	181	5.5	4.4	18.1
F2	-5	106	83	76	7	1003	363	641	15.7	8.6	29.1
	-3	57	78	73	5	765	765	0	6.2	6.2	-
	-7	99	120	113	7	519	431	88	5.3	4.7	14.7
	-6	110	122	121	1	600	543	56	8.1	7.5	28.1
	-8	98	120	116	4	567	567	0	4.4	4.4	-
	-7	100	114	110	4	647	556	91	5.9	5.2	22.8
	-8	129	123	121	2	488	392	96	4.3	3.6	15.9
	-9	99	116	109	7	537	451	85	5.1	4.4	21.4
	-8	114	122	122	0	412	382	30	5.4	5.2	14.8
	-6	74	77	70	7	573	460	113	6.1	5.2	18.9
S1	3	61	55	54	1	681	681	0	13.1	13.1	-
	7	27	59	45	14	1285	1009	276	15.7	14	27.6
	6	62	71	49	22	911	255	657	14.7	6.4	29.8
	5.5	52	60	42	18	1216	563	653	19.6	14.8	27.2
	7	78	51	32	19	1073	524	548	14.1	9	30.5
	0	55	67	52	15	1300	822	479	12.7	10	23.9
	1	76	63	44	19	779	358	421	14.4	9.4	26.3
	-1	65	57	44	13	773	681	92	12.5	11.7	22.9
	-3	54	59	44	15	1061	664	397	16.6	13.3	28.4
	-2	66	54	34	20	661	383	279	15.7	12.8	23.2
S2	4	69	60	56	4	927	787	140	16.6	15.1	35.1
	5	47	48	35	13	935	335	600	16.1	9.8	25
	2.5	60	56	54	2	513	470	44	9.9	9.4	21.9
	5	52	59	51	8	654	539	115	19.2	18	28.6
	-2	48	48	47	1	580	580	0	13.2	13.2	-
	-3	63	57	54	3	364	364	0	7.6	7.6	-
	-1	50	55	55	0	551	551	0	9.8	9.8	-
	-4	64	55	55	0	661	661	0	11.4	11.4	-
	-1	50	46	46	0	497	382	115	11.8	10	28.8
	2	52	50	47	3	496	496	0	11.3	11.3	-
U1	10	27	36	36	0	554	554	0	15.4	15.4	-
	12	29	68	43	25	808	376	431	17.6	15.7	19.6
	13	54	50	49	1	718	718	0	15.6	15.6	-
	27	56	57	54	3	760	723	37	21.1	21.3	18.3
	12	67	40	40	0	622	622	0	13	13	-
	3	78	51	45	6	878	733	145	17.6	15.3	72.3
	14	29	67	67	0	886	886	0	17	17	-
	8	70	49	48	1	1436	950	486	16.7	14	27
	14	62	53	51	2	832	832	0	13.4	13.4	-
	10	46	54	50	4	978	978	0	14.8	14.8	-
U2	9	30	62	62	0	816	766	49	12.7	12.4	24.6
	8	36	56	56	0	981	981	0	17.5	17.5	-
	12	23	57	56	1	826	826	0	12.5	12.5	-
	7	24	70	67	3	1179	1096	84	14.4	14	21
	7	12	60	60	0	979	939	40	16.3	16.2	20.2
	12	31	65	65	0	937	866	71	18	17.3	35.6
	8	69	56	51	5	962	816	146	16.6	15.7	24.4
	15	38	60	57	3	1426	1265	161	17	16.2	26.9
	9.5	64	52	43	9	870	713	157	15.5	14.3	26.1
	14.5	41	48	40	8	820	686	135	14.6	13.2	33.6

cont'd...

Table A2. (cont'd)

