INFLUENCE OF SOIL FLOODING AND NUTRIENT LOAD ON GROWTH OF SELECTED WETLAND PLANTS

By

ROBERT ERNEST BORER

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

1994

ACKNOWLEDGMENTS

My sincere appreciation goes to my major professor, Dr. G. Ronnie Best, for his support, guidance, and direction in this endeavor. Thanks also go to Dr. K.R. Reddy for the use of the Wetland Soils Research Laboratory equipment and facilities. Appreciation is expressed to Dr. Reddy and Dr. T.L. Crisman for being part of my advisory committee, providing suggestions, assistance, and review of the manuscript.

Great appreciation is expressed to Mr. Matthew Fisher, research assistant at the Wetland Soils Research Laboratory, for his guidance and assistance with the nutrient analysis. Thanks are also expressed to Mr. Charles D. Kincaid for his thoughts and assistance with the statistical analysis.

Most of all, I would like to thank my wife, Kerry, for her patience, support, and understanding throughout this process.

TABLE OF CONTENTS

Abstract of Thesis Presented to the Graduate School
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Robert Ernest Borer

August, 1994

Chairman: Dr. G.R. Best
Major Department: Environmental Engineering Sciences

The effects of soil flooding on four wetland plant species, *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* were observed in nutrient rich (primary wastewater) and nutrient poor (oligotrophic marsh water) microcosms. Species performance was based on survival, plant height, above and below ground biomass production, nutrient assimilation, and litter production. Both *T. domingensis* and *S. caroliniana* had 100% survival throughout the five month study period. *S. canadensis* survival ranged from 90% survival in saturated high nutrient(SH) conditions to 17% survival in inundated low nutrient(IL) conditions. *S. latifolia* succumbed to natural end of growing season senescence after week fifteen of the study. Both *T. domingensis* and *S. latifolia* individuals were

significantly taller in inundated high nutrient(IH) conditions compared to SH conditions. Heights for these species did not differ between IL and saturated low nutrient(SL) conditions. *S. caroliniana* had significantly taller plants in both IH and SH conditions compared to IL and SL conditions. *S. canadensis* exhibited no differences in height over the study. *T. domingensis* produced the greatest amount of aboveground biomass in the IH condition. SH also produced significantly more biomass than individuals in SL conditions. Plants in IH conditions also produced the greatest amount of below ground biomass. *S. latifolia* and *S. canadensis* exhibited no significant differences in above or below ground biomass between conditions. *S. caroliniana* produced the greatest above ground biomass in IH conditions and the greatest below ground biomass in SH conditions. *T. domingensis* had no statistical variation in nutrient assimilation (N or P). *S. latifolia* SH had the highest tissue N levels and IH conditions produced the greatest tissue P levels. Both woody species produced greater N and P amounts in the IH conditions. Litter was produced by only the herbaceous species. Individuals of both *T. domingensis* and *S. latifolia* had the greatest levels of litter production and nutrient assimilation (N and P) per plant in IH conditions.

INTRODUCTION

Many natural ecosystems are continually being changed by anthropogenic factors which interrupt the function of these systems. Disposal of treated wastewater has become a problem in Florida. Many natural marsh ecosystems that are influenced by high nutrient wastewaters are experiencing changes in vegetative composition and function.

Freshwater marshes undergo periodic natural water level fluctuations over time periods of several years to several decades that cause changes in the species composition and productivity of marsh vegetation. Flooding and drying associated with water level fluctuations affect marsh nutrient cycles and ultimately plant growth (Neill, 1990). The question has been raised whether hydrologic regime or nutrient loading has initiated the transition of vegetation of these ecosystems.

The purpose of this research was to determine how well two woody species, *Salix caroliniana* and *Sambucus canadensis*, and two herbaceous species, *Typha domingensis* and *Sagittaria latifolia*, found throughout Florida, respond to two different nutrient levels and two different hydrologic regimes (species referred to during the study as *Salix*, *Sambucus*, *Typha* and *Sagittaria*, respectively). Information about how well these plants survive and grow under these conditions may be considered when management of these systems as marsh ecosystems becomes necessary.

Specific objectives of this study were to (1) compare the survival of these species in various study environments, (2) compare growth characteristics (height, above and below ground biomass production) in the four specified environments, and (3) compare nutrient assimilation abilities of the four species in these environments.

