

THE EFFECT OF *PHRAGMITES AUSTRALIS* INVASION
ON COMMUNITY PROCESSES IN A TIDAL FRESHWATER MARSH

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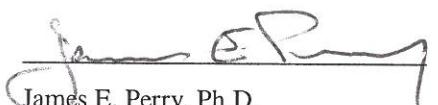
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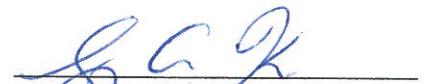
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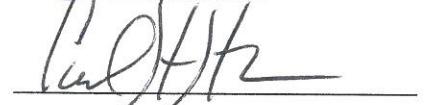
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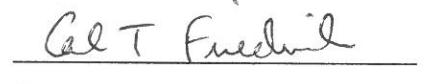
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To everyone who ever believed in me.

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ABSTRACT

Nutrient flux, sedimentation, and plant community structure and species diversity within 3 paired *Phragmites australis* (Cav.) Trin. ex Steud. and *Spartina cynosuroides* (L.) Roth wetland plant communities were compared to investigate the effect of *P. australis* invasion on tidal freshwater marsh processes at Sweet Hall Marsh, Virginia. Nutrient flux (PO_4^{3-} , NH_4^+ , $\text{NO}_3^-+\text{NO}_2^-$, DIN) was measured 3 times during the growing season using a benthic chamber method. Net annual inorganic mass flux and accretion rates were measured using depth of peak ^{137}Cs deposition. Vascular plant species richness, species diversity, species evenness, and community structure were investigated using ground cover, stem density, and frequency of occurrence measurements taken 3 times during the growing season. The invasive *P. australis* communities exhibited lower PO_4^{3-} release to tidal waters late in the growing season (-3.9 $\mu\text{mol m}^{-2} \text{ h}^{-1}$ and 28.3 $\mu\text{mol m}^{-2} \text{ h}^{-1}$ respectively), lower $\text{NO}_3^-+\text{NO}_2^-$ uptake from tidal waters throughout the growing season (-58 $\mu\text{mol m}^{-2} \text{ h}^{-1}$ and -159.9 $\mu\text{mol m}^{-2} \text{ h}^{-1}$ respectively), and slightly higher values of species richness (14.3 and 11.7 respectively) and diversity (1.937 and 1.683 respectively) mid-season than the native *S. cynosuroides* communities. No differences in inorganic mass flux or accretion rates between the two communities were detected. Results indicate that predicting the effect of changes in species composition on community, and potentially ecosystem processes, is dependent on the species' role in the system and the type of process. In addition, invasive *P. australis* communities do not appear to be devoid of water quality (nutrient/sediment buffering) or habitat (richness/diversity) value compared to native communities in this marsh. Recognition of this potential ecological value in other ecosystems should be incorporated into the resource management decision-making process.

THE EFFECT OF *PHRAGMITES AUSTRALIS* INVASION
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INTRODUCTION

One of the primary disturbances being imposed on ecosystems is the loss or replacement of species. The relation of these species changes to ecosystem processes is unclear (Lawton 1994). One method of investigating the impact of species change on an ecosystem is by studying invasive species (Vitousek and Walker 1989). Invasive species are community members that are new to an ecosystem and, usually, invade at the expense of one or more of the original species. The invading species occupies a previously unexploited niche or is a better competitor for the niches occupied by the original species (Elton 1958; Mooney and Drake 1989). The former situation represents an inverse of the problem of species loss; it is a species gain. The latter situation is species replacement and may lead to an overall species loss if the replacement interferes with other niches. In both cases, the invasive species may have an effect on the functioning of the ecosystem.

Common reed (*Phragmites australis* Trin. [Cav.] ex Steudal) is an invasive species along the east and gulf coast of North America (Silberhorn 1991; Hugo 1996; Stapleton 1996). Stable, natural communities of this species are usually found in wetland transition zones from ocean, estuary, river, or lake to upland. They also may be found in groundwater or precipitation fed freshwater marshes or swamps. *P. australis* communities are ubiquitous across Europe and may enhance ecosystem value by contributing to erosion control, water quality, wildlife habitat, and the export of productivity (Ostendorp 1989,1993).

P. australis is regarded by resource managers in the United States to be a pest species of little value. The U.S. Fish and Wildlife Service recommends control of *P. australis* in wetlands (Cross and Fleming 1989). In Virginia, the Virginia Marine Resources Commission (VMRC) Wetlands Guidelines (1993) classify marshes dominated by *P. australis* as Group 5 marshes. These marshes have "few values of significance" and are preferred for development over any other type of coastal wetland except saltwort

communities. Extensive effort and expense is invested towards the control of the *P. australis* invasion (Jones and Lehman 1987; Bryant 1985).

The primary rationale for this effort and expense is that *P. australis* is poor habitat for waterfowl and small mammals that use wetlands. Also, *P. australis* reduces the diversity of native plants when it invades an area and, as an aggressive, rapidly expanding invader, may cause a region-wide decline in habitat and species diversity. These threats and others have been reviewed by Marks *et al* (1994). In addition, *P. australis* clogs drainage ditches, increases the probability of marsh fires, increases the probability of airplane accidents caused by redwing blackbirds (*Agelaius phoeniceus*) that nest in *P. australis* stands, makes monitoring and control of mosquito populations difficult, and obstructs the view of coastal sights by coastal residents and visitors (Hellings and Gallagher 1992). Thus, *P. australis* is considered a deleterious pest species.

The attitudes in Europe diverge widely from those expressed in North America. In Europe, *P. australis* is valued for its contributions to ecosystem functioning. Presently, Europe is experiencing a decline in *P. australis* populations. Concern over this issue in Europe is reflected by dedication of an entire issue of the journal Aquatic Botany (v. 35, 1989) to this one problem. The extreme divergence of opinion in Europe indicates that even as an invasive species, *P. australis* may be a valuable contributor to the functioning of a wetland ecosystem.

In the mid-Atlantic region of the N. American coast, *P. australis* tends to displace vegetative communities characterized by saltmeadow hay (*Spartina patens* [Ait.] Muhl.), big cordgrass (*Spartina cynosuroides* [L.] Roth), and wild rice (*Zizania aquatica* L.) (Silberhorn 1991). *S. cynosuroides* is found in tidal brackish to tidal freshwater marshes along the east coast of N. America (Radford *et al* 1968; Silberhorn 1992). *S. cynosuroides* is morphologically similar to *P. australis*. Both are tall perennial plants that tend to form large, dense, nearly monodominant communities. They are both highly productive with a complex underground system of rhizomes and roots (Gleason and Cronquist 1991). Therefore, the replacement of *S. cynosuroides* by *P. australis* is an excellent case to study the problem of species effects

on ecosystems at a community-level since the confounding effect of physical structural change, another factor relating to ecosystem processes, is limited.

The functions of tidal freshwater and brackish marshes are related to their placement in the estuarine setting. These marshes may play a role in maintaining water quality by nutrient (e.g., Grant and Patrick 1970) and sediment retention (VMRC 1993), providing wildlife habitat (e.g., Odum et al 1984; Odum 1988), minimizing erosion (VMRC 1993), and supporting estuarine fish populations (e.g., Bender and Correll 1974). In addition, tidal freshwater marshes support a diverse assemblage of plant and animal species (Odum 1988). *S. cynosuroides* communities may contribute in varying degrees to these functions, and *P. australis* may change any of these functions when it replaces *S. cynosuroides*.

This study compares the functioning within adjacent communities of *P. australis* and *S. cynosuroides* to evaluate the potential effect of *P. australis* invasion on *S. cynosuroides* communities in a tidal freshwater marsh. For this study, two potentially valuable aspects of tidal freshwater marshes were investigated, water quality and habitat. Water quality incorporates two processes, nutrient flux and sedimentation. Habitat was evaluated using plant community structure and species diversity. This study provides data to help evaluate the management rationale adopted for *P. australis* invasion. In addition, it will provide insight into the relationship of ecosystem processes with respect to community species structure.

LITERATURE REVIEW

I. Biology and Ecology of *P. australis* and *S. cynosuroides*

P. australis is a cosmopolitan perennial grass (Poaceae) of wetland areas. The rapid increase of *P. australis* along the east and gulf coasts of North America over the last few decades has raised speculation that *P. australis* is a recently introduced species or that a new more invasive genotype was recently introduced. Tidal marsh peat cores from Connecticut show evidence that *P. australis* was part of these marshes at least two centuries ago (although exact dating was not done; Niering et al 1977) contradicting the argument that *P. australis* was recently introduced. Isozyme studies in gulf coast marshes indicate a significant genetic variation between invasive and more stable patches of *P. australis* (Hauber et al 1991); this variation may represent a more recently introduced invasive genotype. Hauber et al (1991) also note that this genetic variation is consistent with variation seen in *P. australis* stands of Europe, N. Africa, and C. Asia. At this time, the consensus is that *P. australis* was not introduced recently and is an indigenous species of N. America.

A number of reviews of the biology and ecology of *P. australis* have been written in the past twenty-five years (e.g., Haslam 1971a, 1971b, 1972, 1973; Hocking et al 1983). The following description of the morphology and life history of *P. australis* draws heavily from these reviews.

P. australis is primarily found in wet freshwater habitats. It is capable of surviving in drier areas, but appears to be outcompeted in these areas by other species (Haslam 1971b). It tends to be found most often in areas characterized by stable, shallow, low-flow water conditions. Unstable conditions such as high wave energy can cause stem breakage (Ostendorp 1989). Prolonged high water levels lead to death (Shay and Shay 1986) while higher flow rates lead to competition from other species (Haslam 1971b).

Finally, high salinity inhibits *P. australis* bud formation (Haslam 1971a). Therefore, *P. australis* communities may be found in wetland transition zones from ocean, estuary, river, or lake to uplands. They also may be found in groundwater or precipitation fed freshwater marshes or swamps and on wetland levees. Limiting this potential is the presence of other species assemblages.

The morphology of *P. australis* may be split into the belowground and aboveground system. The belowground system consists of a network of vertical and horizontal rhizomes (underground stems). Rhizomes usually live from 3-6 years, and roots of the vertical rhizomes form a dense mat. Culms (shoots) emerge from vertical rhizomes in early spring and grow to approximately 2-4 m tall, although variation in climatic conditions can lead to significantly taller culms. Culms senesce after one growing season but remain standing throughout the year. Leaves form a sheath on culms and, after the initial transitional leaves, become large (up to 0.5 m; Silberhorn 1991). Culms may terminate in a large panicle inflorescence bearing caryopsis fruits. In addition, long stolons (runners) up to 10 m in length known as legehalme may emerge from above or belowground stems. The basic morphology of *P. australis* is highly plastic and varies depending on environmental conditions (Haslam 1972).

Once an area has been colonized or invaded by *P. australis*, the individual expands by vegetative propagation. Propagation is primarily by rhizome growth although legehalme enhance the speed of expansion. Rhizome growth begins mid-summer as nutrients are translocated from shoots to the rhizomes (Thompson and Shay 1985). In the late summer, buds develop near the base of the vertical rhizomes. Horizontal rhizomes grow from these buds approximately 1 m before turning upward. Next, vertical rhizomes grow near the soil surface and become dormant until spring. In the early spring, culms grow rapidly above the soil surface from the vertical rhizome using stored nutrients in the rhizomes. Culm growth appears to be integrated throughout the rhizome system so smaller shoots are not suppressed by larger shoots (Hara et al 1993). Hara et al (1993) also describe that culm growth is primarily in height; stem diameter does not change through the growing season.

P. australis communities are characterized by the presence of dead and living culms that together form dense stands ($30-65 \text{ culms m}^{-2}$; Silberhorn 1991). A litter mat of toppled culms forms over the

ground because of slow decomposition and physical removal (Haslam 1971a). This litter mat contributes to the survival of the community by inhibiting growth and invasion by other species. As a consequence of this litter mat, early rapid growth, and tall dense shading culms, *P. australis* communities are monodominant and may be monospecific.

Despite this condition, these communities remain highly productive. In lakeshore situations, aboveground productivity has been estimated to range from 551 g m⁻² yr⁻¹ (Mason and Bryant 1975) to 2318 g m⁻² yr⁻¹ (Hopkinson et al 1978). Odum *et al* (1984) summarized studies of *P. australis* productivity for tidal freshwater marshes and calculated a mean annual aboveground productivity of 1872 g m⁻² yr⁻¹. Gallagher and Plumley (1979) estimated belowground productivity at 3649 g m⁻² yr⁻¹ in a Delaware marsh, while Good and Walker (1977; in Good et al 1982) estimated productivity of 2810 g m⁻² yr⁻¹ in a New Jersey marsh. The combination of aboveground and belowground productivity estimates establishes *P. australis* as one of the most productive wetland species.

S. cynosuroides is another perennial grass (Poaceae) found in wetlands but, unlike *P. australis*, exhibits a more limited range. It is distributed almost exclusively in tidal brackish to tidal freshwater marshes along the east and gulf coast of N. America. Within these marshes, *S. cynosuroides* is found above mean high water and below the upland transition in the high marsh area. *S. cynosuroides* may also be found in narrow bands along levees, tidal creeks, and sloughs (Odum et al 1984).

S. cynosuroides forms a dense mat of thick belowground rhizomes and roots (VMRC 1993). Rhizome growth can cause rapid and extensive expansion of *S. cynosuroides* communities. Culms emerging from rhizomes of *S. cynosuroides* are tall (2-4 m), and covered by a large number of long 0.5 - 1.5 m leaf blades. The blades are characterized by micro-serrated edges. In late August and September, a large coarsely branched inflorescence develops terminally above the leaves of the culm (Silberhorn 1992).

S. cynosuroides communities are dense (100-160 culms m⁻²; Silberhorn 1992) and often monodominant. Stand density is a component that makes *S. cynosuroides* one of the most productive wetland species. Aboveground productivity has been reported as low as 1355 g m⁻² yr⁻¹ for a brackish marsh of the Louisiana coast (Hopkinson et al 1978) to as high as 3080 g m⁻² yr⁻¹ for a Georgia brackish

marsh (Schubauer and Hopkinson 1984). For tidal freshwater marshes, Johnson (1970) reported a productivity of $1572 \text{ g m}^{-2} \text{ yr}^{-1}$ in Maryland (in Odum et al 1984) whereas Booth (1989) calculated a productivity of $2462 \text{ g m}^{-2} \text{ yr}^{-1}$ in Virginia. Booth (1989) also estimated a belowground productivity of $4544 \text{ g m}^{-2} \text{ yr}^{-1}$ for the same study. This estimate is similar to the $4628 \text{ g m}^{-2} \text{ yr}^{-1}$ reported for the Georgia brackish marsh (Schubauer and Hopkinson 1984) and higher than another estimate, $3562 \text{ g m}^{-2} \text{ yr}^{-1}$, from the same area (Gallagher and Plumley 1979). Hackney and de la Cruz (1986) estimated a much lower number, $2200 \text{ g m}^{-2} \text{ yr}^{-1}$, for a Mississippi brackish marsh. The variability in measurements for *S. cynosuroides* communities does not mask the overall productivity of these communities.

P. australis and *S. cynosuroides* share in common their morphology and life history characteristics. As a part of marsh vegetative community structure, they are nearly identical. Physiologically however, they are different species, and these differences may have a significant effect on their contribution to ecosystem processes. Physiological differences are represented by the wider niche of *P. australis*. In addition, *P. australis* uses a C₃ pathway for carbon fixation (Gloser 1978) whereas *S. cynosuroides* uses a C₄ pathway (Giurgevich and Dunn 1981). This difference may have a significant impact on productivity and nutrient use (Ramakrishnan and Vitousek 1989). Therefore, the impact of changing from *S. cynosuroides* to *P. australis* may depend on the relative importance of vegetative morphology or physiology to ecosystem processes.

II. Ecological Values of Tidal Freshwater Marshes

II. A. Water Quality

II. A. 1. Nutrient Flux: Eutrophication is a major problem in water bodies that serve as drainage basins for marshes. Eutrophication is a process where excess nutrients enter a body of water, causing overgrowth of algae and other aquatic plants. This overgrowth can lead to oxygen depletion in the water, which can kill fish and other aquatic organisms. Eutrophication is caused by various factors, including agricultural runoff, urban wastewater discharge, and atmospheric deposition. It is a complex issue that requires a multi-faceted approach to address effectively.

Consequent decomposition of these blooms can cause hypoxic and anoxic conditions that affect other species in these water bodies. The Chesapeake Bay experiences eutrophication during the summer in its bottom waters as stratification and microbial oxygen consumption leaves these waters hypoxic (Smullen et al 1982).

Tidal freshwater marshes form borders along the gently grading coasts of estuaries in the transition from open water to upland. The placement of these marshes in the landscape implies that they could provide a protective buffer to estuarine waters from nutrient loads (Simpson et al 1983a). Studies of wetlands in this landscape position determined that they may serve as a nutrient sink (e.g., Grant and Patrick 1970), source (e.g., Stevenson et al 1977), or transformer (e.g., Mason and Bryant 1975) to the estuary. The role any individual marsh may play is influenced by the surrounding landscape and the temporal scale considered. Seasonal and spatial variation of these marshes is high (Simpson et al 1983b). If these marshes are sinks for nutrients, they may also act as buffers to the surrounding estuary. If they act as transformers, they may shift the time of nutrient loading to a time of the year such as the winter months when the estuary is less vulnerable to algal blooms (Mason and Bryant 1975).

The processes involved in wetlands that may provide their nutrient buffering capability are microbial transformations, biological uptake, and burial in sediments. The importance of these three processes is temporally and spatially variable.

Microbial transformations are important for consideration of nitrogen retention. In coastal systems, nitrogen is usually the limiting nutrient for biological growth. The primary microbial process for loss of nitrogen from aquatic systems is denitrification. Denitrification converts nitrate to gaseous nitrogen that escapes into the large atmospheric pool. This process occurs in anoxic environments. The rate of denitrification is limited primarily by the nitrification rate in wetlands that are not receiving large amounts of anthropogenic nitrate runoff (Bowmer 1987). Nitrification converts ammonium to nitrate, thus, providing the precursor for denitrification from the largest pool of nitrogen in wetlands, ammonium. Denitrification is the only process that leads to loss, not storage, of nutrients from aquatic systems.

Biological uptake may provide a short- (monthly) or long-term (annual) sink for nutrients. Plants and microbes use nutrients for growth and remove it from sediment and interstitial waters. The greater the productivity and ratio of nutrients to carbon in the organism the greater the uptake of nutrients. Nutrients taken up by plants are either released back into the system by decomposition or stored by perennial plants over multiple growing seasons. The latter processes are key aspects of long-term storage of nutrients in wetland systems.

Sediment burial is a long-term sink for nutrients. It is dependent, in part, on the efficiency of biological uptake from sediments, the rate of biological release, and the overall sedimentation rate. Slow decomposition rates because of anoxic conditions may cause a high organic soil content, and a significant amount of nutrients may not be remobilized. This situation is relevant to the belowground system of perennial marsh species. Burial may be especially important for phosphorus. Inorganic phosphorus is delivered and remains in wetland systems adsorbed to sediments or precipitated with metals. If this phosphorus is not taken up by biological organisms or dissolved to interstitial waters, it may become buried in the wetland system.

P. australis may increase the ability of tidal freshwater marshes to act as nutrient sinks. It is highly productive and, therefore, uses a large amount of nutrients. *P. australis* is also perennial and may translocate a large amount of nutrients to its underground rhizomes. Rhizomes live for many more years than culms and are often already in periodically anoxic soil. Therefore, they hold nutrients for multiple growing seasons, and their decomposition may be slow due to low oxygen availability. This slow decomposition may enhance permanent burial of nutrients depending on the efficiency of mobilization of nutrients from the dying rhizome to younger tissues.

Includ *P. australis* may serve the function of nutrient retention in lacustrine situations (Tóth 1972; Guilizzoni and Galanti 1989). Mason and Bryant (1975) hypothesized that *P. australis* communities may serve as a valuable transformer and temporal shifter of nitrogen fluxes to a shallow eutrophic lake. Furthermore, invasive species may improve nutrient removal in wetlands, thus, enhancing the water quality value (Mitsch 1977).

S. cynosuroides has similar potential as *P. australis*, although differences in aboveground and belowground productivity, decomposition rates, and nutrient use efficiency may make one species more effective than the other one. Productivity studies appear to indicate that *S. cynosuroides* has a higher range of production than *P. australis* (Table 1). Schubauer and Hopkinson (1984) noted that comparisons of different studies are difficult because of varying methodology. Even studies that looked at both species with the same methods are not necessarily comparable because sampling was in different marsh-types (Hopkinson et al 1978) or different geographic regions (Gallagher and Plumley 1979). Furthermore, productivity measurements may be inaccurate because they separate aboveground and belowground components without accounting for the translocation between these systems. Therefore, it is clear from past research that both *P. australis* and *S. cynosuroides* are highly productive.

The different photosynthetic pathways of *P. australis* and *S. cynosuroides* may impact productivity as well. The C₄ photosynthetic pathway is hypothesized to enable species to achieve higher production rates under high temperature and irradiance conditions relative to the C₃ photosynthetic pathway by decreasing photorespiration. Saxena and Ramakrishnan (1984) observed that C₄ species were more productive than C₃ species early in the Indian growing season when solar irradiance and temperature were high and vice-versa late in the growing season when temperature and irradiance were relatively lower. Therefore, *P. australis* and *S. cynosuroides* may exhibit different periods of maximum productivity rates. This difference might cause asynchronous periods of higher nutrient demand during the growing season.