Plot	Understorey aboveground biomass (g·m <sup>-2</sup> ):						Total understorey biomass	Total community biomass
	<i>Sonchus arvensis</i>	<i>Cirsium arvense</i>	<i>Atriplex patula</i>	<i>Rumex maritimus</i>	<i>Aster</i> sp.	Unknown species		
F1	0	0	0	0	0	0	0	512.7
	0	0	0	0	0	0	0	638.9
	0	0	0	0	0	0	0	689
	0	0	0	0	0	0	0	778.6
	0	0	0	0	0	0	0	550.8
	0.1	0	0	0	0	0	0.1	584.9
	0	0	0	0	0	0.1	0.1	626.6
	0	0	0	0	0	0	0	563.6
	0	0	0	0	0	0	0	658.6
	0	0.4	1.1	0	0	0	1.6	702.2
F2	0	0	0	0	0	0	0	1003.4
	0	0	0	0	0	0	0	765.4
	0	0	0	0	0	0	0	518.7
	0	0	0	0	0	0	0	599.7
	0	0	0	0	0	0	0	566.7
	0	0	0	0	0	0	0	646.7
	0	0	0	0	0	0	0	487.9
	0.1	0	0	0	0	0	0.1	536.7
	0	0	0	0	0	0.3	0.3	412.3
	0	0	0	0	0	0	0	573.1
S1	0	0	0	0	0	0	0	680.5
	0	0	0	0	0	0	0	1285.2
	0	0	0	0	0	0	0	911.2
	0	0	0	0	0	0	0	1216.1
	0.7	0.7	0	0	0	0	1.4	1073.9
	0	0	0	0	0	0	0	1300.1
	0	0	0	0	0	0	0	779.3
	0	0	0	0	0	0	0	772.7
	0	0	0	0	0	0	0	1061.1
	0	0	0	0	0	0	0	661.4
S2	0	0	0	0	0	0	0	926.9
	0	0	0	0	0	0	0	935.1
	0	6.6	5	0	0	0	11.6	525
	0	0	0	0	0	0	0	653.6
	0	0	0	0	0	0	0	579.5
	0.5	0	0.5	0.2	0.4	0	1.6	366
	0	2	2	0	0	0	4	554.7
	0.2	0	2.3	0	0	0	2.5	663.5
	0	0	0	0	0	0	0	496.5
	0	0	0	0	0	0	0	496.3
U1	0	0	0	0	0	0	0	554.4
	0	0	0	0	0	0	0	807.6
	0	0	0	0	0	0	0	717.9
	0	0	0	0	0	0	0	759.9
	0	0	0	0	0	0	0	622.4
	0	0	0	0	0	0	0	878
	0	0	0	0	0	0	0	886.3
	0	0	0	0	0	0	0	1436.4
	0	0	0	0	0	0	0	831.5
	0	0	0	0	0	0	0	978.4
U2	0	0	0	0	0	0	166.1	981.7
	0	0	0	0	0	0	0	981.1
	0	0	0	0	0	0	80.5	906.5
	0	0	0	0	0	0	0	1179.3
	0	0	0	0	0	0	0	979
	0	0	0	0	0	0	0	936.7
	0	0	0	0	0	0	0	961.7
	0	0	0	0	0	0	0	1426.3
	0	0	0	0	0	0	0	869.9
	0	0	0	0	0	0	0	820.3

cont'd....

Table A3. Results of water level and vegetation sampling in Phragmites communities.