LITERATURE REVIEW

Biomass Production and Nutrient Assimilation

Both the herbaceous and woody species used in this study are classified as emergent aquatic plants. *Typha domingensis* Pers.(Southern Cattail) and *Sagittaria latifolia* Willd.(Common Arrowhead) are erect, perennial, rhizomatous herbs and are listed as obligate hydrophytes in the National List of Plant Species that occur in Wetlands: Florida (Reed, 1988). *Salix caroliniana* Michx.(Coastal Plain Willow) is a tree or shrub to 20 m, often with several trunks. This species commonly and abundantly colonizes wet disturbed areas and is also a obligate hydrophyte in Florida. *Sambucus canadensis* L.(Elderberry) is a soft stemmed shrub to 4 m tall. Elderberry is listed as a facultative wet species in Florida and inhabits moist to wet open places, and abundantly colonizes wet clearings and wet disturbed sites (Godrey and Wooten, 1979).

Macrophytes Biomass production in wetlands can vary considerably with hydrologic regime and latitude (Hill, 1987). The high primary production of emergent macrophyte communities generally is attributed to adequate supplies of light, water, and nutrients in the wetland environment (Neely and Davis, 1985). Cattail generally is one of the most studied species due to its ubiquitous growth range from tropical to temperate regions (Debusk and Ryther, 1980). The southern cattail is primarily found in the lower latitudes, and most of the literature available on this species originates from the southeastern USA. Cattail is considered a highly productive emergent macrophyte accompanied by a rapid growth rate (Sharitz et al., 1984). A study at Par Pond in South Carolina by Sharitz et al. (1984) found *T. domingensis* to be highly productive. Par Pond is a thermally graded nuclear reactor reservoir in which the southern cattail inhabited only the ambient and intermediate temperature regimes. They found maximum shoot biomass accumulation in the ambient conditions to be 82.4 ± 36.8 g/plant. The growth rate of this species was 0.70 g/plant/day. The ambient community had the highest standing crop production due to the species' intolerance of elevated water temperatures.

In a brackish estuarine system in North Carolina, Bellis and Gaither (1985) studied annual plant biomass production over an eighteen month period on a tract of low salinity estuarine shoreline. The researchers found end of season live standing crops for *Typha domingensis* ranging from 0.25 to 0.60 kg m^{-2}. Below ground live standing crop ranged from 7.01 to 8.17 kg m^{-2}. These production estimates produced an extremely high annual average ratio of below ground to above ground biomass (B/A) of 11.26. Below ground production tends to be greater than above ground production in the early growing season and decreases throughout the growing season before increasing again during the senescence period (Hill, 1987). The evidence of this increase suggests that a translocation of plant constituents from the senescing above ground structures to the over wintering below ground structures. Hill (1987) also suggested that the lower B/A ratios from the biomass peaks of the two growing seasons of a study in Texas, were indicative of cattails growing in equitable climates, such as those found in lower latitudes. Under the long growing seasons of these regions, little biomass would be expected to be accrued in over wintering organs.

Ogwada (1983) studied cattail production and yields grown in agricultural drainage water in Florida. Total biomass ranged from 0.633 to 1.075 kg m^{-2}. Seasonal standing crop yields ranged from 0.334 to 1.457 kg m^{-2} for shoots and 0.189 to 0.499 kg m^{-2} for rhizomes. The mean seasonal total biomass yield (shoot + rhizome) was 1.048 kg m^{-2}. The study also included a microcosm study where agricultural drainage water was enriched with both N and P. Under the enriched conditions, the biomass yield was 1.067 kg m^{-2} for shoots and 0.908 kg m^{-2} for rhizomes. Total biomass yield for the enriched *Typha* microcosms was 1.975 kg m^{-2} with a shoot to root ratio of 1.2. Tissue nutrient concentrations of the cattails grown in low nutrient agricultural drainage water were 11.46 mg g^{-1} for N and 0.93 mg g^{-1} for P for shoots and 12.34 mg g^{-1} and 0.89 mg g^{-1} for rhizomes, respectively.

Growth, decomposition, and nutrient retention of *Typha domingensis* was studied by Davis (1991) in the Florida Everglades. Study plots were examined over a nutrient enrichment gradient. Leaf tissue concentrations of P, but not N, reflected surface water concentrations and tissue nutrient concentrations were significantly higher in living leaves of *T. domingensis* compared with dead leaves. Concentrations exceeded those in dead leaves by factors of 4.4 for P and 2.0 for N. High nutrient concentrations in live leaves, compared with dead leaves, indicated substantial translocation or leaching from leaves during senescence. Compared with *Cladium jamaicense*, *T. domingensis* allocated larger quantities of P and N to growing leaves, translocated or leached larger quantities from dying leaves, and retained larger quantities in dead leaves. The researcher found that dying *T. domingensis* leaves lost 71-83% of the P and 33-63% of the N which they accumulated during growth.