Decomposition rates of *P. australis* and *S. cynosuroides* appear similar. Hopkinson et al (1978) calculated an annual instantaneous loss rate of 4.0 mg g⁻¹ day⁻¹ and 4.7 mg g⁻¹ day⁻¹ for *P. australis* and *S. cynosuroides* respectively. The instantaneous loss rate integrates all processes of biomass removal including decomposition. Measurements in this study were taken in different marsh-types. Gallagher and Plumley (1979) estimated turnover times of 27 months and 28 months for belowground biomass of *P. australis* and *S. cynosuroides* respectively. Turnover times are equivalent to loss rates when all living and dead biomass is included. These studies indicate that differences in decomposition appear to be small. Van der Valk et al (1991) reported a decay rate of 0.0005 for *P. australis* in prairie potholes. This unitless

Table 1. Summary of literature values for aboveground and belowground primary productivity of *S. cynosuroides* communities and *P. australis* communities.

Species	Primary Productivity ($\text{g m}^{-2} \text{y}^{-1}$)		Marsh-type	Location	Study
	Aboveground	Belowground			
<i>S. cynosuroides</i>	1572	-	Tidal Freshwater	Maryland	Johnson 1970
	1355	-	Brackish	Louisiana	Hopkinson <i>et al</i> 1978
	-	2200	Brackish	Mississippi	Hackney and de la Cruz 1986
	-	3562	Brackish	Georgia	Gallagher and Plumley 1979
	3080	4628	Brackish	Georgia	Schubauer and Hopkinson 1984
	2462	4544	Tidal Freshwater	Virginia	Booth 1989
	Mean	3734			
	1080/551	-	Freshwater	Great Britain	Mason and Bryant 1975
	1372	-	Freshwater	Italy	Guilizzoni and Galanti 1989
	2318	-	Freshwater	Louisiana	Hopkinson <i>et al</i> 1978
<i>P. australis</i>	-	3649	-	Delaware	Gallagher and Plumley 1979
	-	2810	-	New Jersey	Good and Walker 1977
	Mean	3230			

rate based on a single exponential decay-rate model was three times lower than the next sampled vegetation, *Typha x glauca* Godr. These studies indicate that decomposition rates are similar for both species under various conditions.

Comparison of the relative nutrient use efficiency of *P. australis* and *S. cynosuroides* from past studies is difficult. Guilizzoni and Galanti (1989) calculated an average nitrogen concentration of 1.75% dry weight for *P. australis*. Mason and Bryant (1975) calculated a much higher nitrogen concentration of 2.84% dry weight. Booth (1989) calculated a mean nitrogen concentration of 1.44% dry weight for *S. cynosuroides*. Nutrient concentrations vary depending on environmental availability so direct comparison of studies cannot be done without reference to total available nutrients. Physiologically, Saxena and Ramakrishnan (1984) observed that C₄ species *on average* use nutrients more efficiently than C₃ species under the same conditions. Therefore, *S. cynosuroides* may be a more efficient nutrient collector and not provide as great a nutrient buffer or sink as *P. australis* per unit of production.

In conclusion, it is not evident from previous literature if *P. australis* is more influential on nutrient fluxes than *S. cynosuroides*. *S. cynosuroides* may be capable of the same level or higher levels of nutrient buffering in tidal freshwater marshes as *P. australis* in other wetland situations.

II. A. 2. Sedimentation: Estuaries receive large inputs of sediment from their tributaries. These sediments are either flushed out of the system or settle in the system, subject to resuspension. Sediments are important for several reasons. First, they are important to water quality as carriers of pollutants (Hall and Pulliam 1995) and phosphorus adsorbed to the sediment. Pollutants lead to general habitat degradation, primarily in this case, for benthic-associated species. Phosphorus may also be an important contributor to damaging algal blooms. Second, excessive sediment loads may lead to infilling of channels and shellfish beds (VMRC 1993). This infilling increases the need for channel dredging. Third, sedimentation in coastal wetlands is beneficial for maintenance of present wetland areas. Sea-level rise and subsidence in many areas is occurring at a rate faster than accretion and, therefore, wetlands are being lost (DeLaune et al 1983). High sedimentation rates in coastal wetlands may increase wetland surface accretion

and conserve wetland area. Thus, increased sedimentation outside estuarine waters may be beneficial to the wetland as well as the estuary. Tidal freshwater marshes along estuaries serve as prime areas for sediment removal from tidal waters or surface runoff because they are frequently located within the turbidity maximum of estuaries (Odum et al 1984; Odum 1988).

Sedimentary processes in wetlands are influenced by frequency of inundation, water volume entering the wetland, sediment load of this volume, topography of the wetland, and vegetation (Friedrichs and Perry in press). The capacity of water to maintain sediment in suspension decreases as velocity decreases. Sediment in suspension is deposited when water velocities go below a critical point. Ease of suspension depends on the weight and shape of the sediment. Therefore, different grain sizes are deposited at different points. Sedimentation is enhanced for a given load of sediment if velocities are slowed enough to drop the finer grain sizes, silts and clays. Maximum sediment dumping on flood tides occurs along the edges of wetland creek channels from the large reduction in tidal velocity associated with tidal inundation of the wetland (French et al 1995). The influence of vegetation on flood tide sedimentation is through reduction in water velocity by the physical interference of stems (Redfield 1972), although French *et al* (1995) indicated that various vegetation properties appeared to be less important than location relative to the tidal channel.

P. australis forms dense communities and has the potential to enhance sedimentation by reduction of water velocity. Its role as a sediment sink is not limited to the growing season because culms remain standing throughout the year, an important consideration in tidal freshwater marshes where rapid decomposition during the winter leaves exposed mudflats. Tempering this ability is the location of *P. australis* in the marsh. *P. australis* is usually located on creek levees and high marsh. Creek levees are prime areas for sedimentation, often independent of vegetation (French et al 1995). However, high marsh areas by definition are not inundated on a regular basis by tidal action. Inundation of high marsh does occur during storm surges, and this inundation may deposit significant amounts of sediment in *P. australis* communities relative to other communities (Rejmánek et al 1988). High marshes may receive sediment from surface runoff directly into the wetland as well.

Resuspension of sediment also is important in the consideration of net sedimentation. On ebb tides, wetland vegetation maintains low velocities within the wetland inhibiting resuspension and trapping organic litter. *P. australis* has been demonstrated to be effective in reducing scouring and erosion of sediments by storms (Schleyer and Roberts 1987). Takeda and Kurihara (1988) implied that *P. australis* communities reduce resuspension and stabilize the substratum under daily wave conditions. Furthermore, the underground net of roots and rhizomes of *P. australis* may prevent erosion and sediment loss from wetlands. Finally, *P. australis* communities accumulate autochthonous and allochthonous detritus to form a thick litter mat (Schleyer and Roberts 1987) that may contribute to higher wetland accretion. The organic contribution to accretion is important to conservation of wetland area in the face of sea-level rise (Nyman et al 1993) as well as possibly enhancing heavy metal retention from inorganic sediment delivery (Sprague 1985).

The potential of *P. australis* as a valuable sediment sink in the high marsh of tidal areas is largely related to its dense year-round stands, extensive root and rhizome system, and its decomposition resistant culms. *S. cynosuroides* as a morphologically similar species may also act as a sediment sink, although higher turnover rates of *S. cynosuroides* may limit its ability to accumulate autochthonous organic matter.

II. B. Habitat

Species live in areas referred to as their habitat. Habitat has several definitions and is often used interchangeably with biological community. For example, migratory or territorial animals may be referred to as using multiple habitats when they move from area to area. In the most specific sense, habitat is tied directly to the species. In this case, habitat is the physical and biological environment experienced by a species. The latter definition will be used for habitat.

Changes in a system can cause habitat degradation for a species that may lead to the decline or loss of that species' population. The loss or decline of a particular species may cause:

1. *functional disruption.* Ecosystem functions to which the declining or lost species contribute may be affected. These functions may be valuable to society and have an impact on the landscape-level as in the case of water quality.
2. *habitat disruption.* The loss or decline of one species population may impact other species' habitat that includes the first species as an element. This impact could be a decrease in other species populations, a local loss of populations, or population instability. In terms of societal impact, change of a single species can impact populations of economic value like waterfowl and fish. Loss or degradation of these species' populations can have direct economic impact on people dependent on these markets. Furthermore, each habitat disruption may enhance functional disruption even more.
3. *system instability.* The loss of species can impact the long-term stability of ecosystems. High species richness may buffer the impact of a perturbation on ecosystem biomass relative to a less rich system (Tilman 1996).

Therefore, loss or decline of a species population may change an ecosystem's functional value, habitat value, or long-term stability.

Habitat value may be defined as the quality of the habitat for each species. At a system-level, habitat value is the ability of the system to support a number of species, i.e., provide complete or partial habitat for more species. The system's ability to support a number of species is related to numerous factors like structure and ecological equilibrium (Begon et al 1990). The importance of any one factor depends on the system.

Tidal freshwater marshes by increasing landscape heterogeneity play a valuable role in species diversity at a regional-level. These marshes have a high diversity of annual and perennial plants relative to tidal salt marshes (Odum 1988). Avian species richness in tidal freshwater marshes is high as well (Odum et al 1984). Odum et al (1984) relates this richness to the high diversity of vegetative structure. Therefore, the high diversity of vascular plants may indirectly relate to high avian diversity including economically

important species like waterfowl. In addition, tidal freshwater marshes often provide habitat for rare and endangered species (Hershner and Perry 1988; Odum 1988).

P. australis has been identified as a primary contributor in the decline of overall species diversity in the systems it invades (Marks et al 1994). Concern is centered on observed declines in waterfowl populations. This decline is surmised to be the result of reduced structural heterogeneity and food quality of the system (Jones and Lehman 1987). In addition, the tendency of *P. australis* communities to be monodominant may choke out other species especially more fragile rare and endangered species populations. Therefore, *P. australis* is believed to decrease the habitat quality of the system for other organisms. The rapid expansion of *P. australis* communities within an ecosystem exacerbates the problem by decreasing ecosystem species richness. This decrease may compromise overall ecosystem stability (Tilman 1996).

The change in species structure from *S. cynosuroides* to *P. australis* may affect the species diversity of the wetland. Evidence for these changes remains primarily anecdotal. In particular, *P. australis* may decrease plant species diversity because the dense, tall, monodominant communities tend to crowd and shade out other species. *S. cynosuroides*, as a structurally similar species, may not provide better habitat than *P. australis*. Therefore, there may be no difference in plant species diversity when *P. australis* invades *S. cynosuroides* communities in a tidal freshwater marsh. There may be a difference at the ecosystem-level if *P. australis* encroaches into other marsh communities.

III. Background for Study Methodology

III. A. Nutrient Flux

Nutrient flux through tidal marshes is difficult to quantify accurately because of the numerous potential sources and outlets. Flux studies are limited to sampling directly one or two potential sources and outlets assuming other sources and outlets are minor, or sampling indirectly through standing stock changes.

One common method for measuring nutrient flux is a standing stock mass balance (e.g., Hopkinson and Schubauer 1984). The standing nutrient stocks of aboveground and belowground vegetation and sediments are sampled over the course of a year. Net changes indicate flux of nutrients through the vegetative system and marsh environment.

A second common method uses benthic chambers to measure nutrient flux between tidal waters and the marsh surface (e.g., Neikirk 1996). Open sediment chambers are placed on the marsh surface. Tidal waters fill the chamber on the rising tide. Chambers are stopped and samples are taken from the chamber at time intervals. Nutrient flux is determined from a regression of each time sample. Modifications of this method using an autosampling technique (Hargrave and Connolly 1978) and a closed water reservoir (Chambers 1992) exist.

A third method uses hydrodynamic sampling to measure nutrient flux (e.g., Whiting et al 1985). Nutrient samples are removed from a tidal creek several times over the course of a tidal cycle. Nutrient flux is determined from the difference in flood and ebb nutrient levels.

A final method for measuring nutrient flux uses constructed flumes (e.g., Wolaver et al 1983). A flume is established perpendicular to tidal flow to prevent lateral flow movement. Water samples are taken from the mouth of the flume at time intervals over the course of a tidal cycle. Nutrient flux is calculated from differences in flood and ebb nutrients. The technique was modified for throughflow situations by Childers and Day (1988) so that sampling occurs at both ends of the flume.

III. B. Sedimentation

Sedimentation under wetland conditions may be measured using a variety of techniques. These techniques may be separated into long-term measurements and short-term measurements. Long-term measurements determine average sedimentation trends over decades and centuries. Long-term methods are limited primarily to the use of different radioisotopes:

1. *Cesium-137* (e.g., DeLaune et al 1987; Sharma et al 1987) - a radioactive isotope introduced into the atmosphere in variable quantities by nuclear weapons testing. This isotope adsorbs strongly to sediment and organic matter and is effectively immobilized (Davis 1963). It may be used to measure sedimentation rates by evaluating the point of appearance (year 1954) in a sediment core and the peak activity (year 1963) in the core (Wise 1980).
2. *Lead-210* - an isotope produced from the decay of ^{222}Rn in the atmosphere that has a relatively constant atmospheric deposition. ^{222}Rn is produced from ^{226}Ra in soils and rocks. ^{210}Pb is primarily insoluble and associates with sediments (Sharma et al 1987). Assuming steady-state conditions, sedimentation rates may be determined from cores using ^{210}Pb 's half-life of 22.3 years. ^{210}Pb is usually measured indirectly using its daughter isotope ^{210}Bi or granddaughter isotope ^{210}Po (Nittrouer et al 1979).

These measurements are useful in integrating stochastic events or alternating periods of sedimentation and erosion as well as subsequent sediment compaction missed by short-term measurements.

Short-term measurements are used primarily to determine present sedimentary conditions and have a resolution from hours to years. Short-term measurements include:

1. *graduated stakes* (e.g., Ranwell 1964) - graduated stakes are placed in the ground and allowed to settle. Subsequent sedimentation measurements are made using the stake. This method is simple and allows for frequent measurements of the same point.
2. *artificial marker horizon* (e.g., Baumann et al 1984; Rejmánek et al 1988) - ground is covered in plots using clay dust or any material that provides an easily identifiable marker horizon for subsequent measurements of sedimentation over this horizon. The risk with this method is loss of the marker horizon by scouring.
3. *dyed core* (e.g., Ledwin 1988) - a sediment core of known-length is removed, dyed, and replaced level with the marsh surface. At the end of the study, the plug and any sediment above the plug

are measured to determine net sedimentation or erosion over a specified time period. This method is sensitive to sediment loss as well as sediment accumulation.

4. *sediment traps* (e.g., French et al 1995; Meeker 1996) - a series of traps, usually petri dishes, are placed on the marsh surface and collected after the period of interest. Sediment trapped is dried and weighed. This method requires a large distribution of traps but will give a high resolution profile of sedimentation in the marsh.

The first three methods give sedimentation rates in terms of elevation change (height time^{-1}) whereas the fourth method gives sedimentation in terms of mass change (mass time^{-1}). All these short-term measurements are useful in determining the influence of specific events or seasons on sedimentation. They cannot account for subsequent processes like compaction for studies attempting to determine marsh accretion rates.

III. C. Plant Community Structure and Species Diversity

The description of vegetative communities may use a variety of parameters. These potential parameters and their strengths and weaknesses have been reviewed by Daubenmire (1968) and Mueller-Dombois and Ellenberg (1974). Four common, simple, nondestructive methods are:

1. *species richness* - the total number of species growing within a certain area.
2. *ground cover* - the surface area overlaid by each species biomass. Cover is a measure of species dominance.
3. *stem density* - the number of species individuals or stems within a specified area.
4. *species frequency* - a measure of the patchiness of species within a specified area.

The four basic measurements may be used to calculate two characteristic community quantities. Importance values may be calculated as a descriptor of vegetative community structure. The importance value is the sum of the relative cover, relative density, and the relative frequency. It produces an integrated

number of the importance of each species to the community although the use of relative values limits its use as a measure of the importance of the environment to the members of the community (Mueller-Dombois and Ellenberg 1974). Also, addition of the 3 measurements can obscure interpretation of the data (Daubenmire 1968). For example, frequency measures are subjective to the size of the sampling quadrat. Nevertheless, the importance value is a useful method of integrating vegetative parameters to rank species importance in a community.

Species diversity index values may also be calculated. Species diversity indices are used as quantitative descriptors for communities and ecosystems. These indices take into account species richness as well as the relative abundance of each species. In general, species diversity indices are limited by their obscure relationship to actual ecological structure (Hurlbert 1971).

The Shannon diversity index is the most common index of diversity. MacArthur (1955) first proposed this index for ecology as a measure of community stability although it is primarily used now as an index of the uncertainty of a randomly selected individual being of a certain species (Pielou 1966). It was developed from the principles developed by Shannon and Weaver (1949) for information theory.

Most measurements of species diversity are based on the number of population individuals (e.g. Margalef 1958) although MacArthur (1955) used energy flow. However, for plant species, individuals are difficult to define, and energy is difficult to measure and quantify. Practically, biomass is the best measure of species proportions for plant diversity estimation because it accounts quantitatively for the 3-dimensional structure of the community, but biomass measurements can be destructive. Ground cover represents the best 2-dimensional representation of biomass dominance (Daubenmire 1968) and may also be used as a measure of species proportions.

HYPOTHESIS

The replacement of *S. cynosuroides* by *P. australis* will cause minimal changes in the value of tidal freshwater marshes. The effect will be minimal because of the similar morphology and life history of the two species. This hypothesis will be tested by examining two values of tidal freshwater marshes, water quality and habitat. Water quality impact will be assessed by a comparison of nutrient fluxes and sedimentation in adjacent *S. cynosuroides* and *P. australis* communities. Habitat impact will be assessed by comparison of plant community structure and species diversity in adjacent stands. For any statistical treatment of the three studied aspects, a null hypothesis of no change will be used:

$$H_0: f_x(S. \text{cynosuroides}) = f_x(P. \text{australis})$$

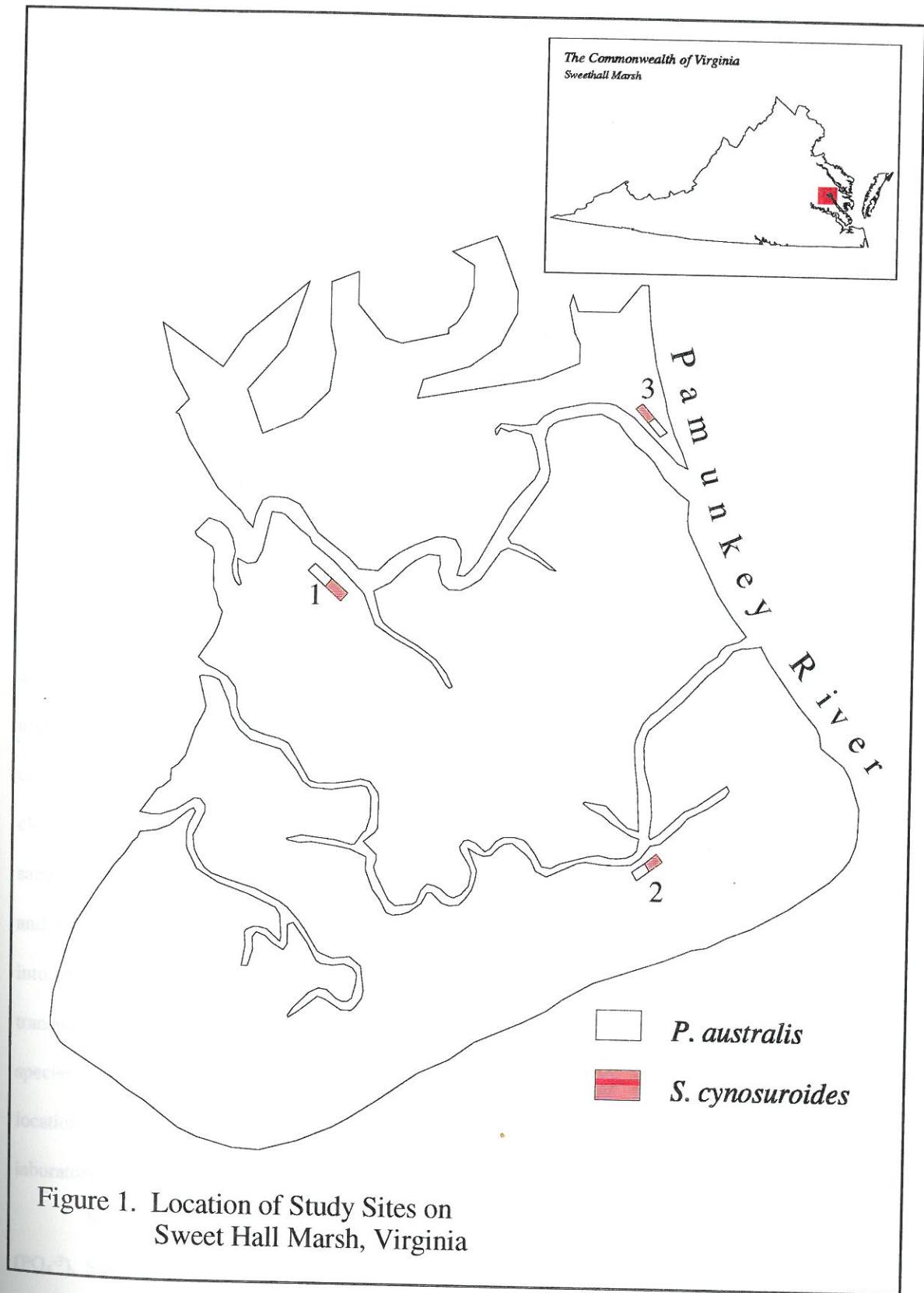
MATERIALS AND METHODS

I. Site Description

The study was conducted on Sweet Hall Marsh ($37^{\circ} 34' N$ $76^{\circ} 33' W$) of the National Estuarine Research Reserve System (NERRS). Sweet Hall Marsh is a large (444 ha) tidal freshwater marsh of the Pamunkey River, a tributary of the York River, Virginia in the Chesapeake Bay watershed (Doumlele 1981). The marsh is approximately 25 km upstream from the confluence of the Pamunkey and Mattaponi Rivers into the York. River salinity ranges from 0-7 ppt with an average salinity of 0.45 ppt and a mean tide range of 0.83 m (Perry 1991). Silviculture and agriculture are among the prominent surrounding land uses (Hobbs et al 1975). Three sampling sites of adjacent (paired) communities of *S. cynosuroides* and *P. australis* were used to investigate sedimentation and plant structure and species diversity (Fig. 1). These sites are located on tidal creek levees and dominated by *S. cynosuroides* and *P. australis* as well as arrow-arum (*Peltandra virginica* [L.] Schott & Endl.), rice cutgrass (*Leersia oryzoides* [L.] Swartz), and smartweed (*Polygonum punctatum* Elliott) (Perry and Atkinson 1997). One of these sites of paired communities was used to investigate nutrient flux.