Plot	Water level (cm)	Shoot Density (shoots·m <sup>-2</sup> ):				Phragmites biomass (g·m <sup>-2</sup> ):			Mean biomass per shoot (g):		
		May	August (Total)	Vegetative shoots	Flowering shoots	Total	Vegetative shoots	Flowering shoots	Overall	Vegetative shoots	Flowering shoots
F1	-4	81	120	70	50	659	302	356	5.5	4.3	7.1
	-2	51	154	80	74	1051	-	-	6.8	-	-
	-3	105	80	58	22	519	-	-	6.5	-	-
	1	88	132	66	66	915	313	603	6.9	4.7	9.1
	-4	121	148	112	36	650	355	295	4.4	3.2	8.2
	-5	112	174	116	58	902	444	458	5.2	3.8	7.9
	-4	107	164	122	42	964	-	-	5.9	-	-
	2	124	158	98	60	815	414	401	5.2	4.2	6.7
	-4	109	130	86	44	685	384	301	5.3	4.5	6.9
	-2	100	132	94	38	752	406	347	5.7	4.3	9.1
F2	4	61	124	102	22	529	343	186	4.3	3.4	8.5
	-5	71	116	60	56	721	283	438	6.2	4.7	7.8
	-2	82	146	112	34	933	-	-	6.4	-	-
	-3	104	156	108	48	812	447	366	5.2	4.1	7.6
	-6	99	150	106	44	988	-	-	6.6	-	-
	-5	60	148	104	44	886	-	-	6.0	-	-
	-2	93	94	60	34	716	295	421	7.6	4.9	12.4
	-1	44	90	68	22	499	-	-	5.5	-	-
	-8	93	118	98	20	375	241	134	3.2	2.5	6.7
	0	92	118	74	44	879	331	547	7.4	4.5	12.4
S1	-16.5	71	58	58	0	344	344	0	5.9	5.9	0.0
	-33.5	100	102	84	18	569	402	168	5.6	4.8	9.3
	-27	76	106	78	28	925	616	309	8.7	7.9	11.0
	-56	87	94	92	2	568	-	-	6.0	-	-
	-22.5	86	92	70	22	836	-	-	9.1	-	-
	-36.5	73	68	28	40	815	361	454	12.0	12.9	11.3
	-11	68	66	60	6	452	393	59	6.8	6.5	9.9
	-66	85	64	58	6	476	396	80	7.4	6.8	13.3
	-47	77	60	58	2	494	481	13	8.2	8.3	6.4
	-64	76	58	56	2	402	-	-	6.9	-	-
S2	-40	126	88	86	2	525	505	20	6.0	5.9	9.9
	-29	121	54	14	40	524	-	-	9.7	-	-
	-41.5	75	52	44	8	342	-	-	6.6	-	-
	-26	104	108	48	60	1090	-	-	10.1	-	-
	-40	95	74	58	16	557	409	148	7.5	7.1	9.3
	-2	130	98	34	64	1210	333	878	12.3	9.8	13.7
	-25	116	90	50	40	805	366	439	8.9	7.3	11.0
	-5	84	72	46	26	862	-	-	12.0	-	-
	-37.5	89	76	72	4	393	357	36	5.2	5.0	9.1
	-6	99	96	42	54	1545	-	-	16.1	-	-
U1	-49	37	66	48	18	501	-	-	7.6	-	-
	-49	52	44	26	18	392	-	-	8.9	-	-
	-56	43	36	28	8	254	-	-	7.0	-	-
	-50	47	32	18	14	273	-	-	8.5	-	-
	-53	26	46	32	14	408	-	-	8.9	-	-
	-54	31	70	50	20	502	314	188	7.2	6.3	9.4
	-42	42	60	56	4	343	302	42	5.7	5.4	10.4
	-50	67	42	22	20	358	151	207	8.5	6.9	10.3
	-48	51	58	40	18	474	295	179	8.2	7.4	10.0
	-46	50	76	76	0	519	519	0	6.8	6.8	-
U2	-52	37	46	42	4	341	-	-	7.4	-	-
	-52	42	42	36	6	400	-	-	9.5	-	-
	-56	38	50	40	10	481	-	-	9.6	-	-
	-58	43	60	50	10	461	348	113	7.7	7.0	11.3
	-50	62	52	44	8	336	-	-	6.5	-	-
	-51	52	62	42	20	533	-	-	8.6	-	-
	-49	51	48	30	18	426	215	210	8.9	7.2	11.7
	-52	55	32	26	6	344	254	89	10.7	9.8	14.9
	-49	51	50	32	18	534	-	-	10.7	-	-
	-47	63	32	18	14	378	210	168	11.8	11.6	12.0

cont'd...

Table A3. (cont'd)