Factors such as growth response to changing nutrient availability, higher rate of nutrient allocation to growing leaves, higher rates of nutrient loss from senescing leaves, shorter leaf longevity, and rapid leaf turnover are all characteristics of high nutrient status plants. With a combination of these physiological adaptations, the high nutrient status plants, in many instances, may out compete other plants when nutrient levels increase (Davis, 1991).

Cattails grown in effluent with a high eutrophic potential produced biomass which was greater than 600 g /plant (Martin and Fernandez, 1992). Harvesting for this study took place in November when 34% of the total plant biomass was incorporated in the rhizomes. The total productivity of the plants at the end of their vegetative cycle was estimated at 13 kg m^{-2}. This estimate is fairly high compared to estimates from naturally occurring stands in nutrient poor conditions of 1 to 5 kg m^{-2}. Martin and Fernandez (1992) found that plants grown in the effluent water exhibited a delay of natural leaf senescence when compared to natural, nutrient poor stands. They noted that the induction of leaf senescence in response to a nutrient deficiency appeared frequently in plants, resulting in redistribution of the limiting nutrient from older tissue to developing structures (Martin and Fernandez, 1992). The authors also found decreasing tissue nutrient concentrations over time throughout the growing period. This condition was present event when net biomass production was increasing. Boyd (1970) predicted that this phenomenon is due to a decrease in the rate of nutrient absorption per unit of net production and suggested that total plant nutrient storage continued to increase over the same period due to continued increases in net production. Many nutrient accumulation studies (Martin and Fernandez, 1992; Sharitz et al., 1984; Bernard and Fitz, 1979; Dean and Biesboer, 1986; Krolikowska, 1981; Ulrich and Burton, 1988; Neely and Davis, 1985; and

Jordan et al., 1990) have discussed nutrient loss toward the end of the growing season due to either leaching from live, dead, or dying leaves or translocation of nutrients from above ground structures to below ground structures. Dean and Biesboer (1986) used $^{15}N_2$ to measure uptake and distribution of nitrogen in *Typha latifolia*. The researchers found that dinitrogen was presumably fixed in the rhizosphere and any amounts present in the above ground structures were translocated there from the roots or rhizome structures. After two months of nitrogen addition, the plants were harvested, and total nitrogen per plant was found to be 0.3364 ± 0.0948 g/plant. Sharitz et al. (1984) noted that nutrient loss was probably a result of either dilution of elements in the tissues as biomass increases, or slowdown in absorption following early spring initiation of growth. This hypothesis is in agreement with Boyd's (1970) hypothesis of net production overshadowing nutrient accumulation. Sharitz et al. (1984) also stated that in the southern USA, most of the total net nutrient accumulation occurs by mid spring prior to reaching peak standing crop. Bernhard and Fitz (1979) emphasized that the loss of nutrients from the above ground structures in the *Typha glauca* ecosystem they studied was not caused by translocation but most likely from leaching from dying leaves. The *Typha glauca* ecosystem in their study is located in upstate New York where rapid temperature change at the end of the growing period causes rapid senescence and limited translocation of nutrients from above to below ground structures.

Krolikowska (1981) investigated the influence of nitrogen and potassium fertilization on the production and water relations of *Typha latifolia* L. The researcher dosed plants with either 0,1,2, or 3 N or K with a 1 N dose equaling 1.374 g of ammonium nitrate and 1 K dose equaling 1.377 g of potassium salt. The highest total dry weight biomass values were found with fertilization with 2 N. A lowered total biomass with fertilization of 3 N was caused possibly by low biomass of the underground parts due to the intense fertilization. Addition of nitrogen to the substrate caused a greater increase in biomass production and a faster growth in height than did a treatment with potassium. The researcher found that potassium did not cause any significant changes in plant growth rate. Plants treated with nitrogen, even when potassium content was low, exhibited high production and growth rate compared to control plants because the nitrogen had a beneficial influence on the nitrogen uptake from the substrate. The author also found that transpiration was favorably affected by nitrogen and potassium addition. In the higher treatment doses of nitrogen and nitrogen-potassium, the transpiration coefficient was lowered suggesting more economical use of water by the plant.

In a similar study using nitrogen and phosphorus fertilizers by Ulrich and Burton (1988), shoot production indicated that nitrate limited growth and that phosphate was present in great excess of need for growth. In was also found that *Typha* species above ground N or P content can be more than doubled by increasing the respective fertilizer application beyond that needed for maximum growth. Below ground N and P tissue contents can also be increased substantially without increases in biomass. This luxury uptake of nutrients may be of benefit when considering the use of *Typha* spp. in wastewater treatment systems.