II. Nutrient Flux

Nutrient fluxes on site 1 were measured using a benthic chamber method (Chambers 1992; Neikirk 1996). This technique allows for measurement of the flux of nutrients between the water column and the sediment surface for each community. Other common methods for measuring nutrient fluxes such as hydrodynamic sampling (e.g., Whiting et al 1985) and flume sampling (e.g., Wolaver et al 1983) are inappropriate as the former measures over the entire marsh surface and the latter measures the integrated effect of multiple communities along the gradient of tidal inundation.



Benthic and water column chambers were constructed from polypropylene-lined aluminum coil.

The aluminum coil was cut into 1.525 m strips and sealed with bolts. Chambers were maintained water tight with closed-cell foam stripping and rubber washers. Two 2.54 cm diameter holes were cut at opposite ends of the sealed cylinder 10 cm above the bottom. Water column chambers were closed and had an aluminum bottom sealed with silicone previous to sampling placement. Benthic chambers were sealed on site. Benthic chambers were 51 cm in height above the sediment surface and 0.1555 m² in area during sampling whereas water column chambers were 61 cm tall with the same area.

Nutrient fluxes were measured over the course of spring high tide inundation in September 1997, April 1998, and July 1998. One week prior to spring tide, five benthic chambers were placed in each community along a central transect (Fig. 2). Surface root mass was cut, and the chambers were twisted into the sediment approximately 10 cm deep. Tidal waters were allowed to rise and fall through chamber openings for the course of the next week.

The day of maximum spring tide, two water column chambers with fixed bottoms were placed along each transect. Benthic chambers were cleaned *in situ* to remove algal growth. All chambers were allowed to fill on the rising tide. One hour prior to high tide, ambient water temperature in each community was recorded, battery-powered mixers were placed in each chamber, and chamber openings were closed with neoprene stoppers. During 5 sampling times over the course of the next 2 hours, triplicate samples were taken from each chamber using 30 ml acid-washed syringes. At each sampling time, the time and water height for each chamber was recorded. Samples were filtered through a 0.45 µm syringe filter into whirlpak bags with the first 2 ml of filtered water discarded. All filtered samples were stored on ice for transport. After sampling was complete, individual chamber water temperatures were recorded, plant species were identified and stem density counted within each chamber, all chambers were removed, and the location of each chamber and site marked for future sampling dates. Samples were frozen and stored until laboratory analysis.

Samples were analyzed for ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), and orthophosphate (PO_4^{3-}). Samples were removed from the freezer and thawed in a refrigerator overnight. Phosphate

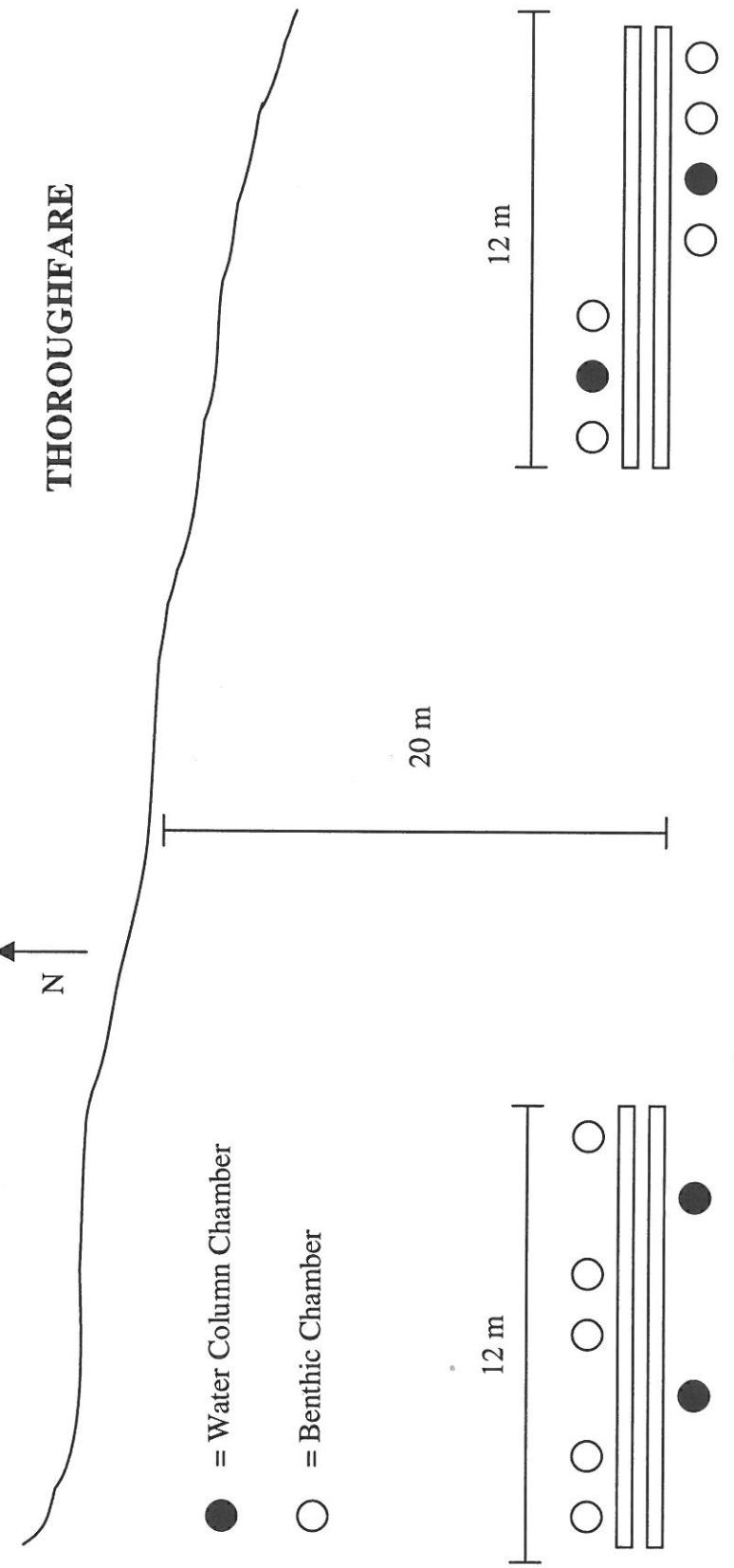


Figure 2. Chamber layout on site 1 for nutrient flux sampling. *P. australis* community is located on left, and *S. cynosuroides* community is located on right. Drawing is not to scale.

concentrations were determined by adding an acidified solution of ammonium molybdate with antimony to samples and phosphate standards. Samples were then mixed and read on a spectrophotometer at 880 nm after 10 minutes (Murphy and Riley 1962). Ammonium concentrations were determined by the phenolhypochlorite method outlined by Solórzano (1969). After all reagents were added, samples and standards were mixed, covered, and placed in dark conditions for 24 hours. Samples were read on a spectrophotometer at 630 nm. Analytic replicates were performed for each ammonium sample. Nitrite and nitrate concentrations were determined using an Alpkem Flow Solution Autoanalyzer (Perstorp 1992).

Nutrient fluxes between the sediments and the tidal waters were calculated using a linear regression against time. First, mean nutrient concentrations for each sampling time were determined from the triplicate samples. Dissolved inorganic nitrogen (DIN) concentrations were calculated as the sum of nitrate, nitrite, and ammonium concentrations. Next, for each water column chamber, a linear regression of mean concentration against time for each nutrient was performed to calculate a water column chamber flux ($\mu\text{mol L}^{-1} \text{ h}^{-1}$). A mean water column chamber flux was then determined for each community.

Fluxes between the sediments and the water column were then calculated. First, mean nutrient concentrations ($\mu\text{mol L}^{-1}$) at each sampling time were multiplied by benthic chamber volume (L) to determine the mass of nutrients (μmol) in each chamber at each sampling time. Two mass adjustments were then calculated. The first adjustment corrected for leakage from the chambers by multiplying the apparent gain or loss of water volume between sampling times by the average nutrient concentration during the interval:

$$\text{LA}_n = \sum_{i=1}^n \{[(C_n + C_{n-1})/2] (V_n - V_{n-1})\}$$

where LA = leakage adjustment (μmol)
 C = nutrient concentration ($\mu\text{mol L}^{-1}$)
 V = water volume (L)
 n = sampling time index (0, 1, 2, 3, 4)

The second adjustment corrected for water column processes by multiplying the mean water column chamber flux for each community by the time interval between sampling times and the average water volume of the benthic chamber during this interval:

$$WA_n = \sum_{i=1}^n \{(WCCF_s) (t_n - t_{n-1}) [(V_n - V_{n-1})/2]\}$$

where WA = water adjustment (μmol)
 $WCCF_s$ = water chamber column flux ($\mu\text{mol L}^{-1} \text{ h}^{-1}$) by community (s)
 t = time (h)
 V = water volume (L)
 n = sampling time index (0, 1, 2, 3, 4)

Adjustments for the initial sampling time ($n=0$) were zero. The two adjustments were then subtracted from the chamber masses:

$$\text{mass} = C_n V_n - LA_n - WA_n$$

where C = nutrient concentration ($\mu\text{mol L}^{-1}$)
 V = water volume (L)
 LA = leakage adjustment (μmol)
 WA = water adjustment (μmol)
 n = sampling time index (0, 1, 2, 3, 4)

The corrected masses were then regressed against time ($\mu\text{mol h}^{-1}$). Slope coefficients were divided by the chamber area to determine the nutrient fluxes between the tidal waters and sediments ($\mu\text{mol m}^{-2} \text{ h}^{-1}$). The 5 benthic chamber fluxes in each community were averaged to determine the mean nutrient flux of the *P. australis* community and the *S. cynosuroides* community for each sampling date.

The benthic chamber fluxes were analyzed using a Welch's t-test to compare the stand fluxes for each nutrient during each sampling date. In addition, benthic chamber fluxes were analyzed using a 2-way ANOVA to compare overall community differences while controlling for seasonal variability. Nitrate and nitrite fluxes were combined for analysis. Initial nutrient concentrations in each community were compared using a Welch's t-test for each sampling date. All statistical analyses were carried out on the MINITAB statistical package (MINITAB, Inc.).

III. Sedimentation

A long-term measurement was used to determine net sedimentation trends over the last 40 years.

Cesium-137 is sufficient for this time frame of interest as sites were invaded prior to the 1950s and have been relatively stable since that time (Perry personal communication 1997).

Two sediment cores were taken at the center of each community during a period of low tide for analysis using ^{137}Cs (DeLaune et al 1987; Sharma et al 1987). One core from each community was used for ^{137}Cs analyses while the second core from each community was used for measurement of sediment properties. Cores were taken using a 1.5 m long, 7.5 cm diameter aluminum core tube and vibracorer as well as 0.5 m long, 15 cm diameter PVC core tubes pushed into the ground (Table 2). The difference between the core surface and the sediment surface was measured to estimate compaction of the cores. The core tubes were capped, extracted from the ground, and returned to the lab for analysis. Cores used for ^{137}Cs analyses were collected during the summer of 1997 whereas cores used to determine sediment properties were collected during the winter of 1998.

The six cores for ^{137}Cs analyses were extruded from the core tubes and cut into 1 cm slices. Extraneous living and dead plant materials were removed from the slices. Gamma counting of the 661.62 keV photopeak of ^{137}Cs was performed for 24 hours using high-purity germanium detectors. Vibracore samples were dried and ground before counting whereas push cores were counted wet. Resultant counts of ^{137}Cs were converted to activities using known efficiency factors and plotted against depth. The point of 1963-64 peak levels was determined and an average annual accretion rate calculated for each community. For cores collected from site 1, the depth of peak ^{137}Cs activity was multiplied by the ratio of core depth to the actual core length to correct for sampling compaction. Compaction was not apparent during push core sampling.

The remaining six cores were extruded from core tubes and cut into 2 cm slices. Every other slice was weighed, dried completely, and reweighed. Dry weight and the volume of each slice were used to calculate average bulk density (g cm^{-3}):

Table 2. Summary of data collection for nutrient flux, sedimentation, and plant community structure and species diversity from paired *S. cynosuroides* communities and *P. australis* communities located on Sweet Hall Marsh, Virginia.

Site	Community	Sampling	Chamber Placement Date	Nutrient Flux	Sampling Date	Time of Sampling	Sampling Date	Sedimentation	Purpose	Plant Species Diversity	Sampling Date
1	<i>S. cynosuroides</i>	1	9 September, 1997	17 September, 1997	1315 - 1530	6 June, 1997	vibracore	¹³⁷ Cs	3 October, 1997		
		2	14 April, 1998	24 April, 1998	1100 - 1315	19 February, 1998	push	Bulk Density	19 May, 1998		
		3	30 June, 1998	9 July, 1998	1245 - 1500	-	-	-	16 July, 1998		
P. australis	<i>P. australis</i>	1	9 September, 1997	17 September, 1997	1315 - 1530	7 July, 1997	vibracore	¹³⁷ Cs	3 October, 1997		
		2	14 April, 1998	24 April, 1998	1100 - 1315	19 February, 1998	push	Bulk Density	19 May, 1998		
		3	30 June, 1998	9 July, 1998	1245 - 1500	-	-	-	16 July, 1998		
2	<i>S. cynosuroides</i>	1	-	-	-	7 July, 1997	push	¹³⁷ Cs	23 September, 1997		
		2	-	-	-	19 February, 1998	push	Bulk Density	20 May, 1998		
		3	-	-	-	-	-	-	17 July, 1998		
P. australis	<i>P. australis</i>	1	-	-	-	7 July, 1997	push	¹³⁷ Cs	23 September, 1997		
		2	-	-	-	19 February, 1998	push	Bulk Density	20 May, 1998		
		3	-	-	-	-	-	-	17 July, 1998		
3	<i>S. cynosuroides</i>	1	-	-	-	7 August, 1997	push	¹³⁷ Cs	24 September, 1997		
		2	-	-	-	5 March, 1998	push	Bulk Density	19 May, 1998		
		3	-	-	-	-	-	-	16 July, 1998		
P. australis	<i>P. australis</i>	1	-	-	-	7 August, 1997	push	¹³⁷ Cs	24 September, 1997		
		2	-	-	-	5 March, 1998	push	Bulk Density	19 May, 1998		
		3	-	-	-	-	-	-	16 July, 1998		

$$BD = \frac{\sum_{i=1}^n DW_i/V}{n}$$

where BD = mean dry bulk density (g cm^{-3})
 DW_i = dry weight of *i*th slice (g)
 V = volume of slice (cm^{-3})
 n = total number of slices

Samples were then combusted at 500 °C for at least 5 hours in a muffle oven and reweighed. Organic content was calculated as ash-free dry weight divided by initial dry weight:

$$OC = \frac{\sum_{i=1}^n (AFDW_i/DW_i)}{n} \cdot 100$$

where OC = mean organic content by dry weight (%)
 AFDW_i = ash-free dry weight of *i*th slice (g)
 = (dry weight) - (ash weight)
 n = total number of slices

Using the inorganic content of each slice and the ^{137}Cs horizon depth, an inorganic mass flux or accumulation rate was calculated ($\text{g m}^{-2} \text{y}^{-1}$):

$$MF = \frac{D \left(\sum_{i=1}^n AW_i/n \right)}{A \cdot t}$$

where MF = inorganic mass flux ($\text{g m}^{-2} \text{y}^{-1}$)
 AW_i = measured or estimated inorganic mass of *i*th centimeter (g)
 n = midpoint depth of nearest measured slice below ^{137}Cs peak horizon (cm)
 D = depth of ^{137}Cs peak horizon (cm)
 A = area of sediment property core (m^2)
 t = time of ^{137}Cs horizon deposition (34 y)

For this calculation, the inorganic mass of intervening unmeasured slices was estimated by averaging the adjacent slices.

Accretion rates, inorganic mass flux, organic content, and bulk density were compared between *P. australis* communities and *S. cynosuroides* communities using an ANOVA blocked by site. All statistical analyses were performed on the MINITAB statistical package.

IV. Plant Community Structure and Species Diversity

Plant community structure and species diversity was determined for all communities in September 1997, May 1998, and July 1998 using species identification and counting, ground cover, stem density, and frequency of species occurrence (Mueller-Dombois and Ellenberg 1974). Ten random 1 m² quadrats were chosen in each community. All species in each quadrat were identified. Vascular plant nomenclature followed Gleason and Cronquist (1991). Once each species had been identified, ground cover for each species in a quadrat was estimated by sight into a modified Daubenmire (1959) cover class scale (Perry and Atkinson 1997; Table 3). Individual species stems rooted in each quadrat were then counted.

Using these data, richness, mean ground cover, mean stem density, and frequency of species occurrence were calculated for all six communities. Species richness was measured by adding the number of species identified in each community. Cover class data recorded in the field were converted to species midpoint cover values (Table 3) for analysis. Mean species cover was determined by adding the midpoint cover values from the sampled quadrats in a community and dividing by 10 (% species cover). The mean species stem density was calculated by adding the total number of stems of each species counted in the ten quadrats of a community and dividing by 10 m² (stems m⁻²). Frequency was measured by the number of quadrats in a community in which an individual species appeared divided by the number of quadrats sampled (10).

Pooled values for richness, cover, density, and frequency were also calculated. Pooled species richness of the *P. australis* communities was measured by adding the number of species identified in the *P. australis* communities on all sites. Pooled species cover for the *P. australis* communities was calculated by averaging the mean species cover value for the *P. australis* communities on all sites. Pooled species stem density was calculated for the *P. australis* communities by adding stem counts for each species from all thirty quadrats on *P. australis* communities and dividing by thirty. Pooled species frequency was calculated by averaging the frequency measurements from all the *P. australis* communities. Therefore, standard errors for pooled species cover and pooled species frequencies represent variability between *P. australis* communities whereas standard errors for pooled species stem density represent variability between

Table 3. Cover class scale (modified from Daubenmire 1959) for estimation of species ground cover.

Cover Class	Range of Cover (%)	Class Midpoints (%)
6	95 - 100	97.5
5	75 - 95	85
4	50 - 75	62.5
3	25 - 50	37.5
2	5 - 25	15
1	1 - 5	2.5
trace	0 - 1	0.5

sampled quadrats in the *P. australis* communities. Pooled species richness has no associated error. Pooled values were calculated for the *S. cynosuroides* communities by the same methods.

Importance values for pooled community data were calculated from relative cover, relative density, and relative frequency:

$$IV_i = \frac{\text{species frequency}_i}{\sum_{i=1}^S \text{species frequency}_i} + \frac{\text{ground cover}_i}{\sum_{i=1}^S \text{ground cover}_i} + \frac{\text{stem density}_i}{\sum_{i=1}^S \text{stem density}_i}$$

where IV_i = importance value of i th species
 S = total number of species (species richness)

(from Mueller-Dombois and Ellenberg 1974)

Importance values were used to rank each species. Shannon's diversity index and evenness were calculated for the communities on each site and pooled community data to quantify plant species diversity (Pielou 1966). Species proportion values for the index and evenness were calculated using relative ground cover:

$$H' = - \sum_{i=1}^S P_i \ln P_i$$

$$J' = \frac{H'}{\ln S}$$

where H' = diversity index
 J' = evenness
 P_i = proportion of i th species
 $= \frac{\text{species cover}_i}{\sum_{i=1}^S \text{species cover}_i}$
 S = species richness

Friedman's tests were used to compare values obtained from the index, evenness, and richness between *P. australis* and *S. cynosuroides* communities; comparisons were made for each sampling date with data blocked by site and for the study with pooled data blocked by sampling date. A Welch's t-test was used to compare community structure by looking at the difference between pooled community stem densities of the 3-4 most frequently occurring species plus *S. cynosuroides* and *P. australis*. Friedman's tests were used to

compare total ground cover between *S. cynosuroides* and *P. australis* communities for each sampling date with data blocked by site. In addition, a Friedman's test was used to compare total pooled ground cover between the communities across seasons with data blocked by sampling date. All statistical analyses were performed on the MINITAB statistical package.