Understorey aboveground biomass (g•m <sup>-2</sup> ):												
Plot	<i>Cirsium arvense</i>	<i>Sonchus arvensis</i>	<i>Urtica dioica</i>	<i>Teucrium occidentale</i>	<i>Lycopus asper</i>	<i>Mentha arvensis</i>	<i>Stachys palustris</i>	<i>Scolochloa festucacea</i>	<i>Spartina pectinata</i>	<i>Carex atherodes</i>	<i>Cuscuta gronovii</i>	<i>Convolvulus sepium</i>
F1	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	9.14	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
F2	0	0	0	0	0	0	0	0	0	0	0	0
	1.58	4.22	0	0	0	0	0	0	0	0	0	0
	3.62	0	0	0	0	6.46	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	1.84	5.28	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
	0	0.96	0	0	0	1.82	0	0	0	0	0	0
	0	0	0	0	0	0	0	0	0	0	0	0
S1	556	30.1	5.24	11.9	0	0	0	0	0	0	0	21.1
	160	0	0	11	0	0	0	0	0	0	1.1	0
	87.7	0	1.78	7.14	0	0	0	0	0	0	0	0
	341	0	4.86	6.86	0	0	0	0	0	0	0	0
	42.4	0	0	0	0	0	0	0	0	0	0	0
	109	0	0	1.52	0	0	0	0	0	0	0	0
	270	0	0	4.62	0	0	2.52	0	0	65.44	0	0
	202	33.5	8.28	2.12	0	0	0	0	0	8.26	0	0
	331	11.2	0	5.46	0	0	0	0	0	18.36	0	0
	569	0	23.1	3.62	0	0	0	0	0	0	19	0
S2	253	0	0	7.7	0	0.94	19.9	0	0	0	0	0
	90.3	10.9	0	17.2	0	3.76	35.4	0	0	0	3.9	0
	244	0	72.4	0	0	0.78	9.64	0	0	0	0	0
	109	0	0	0	0	2.8	32.5	0	0	0	0	0
	328	0	0	20	0	3.86	3.7	0	0	0	0	0
	0	0	0	0	0.82	0	0	0	0	0	0	0
	224	0	0	6.06	1.92	10.28	24	0	0	0	0	0
	38.3	0	0	23.1	0	10	29.4	0	0	0	0	0
	346	0	2.44	0	0	0	17.9	0	0	0	3.4	0
	65.4	0	0	0	0	0	67.3	0	0	0	0	0
U1	153	72.5	0	7.96	0	0	1.98	0	152.52	0	0	0
	21	94	0.16	7.54	0	0	0.56	0	0	0	0	0
	86.2	119	0	3.3	0	0	0	0	149.26	0	0	0
	104	107	0	15.5	4.8	0	5.68	0	148.86	0	0	0
	126	53.5	37.8	7.14	0	0.26	0.88	0	15.96	0	0	0
	167	34.8	22.8	1.44	0	0	0	0	0	0	0	0
	229	9.76	0.92	6.78	0	0	0	0	0	0	0	0
	35.8	31.5	12.8	0	0	0.76	0	11.06	0	0	0	0
	95.8	81.6	0	11.9	3.32	0	0	0	0	0	0	0
	35.4	110	7.98	19.9	5.04	0.38	2.62	98.54	0	0	0	0
U2	239	0	27.5	7.26	0	0	0	0	0	0	0	0
	159	0	6.8	42.6	0	0	0	0	0	0	0	0
	140	0	0	32.4	0	0	0	0	0	0	0	0
	92.8	0	0	27	0	0	0	0	0	0	0	0
	161	88.3	0	18.5	0	0	0	0	0	0	0	0
	201	21.8	0	26.9	0	0	0	0	0	0	0	0
	182	28.4	1.36	5.86	0	0	0	0	0	0	0	0
	89.1	0	10.5	4	0	0	0	0	0	34.72	0	0
	91.2	0	9.62	21.3	0	0	0	0	0	0	0	0
	38.4	0	30.9	13.1	0	0	0	0	0	21.98	0	0

cont'd...

Table A3. (cont'd)