Neely and Davis (1985) stressed that the response of emergent vegetation to surface applied fertilizers is dependent on movement of the fertilizer into the sediment or interstitial water of the root zone. In their study, fertilizers influenced interstitial waters to a depth of 15 cm during surface application of the fertilizer. Since a majority of wetland species root zones are found in the first 10 cm of sediment, adequate amounts of nutrients would be able to penetrate, via the interstitial water, to this depth (Neely and Davis, 1985). Average summer biomass production for fertilized plots was significantly higher than in unfertilized plots in this study. *Typha glauca* produced a maximum biomass of 1.726 kg m^{-2} in control plots and 2.343 kg m^{-2} in fertilized plots. The same population produced 1.351 kg m^{-2} and 1.781 kg m^{-2}, respectively, the year before. The authors also noted that below ground production of *Typha glauca* in prairie marsh systems in the northwest during autumnal senescence was in the range of 1.431 kg m^{-2} to 1.450 kg m^{-2}.

Nutrient applications to a *Typha angustifolia* L. stand increased maximum above ground biomass by 13% in the first growing season and by 22% in the second growing season compared to control stands during a study by Jordan et al. (1990). The researchers found that although only a small proportion of the added nutrients were taken up into above ground biomass, the total amount of nutrients in above ground structures increased substantially in response to added nutrients. During a highly productive year, tissue nutrient storage potentials were 6.2 g N m^{-2} and 1.2 g P m^{-2} in above ground tissues. These values represent 10% of the N and 2.2% of the P added as fertilizer to the stands. As compared to control stands, these values represent a 66% increase in N and a 55% increase in P in the above ground biomass.

Clark and Clay (1984) estimated the standing crop of *Sagittaria latifolia* and *Sagittaria rigida* in the upper Mississippi River. They estimated that the above ground standing crop of *Sagittaria latifolia* at peak growth was in the range of 0.270-0.765 kg m^{-2}. Below ground standing crop was in the range of 0.072-0.372 kg m^{-2}. This range was similar to the range of 0.706-0.999 kg m^{-2} for above ground production that had been previously reported from the same study area. The researchers noted that estimates of peak standing crops in riverine habitats are different than estimates made in habitats such as prairie marshes (460 g

m^{-2}). The researchers stressed that limited data have been published on *Sagittaria* spp. grown in varying water level regimes in marsh systems. Clark and Clay (1984) found a relationship between water level and increased plant production as a function of light penetration during emergence. Shallower water may have also attributed to a reduction in the number of flowering stems during the study period. The data of their study supported the view that shallower water results in more stressful environmental conditions in *Sagittaria* spp., resulting in lower plant densities, above ground production, and below ground production.

Whigham et al. (1978) found, in their review, that peak above ground standing crop for *Sagittaria latifolia* ranged from 0.214 to 0.649 kg m^{-2} for freshwater tidal wetlands. The researchers also stated that due to the extensive variability in available data, it was impossible to make any valid comparisons between production of tidal and nontidal freshwater wetlands.

Burgoon et al. (1991) assessed biomass and nutrient uptake rates for *Sagittaria latifolia* and *Typha latifolia* grown in wastewater effluent. The study used vegetated submerged beds containing gravel or plastic pellets as substrate, and the study focused on nutrient removal efficiencies of certain aquatic macrophytes using these vegetated beds. The beds were planted with four aquatic macrophytes and analyzed for plant biomass and nutrient removal efficiencies. The plants were grown in three successive hydraulic loading rates. *Sagittaria* above ground biomass ranged from 1.384 kg m^{-2} to 2.012 kg m^{-2} and *Typha* above ground biomass ranged from 1.037 kg m^{-2} to 1.160 kg m^{-2}. Below ground biomass for *Sagittaria* ranged from 0.900 kg m^{-2} to 1.500 kg m^{-2} and *Typha* below ground biomass was 1.500 kg m^{-2}. The researchers also analyzed the plant tissue for nitrogen and phosphorus to determine the ability of aquatic macrophytes for nutrient removal. *Sagittaria* contained from 17.1 to 28.4 mg N g^{-1} and 3.2 to 4.4 mg P g^{-1} during the study. *Typha* contained from 19.1 to 25.1 mg N g^{-1} and 3.2 to 5.0 mg P g^{-1}.

Woody species. There has been limited research on the production of the woody species used in this study, *Salix caroliniana* and *Sambucus canadensis*. Muzika et al. (1987) found that biomass estimates for *Salix* spp. (including *Salix caroliniana*) in Southeastern floodplain forests ranged from 113.5 to 227 g dry wt m^{-2} yr^{-1} of bolewood (wood and bark only) production. Literature on *Sambucus canadensis* only explored its use as a small fruit crop species. No current estimates of production or growth in varying water regimes exist.