RESULTS

I. Nutrient Flux

Benthic chamber flux data is summarized in Table 4. Positive fluxes indicate delivery of the nutrient from the sediment to the overlying tidal waters. Negative fluxes indicate uptake of the nutrient from the tidal waters to the sediment. For sampling in September 1997 and April 1998, one chamber in the *P. australis* community was not sampled because of excess leakage or overtopping by tidal waters.

Fluxes of phosphate showed a significant difference between the *P. australis* community and the *S. cynosuroides* community in September ($28.3 \mu\text{mol m}^{-2} \text{ h}^{-1}$ and $-3.9 \mu\text{mol m}^{-2} \text{ h}^{-1}$ respectively; $t=3.88$, $df=5$, $p=0.012$). Release of phosphate occurred from both *S. cynosuroides* and *P. australis* communities in April ($57.2 \mu\text{mol m}^{-2} \text{ h}^{-1}$ and $51.7 \mu\text{mol m}^{-2} \text{ h}^{-1}$ respectively). Uptake of phosphate occurred from both communities in July ($-19.0 \mu\text{mol m}^{-2} \text{ h}^{-1}$ and $-16.0 \mu\text{mol m}^{-2} \text{ h}^{-1}$ respectively). No significant differences for phosphate fluxes were observed during these months ($t=0.21$, $df=6$, $p=0.84$ and $t=-0.26$, $df=6$, $p=0.81$ respectively; Fig. 3). Controlling for seasonal variability, no significant difference occurred between community phosphate fluxes ($F=1.26$, $df=1$, $p=0.272$).

In September and April, both the *S. cynosuroides* community and the *P. australis* community showed a net release of ammonium ($32.9 \mu\text{mol m}^{-2} \text{ h}^{-1}$ and $100.0 \mu\text{mol m}^{-2} \text{ h}^{-1}$ in September, $34.1 \mu\text{mol m}^{-2} \text{ h}^{-1}$ and $10.5 \mu\text{mol m}^{-2} \text{ h}^{-1}$ in April respectively). In July, both communities had a net uptake of ammonium ($-18.8 \mu\text{mol m}^{-2} \text{ h}^{-1}$ and $-43.7 \mu\text{mol m}^{-2} \text{ h}^{-1}$ respectively). Ammonium fluxes were small for all sampling dates (Fig. 4) without significant differences for individual sampling dates ($t=-1.72$, $df=5$, $p=0.15$; $t=0.74$, $df=5$, $p=0.49$; $t=0.28$, $df=4$, $p=0.33$) or across seasons ($F=0.02$, $df=1$, $p=0.891$).

Combined nitrate and nitrite fluxes were only significantly different in July ($t=-2.44$, $df=8$, $p=0.041$). *S. cynosuroides* communities showed more intensive uptake of nitrate/nitrite ($-378.1 \mu\text{mol m}^{-2}$

h^{-1}) relative to the *P. australis* community ($-188.9 \mu\text{mol m}^{-2} \text{h}^{-1}$). In September and April, both communities showed little net nitrate/nitrite activity compared to July rates (Fig. 5). Small uptake occurred in September in *S. cynosuroides* communities and *P. australis* communities ($-18.8 \mu\text{mol m}^{-2} \text{h}^{-1}$ and $-31.4 \mu\text{mol m}^{-2} \text{h}^{-1}$ respectively). In April, the *S. cynosuroides* community continued to uptake nitrate/nitrite ($-82.9253 \mu\text{mol m}^{-2} \text{h}^{-1}$) whereas the *P. australis* community showed a net release of nitrate/nitrite ($46.2 \mu\text{mol m}^{-2} \text{h}^{-1}$). Nitrate/nitrite flux differences in September and April were not significant ($t=0.31$, $df=3$, $p=0.77$; $t=-1.05$, $df=6$, $p=0.33$). There was an overall difference between the communities across seasons ($F=4.34$, $df=1$, $p=0.048$).

In September, release of DIN occurred in both *S. cynosuroides* communities and *P. australis* communities ($14.1 \mu\text{mol m}^{-2} \text{h}^{-1}$ and $68.6 \mu\text{mol m}^{-2} \text{h}^{-1}$ respectively; $t=-1.01$, $df=4$, $p=0.37$). In April, the *S. cynosuroides* community was taking up DIN ($-48.8 \mu\text{mol m}^{-2} \text{h}^{-1}$) whereas the *P. australis* community still released DIN ($56.3 \mu\text{mol m}^{-2} \text{h}^{-1}$; $t=-0.79$, $df=6$, $p=0.46$). In July, both communities were taking up relatively large amounts of DIN ($-397.0 \mu\text{mol m}^{-2} \text{h}^{-1}$ and $-232.6 \mu\text{mol m}^{-2} \text{h}^{-1}$; $t=-1.07$, $df=5$, $p=0.33$). No significant difference between communities was detected for any of these sampling dates (Fig. 6). In addition, there was no overall significant difference in DIN flux between the communities ($F=2.45$, $df=1$, $p=0.131$).

Initial nutrient concentrations were not found to differ between communities in most situations (Table 5). Differences were observed between initial concentrations for phosphate during July sampling ($t=2.04$, $df=7$, $p=0.081$) and DIN during September sampling ($t=2.31$, $df=9$, $p=0.046$).

II. Sedimentation

Sedimentation data is summarized in Table 6. All ^{137}Cs profiles were interpretable except from the core taken from the *S. cynosuroides* community on site 3 (Fig. 7). This core was found to have a *P. virginica* rhizome from approximately 28-40 cm depth in the core. Presence of the rhizome affected extrusion of the core leading to a disturbance of the ^{137}Cs profile. Cesium-137 activity readings for all cores are presented in Table 7. The calculated accretion rates for the remaining cores from *S. cynosuroides*

Table 4. Relative inorganic nutrient flux (No./ $\mu\text{mol m}^{-2} \text{h}^{-1} \pm \text{SE}$) from paired *S. cynosuroides* community and *P. australis* community to overlying tidal waters. Superscripts indicate differences between communities using Welch's t-test (a: $p < .1$, b: $p < .05$).

Season	Community	Nutrient Flux			
		PO_4^{3-}	$\text{NO}_3^- + \text{NO}_2^-$	NH_4^+	DIN
September	<i>S. cynosuroides</i>	28.3 ± 7.6^b	-18.8 ± 14.8	32.9 ± 23.7	14.1 ± 26.0
	<i>P. australis</i>	-3.9 ± 3.5	-31.4 ± 37.3	100.0 ± 31.1	68.6 ± 47.3
April	<i>S. cynosuroides</i>	57.2 ± 17.0	-82.9 ± 82.4	34.1 ± 28.6	-48.8 ± 104.0
	<i>P. australis</i>	51.7 ± 19.4	46.2 ± 91.0	10.5 ± 14.5	56.3 ± 84.0
July	<i>S. cynosuroides</i>	-19.0 ± 10.0	-378.1 ± 62.7^b	-18.8 ± 84.9	-397.0 ± 140.1
	<i>P. australis</i>	-16.0 ± 6.4	-188.9 ± 45.7	-43.7 ± 26.3	-232.6 ± 63.0
Mean	<i>S. cynosuroides</i>	22.2 ± 22.2	-159.9 ± 110.6	16.1 ± 17.4	-143.9 ± 127.9^a
	<i>P. australis</i>	10.6 ± 20.8	-58.0 ± 69.2	22.3 ± 41.9	-35.9 ± 98.4

Table 5. Initial chamber concentrations (No./ $\mu\text{mol L}^{-1} \pm \text{SE}$) of inorganic nutrients for paired *S. cynosuroides* community and *P. australis* community. Superscripts indicate differences between communities using Welch's t-test (a: $p < .1$, b: $p < .05$).

Season	Community	Initial Concentration			
		PO_4^{3-}	$\text{NO}_3^- + \text{NO}_2^-$	NH_4^+	DIN
September	<i>S. cynosuroides</i>	0.66 ± 0.08	2.59 ± 0.09	3.40 ± 0.63	5.99 ± 0.56^a
	<i>P. australis</i>	0.55 ± 0.01	2.30 ± 0.20	2.19 ± 0.15	4.50 ± 0.32
April	<i>S. cynosuroides</i>	0.62 ± 0.03	14.97 ± 3.53	3.52 ± 0.28	23.67 ± 0.64
	<i>P. australis</i>	0.60 ± 0.03	14.11 ± 3.98	3.42 ± 0.10	23.38 ± 0.29
July	<i>S. cynosuroides</i>	0.86 ± 0.08^b	11.41 ± 0.78	2.51 ± 0.37	13.92 ± 0.46
	<i>P. australis</i>	0.68 ± 0.03	10.94 ± 0.75	2.24 ± 0.29	13.17 ± 0.61

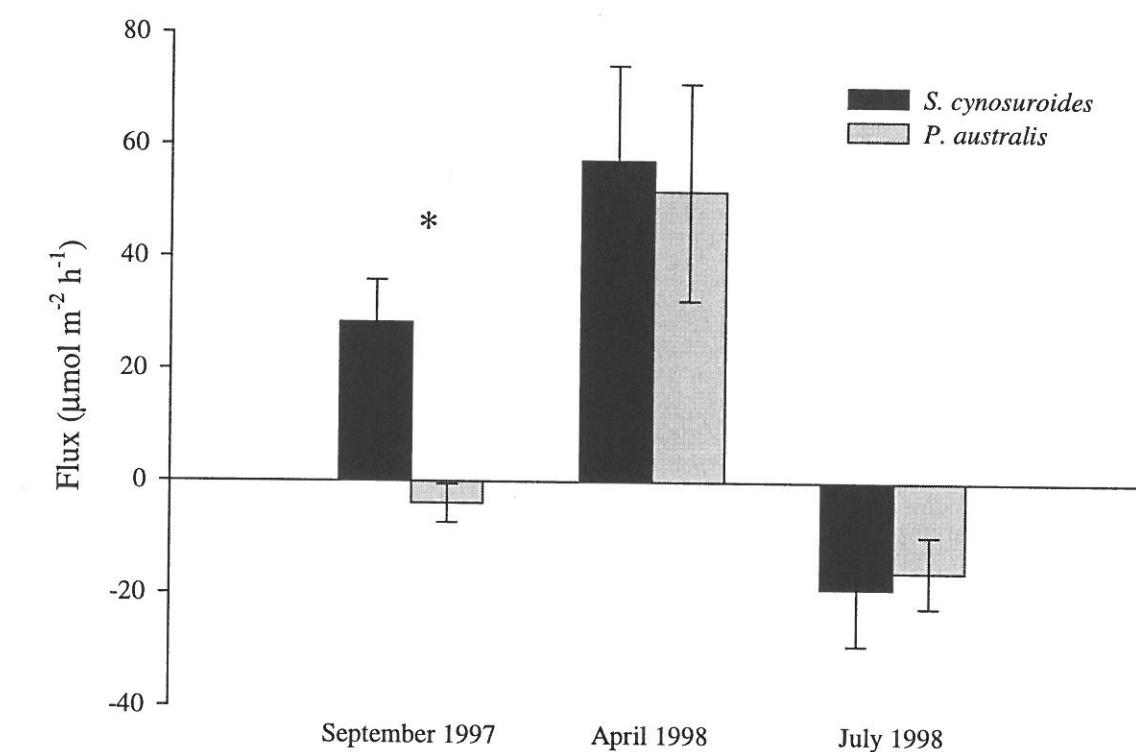


Figure 3. Relative phosphate (PO_4^{3-}) flux ($\pm\text{SE}$) from paired *S. cynosuroides* community and *P. australis* community to overlying tidal waters. Asterix indicate significant differences ($p < .05$) between communities using Welch's t-test.

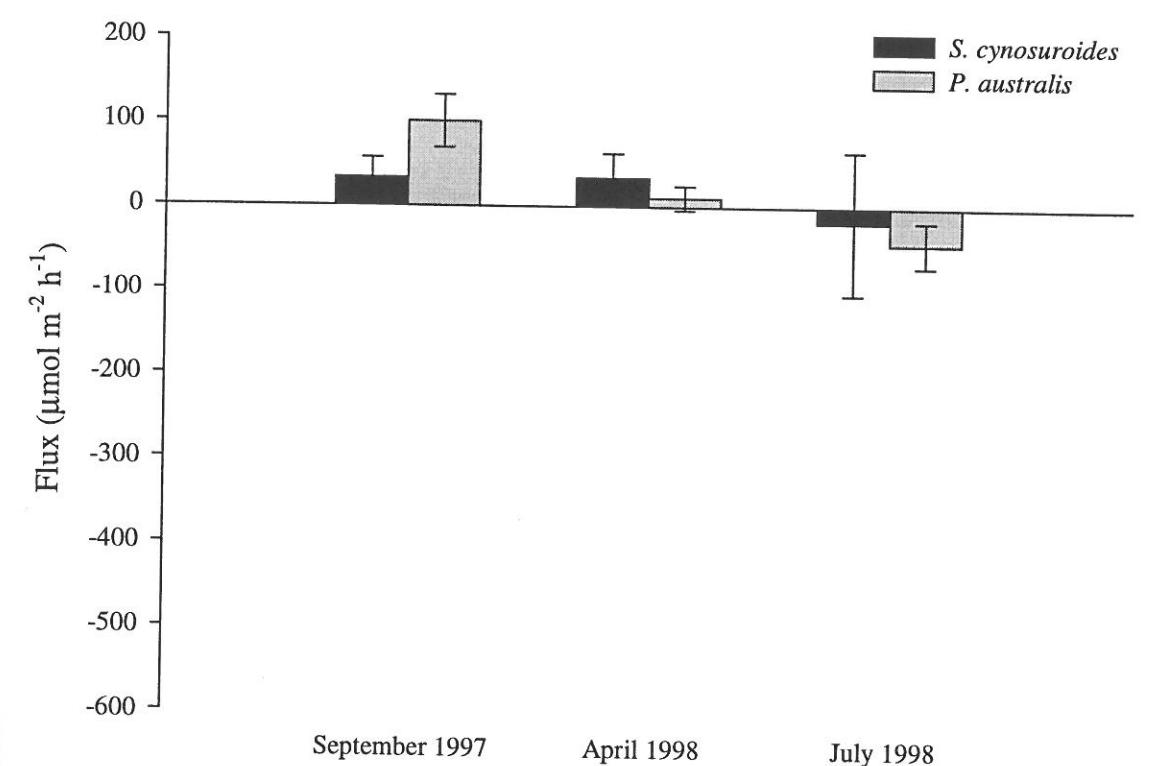


Figure 4. Relative ammonium (NH_4^+) flux ($\pm\text{SE}$) from paired *S. cynosuroides* community and *P. australis* community to overlying tidal waters.

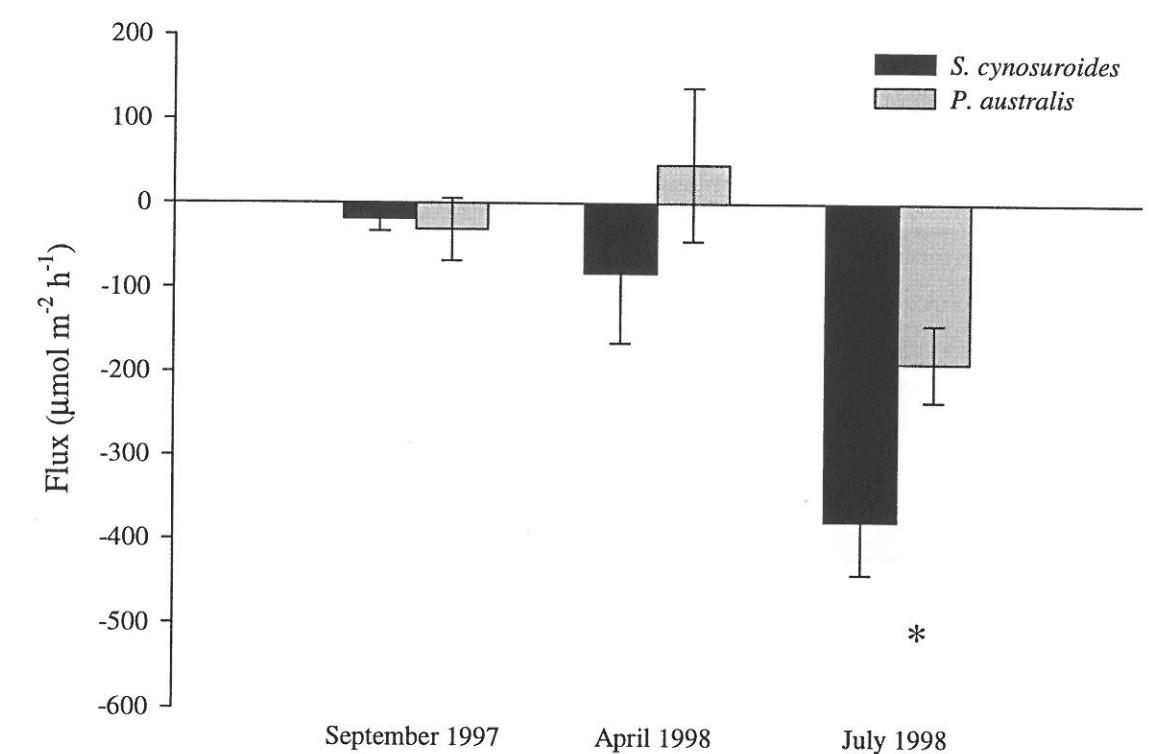


Figure 5. Relative nitrate/nitrite ($\text{NO}_3^- + \text{NO}_2^-$) flux ($\pm \text{SE}$) from paired *S. cynosuroides* community and *P. australis* community to overlying tidal waters. Asterix indicate significant differences ($p < .05$) between communities using Welch's t-test.

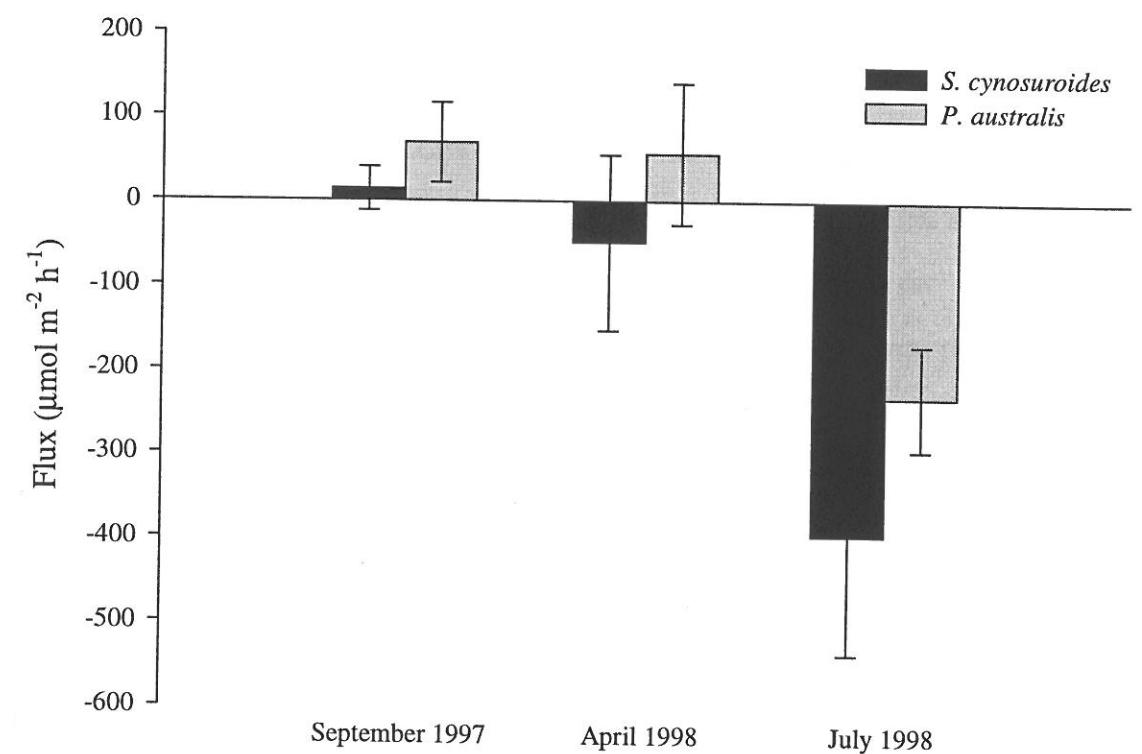


Figure 6. Relative dissolved inorganic nitrogen (DIN) flux (\pm SE) from paired *S. cynosuroides* community and *P. australis* community to overlying tidal waters.

communities on site 1 and site 2 were 5.79 mm y^{-1} and 4.85 mm y^{-1} . Accretion rates for the 3 cores from *P. australis* communities were 4.92 mm y^{-1} , 6.03 mm y^{-1} , and 4.85 mm y^{-1} . Mean accretion rates for the *S. cynosuroides* and *P. australis* communities were nearly identical (5.32 mm y^{-1} and 5.27 mm y^{-1} respectively) and not significantly different ($F=0.02$, $df=1$, $p=0.904$).