Plot	Understorey aboveground biomass (g·m <sup>-2</sup> ):							Total understorey biomass	Total community biomass
	<i>Chenopodium rubrum</i>	<i>Solidago canadensis</i>	<i>Impatiens capensis</i>	<i>Typha glauca</i>	<i>Rumex maritimus</i>	<i>Carex sp.</i>	Unknown species		
F1	1.78	0	0	49.88	0	0	0	51.66	710.18
	0	0	0	11.48	0	0	0	11.48	1062.3
	0	0	0	0	0	0	0	0	518.6
	0	0	0	53.94	0	0	0	53.94	969.42
	0	0	0	84.08	0	0	0	84.08	734.26
	0	0	0	73.28	0	0	0	73.28	975.42
	0	0	0	0	0	0	0	0	963.98
	0	0	0	36.18	0	0	0	45.32	860.62
	0	0	0	27.06	0	0	0	27.06	711.98
	0	0	0	0	0	0	0	0	752.34
F2	0.62	0	0	51.56	0	0	0	52.18	581.48
	0	0	0	171.2	0	0	0	177.04	898.22
	0	0	0	36.36	1.9	6.14	0	54.48	987.28
	2.24	0	0	248.3	2.66	0	0	253.24	1065.5
	25.6	0	0	0	0	0	5.7	38.42	1026
	3.06	0	0	125.1	0	2.58	0	130.78	1016.4
	4.16	0	0	0	0	0	0	4.16	719.9
	0	0	0	291.8	6.16	0	0	297.92	796.7
	0	0	0	0	2.62	3.84	17	26.46	401.8
	0	0	0	0	0	0	0	0	878.5
S1	0	0	0	0	0	0	0	624.14	968.48
	0	0	5.1	0	0	0	0	177.18	746.38
	0	0	2.8	0	0	0	0	99.34	1024.5
	0	0	0	0	0	0	0	353	921.02
	5.9	0	0	0	0	0	0	48.3	884.56
	0	0	0.7	0	0	0	0	111.08	926.14
	0	0	1.6	0	0	0	0	343.68	795.54
	0	86.3	0	0	0	0	0	340.44	816.26
	0	0	1.3	0	0	0	0	367.74	861.62
	0	0	0	0	0	0	0	614.36	1016
S2	0	0	0	0	0	0	0	281.76	806.92
	0	0	0	0	0	0	0	161.38	685.5
	0	0	0	0	0	0	0	327.2	669.08
	0	0	0	0	0	0	0	144.36	1234.4
	0	0	0	0	0	0	0	355.58	912.9
	0	0	9.1	0	0	0	0	9.88	1219.9
	0	0	0	0	0	0	0	266.7	1071.9
	0	0	0	0	0	0	0	100.76	962.6
	0	0	0	0	0	0	0	369.92	763.12
	0	0	0	0	0	0	0	132.72	1678
U1	0	0	0	0	0	0	0	388.12	888.66
	0	0	0	0	0	0	0	123.22	514.78
	0	0	0	0	0	0	0	358.24	612.02
	0	0	0	0	0	0	0	386.2	659.32
	0	0	0	0	0	0	0	241.78	650.06
	0	0	0	0	0	0	0	226.5	728.54
	0	0	0	0	0	0	0	246.46	589.9
	0	0	0	0	0	0	0	91.94	449.46
	0	0	0	0	0	0	0	192.68	666.66
	0	0	0	0	0	0	0	279.98	799.26
U2	0	0	0	0	0	0	0	274.22	615.58
	0	0	0	0	0	0	0	208.14	607.98
	0	0	0	0	0	0	0	172.54	653.94
	0	0	0	0	0	0	0	119.72	581.02
	0	0	0	0	0	0	0	268.12	604.1
	0	0	0	0	0	0	0	250.02	782.96
	0	0	0	0	0	0	0	217.16	642.96
	0	0	0	0	0	0	0	138.34	481.84
	0	0	0	0	0	0	0	122.06	656.42
	0	0	0	0	0	0	0	104.46	482.12

Table A4. Results of water level and vegetation sampling in *Scolochloa* communities.

Plot	Water level (cm)	August Density (shoots·m <sup>-2</sup> ):	<i>Scolochloa</i> biomass (g·m <sup>-2</sup> ):	Mean biomass per shoot (g)	Understorey biomass (g·m <sup>-2</sup> ):					Total understorey biomass	Total community biomass
					<i>Atriplex patula</i>	<i>Mentha arvensis</i>	<i>Teucrium occidentale</i>	<i>Sonchus arvensis</i>	<i>Cirsium arvense</i>		
F1	-17	550	291	0.6	79.5	0	0	0	0	79.5	370.1
	-15	618	346	0.7	79.5	0	0	0	0	79.5	425.1
	-15	550	164	0.3	58.7	0	0	0	0	58.7	222.9
	-17	579	251	0.5	153.1	0	0	0	0	153.1	403.7
	-11	486	157	0.3	139.7	0	0	0	0	139.7	297.1
	-13	605	279	0.5	203.7	0	0	0	0	203.7	482.7
	-14	646	357	0.6	249.6	0	0	0	0	249.6	606.4
	-16	675	481	0.6	94.4	0	0	0	0	94.4	575.5
	-17	410	167	0.4	263.5	0	0	0	0	263.5	430.4
	-16	746	484	0.9	147.7	0	0	0	0	147.7	632
F2	-15	669	866	1.4	55.5	0	4.8	0	0	60.3	926.4
	-19	752	945	1.2	50.1	0	0	0	0	50.1	995.2
	-17	733	775	1	82.1	0	0	0	0	82.1	857.1
	-15	851	960	1.3	47.5	0	0	2.7	0	50.1	1009.6
	-17	736	851	1.1	81.1	0	0	0	0	81.1	932.3
	-16	701	774	1	49.1	0	0	0	0	49.1	822.9
	-16	640	539	0.8	111.5	0	0	0	0	111.5	650.7
	-15	656	745	1	65.1	0	0	0	0	65.1	810.1
	-16	800	714	1.1	53.3	0	0	0	0	53.3	767.5
	-15	854	978	1.1	32.5	0	0	0	0	32.5	1010.7
F3	-21	685	540	0.9	84.8	0	0	0	0	84.8	625.1
	-15	534	315	0.6	204.3	0	0	0	0	204.3	518.9
	-23	570	442	0.8	84.3	0	11.2	0	0	95.5	537.1
	-13	502	451	0.8	124.3	0	0	0	0	124.3	575.5
	-22	678	682	1	69.3	0	1.1	0	0	70.4	752.5
	-23	646	580	1.1	137.6	0	0	0	0	137.6	717.9
	-22	496	445	0.9	219.2	0	0.5	0	0	219.7	664.5
	-16	621	646	0.9	156.3	0	0	0	0	156.3	802.7
	-26	662	488	0.7	144.5	0	0	0	0	144.5	632
	-18	675	561	0.8	173.9	0	0	0	0	173.9	734.9
S1	-22.5	560	619	1.3	35.2	0	10.1	0	0	45.3	664.5
	-22	723	766	1.4	25.1	0	1.1	0	0	26.1	792
	-20	765	1183	1.4	11.2	0	11.7	0	0	22.9	1205.9
	-25	640	1063	1.6	22.9	0	9.6	2.7	7.5	42.7	1105.6
	-20	608	874	1.5	6.4	0	16.5	0	0	22.9	896.5