Effects of Flooding

Macrophytes Many emergent flood tolerant macrophytes possess anatomical or morphological characteristics which allow the transport of oxygen to the roots of plants growing in anaerobic soils. Some of these include aerenchyma, lenticels, and adventitous roots (McKee et al., 1989). Various studies have illustrated that water depth has a pronounced regulatory effect on the distribution and abundance of marsh species (Grace, 1989). Management of marsh ecosystems may include water level manipulations to control invasion of unwanted species.

McKee et al. (1989) studied the differential metabolic responses in five freshwater marsh plants. The currently proposed metabolic theory of flood tolerance suggested that flood sensitivity in intolerant species is due to the accumulation of ethanol in the roots and that tolerant species would avoid ethanol accumulation by limiting alcoholic fermentation and stimulating alternate pathways that produce nontoxic organic acids such as malate. The researchers suggested that changes in metabolism may assist in survival during flooding, especially when other physiological or morphological adaptations have not yet developed or are not yet sufficient to supply the roots with needed oxygen. They also found that *Typha glauca* had a large capacity for gas movement to the root zone compared to other emergent wetland species in the study.

Species presence or absence at either the stressful or the disturbed ends of the exposure gradient (i.e. water depth) is not due to the species out competing other species, nor is it that they are physiologically adapted for the particular stresses, instead these species can physiologically tolerate the extreme conditions (Shipley et al., 1991).

There have been relatively few studies dealing with growth of emergents at different water depths. Squires and Van der Valk (1992) studied water depth tolerances of seven emergent species over a depth gradient of -5 cm to 120 cm. The researchers found that emergent species must be able to maintain sufficient shoot area above the water surface for gas exchange in order to survive in deeper water. Species adjusted their shoot area not by increasing shoot length but by producing fewer sufficiently long shoots. In turn, shoot length per unit of aboveground biomass increased with water depth and mean shoot density decreased with water depth. Increasing height and shoot biomass with increasing water depth was noted in a study by Waters and Shay (1990). They found that *Typha glauca* produced significant differences in height of underwater portions and had relatively constant aerial dimensions. The researchers supported the theory of increased height to maintain proper gas exchange abilities, and they predicted that ethylene may contribute to this response.

Grace (1989) studied the effects of water depth on *Typha latifolia* and *Typha domingensis*. The researcher found a greater tolerance of *T. domingensis* to deeper water because it grew well at all depths of the study. It was also found that both *T. domingensis* and *T. latifolia* exhibited increased height with increasing water depth similarly over the entire depth range. Grace (1989) also found that *T. latifolia* showed no significant differences in unit leaf length per unit biomass over the depth gradient and that *T. domingensis* exhibited a decline in unit leaf length per unit biomass with increasing depth. This finding contradicts the Squires and Van der Valk (1992) study were they found that *T. glauca* shoot length per unit biomass increased over the depth gradient. Grace (1989) suggests that there is an increasing importance of light limitation over increasing depth and a decreasing importance in nutrient and water limitation over the depth gradient. Plants adjust their form to allow adequate photosynthesis to proceed and maintain a positive carbon balance. Squires and Van der Valk (1992) noted that light only became limiting a depths of 70 to 95 cm. They hypothesized that the plant must be able to conduct sufficient gas exchange above the water surface and that this response causes increased height at depth. Grace (1989) also suggested that biomass allocation may shift to greater biomass in the leaves and stems and a reduction in below ground biomass in deeper waters. It has also been assumed that biomass per plant will increase with increasing water depth in correlation with increasing plant height.

A very limited number of studies have examined the effects of both water level and nutrient level on emergent macrophytes (Neill, 1990 and Grace, 1988). Neill (1990) studied growth and nutrient uptake in whitetop (*Scolochloa festucacea*) and cattail (*Typha glauca*) in varying water depths. The researcher found that the combination of higher biomass and higher tissue nitrogen after 1 year of nitrogen fertilization and higher tissue phosphorus but lack of increased growth after phosphorus fertilization supported nitrogen limitation in both species studied. This effect of nitrogen limitation was experienced at both the shallow and deep water study sites. Fertilization with low and high levels of N and fertilization with a combination of N + P produced the greatest increases in biomass for both species in both shallow and deep water. Nutrient treatments had little effect on below ground biomass of whitetop. Cattail showed slight decreases in below ground biomass at the deep water sites. This decrease in below ground biomass may be similar to the results found by Grace (1989) where deeper water plants allocated more biomass to the above ground structures to maintain a positive carbon balance. Neill (1990) found that cattails grown in the deeper water produced significantly less biomass than cattails grown in shallower water even during nutrient additions. This suggested response may be due to an overall limitation of water depth under any nutrient additions. This response seems to be species specific because Grace (1989) found that *T. latifolia* grown in saturated soil conditions produced significantly less biomass than inundated species which had no pronounced differences in biomass over the depth gradient to 115 cm. The researcher also found that *T. domingensis* biomass production increased as water depth increased from 5 to 115 cm. Squires and van der Valk (1992) found that the biomass of *T. glauca* increased to the 45 cm depth and decreased between 70 and 95 cm depths with complete mortality beyond the 95cm depth.