Bulk density and organic content from the second set of cores did not vary significantly between communities. Mean dry bulk density for the *S. cynosuroides* communities and the *P. australis* communities was 0.353 g cm^{-3} and 0.344 g cm^{-3} respectively ($F=0.78$, $df=1$, $p=0.471$). Mean organic content for these communities was 22.3% and 22.2% ($F=0.06$, $df=1$, $p=0.824$). Site 2 though had lower bulk densities (0.2572 g cm^{-3} and 0.2496 g cm^{-3}) and higher organic content (31.2% and 31.4%) than site 1 (0.4029 g cm^{-3} and 0.3768 g cm^{-3} , 17.6% and 17.9%) and site 3 (0.3984 g cm^{-3} and 0.4062 g cm^{-3} , 18.1% and 17.4%). Site 1 and site 3 were located on the same tidal channel whereas site 2 was located on an interior tidal channel (Fig. 1). Sediment load of individual tidal creeks and the hydroperiod of individual sites may account for this difference.

Inorganic mass fluxes for both communities were also not significantly different ($F=0.18$, $df=1$, $p=0.746$). Fluxes for site 1 in the *S. cynosuroides* community and *P. australis* community were $1829 \text{ g m}^{-2} \text{ y}^{-1}$ and $1341 \text{ g m}^{-2} \text{ y}^{-1}$; site 2 mass fluxes were $855 \text{ g m}^{-2} \text{ y}^{-1}$ and $1054 \text{ g m}^{-2} \text{ y}^{-1}$. Site 3 mass fluxes for the *P. australis* community was $1294 \text{ g m}^{-2} \text{ y}^{-1}$. Site 3 mass fluxes for the *S. cynosuroides* community were not calculated because of missing accretion rate data. Mean inorganic mass fluxes were $1340 \text{ g m}^{-2} \text{ y}^{-1}$ and $1230 \text{ g m}^{-2} \text{ y}^{-1}$ for the *S. cynosuroides* and *P. australis* community respectively.

III. Plant Community Structure and Species Diversity

III. A. Species Composition

Over the course of the study, thirty-three species were identified (Table 8). Twenty-three species were identified in both communities; 4 species were identified only in the *S. cynosuroides* communities (*Apios americana* Medikus, *Osmunda regalis* L., *Murdannia keisak* [Hassk.] Hand.-Mazz., *Rumex*

Table 6. Summary of accretion rates, bulk density, organic content, and inorganic mass flux for paired *S. cynosuroides* communities and *P. australis* communities.

Site	Community	Accretion Rate (mm y ⁻¹)	Bulk Density (g cm ⁻³)	Organic Content (%)	Inorganic Mass Flux (g m ⁻² y ⁻¹)
1	<i>S. cynosuroides</i>	5.79	0.4029	17.6	1829
	<i>P. australis</i>	4.92	0.3768	17.9	1341
2	<i>S. cynosuroides</i>	4.85	0.2572	31.2	855
	<i>P. australis</i>	6.03	0.2496	31.4	1054
3	<i>S. cynosuroides</i>	-	0.3984	18.1	-
	<i>P. australis</i>	4.85	0.4062	17.4	1294
Mean ± SE	<i>S. cynosuroides</i>	5.32 ± 0.47	0.353 ± 0.048	22.3 ± 4.4	1340 ± 487
	<i>P. australis</i>	5.27 ± 0.38	0.344 ± 0.048	22.2 ± 4.6	1230 ± 89

Table 7. Cesium-137 activity ($\text{dpm g}^{-1} \pm \text{error}$) with depth of sediment cores from paired *S. cynosuroides* communities and *P. australis* communities. Peak levels are indicated in bold. BD = Below Detection.

Depth (cm)	Activity					
	Site 1		Site 2		Site 3	
	<i>S. cynosuroides</i>	<i>P. australis</i>	<i>S. cynosuroides</i>	<i>P. australis</i>	<i>S. cynosuroides</i>	<i>P. australis</i>
0-1	-	-	-	-	0.808 ± 0.07	0.674 ± 0.08
1-2	-	-	-	0.413 ± 0.07	0.729 ± 0.07	0.802 ± 0.09
2-3	0.935 ± 0.03	-	1.813 ± 0.10	1.169 ± 0.08	0.713 ± 0.07	0.909 ± 0.08
3-4	1.024 ± 0.04	1.161 ± 0.03	1.819 ± 0.12	1.161 ± 0.11	0.848 ± 0.09	0.768 ± 0.09
4-5	1.085 ± 0.03	-	1.039 ± 0.12	1.286 ± 0.09	0.839 ± 0.07	1.140 ± 0.09
5-6	1.091 ± 0.04	1.374 ± 0.04	1.570 ± 0.13	0.958 ± 0.09	0.907 ± 0.08	0.908 ± 0.11
6-7	1.204 ± 0.04	-	1.832 ± 0.11	1.185 ± 0.11	1.052 ± 0.09	1.215 ± 0.10
7-8	1.386 ± 0.04	1.658 ± 0.04	2.469 ± 0.16	1.236 ± 0.10	0.849 ± 0.09	1.154 ± 0.09
8-9	1.568 ± 0.04	2.298 ± 0.05	2.992 ± 0.13	1.389 ± 0.07	0.898 ± 0.06	1.287 ± 0.10
9-10	1.675 ± 0.04	2.679 ± 0.05	3.018 ± 0.13	1.594 ± 0.09	0.971 ± 0.10	1.623 ± 0.12
10-11	2.175 ± 0.05	2.630 ± 0.05	3.397 ± 0.15	1.396 ± 0.10	1.008 ± 0.10	1.576 ± 0.09
11-12	2.340 ± 0.05	3.018 ± 0.05	4.242 ± 0.15	1.825 ± 0.12	1.049 ± 0.08	1.534 ± 0.09
12-13	3.010 ± 0.06	3.290 ± 0.05	5.370 ± 0.15	2.206 ± 0.12	1.231 ± 0.08	1.840 ± 0.12
13-14	4.098 ± 0.07	4.092 ± 0.06	5.092 ± 0.17	2.246 ± 0.12	1.076 ± 0.08	2.128 ± 0.11
14-15	4.108 ± 0.06	3.262 ± 0.06	5.452 ± 0.12	2.554 ± 0.12	1.288 ± 0.06	2.741 ± 0.12
15-16	4.174 ± 0.06	2.653 ± 0.05	5.498 ± 0.16	3.184 ± 0.12	1.349 ± 0.09	2.898 ± 0.12
16-17	3.621 ± 0.06	2.171 ± 0.04	5.712 ± 0.12	3.101 ± 0.12	1.371 ± 0.08	3.049 ± 0.13
17-18	3.817 ± 0.06	1.838 ± 0.04	5.054 ± 0.13	3.200 ± 0.12	1.476 ± 0.08	2.968 ± 0.11
18-19	1.451 ± 0.04	1.529 ± 0.04	4.611 ± 0.13	3.873 ± 0.11	1.215 ± 0.06	2.420 ± 0.08
19-20	1.068 ± 0.03	1.236 ± 0.03	4.213 ± 0.16	3.465 ± 0.12	1.351 ± 0.09	1.906 ± 0.10
20-21	1.534 ± 0.04	1.053 ± 0.03	3.425 ± 0.12	4.354 ± 0.09	1.530 ± 0.08	-
21-22	0.541 ± 0.02	1.020 ± 0.03	2.580 ± 0.12	4.226 ± 0.11	1.549 ± 0.08	1.450 ± 0.10
22-23	0.341 ± 0.02	0.785 ± 0.03	2.058 ± 0.12	3.966 ± 0.10	1.679 ± 0.10	0.593 ± 0.07
23-24	0.221 ± 0.01	0.912 ± 0.03	-	3.124 ± 0.10	1.512 ± 0.07	0.720 ± 0.07
24-25	0.083 ± 0.01	-	-	2.264 ± 0.07	1.776 ± 0.09	0.880 ± 0.08
25-26	0.233 ± 0.01	0.650 ± 0.02	1.667 ± 0.14	1.542 ± 0.11	1.788 ± 0.08	0.279 ± 0.06
26-27	0.155 ± 0.01	-	1.417 ± 0.13	1.139 ± 0.08	1.701 ± 0.11	0.400 ± 0.06
27-28	0.191 ± 0.01	0.695 ± 0.03	0.806 ± 0.10	0.951 ± 0.08	1.685 ± 0.07	0.143 ± 0.04
28-29	0.138 ± 0.01	-	0.523 ± 0.07	0.821 ± 0.07	1.757 ± 0.10	0.264 ± 0.06
29-30	0.109 ± 0.01	0.726 ± 0.03	0.468 ± 0.05	0.273 ± 0.05	1.878 ± 0.09	0.210 ± 0.08
30-31	0.152 ± 0.01	-	0.263 ± 0.06	0.200 ± 0.04	1.973 ± 0.09	0.240 ± 0.06
31-32	0.036 ± 0.01	0.417 ± 0.02	0.109 ± 0.05	0.261 ± 0.04	1.856 ± 0.09	0.194 ± 0.07
32-33	0.020 ± 0.00	-	0.216 ± 0.05	0.387 ± 0.05	1.732 ± 0.09	0.148 ± 0.05
33-34	0.074 ± 0.01	0.326 ± 0.02	0.053 ± 0.04	0.403 ± 0.07	1.672 ± 0.10	BD
34-35	0.137 ± 0.01	-	0.085 ± 0.05	0.705 ± 0.07	1.319 ± 0.08	0.084 ± 0.03
35-36	-	-	0.080 ± 0.05	0.524 ± 0.07	0.866 ± 0.07	0.120 ± 0.04
36-37	BD	0.271 ± 0.02	0.024 ± 0.04	0.483 ± 0.08	0.721 ± 0.07	0.042 ± 0.02
37-38	-	-	0.064 ± 0.05	0.505 ± 0.07	0.719 ± 0.08	-
38-39	-	0.194 ± 0.01	-	-	0.504 ± 0.05	0.061 ± 0.04
39-40	0.021 ± 0.00	BD	0.057 ± 0.04	-	0.273 ± 0.04	0.015 ± 0.03
40-41	-	-	-	-	0.631 ± 0.06	-
41-42	-	BD	-	-	0.625 ± 0.06	-

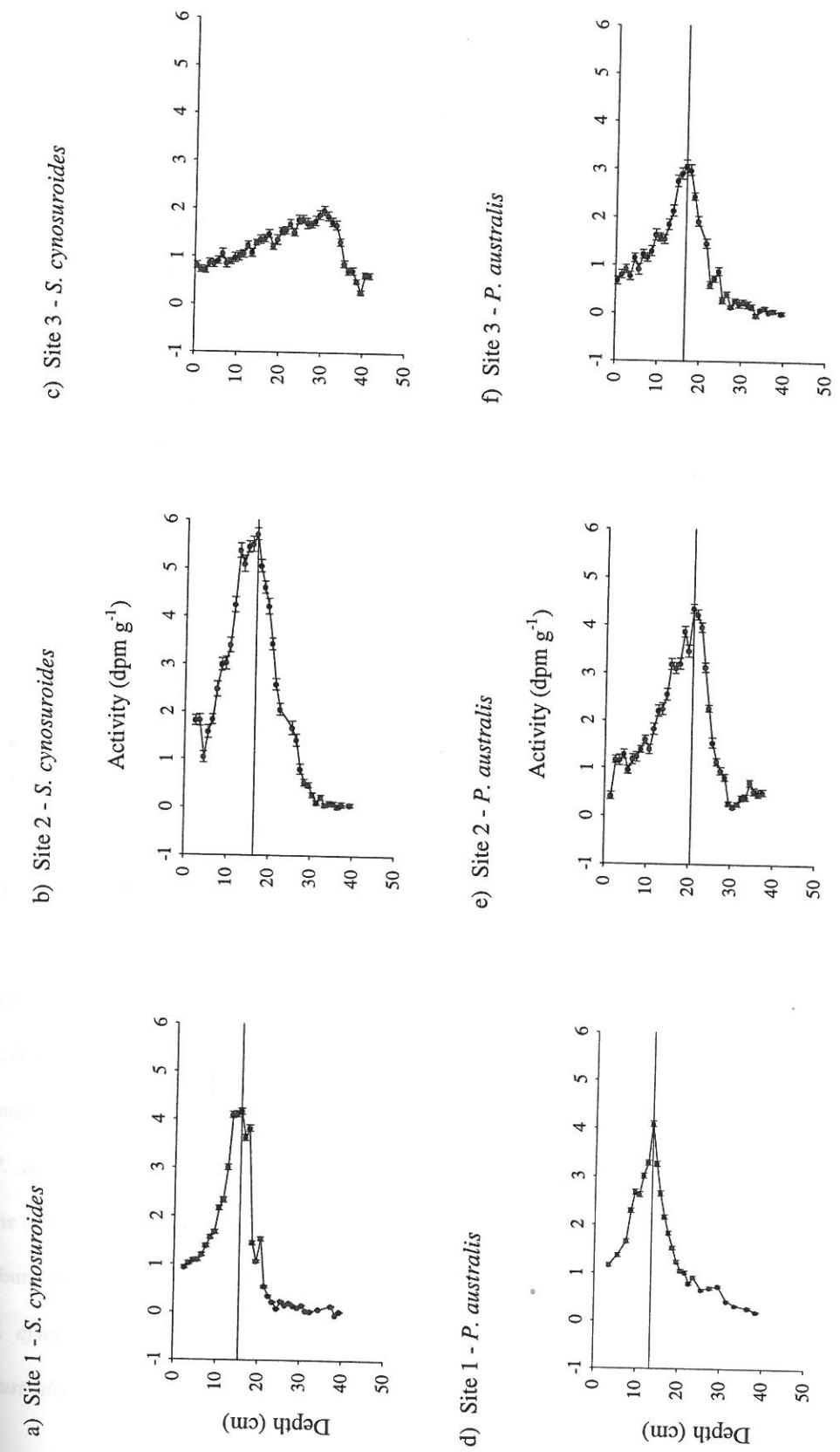


Figure 7. Cesium-137 depth profiles of paired *S. cynosuroides* communities and *P. australis* communities. Interpreted 1963-64 peak level of ¹³⁷Cs is indicated by solid line.

verticillatus L.); and 6 species were identified only in the *P. australis* communities (*Amaranthus cannabinus* [L.] Sauer, *Aster racemosus* Elliott, *Pluchea odorata* [L.] Cass., *Scirpus validus* Vahl, *Sparganium americanum* Nutt., *Teucrium canadense* L.).

Species richness of the *S. cynosuroides* and *P. australis* communities were similar for all sampling dates (Table 9). Maximum numbers for the *P. australis* communities were 17 species on site 2 in July, and minimum numbers were 9 species on site 1 in September. Maximum numbers for the *S. cynosuroides* communities were 14 species on site 2 in May and July, and minimum numbers were 8 species on site 3 in May. Individual site species richness never differed by more than 4 species (site 1, July). Species richness in the *S. cynosuroides* communities was less on all sites in July and less on all but one site in September. During May sampling, both communities had similar site species richness. Pooled species richness was greater in the *S. cynosuroides* communities in May (20 to 18) but less in September (18 to 19) and July (20 to 23) relative to the *P. australis* communities. However, these values did correspond to a slight difference ($S=3.0$, $df=1$, $p=0.083$) between communities. Mean species richness exhibited a slight difference only in July ($S=3.0$, $df=1$, $p=0.083$).

III. B. Ground Cover Values and Stem Density

In September 1997, similar ground cover values were observed between the 2 communities only for *P. virginica* (8.4% and 7.7%; Fig. 8). *L. oryzoides* (18.2% and 3.3%) and *S. cynosuroides* (16.7% and 2.7%) showed a much greater abundance in the native, *S. cynosuroides* communities. The invasive, *P. australis* communities in turn had much larger cover values for *Carex stricta* Lam. (0.0% and 12.5%) and *P. australis* (0.2% and 9.6%). The abundance of *L. oryzoides* and *C. stricta* were primarily derived from the dominance of each species in only one of the sampled communities. *L. oryzoides* occurred with high abundance on site 1 (47.8%) whereas *C. stricta* occurred in high abundance on site 2 (35.6%). Overall the *S. cynosuroides* communities had a higher but non-significant mean ground cover value than the *P. australis* communities (59.8% and 47.5% respectively; $S=0.33$, $df=1$, $p=0.564$; Table 10).

Table 8. Vascular plant species identified by season in *S. cynosuroides* communities and *P. australis* communities (S = September 1997, M = May 1998, J = July 1998). Nomenclature according to Gleason and Cronquist (1991).

Species	Season	
	<i>S. cynosuroides</i>	<i>P. australis</i>
<i>Amaranthus cannabinus</i> (L.) Sauer	-	J
<i>Apio americana</i> Medikus	M	-
<i>Asclepias incarnata</i> L.	J	M
<i>Aster racemosus</i> Elliott	-	S
<i>Bidens coronata</i> (L.) Britton	S,J	J
<i>Bidens laevis</i> (L.) BSP	M,J	M,J
<i>Carex hyalinolepis</i> Steudel	S,M,J	S,M,J
<i>Carex stricta</i> Lam.	M	S,M,J
<i>Echinochloa walteri</i> (Pursh) Heller	S,J	S,J
<i>Eleocharis fallax</i> Weatherby	M,J	M,J
<i>Eleocharis quadrangulata</i> (Michx.) Roemer & Schultes	S,M,J	S,M,J
<i>Hibiscus moscheutos</i> L.	S,M,J	S,M,J
<i>Kosteletzky virginica</i> (L.) C. Presl.	S,J	M,J
<i>Leersia oryzoides</i> (L.) Swartz	S,M,J	S,M,J
<i>Ludwigia palustris</i> (L.) Elliott	J	M,J
<i>Mikania scandens</i> (L.) Willd.	M	M
<i>Murdannia keisak</i> (Hassk.) Hand.-Mazz.	M	-
<i>Osmunda regalis</i> L.	S,M,J	-
<i>Peltandra virginica</i> (L.) Schott & Endl.	S,M,J	S,M,J
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	S,M,J	S,M,J
<i>Pluchea odorata</i> (L.) Cass.	-	S,J
<i>Polygonum arifolium</i> L.	S,M,J	S
<i>Polygonum punctatum</i> Elliott	S,M,J	S,M,J
<i>Pontederia cordata</i> L.	S,M,J	S,M,J
<i>Rumex verticillatus</i> L.	S,M	-
<i>Sagittaria latifolia</i> Willd.	J	J
<i>Scirpus robustus</i> Pursh	S	J
<i>Scirpus validus</i> Vahl	-	S
<i>Sparganium americanum</i> Nutt.	-	S
<i>Spartina cynosuroides</i> (L.) Roth	S,M,J	S,M,J
<i>Teucrium canadense</i> L.	-	S,J
<i>Thelypteris palustris</i> Schott	S,M,J	S,M,J
<i>Zizania aquatica</i> L.	S,M,J	S,M,J
Total	27	29

Table 9. Relative vascular plant species richness for paired *S. cynosuroides* communities and *P. australis* communities. Superscripts indicate difference between communities using Friedman's test (a: $p < .1$).

Site	Community	Richness		
		September 1997	May 1998	July 1998
1	<i>S. cynosuroides</i>	11	10	10
	<i>P. australis</i>	9	10	14
2	<i>S. cynosuroides</i>	11	14	14
	<i>P. australis</i>	13	14	17
3	<i>S. cynosuroides</i>	10	8	11
	<i>P. australis</i>	12	11	12
Pooled	<i>S. cynosuroides</i>	18	20	20
	<i>P. australis</i>	19	18	23
Mean \pm SE		10.7 ± 0.3	10.7 ± 1.8	11.7 ± 1.2^a
		11.3 ± 1.2	11.7 ± 1.2	14.3 ± 1.5

Comparisons of the stem densities between the two communities confirm differences seen in ground cover values (Fig. 9, Table 11). Of the most frequently occurring species, *P. punctatum* was the only species not to show a significant difference between the two communities with stem densities of 2.6 stems m^{-2} in the *S. cynosuroides* communities and 1.8 stems m^{-2} in the *P. australis* communities ($t=1.03$, $df=57$, $p=0.31$). *L. oryzoides* had a mean stem density of 30.8 stems m^{-2} in the *S. cynosuroides* communities and 14.4 stems m^{-2} in the *P. australis* communities ($t=2.63$, $df=42$, $p=0.012$). *S. cynosuroides* had a mean stem density of 17.3 stems m^{-2} in the *S. cynosuroides* communities and 3.7 stems m^{-2} in the *P. australis* communities ($t=5.31$, $df=45$, $p<0.0001$). *P. australis* had a mean stem density of 0.17 stems m^{-2} in the *S. cynosuroides* communities and 10.3 stems m^{-2} in the *P. australis* communities ($t=-6.93$, $df=29$, $p<0.0001$). Even *P. virginica* showed a slight difference in stem densities between the *S. cynosuroides* communities and the *P. australis* communities (16.6 and 13.1 stems m^{-2} respectively; $t=1.71$, $df=57$, $p=0.092$).