cont'd...

Table A4. (cont'd)

Plot	Water level (cm)	August Density (shoots·m <sup>-2</sup> ):	<i>Scolochloa</i> biomass (g·m <sup>-2</sup> ):	Mean biomass per shoot (g)	Understorey biomass (g·m <sup>-2</sup> ):					Total understorey biomass	Total community biomass
					<i>Atriplex patula</i>	<i>Mentha arvensis</i>	<i>Teucrium occidentale</i>	<i>Sonchus arvensis</i>	<i>Cirsium arvense</i>		
S1	-24	733	997	1.4	10.1	0	10.1	0	0	20.3	1017.1
	-14	570	508	0.9	77.9	0	3.2	0	0	81.1	589.3
	-28	755	980	1.3	2.7	0	44.8	0	4.3	51.7	1031.5
	-28	726	942	1.2	6.4	0	6.4	4.8	1.1	18.7	960.5
	-19	755	786	1.2	70.9	0	6.9	1.1	0	78.9	865.1
S2	-24	605	805	1.1	65.1	0	20.8	2.7	0	88.5	893.3
	-23	739	975	1.5	3.2	1.1	4.3	0	0	8.5	983.5
	-25	608	752	1.2	123.7	0	4.8	0	0	128.5	880
	-21	682	862	1.2	21.9	0	24.5	34.1	0	80.5	942.9
	-18	726	922	1.4	34.1	0	17.6	0	0	51.7	973.3
	-19	771	904	1.2	25.1	0	3.7	0	0	28.8	932.3
	-32	675	778	1.2	0	0	1.6	82.7	6.4	90.7	868.8
	-22	720	900	1.2	6.9	0	3.2	0	0	10.1	910.4
	-30	614	832	1.5	0.5	0	18.7	0	58.1	77.3	909.3
	-28	714	832	1.3	0.5	2.7	2.7	35.2	1.6	42.7	874.7
	U1	-10	694	938	1.5	0.5	0	11.7	0	0	12.3
-2		653	748	1.1	0	0	0	0	0	0	748.3
-13		720	1004	1.4	0.5	0	29.3	0	0	29.9	1033.6
-1		762	880	1.2	0	0	0	0	0	0	879.5
-15		486	696	1.2	0	0	7.5	0	0	7.5	703.5
-10		640	697	1	0	0	0	0	0	0	697.1
-13		576	804	1.2	0	0	14.4	0	0	14.4	818.7
-4		605	710	1.2	5.9	0	0	1.1	0	6.9	717.3
-16		493	603	1.2	0	0	0	0	0	0	603.2
-8		493	390	1	1.1	0	0	0	0	1.1	390.9
U2	-16	586	761	1.2	3.7	0	0	9.6	0	13.3	774.4
	-9	598	641	1.1	2.1	0	0	0	0	2.1	642.7
	-24	701	730	1.4	0	0	0	48	0	48	777.6
	-19	822	996	1.3	0	0	6.4	20.3	0	26.7	1022.4
	-20	582	886	1.7	0	0	0	30.9	0	30.9	917.3
	-11	557	700	1.2	9.6	0	2.1	8	0	19.7	719.5
	-17	669	940	1.4	2.7	0	0	27.7	0	30.4	970.7
	-12	419	624	1.5	9.1	0	0	14.4	0	23.5	646.9
	-18	602	700	1.3	0	0	0	76.8	0	76.8	777.1
	-14	576	630	1.2	13.3	0	1.6	22.9	0	37.9	667.7