Grace (1988) also studied the effect of nutrient additions on both *T. domingensis* and *T. latifolia* along a water-depth gradient. The study found that shoot density and total biomass were enhanced with nutrient addition along the depth gradient. Similar to the findings in other studies, *T. latifolia* was only significantly enhanced by nutrients in depths of 5 to 58 cm. *T. latifolia* was completely eliminated under nutrient addition at the 95 cm depth. *T. domingensis* was enhanced in deeper waters by nutrient additions but showed little response in 0 to 58 cm depths and 105 cm depth. The researcher noted that the results suggest that nitrogen, specifically ammonium, was probably the most limiting nutrient. The study also supported the theory that *T. domingensis* has a greater ability to oxidize its rhizosphere but poorer ability to compete for nitrogen resources compared to *T. latifolia*.

<u>Woody Species</u> Injury of plants to waterlogging often has been attributed to dessication induced by increased root resistance to water flow (Pereira and Kozlowski, 1977). Soil waterlogging, synonymous with soil flooding, is not itself a stress since saturation with water is not injurious, but prolonged flooding can lead to the secondary physiochemical stresses of oxygen deficiency with woody species (Donovan et

al., 1988; Iremonger and Kelly, 1988; Gill, 1970). Iremonger and Kelly (1988) conducted waterlogging experiments on four common woody wetland tree species of Ireland: *Alnus glutinosa, Betula pubescens, Fraxinus excelsior* and *Salix cinerea* ssp. *oleifolia*. After waterlogging the soil to half and full saturation, it was found that while all species tolerated the waterlogging, all exhibited decreased growth. The researchers also found that sustained waterlogging during the dormancy season produced a 50% mortality in all individuals. *Salix cinerea* was found to be the only species studied to increase growth throughout the study period. The researchers suggested that the tolerance to flooded conditions was due to special adaptations such as adventitous roots and the ability to initiate anaerobic respiration. Donovan et al. (1988) found that biomass of *Salix nigra* decreased when the plants were flooded. These trees also produced hypertrophied lenticels and adventitous roots in response to flooding. This response of willow species to flooding has been documented in numerous studies (Donovan et al., 1988; Ohmann et al., 1991; Knighton, 1981). Research has also suggested that Salix species eventually succumb to flooding over time (Ohmann et al., 1991). Chlorosis and loss of leaves was apparent toward the end of the growing season in the study of willow tolerance to flooding by Knighton (1981). It has been found that survival of Salix spp. over time in flooded environments is primarily due to adventitous root formation (Ohmann et al., 1991; Knighton, 1981; Donovan et al., 1988; Pereira and Kozlowski, 1977; Hosner, 1960). One of the earliest responses of flooding is stomatal closure, followed by inhibition of root growth, alterations in root and stem morphology, formation of adventitious roots, and leaf senescence (Pereira and Kozlowski, 1977). Gill (1970) noted also that factors such as low light intensity and interference with stomatal function are also critical when floodwater is deep and inundation is complete.