In May 1998, ground cover values for *P. virginica* (45.0% and 45.2%) and *L. oryzoides* (7.5% and 6.3%) were similar between *S. cynosuroides* and *P. australis* communities (Fig. 10, Table 12). As in September, *P. australis* and *S. cynosuroides* abundance showed a reciprocal relationship. *P. australis* was more abundant in the *P. australis* communities (1.5% to 13.2%) and *S. cynosuroides* in the *S. cynosuroides* communities (13.1% to 1.9%) by nearly inverse ratios. In addition, *C. stricta* showed a large abundance in the *P. australis* communities (10.0%) although once again most of this abundance was derived from site 2 (28.6%). Overall ground cover in the two communities was nearly equal (78.8% and 87.8%; $S=0.33$, $df=1$, $p=0.564$).

Significant stem density differences were observed for all frequently occurring species except *P. virginica* ($t=-0.39$, $df=46$, $p=0.70$) and *P. punctatum* ($t=-1.31$, $df=54$, $p=0.26$; Fig. 11, Table 13). *L. oryzoides* had a density of 66.2 stems m^{-2} in the *S. cynosuroides* communities and 39.7 stems m^{-2} in the *P. australis* communities ($t=2.23$, $df=41$, $p=0.031$). Once again, stem density differences between *P. australis* (0.6 stems m^{-2} and 13.4 stems m^{-2}) and *S. cynosuroides* (22.0 stems m^{-2} and 3.1 stems m^{-2}) in

the two communities were highly significant ($t=-6.70$, $df=31$, $p<0.0001$ and $t=5.43$, $df=36$, $p<0.0001$ respectively).

In July 1998 as in September, *P. virginica* was the only species with similar cover values in both communities (29.3% and 25.6%). *P. australis* was less abundant in the *S. cynosuroides* communities relative to the *P. australis* communities (1.1% to 15.2%) and vice versa for *S. cynosuroides* in the *P. australis* communities (11% to 2.6%). *L. oryzoides* was more abundant in the *S. cynosuroides* communities (19.0% to 7.2%) primarily due to high ground cover values of *L. oryzoides* on the site 1 community (43%) as in September. *C. stricta* continued to be abundant in the *P. australis* communities (0.0% to 16.1%) primarily due to high ground cover values of *C. stricta* from the site 2 community (39.3%). In addition, *O. regalis* appeared in high abundance in the *S. cynosuroides* communities (6.2% to 0.0%) although it was only present on site 2 (18.5%). Total mean ground cover for the *S. cynosuroides* and *P. australis* communities were similar (84.7% and 88.6%; $S=0.33$, $df=1$, $p=0.564$; Fig. 12, Table 14).

Stem density differences between the *S. cynosuroides* and *P. australis* communities were not significant for *P. virginica* (21.7 stems m^{-2} and 20.1 stems m^{-2} respectively; $t=0.72$, $df=57$, $p=0.48$) or *Z. aquatica* (3.2 stems m^{-2} and 2.7 stems m^{-2} respectively; $t=0.32$, $df=40$, $p=0.75$; Fig. 13, Table 15). *P. punctatum* had densities of 1.2 stems m^{-2} and 2.9 stems m^{-2} in the *S. cynosuroides* and *P. australis* communities respectively ($t=-1.87$, $df=35$, $p=0.069$). *L. oryzoides* measured densities were 64.1 stems m^{-2} and 33.7 stems m^{-2} in the *S. cynosuroides* and *P. australis* communities ($t=2.08$, $df=55$, $p=0.042$). Highest significant differences between stem densities of a species in the two communities were for *P. australis* (0.6 stems m^{-2} and 12.8 stems m^{-2} , $t=-6.17$, $df=31$, $p<0.0001$) and *S. cynosuroides* (9.3 stems m^{-2} and 1.7 stems m^{-2} ; $t=3.16$, $df=32$, $p=0.0035$).

III. C. Importance Value Rankings

Rankings of species by importance value show a difference of three species between the *S. cynosuroides* and *P. australis* communities in September 1997 and May 1998 and a difference of 4 species

Table 10. Relative pooled community ground cover values (%) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during September 1997. Only species with pooled ground cover greater than 5% in at least one of the two communities are listed.

Site	Community	Ground Cover					Total
		<i>C. stricta</i>	<i>L. oryzoides</i>	<i>P. virginica</i>	<i>P. australis</i>	<i>P. punctatum</i>	
1	<i>S. cynosuroides</i>	-	47.8	7.8	0.6	6.4	17.1
	<i>P. australis</i>	1.8	5.4	9.0	12.6	4.0	83.4
2	<i>S. cynosuroides</i>	-	3.0	8.3	-	7.0	37.0
	<i>P. australis</i>	35.6	3.7	5.2	6.6	4.0	48.1
3	<i>S. cynosuroides</i>	-	3.9	9.0	-	2.1	64.2
	<i>P. australis</i>	-	1.0	9.0	9.6	-	47.8
Pooled ± SE	<i>S. cynosuroides</i>	-	18.2 ± 14.8	8.4 ± 0.4	0.2 ± 0.2	5.1 ± 1.5	16.7 ± 1.7
	<i>P. australis</i>	12.5 ± 11.6	3.3 ± 1.3	7.7 ± 1.3	9.6 ± 1.7	2.7 ± 1.3	2.7 ± 1.5
							59.8 ± 11.8
							47.5 ± 8.5

Table 11. Relative^a pooled community stem density (stems m⁻²) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during September 1997. Only most frequently occurring species are listed. Superscript indicate differences between communities using Welch's t-test (a: p < .1, b: p < .05, c: p < .0001).

Site	Community	Density				
		<i>L. oryzoides</i>	<i>P. virginica</i>	<i>P. australis</i>	<i>P. punctatum</i>	<i>S. cynosuroides</i>
1	<i>S. cynosuroides</i>	68.4	13.1	0.5	4.0	14.4
	<i>P. australis</i>	25.6	15.0	16.4	2.3	-
2	<i>S. cynosuroides</i>	16.4	15.3	-	3.6	25.6
	<i>P. australis</i>	13.8	5.2	6.2	3.0	3.6
3	<i>S. cynosuroides</i>	7.7	21.4	-	0.3	11.9
	<i>P. australis</i>	3.7	15.0	8.4	-	7.5
Pooled ± SE	<i>S. cynosuroides</i>	30.8 ± 5.6 ^b	16.6 ± 1.5 ^a	0.2 ± 0.1 ^c	2.6 ± 0.6	17.3 ± 2.2 ^c
	<i>P. australis</i>	14.4 ± 2.8	13.1 ± 1.4	10.3 ± 1.5	1.8 ± 0.1	3.7 ± 1.2

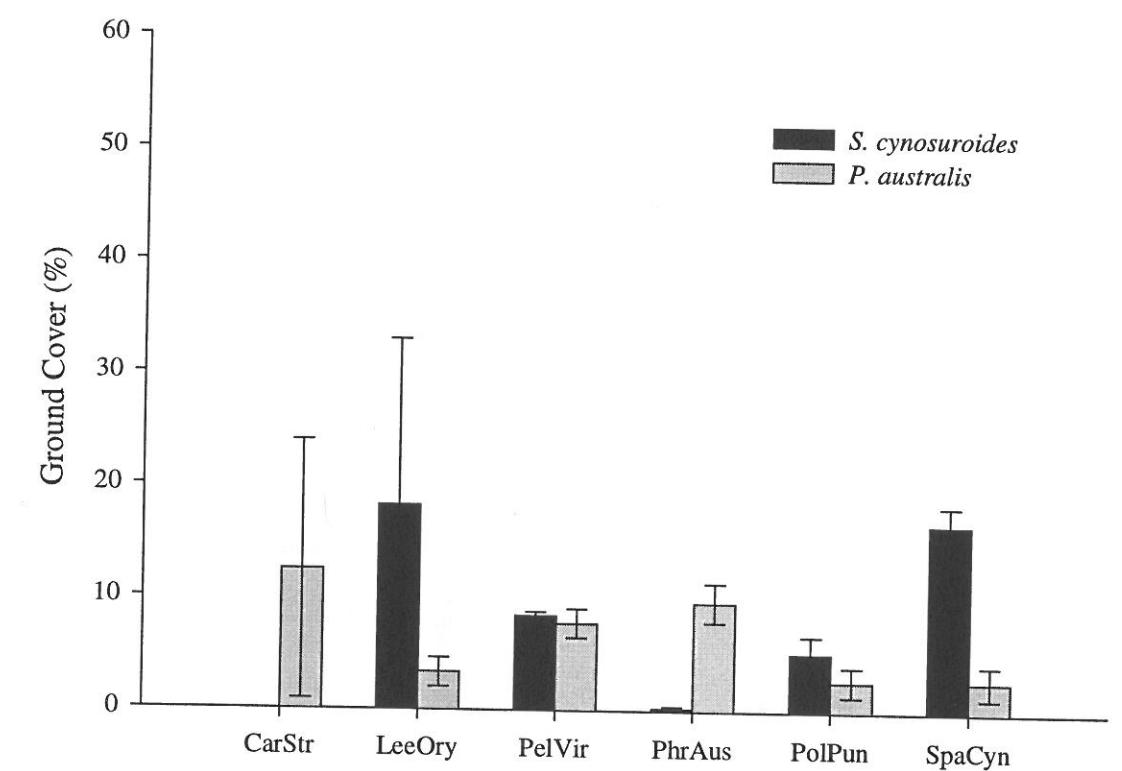


Figure 8. Relative pooled community ground cover (\pm SE) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during September 1997. Only species with pooled ground cover greater than 5% in at least one of the communities are shown. Species are abbreviated by first 3 letters of genus name and species name.

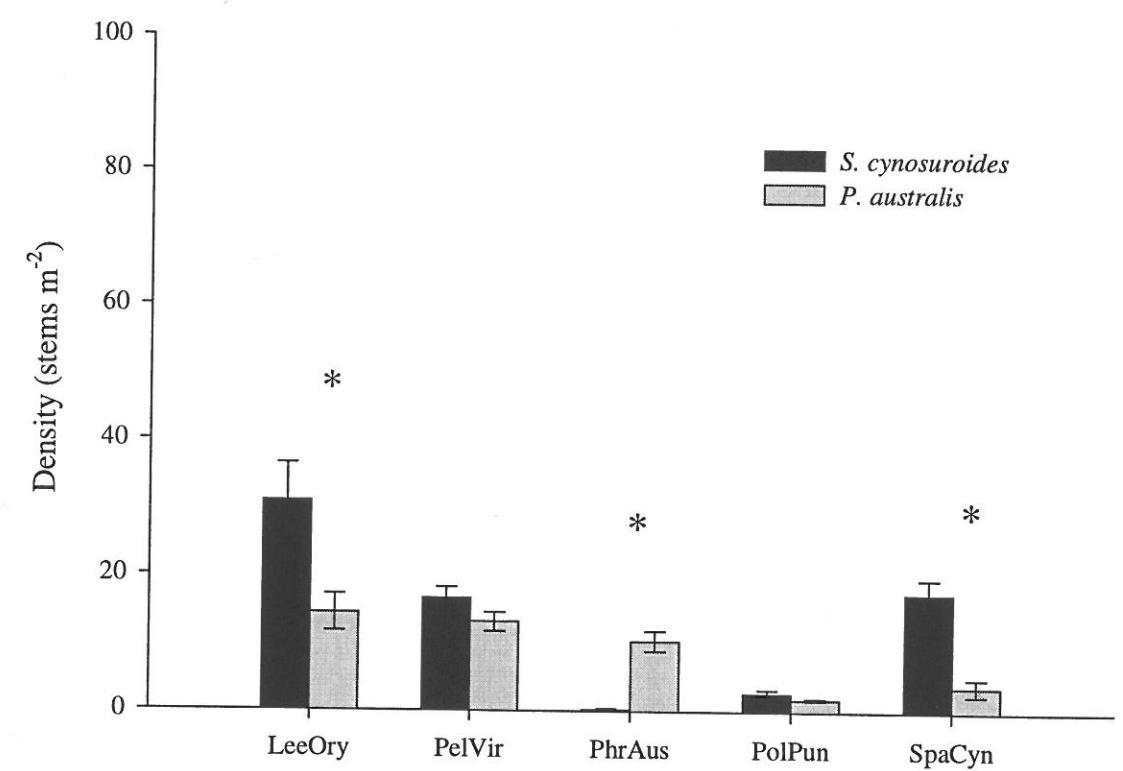


Figure 9. Relative pooled community stem density (\pm SE) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during September 1997. Only most frequently occurring species are shown. Asterix indicate significant differences ($p < .05$) between communities using Welch's t-test. Species are abbreviated by first 3 letters of genus name and species name.

Table 12. Relative pooled community ground cover values (%) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during May 1998. Only species with pooled ground cover greater than 5% in at least one of the two communities are listed.

Site	Community	Ground Cover					Total
		<i>C. stricta</i>	<i>L. oryzoides</i>	<i>P. virginica</i>	<i>P. australis</i>	<i>S. cynosuroides</i>	
1	<i>S. cynosuroides</i>	-	15.0	45.0	4.5	7.5	80.3
	<i>P. australis</i>	1.5	12.6	54.3	13.4	0.6	90.8
2	<i>S. cynosuroides</i>	1.5	6.6	47.5	-	26.3	97.2
	<i>P. australis</i>	28.6	4.2	33.3	6.6	1.2	92.4
3	<i>S. cynosuroides</i>	-	1.0	42.5	-	5.4	58.8
	<i>P. australis</i>	-	2.1	48	9.6	3.9	80.5
Pooled ± SE	<i>S. cynosuroides</i>	0.5 ± 0.5	7.5 ± 6.5	45.0 ± 1.4	1.5 ± 2.3	13.1 ± 5.9	78.8 ± 11.1
	<i>P. australis</i>	10.0 ± 8.4	6.3 ± 5.1	45.2 ± 6.6	13.2 ± 0.3	1.9 ± 1.5	87.8 ± 3.7

Table 13. Relative pooled community stem density (stems m⁻²) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during May 1998. Only most frequently occurring species are listed. Superscript indicate differences between communities using Welch's t-test (a: p < .05, b: p < .0001).

Site	Community	Density				
		<i>L. oryzoides</i>	<i>P. virginica</i>	<i>P. australis</i>	<i>P. punctatum</i>	<i>S. cynosuroides</i>
1	<i>S. cynosuroides</i>	157.3	21.6	2.0	4.7	8.4
	<i>P. australis</i>	69.0	34.7	12.1	7.1	0.5
2	<i>S. cynosuroides</i>	59.1	30.4	-	4.2	46.3
	<i>P. australis</i>	29.7	21.8	16.6	5.4	1.1
3	<i>S. cynosuroides</i>	2.3	37.1	-	-	19.5
	<i>P. australis</i>	7.1	37.0	9.8	0.7	7.5
Pooled ± SE	<i>S. cynosuroides</i>	72.9 ± 15.2 ^a	29.7 ± 1.9	0.7 ± 0.4 ^b	3.0 ± 3.8	24.7 ± 3.8 ^b
	<i>P. australis</i>	35.3 ± 7.3	31.2 ± 3.2	12.8 ± 1.8	4.4 ± 1.0	3.0 ± 1.3

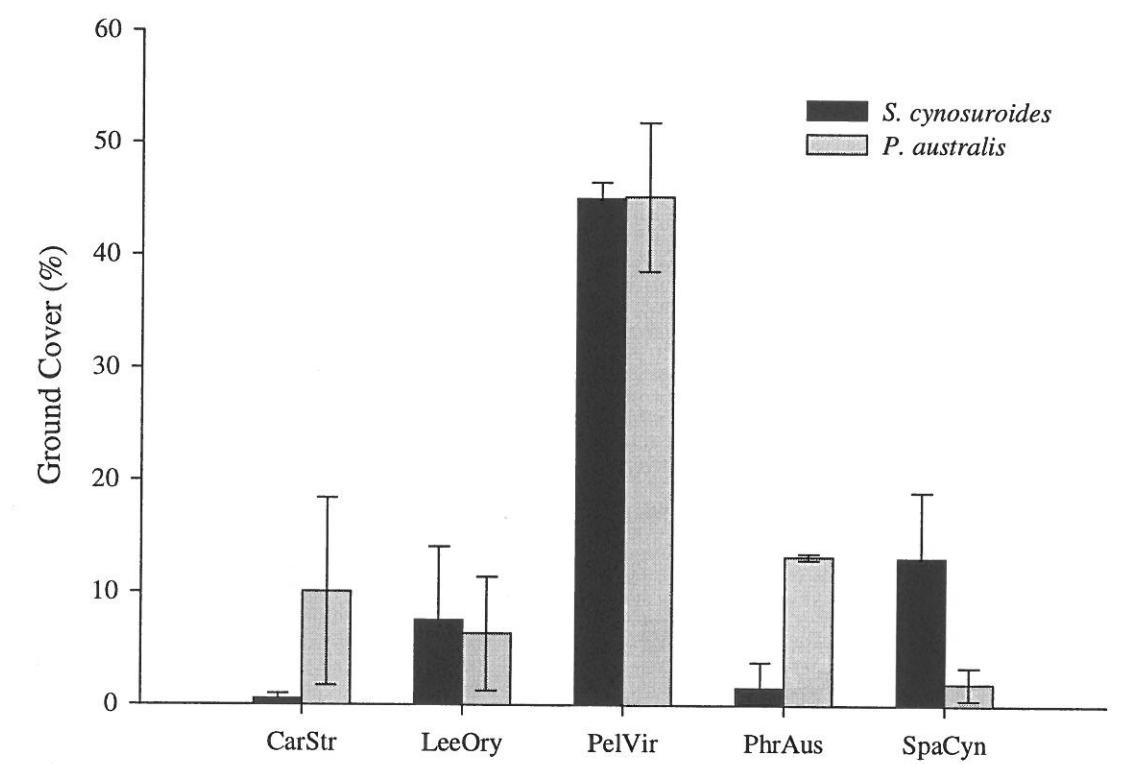


Figure 10. Relative pooled community ground cover (\pm SE) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during May 1998. Only species with pooled ground cover greater than 5% in at least one of the communities are shown. Species are abbreviated by first 3 letters of genus name and species name.

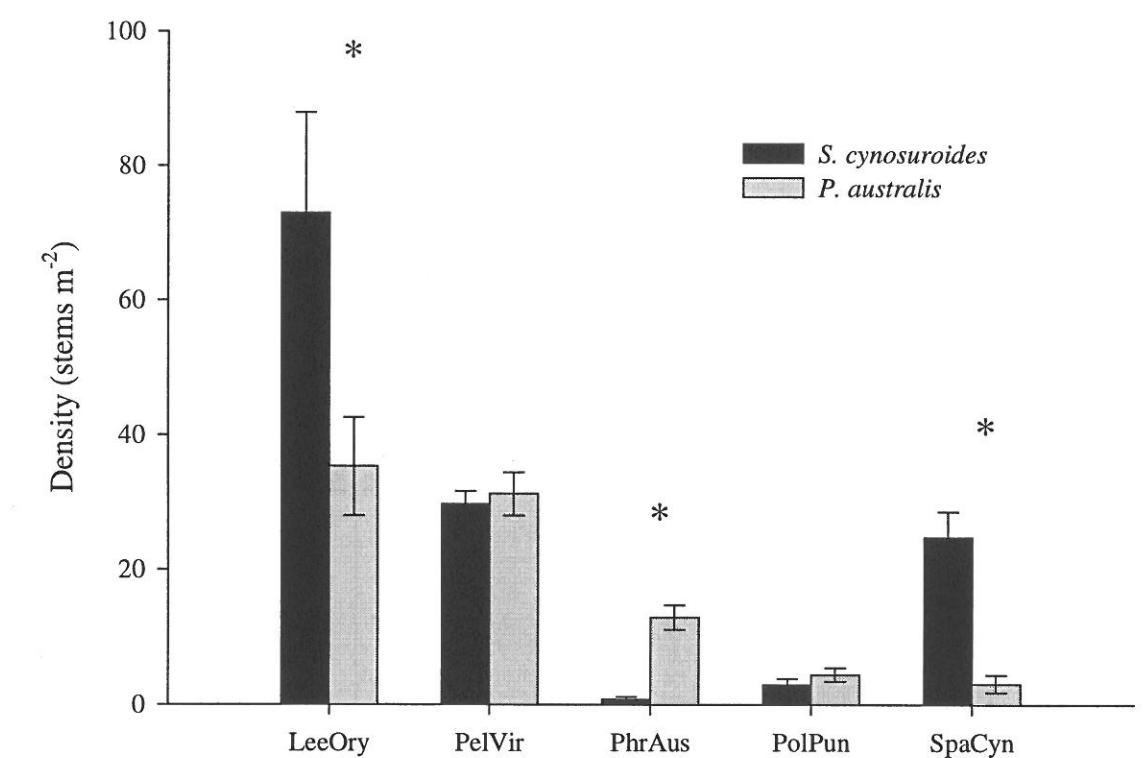


Figure 11. Relative pooled community stem density (\pm SE) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during May 1998. Only most frequently occurring species are shown. Asterix indicate significant differences ($p < .05$) between communities using Welch's t-test. Species are abbreviated by first 3 letters of genus name and species name.

Table 14. Relative pooled community ground cover values (%) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during July 1998. Only species with pooled ground cover greater than 5% in at least one of the two communities are listed.

Site	Community	Ground Cover					Total
		<i>C. stricta</i>	<i>L. oryzoides</i>	<i>O. regalis</i>	<i>P. virginica</i>	<i>P. australis</i>	
1	<i>S. cynosuroides</i>	-	43.0	-	24.0	3.3	11.3
	<i>P. australis</i>	9.0	13.5	-	28.5	14.6	81.5
2	<i>S. cynosuroides</i>	-	7.8	18.5	30.8	-	97.8
	<i>P. australis</i>	39.3	6.4	-	19.5	16.8	117.2
3	<i>S. cynosuroides</i>	-	6.3	-	33.3	-	65.2
	<i>P. australis</i>	-	1.8	-	28.8	14.1	67.2
Pooled ± SE	<i>S. cynosuroides</i>	-	19.0 ± 12.0	6.2 ± 6.2	29.3 ± 2.8	1.1 ± 1.1	84.7 ± 10.0
	<i>P. australis</i>	16.1 ± 11.9	7.2 ± 3.4	-	25.6 ± 3.1	15.2 ± 0.8	88.6 ± 14.9

Table 15. Relative pooled community stem density (stems m⁻²) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during July 1998. Only most frequently occurring species are listed. Superscript indicate differences between communities using Welch's t-test (a: p < .1, b: p < .05, c: p < .01, d: p < .0001).

Site	Community	Density					<i>Z. aquatica</i>
		<i>L. oryzoides</i>	<i>P. virginica</i>	<i>P. australis</i>	<i>P. punctatum</i>	<i>S. cynosuroides</i>	
1	<i>S. cynosuroides</i>	141.3	19.7	1.9	0.9	6.0	2.0
	<i>P. australis</i>	61.5	22.9	9.6	2.5	0.1	1.9
2	<i>S. cynosuroides</i>	33.4	15.9	-	1.7	21.4	-
	<i>P. australis</i>	35.6	11.9	20.2	5.7	2.0	-
3	<i>S. cynosuroides</i>	17.7	29.6	-	0.9	0.4	7.7
	<i>P. australis</i>	4.1	25.4	8.5	0.5	3.0	6.1
Pooled ± SE	<i>S. cynosuroides</i>	64.1 ± 11.3 ^b	21.7 ± 1.5	0.6 ± 0.4 ^d	1.2 ± 0.3 ^a	9.3 ± 2.3 ^c	3.2 ± 1.6
	<i>P. australis</i>	33.7 ± 9.2	20.1 ± 1.7	12.8 ± 1.9	2.9 ± 0.9	1.7 ± 0.6	2.7 ± 0.7

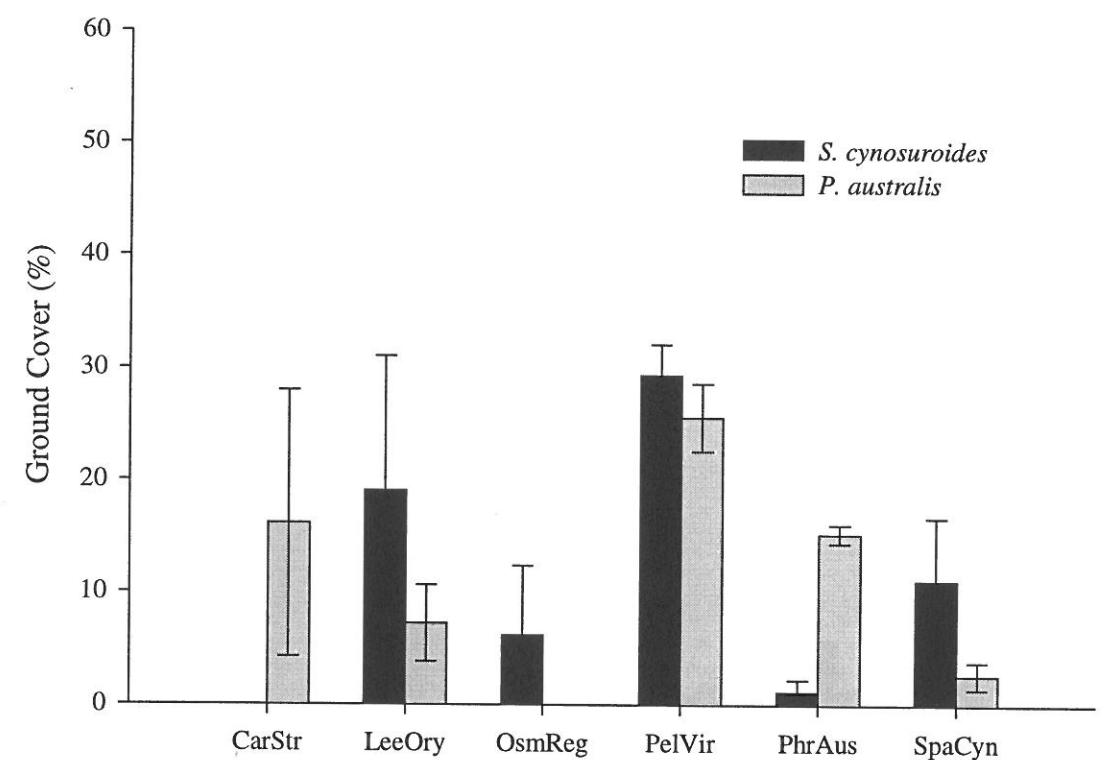


Figure 12. Relative pooled community ground cover (\pm SE) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during July 1998. Only species with pooled ground cover greater than 5% in at least one of the communities are shown. Species are abbreviated by first 3 letters of genus name and species name.

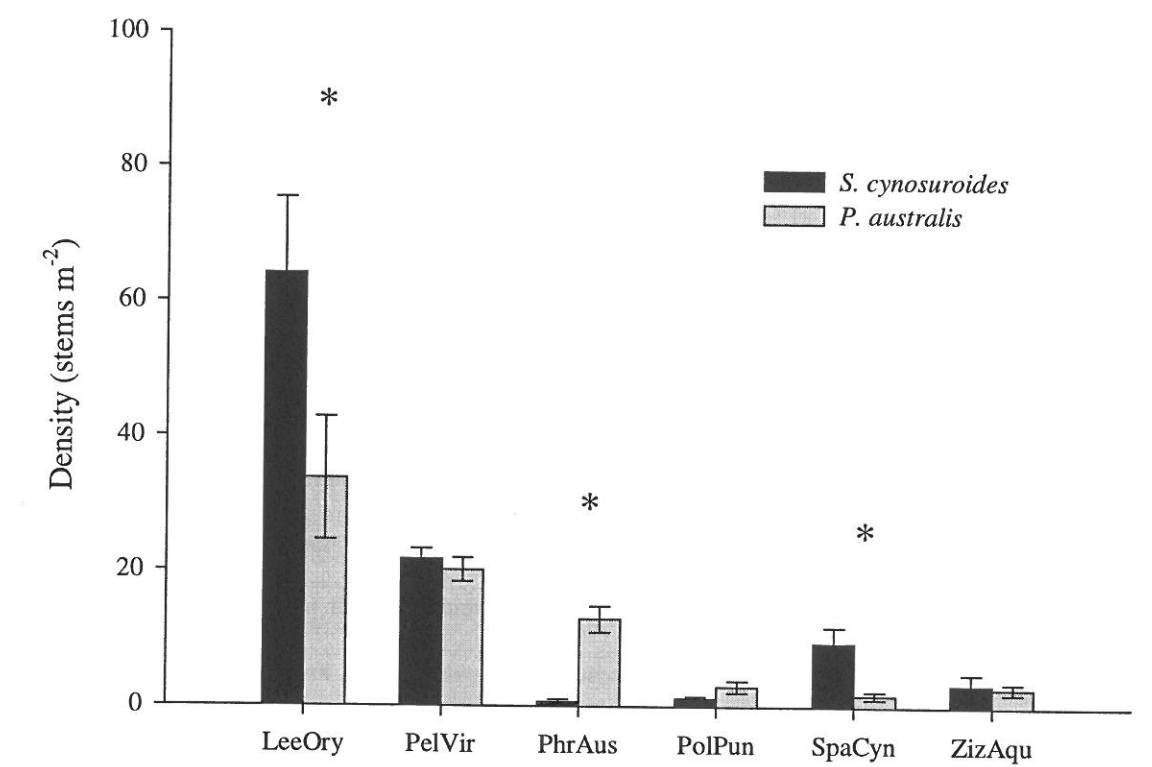


Figure 13. Relative pooled community stem density (\pm SE) of vegetation for paired *S. cynosuroides* communities and *P. australis* communities during July 1998. Only most frequently occurring species are shown. Asterix indicate significant differences ($p < .05$) between communities using Welch's t-test. Species are abbreviated by first 3 letters of genus name and species name.

in July 1998 (Table 16). *C. stricta* and *P. australis* are one of the top four ranked species in the *P. australis* communities for every sampling date but do not occur in the top ranked species of the *S. cynosuroides* communities. The highest ranking difference after *C. stricta* and *P. australis* occurs with *O. regalis* receiving a 10 ranking in September and May and a 5 ranking in July in the *S. cynosuroides* communities without occurring in the *P. australis* communities, and the presence of *Carex hyalinolepis* Steud. ranked as high as 6 in the *S. cynosuroides* communities but never achieving a ranking higher than 14 in *P. australis* communities. Otherwise, the top six species in the *S. cynosuroides* communities always appear in the top 10 rankings of the *P. australis* communities.

III. D. Community Species Diversity

Shannon diversity and evenness were consistently higher on all sites for all seasons in the *P. australis* communities (Table 17). Exceptions were on site 2 in September and site 1 in May. Also, evenness on site 3 in July was greater in the *S. cynosuroides* community than the *P. australis* community. Pooled diversity was found to be greater in the *P. australis* communities ($S=3.0$, $df=1$, $p=0.083$). However, mean diversity in the communities was only different in July ($S=3.0$, $df=1$, $p=0.083$). Pooled and mean evenness were not found to be significantly different for any sampling date or across seasons ($S=0.33$, $df=1$, $p=0.564$).

Rank-abundance curves were constructed based on community species rank by pooled ground cover and mean ground cover values for each sampling date (Fig. 14). These curves show that the mid-ranked species (5-15) have slightly higher abundance values in the *P. australis* communities than the *S. cynosuroides* communities. In addition, in September and July, the lowest ranked species (<15) also have greater abundance in the *P. australis* communities. These curves indicate that greater equitability of subdominant species in the *P. australis* communities may have contributed to diversity differences despite the lack of significant differences in calculated evenness.

Table 16. Top ten ranking by season of vascular plant species occurring in paired *S. cynosuroides* communities and *P. australis* communities. Species are ranked by pooled community importance values.

Species	Rank			
	September 1997 <i>S. cynosuroides</i>	<i>P. australis</i>	May 1998 <i>S. cynosuroides</i>	<i>P. australis</i>
<i>L. oryzoides</i>	1	4	2	3
<i>S. cynosuroides</i>	2	6	3	1
<i>P. virginica</i>	3	3	1	3
<i>P. punctatum</i>	4	5	4	2
<i>Z. aquatica</i>	5	9	9	6
<i>E. walteri</i>	6	8	-	5
<i>P. cordata</i>	7	7	14	18
<i>P. arifolium</i>	8	19	16	12
<i>H. moscheutos</i>	9	14	7	16
<i>O. regalis</i>	10	-	10	10
<i>C. stricta</i>	-	1	13	-
<i>P. australis</i>	13	2	11	4
<i>E. quadrangulata</i>	12	10	8	11
<i>B. laevis</i>	-	-	5	6
<i>C. hyalinolepis</i>	17	12	6	14
<i>T. palustris</i>	11	11	15	9
<i>L. palustris</i>	-	-	-	10
				7
				18

Table 17. Relative Shannon diversity index values and evenness values of vegetation for paired *S. cynosuroides* communities and *P. australis* communities. Superscripts indicate differences between communities using Friedman's test (a: $p < .1$).

Site	Community	September 1997		May 1998		July 1998	
		Diversity	Evenness	Diversity	Evenness	Diversity	Evenness
1	<i>S. cynosuroides</i>	1.298	0.541	1.397	0.607	1.464	0.636
	<i>P. australis</i>	1.749	0.796	1.329	0.577	1.934	0.733
2	<i>S. cynosuroides</i>	1.777	0.741	1.532	0.581	1.880	0.712
	<i>P. australis</i>	1.617	0.630	1.701	0.644	2.124	0.750
3	<i>S. cynosuroides</i>	1.787	0.776	1.033	0.497	1.705	0.711
	<i>P. australis</i>	2.114	0.851	1.437	0.599	1.752	0.705
Pooled	<i>S. cynosuroides</i>	1.883	0.651	1.555	0.519	2.028	0.677
	<i>P. australis</i>	2.205	0.749	1.682	0.582	2.255	0.719
Mean ± SE	<i>S. cynosuroides</i>	1.621 ± 0.16	0.686 ± 0.07	1.321 ± 0.15	0.561 ± 0.03	1.683 ± 0.12 ^a	0.666 ± 0.03
	<i>P. australis</i>	1.827 ± 0.15	0.759 ± 0.07	1.489 ± 0.11	0.607 ± 0.02	1.937 ± 0.11	0.729 ± 0.01

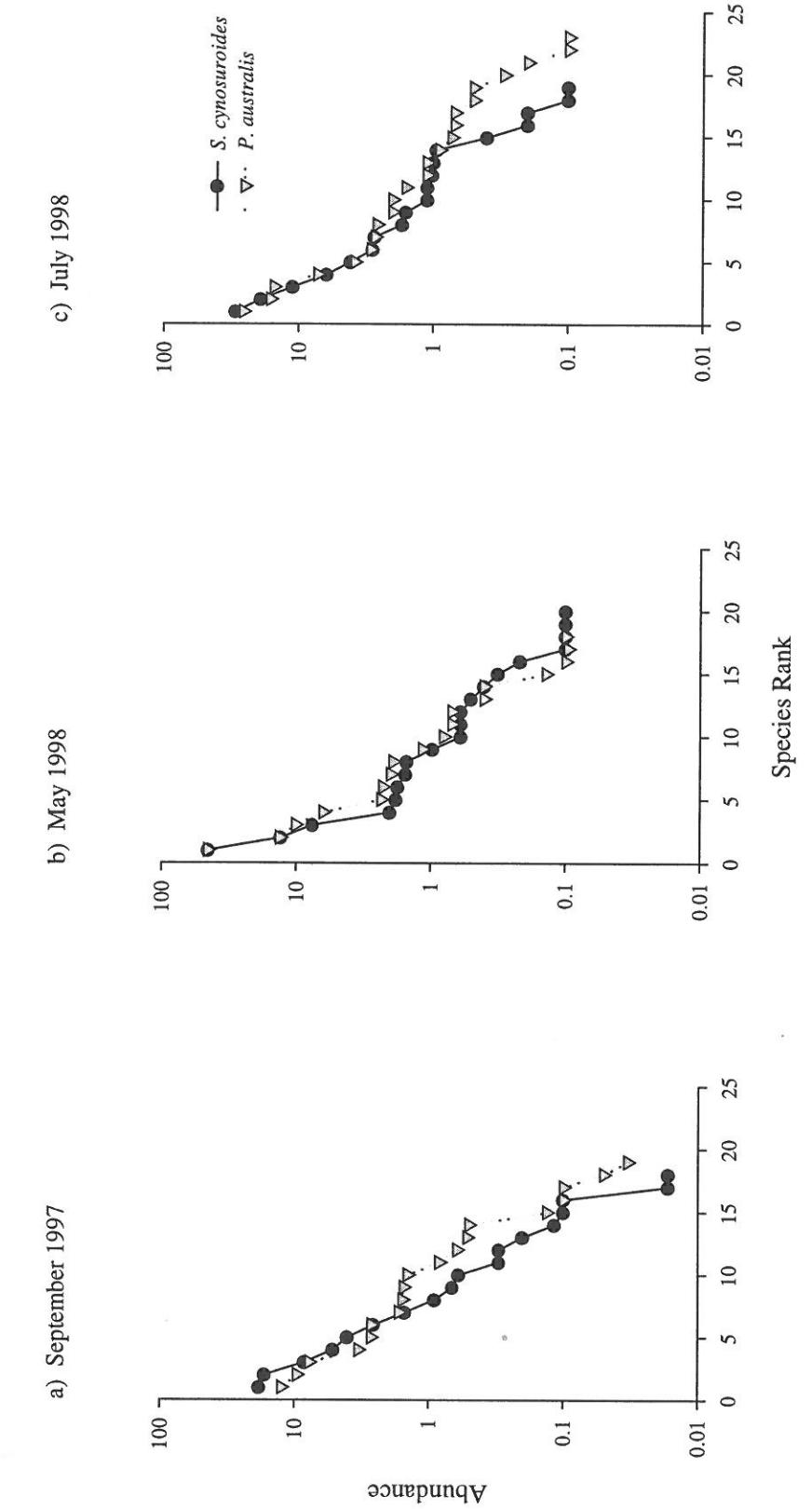


Figure 14. Seasonal rank-abundance curves for paired *S. cynosuroides* communities and *P. australis* communities based on pooled community ground cover values.

DISCUSSION

I. Water Quality

I. A. Nutrient Flux

Nutrient fluxes may indicate differences in the ability of each community to protect the quality of surrounding waters by reducing nutrient loads. The null hypothesis of no difference in nutrient fluxes between the *S. cynosuroides* community and the *P. australis* community could only be rejected in 3 of the 16 comparisons made. Differences in fluxes represent differences in sediment concentrations between the communities as initial concentrations in the tidal waters are the same in nearly all cases (Table 5). In turn, differences in sediment concentrations are indicative of variable rates of processes that influence these concentrations between the two communities.

In September, the *S. cynosuroides* community had a greater flux of phosphate from the sediments to the tidal waters whereas the *P. australis* community had a slight uptake of phosphate. This difference would favor the *P. australis* community in terms of water quality value. However, in April and July, the two communities exhibited similar fluxes. Therefore, no clear trend across seasons exists in the phosphate fluxes.

There are a number of possible explanations for the phosphate flux difference in September. First, it may represent a difference in uptake of the vegetative or microbial populations between the two communities. Second, it may represent a difference in the mineralization from sediment detritus between the communities. If the *S. cynosuroides* community has higher sediment organic content, higher mineralization rates, or organic matter with lower C:P ratios, then this community may have greater mineralization and higher sediment phosphate concentrations. Higher sediment organic content does not

appear to be supported by sediment core data from this study (Table 6). A third explanation for higher phosphate flux in the *P. australis* community is that if more aerobic conditions exist in this community, it could lead to precipitation of phosphate with ferric iron, calcium, and aluminum (Faulkner and Richardson 1989). Armstrong and Armstrong (1988) demonstrated that *P. australis* does aerate its root zone. It is not clear if *S. cynosuroides* aerates its root zone to the same degree. Finally, pH differences may influence the amounts of soluble orthophosphate. Low pH may cause release of phosphate from insoluble salts, but in turn, increase the sorption of phosphate to clay particles (Mitsch and Gosselink 1993). Any of these processes may cause a difference in sediment phosphate concentrations between the two communities.

The second significant difference between the communities occurred with nitrate/nitrite fluxes in July and across seasons. The *S. cynosuroides* community exhibited a significantly larger uptake of nitrate/nitrite especially in July. This difference would indicate an increased buffering capability for nitrate/nitrite in the native community. Nitrate/nitrite fluxes showed similar but insignificant trends to July fluxes in April and no difference in September. Fluxes from these months were close to zero relative to variability. Therefore, the overall significant difference in nitrate/nitrite fluxes across seasons was apparently dominated by the July difference.

Nitrate/nitrite fluxes into the sediment from tidal waters are affected by processes that produce and consume nitrate/nitrite. The primary consumptive processes are assimilatory nitrate reduction, dissimilatory nitrate reduction to ammonium (DNRA), and denitrification. The primary productive process is nitrification. The larger flux of nitrate into the *S. cynosuroides* community shows that the difference between consumptive and productive processes is larger than the difference in the *P. australis* community. The two most likely processes that would produce a difference are assimilatory nitrate reduction and denitrification. Changes due to DNRA or nitrification would be reflected in ammonium fluxes. No signal is observed for ammonium fluxes although it may be hidden by differences in production of ammonium from mineralization.

DR: Assimilatory nitrate reduction is the uptake of nitrate by vegetation and microbes for assimilation in structural molecules like amino acids. The rate of assimilatory nitrate reduction may differ between the

communities during the growing season if the productivity maxima of *P. australis* and *S. cynosuroides* differ. As a C₄ species, *S. cynosuroides* may be exhibiting higher mid-season productivity than the C₃ species, *P. australis*, because of the ability to avoid the inefficiency of photorespiration (Saxena and Ramakrishnan 1984). Assimilatory nitrate reduction may be a minor process though as ammonium is a more favorable substrate for assimilation.

Denitrification is an anaerobic process that converts nitrate to nitrogenous gases. With no large allochthonous source of nitrate, it is linked closely to the aerobic process of nitrate production from nitrification (Bowmer 1987). In tidal freshwater marshes though, allochthonous nitrate delivered from tidal waters may be a more important source of nitrate for denitrification (Bowden 1986). Temperature and redox potential are two physical characteristics that may explain intensity differences in denitrification rates. Based on vegetative ground cover (Tables 10, 12, 14), insolation of the marsh surface is equivalent, and sediment temperatures may not differ. Potential root aeration by *P. australis* (Armstrong and Armstrong 1988) may affect sediment redox potential although oxygen delivery may only be sufficient to support root and rhizome respiration (Brix 1989). Sediment temperature and redox potential were not measured.