Nutrient Dynamics

Nitrogen and phosphorus macronutrients are utilized by all plants during photosynthesis and respiration for growth and maintenance of tissues. Aquatic plants must obtain these needed nutrients from flooded sediment or the overlying water column. The flooding of soils separates the biotic environment into an oxygenated or aerobic zone and an oxygen depleted or anaerobic zone (Ogwada, 1983; Ponnamperuma, 1984; Reddy and Patrick, 1986,1984). Nitrogen and phosphorus undergo distinct processes under flooded conditions. Nitrogen transformations in flooded soils include mineralization, nitrification, volatilization, and denitrication (Reddy and Patrick, 1984; Reddy and Patrick, 1986; Ogwada, 1983; Ponnamperuma, 1984). Mineralization is the conversion of organic nitrogen to inorganic forms in flooded soils. The process usually stops at the ammonium stage due to the lack of oxygen in the flooded conditions to continue the process to nitrate. Nitrification is the microbially mediated reaction where ammonium (NH^{+}_{4}) is oxidized to nitrate (NO^{-}_{3}) (Reddy and Patrick, 1986). Volatilization is a physiochemically mediated equilibrium process where gaseous ammonia is evolved from the hydroxyl form. This process is dependent on the pH and temperature of the flooded soil system (Reddy and Patrick, 1986, 1984). The nitrate formed during the nitrification process moves into the anaerobic zone of the flooded soil by diffusion and is biologically reduced to molecular N_2 and N_2O (Ponnamperuma, 1984; Reddy and Patrick, 1986). Other nitrogen transformations include chemical and biological immobilization of nitrogen in the flooded soils. Chemical immobilization incorporates ammonium into the clay lattice, absorbed on soil colloids, or synthesized in the humus. Biological immobilization removes a portion of the inorganic nitrogen via the synthesis of microbial tissue.

Phosphorus occurs in all known mineral systems as orthophosphate ($[PO_4]^{3-}$) (Berkheiser et al., 1980). This form may be present as soluble phosphates, organic or inorganic, and as slightly soluble solids. Inorganic forms are most readily available for plant uptake and are dependent on the redox potential and amounts of Fe, Ca, clay, and hydrous oxides of Al in the soil substrate (Ogwada, 1983).

MATERIALS AND METHODS

Experimental Set Up

A 7.2 x 4.8 m greenhouse was constructed adjacent to the Center for Wetlands and Water Resources, University of Florida, Gainesville, Florida. The greenhouse was used as an outdoor laboratory to allow all natural conditions to occur while removing only precipitation from the experiment. Venting was incorporated by installing horticultural shade cloth on the sides of the greenhouse to a height of 1 m. The venting allowed air flow through the greenhouse to incorporate natural atmospheric conditions during the study period.

Eight 680 l polyethylene containers were used as individual microcosms. Each container was 37 cm deep and 153 cm in diameter. The containers were arranged in two rows of four inside the greenhouse. Tapped drains on the bottom of the containers were used in combination with standpipes to control water level in the microcosms.

The water application system consisted of a flow through design with a 5 cm per week application rate. Water was collected from both a natural wetland and from the University of Florida waste water treatment plant. The background wetland water was collected just north of the main canal control structure at Paynes Prairie State Preserve, Alachua County, Florida. This water was transported and temporarily stored in 190 l synthetic drums. The waste water was pumped directly from a primary clarifier at the waste water treatment plant to the greenhouse. The waste water was also temporarily stored in synthetic plastic drums.

In order to create both saturated and inundated conditions within each microcosm, platforms were built to elevate the saturated plants. The platform design was necessary to minimize shading effects from the saturated plants on the inundated plants. The platforms were constructed of a flat wooden surface which was supported by upright standing bricks. The platform surfaces were designed in a triangular pattern to allow the platform to fit into one half of the microcosm. Rinsed pea gravel was placed in the microcosms to create a uniform bottom. The completed platforms were placed in the microcosms at counter clockwise quarter turns. This allowed random orientation to the sun for both the saturated and inundated plants.

The individual plant containers were 11 l polyethylene containers purchased from V-G Growers, Inc., Apopka, Florida. Holes were first drilled in the containers in the top 4 cm of the containers at each quarter mark. These holes allowed water movement in the upper third of the container to emulate natural conditions in the saturated plants. The containers were filled with a homogenized peat-topsoil mixture from Traxler's Peat Mines Inc., Florahome, Florida. The filled containers were covered with poly sheeting until planting occurred.

The plants used in the study were collected at various locations throughout Gainesville, Florida. The woody species, Coastal Plain Willow(*Salix caroliniana*) and Elderberry(*Sambucus canadensis*), were collected in wet roadside ditches. The individual plants were removed so that a substantial root "ball" was retained with soil attached for transport. Elderberry can reproduce vegetatively with runners, and in many instances these runners had to be cut prior to plant removal. Immediately after transport, the plants were misted regularly to reduce drying. Both herbaceous species, cattail(*Typha domingensis*) and common arrowhead(*Sagittaria latifolia*), reproduce vegetatively through rhizomatous spreading so removal consisted of cutting the rhizome of an individual clone and removing the plant with remaining roots attached. These species were placed in buckets containing water for transport. All four species were rinsed with water to remove all debris and soil, towel dried, and weighed before planting.

An acclimation period of three weeks was initiated after planting. During the first week, the plants were misted and watered daily. Beginning the second week, misting was decreased and watering increased to saturate the soil. During the third week of the acclimation period, the microcosms were filled with their respective water. The microcosms were equipped with a small (304 l/hr) magnetic project pump that circulated the water in the microcosms throughout the study. Styrofoam packing "peanuts" were spread over the water surface in all of the microcosms to prevent severe algal blooms.