No significant difference in ammonium fluxes was observed between the two communities for any sampling date or across seasons. Mean differences between communities were small with variability between individual chambers relatively high. In addition, the ammonium flux never differed far from zero relative to variability. These results suggest that there is an equivalent balance between productive and consumptive processes involving ammonium in the two communities. Among these processes are mineralization of organic matter, nitrification, DNRA, and biological immobilization. These results do not necessarily imply that rates of each individual process is equal in each community, but the net effect of the combined action of these processes is equivalent in each community.

Differences between combined DIN fluxes were not significant for any season or across seasons. In September and April, ammonium and nitrate/nitrite fluxes were approximately equal contributors to the DIN flux, and when combined in the DIN flux, decreased any differences between the communities exhibited in the individual flux. In July, the nitrate/nitrite flux dominated the comparison between

community DIN fluxes. Overall in September, April, and May, the *P. australis* community exhibited larger release or smaller uptake of DIN. Unlike the nitrate/nitrite flux, though, the high variability incorporated in the DIN flux from the ammonium flux prevented any significant differences. Processes explained for nitrate/nitrite fluxes and ammonium fluxes all contribute to the overall effect on inorganic nitrogen represented by DIN fluxes.

Few direct comparisons between *P. australis* and *S. cynosuroides* communities have been performed. Thut (1989) compared the ability of artificial marshes of *P. australis*, *S. cynosuroides*, and *Typha latifolia* L. to filter pulp mill effluents in Mississippi. He compared influent and effluent water samples for total suspended solids, biological oxygen demand, ammonia, organic nitrogen, and phosphorus on a weekly and biweekly basis for 15 weeks. He found that the artificial marshes were most effective at removing ammonia and phosphorus with little difference between each species over a 24 hour period. However, *S. cynosuroides* did appear to be more effective at phosphorus and ammonia removal than *P. australis* over a 6 hour period. Thut (1989) does not consider this difference, but it may indicate temporal differences between community processes over a daily cycle. This difference does suggest that while the net effect of nutrient processes was the same in each community, the rate of processes were not identical.

The relative ability of the two communities to contribute to buffering of surrounding waters from excess nutrient delivery appears to differ slightly. Phosphate fluxes indicate that both communities are a source of phosphate to surrounding waters during the spring and a sink for phosphate during the mid-summer. Late season data indicates that the *P. australis* community does retain the phosphate later into the summer. However, this community may have a higher release later in the autumn. Based on the data collected, both communities would appear to function as a growing season phosphate buffer with the *P. australis* community possessing some potential advantage.

Nitrate/nitrite fluxes indicate that both communities may be a net sink for nitrate/nitrite. The *S. cynosuroides* community did demonstrate a superior ability to take up nitrate/nitrite during the heart of the growing season. In addition, the *S. cynosuroides* community showed that it may also be less likely to release nitrate/nitrite during other portions of the growing season. In combination with studies that have

demonstrated little winter nitrate/nitrite flux activity (Anderson et al 1998), these results suggest that both communities contribute to nitrate/nitrite buffering of surrounding waters, but the *S. cynosuroides* community may have a slightly greater potential. Furthermore, general trends exhibited in DIN fluxes and the dominance of large DIN fluxes by nitrate/nitrite suggest this conclusion may be extended to DIN. It is important to note that differences in water quality are potentials based on three nonweighted seasonal measurements over a short time period.

I. B. Sedimentation

Sedimentation was described by inorganic mass fluxes and accretion rates. Inorganic mass fluxes represent the allochthonous sediment captured by these communities. These sediments are often carriers of inorganic phosphorus and toxic substances. The capture of this sediment represents the contribution of sedimentation to water quality. No significant difference was detected between the mass fluxes between the two communities.

The inorganic mass flux is primarily influenced by the physical factors of proximity to the sediment source, concentration of sediment in waters, and duration of inundation (Friedrichs and Perry in press). The design of this study attempted to limit the influence of all these factors by choosing paired communities of *P. australis* and *S. cynosuroides*. The final factor that may influence the inorganic mass flux would be the physical environment created by the vegetative communities. The finding of no difference implies that there is no difference in the physical environment created by the vegetative communities or that any difference is not large enough to influence sedimentation processes. Vegetative data collected show that there is a difference in vegetative composition and density between the communities. However, this structural difference in vegetation may not be large enough to affect the inorganic mass flux.

The second value of sedimentation is its effect on marsh accretion rates. Changes in local sea-level rise and subsidence require changes in marsh elevation to maintain the stability of the system (DeLaune et al 1983). No significant difference was detected between the accretion rates of the two communities.

Accretion rates are influenced by the inorganic mass flux discussed previously as well as autochthonous and allochthonous organic fluxes and sediment processes like compaction and mineralization of organic materials. Inorganic mass fluxes were found to be similar for both communities. If similar processes influence allochthonous organic mass fluxes these fluxes would be expected to be the same as well. Autochthonous organic fluxes are represented by the on site organic production and any physical processes that may remove it. Cover values are rough surrogates for biomass and, thus, productivity data (Daubenmire 1968). The finding of little difference in overall cover between the communities indicates that production of the communities is similar (Table 10, 12, 14). Physical processes and compaction are assumed to be equivalent by design. Mineralization of organic material is likely not different since productivity and overall sediment organic content of both communities is the same. Therefore, the lack of difference in community accretion rates shows the similarity of community physical processes and structure in the invasive and native communities.

The accretion rates for both communities are on the higher end of estimates for combined sea-level rise and subsidence in the study area. Rates have been estimated to be in the range of 3.5 - 4.5 mm y^{-1} (CBNERRVA 1989). If the marsh is maintaining itself, then accretion rates would be expected to be in the range of combined sea-level rise and subsidence. The higher rates measured in this study may be the result of the location of the study sites on the creek levees. Levees proximity to the sediment source leads to higher rates of deposition despite decreased duration of inundation (Leonard 1997). Therefore, Sweet Hall Marsh in general may be accreting at a rate closer to sea-level rise and subsidence.

Accretion rates from ^{137}Cs profiles may also represent high-end estimates. The accuracy of this method depends on the stability of the peak horizon in the core profile. High levels of vertical mixing of sediments can displace the horizon downward or eliminate it completely (Guinasso and Schink 1975). The presence of fiddler crabs and perennial plants with extensive underground growth in the study area present the means for this mixing. In addition, mineralization in high organic soils has been demonstrated to release ^{137}Cs from its original deposition point and sink the peak horizon in some situations (Torgenson

and Longmore 1984). Finally, autocompaction of sediments below the peak horizon is not accounted for in ^{137}Cs measurements of accretion (Nyman et al 1993).

Despite these potential inaccuracies in calculating accretion rates and inorganic mass fluxes from the ^{137}Cs deposition profile, relative comparisons between the two communities should be accurate assuming this error is not systematic by community, e.g., mixing is greater in one community than the other. Furthermore, evidence indicates that most mixing and diffusion of sediments leads to a spreading of the peak horizon but not necessarily a movement downward (Wise 1980). In terms of the value of each community through sedimentation to the quality of surrounding water, there does not appear to be any difference as represented by inorganic mass fluxes. In terms of the value of each community to the physical maintenance of the marsh surface relative to sea-level rise and subsidence, there does not appear to be any difference as represented by accretion rates. Therefore, changes in the biological community represented by the *P. australis* invasion do not appear to affect this process.

II. Habitat

Habitat value was measured using plant species richness, species diversity, species evenness, and community structure. The null hypothesis of no differences was rejected in favor of the *P. australis* communities for richness and diversity in July and across seasons as well using pooled numbers from individual sampling dates. No significant differences were determined for richness or diversity in September or May though, and no significant differences were determined for evenness in September, May, July, or across seasons. Structure of the two communities was similar but not identical.

The lack of significant difference between evenness measurements implies that the difference in species diversity is primarily because of the increase in species richness in the *P. australis* communities. Richness was higher overall in the *S. cynosuroides* communities during May sampling, but diversity overall was higher because of increased evenness (Fig. 14b). Therefore, there is not a simple relationship trend between the richness and diversity.

The greater richness and diversity in the *P. australis* communities may be attributed to the displacement rather than complete replacement of native species from the invasive communities. The invasive communities have two new dominant species (*P. australis* and *C. stricta*) but do not necessarily exclude any of the dominant or subdominant species from the original native communities (Table 16). Plant species diversity may be related to spatial and temporal heterogeneity (Tilman and Pacala 1993). A more heterogeneous or patchy environment may support more species.

Disturbance may produce heterogeneity. Intermediate-intensity disturbances tend to increase plant species diversity whereas low- and high-intensity disturbances tend to decrease it. Low disturbance areas do not differ from the original successional communities and high disturbance areas create homogenous environments; intermediate disturbance areas maximize spatial heterogeneity with old and new environments (Levin and Paine 1974). The invasion of *P. australis* on Sweet Hall Marsh may represent an intermediate-level disturbance. Alternatively, *P. australis* is suspected to be an opportunistic species that takes advantage of disturbed wetland areas (Geller 1972; Ricciuti 1983; Roman et al 1984). Therefore, the higher richness and diversity in the *P. australis* communities may ultimately be the result of the initial disturbance of the marsh levees. Potential disturbances in tidal freshwater marshes include muskrat activity, dredging, eutrophication, sea-level rise, and subsidence. In any case, the invasive communities apparently are providing an equivalent or slightly superior habitat for herbaceous plant species than the native community.

Previous studies of Sweet Hall Marsh have yielded much higher numbers for species richness and lower numbers for species diversity. Doumlele (1981) identified 43 species and calculated an average diversity of 0.955. Perry (1991) identified 45 species and calculated an average diversity of 0.951. Perry and Atkinson (1997) identified 56 species and calculated an average diversity of 1.351. All of the previous studies were conducted on transects throughout the marsh whereas this study was limited to the major levee communities. Doumlele (1981) noted that high marsh areas including levees had higher diversity. Therefore, richness and diversity from this study are reasonable compared to previous studies.

While overall structure of the communities in terms of cover is similar, the two communities do exhibit some differences structurally. While *P. australis* and *S. cynosuroides* represent the primary difference in dominant species between the invasive and native communities for all sites, the communities are not strictly dominated by *P. australis* and *S. cynosuroides*. *P. virginica* is also dominant in both communities. *C. stricta* shows up in much higher abundance in the *P. australis* communities as does *L. oryzoides* in the *S. cynosuroides* communities. Unlike *P. australis* and *S. cynosuroides* that have similar growth habits, *C. stricta* and *L. oryzoides* do not. *C. stricta* tends to form dense clumps whereas *L. oryzoides* forms less dense and more diffuse coverage. This difference is primarily restricted to site 1 and site 2.

Differences in structural components of plant communities are considered to be an essential component of community avian species diversity. MacArthur and MacArthur (1961) explained that plant species diversity is an accurate predictor of avian species diversity primarily because higher plant species diversity values correspond to higher plant structural diversity. Plant species diversity numbers for the two communities are similar as are structural differences with the primary exception noted above. Most likely any difference in avian diversity between the communities within this ecosystem would be minor because of the general structural similarity. Above this baseline diversity, variability may exist though based on the structural differences that do exist and differences in species composition.

Habitat for other species has recently been investigated in invasive *P. australis* communities. Fell *et al* (1998) investigated macroinvertebrate populations and mummichog (*Fundulus heteroclitus* L.) use for foraging of *P. australis* communities and native communities in the Connecticut River Estuary. In addition, they looked at the tidal creeks fringed and non-fringed by *P. australis* to see if invertebrate and fish population's use were different. They found that invertebrate populations in *P. australis* and native communities were not significantly different nor were they different in *P. australis* fringed and non-fringed creeks. In addition, *F. heteroclitus* use of *P. australis* marshes and creeks were equivalent based on numbers and gut contents. Fell *et al* (1998) concluded that the *P. australis* communities and native communities had similar habitat value for macroinvertebrate and *F. heteroclitus* populations. Therefore,

the possibility of equivalent habitat between *P. australis* communities and native communities for faunal species is possible.

While a statistical difference in plant species richness, species diversity, and some community structure measures was found between the two communities, it is not clear if these differences represent a difference in habitat for plant or faunal species. When all identified species were pooled together from the entire project only two more species were identified in the *P. australis* communities than the *S. cynosuroides* communities. A difference of two species may only represent sampling error rather than any real difference between the two communities. Furthermore, while a consistent one or two species difference between communities may represent a statistical difference, it is difficult to ascertain if this is an ecologically significant difference. However, the null hypothesis of no difference must be rejected in favor of the *P. australis* communities for habitat value.

III. Implications

III. A. Theoretical Ecology

Lawton (1994) proposed four hypotheses to explain the possible effect of species changes on ecosystem processes:

1. *rivet hypothesis* - each individual species has a unique role in the ecosystem like a rivet in a machine, and the loss of each successive species causes an incremental decline in the ecosystem process rate.
2. *idiosyncratic hypothesis* - each lost species changes the ecosystem process rate, but the character of the change is unpredictable and depends on the role of the species lost.
3. *redundant species hypothesis* - there is a threshold of species that may be lost before the ecosystem process rate is compromised.
4. *null hypothesis* - there is no change in the ecosystem process rate when species are lost.

The first two hypotheses are identical except that the rivet hypothesis assumes that the ecosystem process rate decreases as species are lost. The redundant species hypothesis stands in opposition to the first two hypotheses by predicting the consistent possibility of no change when species are lost. The null hypothesis is mentioned for completeness, but does not appear a true alternative at extreme cases of species loss.

The relationship of species change to ecosystem processes will be discussed only for inorganic nutrient flux and sedimentation. Plant species diversity and structure do not fall directly under the definition of ecosystem processes defined by Lawton (1994) and Likens (1992), "the transformation of energy and matter".

The null hypothesis of this study is that no difference in community processes exists between the invasive and native communities. Rejection of the null hypothesis of this study would be equivalent to a rejection of the redundant species hypothesis assuming that the communities sampled are diverse enough to support redundant species. For nutrient fluxes, nitrate/nitrite and phosphate flux allowed for rejection of the null hypothesis on a seasonal basis, and nitrate/nitrite flux allowed rejection when comparisons were made for all seasons simultaneously. The null hypothesis was accepted for inorganic mass fluxes between the communities. This acceptance does not allow for rejection of Lawton's rivet hypothesis or idiosyncratic hypothesis but does provide support for the redundant species hypothesis.

P. australis and *S. cynosuroides* appear to be structurally redundant species but not physiologically redundant. Sedimentation, a physical process, was not affected by the species replacement. However, nutrient flux that combines physical and biological processes was affected by the species replacement even if the difference was small and not seasonally consistent. These results imply that physiological differences in similar plant species are significant enough to affect community processes that are biologically oriented. Any morphological differences between the species were not enough to change community structure sufficiently to affect physical processes. Therefore, the effect of species changes on ecosystems processes would be dependent on the type of process and the type of species. Considering the number of different processes and the variability between species, it seems unlikely that a completely

redundant species exists. Questions must then be asked about the species richness sufficient to have structural and physiological redundancy among an assemblage of species to replace a single species from an ecosystem.

A number of limitations to these conclusions exist. First, statistically significant differences in processes do not necessarily imply ecologically significant differences, i.e., other communities within the ecosystem may buffer the impact of the single community change. Second, it is assumed ecosystem nutrient flux and sedimentation are cumulative properties of community processes. If emergent components of these processes from community relationships exist, the methodology does not account for them. Third, this study is one example from one system. Extrapolation would be tenuous. Despite these limitations, the comparisons of this study do provide evidence that functional redundancy may exist for individual processes but may exist overall only at the level of species assemblages.

III. B. Management and Policy

Interpreting this data for management purposes is difficult since no strong clear trends between the *P. australis* and *S. cynosuroides* communities exist. Management of *P. australis* populations in the mid-Atlantic region has taken a stance towards eradication and control. Feared losses of plant and animal diversity as well as other potential concerns have instigated this policy. A similar policy is outlined in the VMRC Wetlands Guidelines (1993). The VMRC has listed *P. australis* communities as group 5 marshes with few known values of significance and preferable for development over any other coastal wetland systems except saltwort communities. In contrast, *S. cynosuroides* communities are group 2 marshes with high value for water quality, erosion control, flood buffering, and habitat. This study addressed aspects of water quality and habitat.

In terms of the policy on eradication and control, invasive *P. australis* communities may not be detrimental in all situations. Water quality results were inconclusive with the native, *S. cynosuroides* community showing superior potential for water quality improvement through inorganic nitrogen uptake and the invasive, *P. australis* community showing greater potential for water quality improvement through

phosphate retention. Sedimentation processes were the same for both native and invasive communities indicating no impact to this aspect of water quality. Habitat for plant species as interpreted by species richness and diversity values was greater in the *P. australis* communities. Compared to previous analyses of the *P. australis* problem, water quality data brings into consideration a functional value of ecological systems that is often subordinated to habitat concerns. Plant species richness and diversity numbers directly contradict the present management assertion. These data indicate that, in some situations, the value of invasive *P. australis* communities may not be greatly different from the value of native communities.

If this statement is true, any blanket policy initiative towards control and eradication of *P. australis* may be inefficient by incurring control costs without any net functional benefits. In the end, the decision to control or not control *P. australis* and the level this control should take needs to be decided on a case by case basis. The decision should weigh the costs and benefits of the invasive communities relative to the costs and benefits of the native communities and determine if the differences justify the cost of control.

In terms of the VMRC policy on development, data from this study implies that *P. australis* communities have been undervalued. These communities can share sediment trapping, nutrient sink, and plant habitat value similar to *S. cynosuroides* communities. Faunal habitat value has not been demonstrated but other communities without faunal habitat value have received higher rankings, e.g. the black needlerush community, group 3. One difficulty in increasing the classification value of the *P. australis* communities is its wide ecological tolerances. Unlike other communities considered, the *P. australis* communities may be found from saline to fresh water and inundated to dry regions. Depending on the physiographic situation, the value or lack of value of the community may change. Under the present community classification scheme that does not consider specific ecosystem situations, an accurate classification value of the *P. australis* communities is difficult.

Limiting the management implications of this study is the consideration that the study sites may represent an atypical situation. Density values for *P. australis* and *S. cynosuroides* are on the low end of

literature values and would indicate that neither community shows a vigorous presence on Sweet Hall Marsh. Even if these communities do represent an atypical situation, this study still demonstrates that a situation may exist where the invasive communities are not valueless and may be comparable to the native communities. *P. australis* communities that tend towards monospecificity may also be replacing native communities that have the same tendency, e.g., *S. patens* communities. Therefore, absolute numbers may not be "normal" for either community, but the relative comparison may be accurate for a variety of situations.

Of final consideration is how to deal with the importance of the invasive element of *P. australis* communities. Individual studies comparing the functioning of the *P. australis* communities to other communities it replaces may come to similar conclusions that the invasive communities have some advantages and some disadvantages but are clearly not disastrous alternatives to the native communities. On a regional scale however, if *P. australis* communities replace a variety of other communities or threaten to take over an entire ecosystem, there may be some loss in habitat diversity. Studying the problem at this scale is a difficult task because of problems differentiating between changes caused by the *P. australis* invasion and changes caused by other disturbances over time. This problem is especially prevalent with *P. australis* since questions still remain regarding its invasive status. Is the apparent increase in *P. australis* communities in N. America caused by an exotic genetic strain of the species; or is the invasion an indicator of ecosystem disturbance with concomitant explosion of opportunistic populations?

This study has attempted to provide quantitative data to evaluate the relative ecological value of the invasive and a native community by comparing community functions. Management decisions consider more than ecological value though. Future studies should look at the relative social value of *P. australis* compared to native communities as well as other functions native communities may provide. An efficient policy for control and development of *P. australis* communities may be developed then to replace earlier policies based on anecdotal observations and shot-gun decision-making.

CONCLUSION

The results of this study showed that several natural processes provided by invasive, *P. australis* communities are similar but not necessarily equivalent to those provided by native, *S. cynosuroides* communities. Both communities were sinks for inorganic nitrogen and phosphorus fluxes; both communities exhibited similar ability to trap sediments; and both communities had similar values of plant species richness and diversity. However, the native community did appear to be a potentially superior sink for nitrate/nitrite from tidal waters whereas the invasive community did appear to be a potentially superior sink for phosphate. In addition, the invasive communities did have slightly higher values for species richness and diversity and differing community structure.

Applied to ecological theory, this study indicated that the effect of changes in species composition to ecosystem processes is dependent on the structural and physiological role played by the species in the ecosystem and the type of process. The change in dominant vegetation from *S. cynosuroides* to *P. australis* did not affect the physically dependent process of sedimentation but did affect significantly the biologically dependent process of nutrient flux. Hypotheses that describe functional changes with species changes were supported in the latter case but not in the former. These results imply functional redundancy is more likely to occur at the level of species assemblages than individual species.

Applied to management policy, this study demonstrated that *P. australis* communities do have ecological value based on community functions. This value was similar to the value of the native, *S. cynosuroides* communities. Recognition of this potential ecological value in other situations should be incorporated into management decisions on control and development of *P. australis* communities. Ideally, these considerations should be weighed with other non-ecological costs and benefits against the costs and benefits of control.

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