Methodology

Plant Measurement and Preparation

After the acclimation period, the plants were first measured for maximum height and then placed in the microcosms. Six individuals of each species were placed in each microcosm, three saturated individuals and three inundated individuals.

Height measurements followed on a biweekly sampling schedule. Plants were measured from the soil surface to the primary terminal bud on the woody species, and to the end of the tallest leaf of the herbaceous species. Number of existing live shoots were counted for the herbaceous species at the time of height measurement. The woody species persisted with one shoot or stem throughout the study. Standing and fallen dead plant material was collected during the height measurements. The litter material was cut and placed in paper bags and dried in the Soil and Water Science Department walk-in plant drying facility. Total litter weights for each individual were tabulated at each 5 week harvest. The litter samples were analyzed with all other plant samples (described below). Height and shoot measurements were taken over the five month study period.

Microcosm harvesting followed a 5 week harvest schedule. One low nutrient microcosm and one high nutrient microcosm were harvested on each 5 week sampling date. Plants were removed by species and height was measured. Above ground biomass was collected by clipping all above ground plant structures at the soil surface. The above ground plant material was separated according to living or dead material. Living above ground material was cut into smaller portions and placed in paper bags. The dead above ground material was added to the previously collected litter. The below ground plant material and soil were removed from the containers and thoroughly rinsed to clean all soil and debris from the below ground plant structures. All below ground plant material was then towel dried and placed in paper bags. Both above and below ground plant material was weighed to determine fresh weight biomass.

All harvested plant material was placed in the walk-in dryer at the Soil and Water Science Department plant preparation building on campus. The plant material was dried at 70 degrees C for 144 hours to obtain a constant dry weight for both the herbaceous and woody plants. The plant material was again weighed to attain dry weight biomass. After weighing, the plants were ground in a number 3 Wiley mill with a 1 mm mesh screen. To attain a finer homogeneous sample, the plants were reground in a small Wiley mill using a 40 mesh screen.

Nutrient Analysis

Plant digestion followed procedures outlined by Gallaher et al. (1976) and current Wetland Soils Research Laboratory guidelines. A 0.1 g portion of the dried and ground plant samples was placed in digestion tubes along with approximately 1 g of prepared salt catalyst mixture (96% K_2SO_4 and 3% $CuSO_4$). Three milliliters of concentrated H_2SO_4 were then added. The digestion tubes were placed in a 40 sample capacity Technicon BD40 Aluminum block digester at the Center for Wetlands and Water Resources. Samples were heated at 380°C for approximately 3 hours. After cooling, the samples were brought to 50 ml volume in the digestion tubes with deionized water and mixed using a vortex test-tube mixer.

Plant nutrient tissue analysis followed procedures outlined in Standard Methods for the Examination of Water and Wastewater (APHA, 1989). The plant samples were analyzed for total nitrogen and total phosphorus. Nitrogen analysis followed procedure 4500-NH_3 H. Automated Phenate Method and Phosphorus analysis followed procedure 4500-P F. Automated Ascorbic Acid Reduction Method. Actual analyses were performed on a Technicon Autoanalyzer at the Wetland Soils Research Laboratory. All nutrient analyses were performed using standard analytical methods and certified reagents and standards. Controls, duplicates, and/or spiked samples were run with each analysis.

Statistical Analysis

The description of the design of the experiment, given above, shows that there are three sources of random variation arranged in the form of a split-split plot. Analysis of Variance (ANOVA) was completed using the General Linear Models Procedure. The four general comparisons were applied to each species and parameter analyzed. These comparisons included plants grown in (1) inundated low nutrient conditions versus saturated low nutrient conditions, (2) inundated high nutrient conditions versus saturated high nutrient conditions, (3) inundated high nutrient conditions versus inundated low nutrient conditions, and (4) saturated high nutrient conditions versus saturated low nutrient conditions.

RESULTS

Plant Performance

Survival

Both *Typha* and *Salix* had 100% survival throughout the study (Figure 2-1, 2-2). As for woody plant survival, *Sambucus* had only 33% of the inundated high nutrient individuals remaining by the first harvest and maintained this survival percentage throughout the study (Figure 2-1). Saturated high nutrient plants decreased from 100% survival at the first harvest to 90% survival for the remainder of the study. Inundated low nutrient individuals had only a 17% survival by the first harvest and were eliminated by the second harvest. Saturated low nutrient plants exhibited a sporadic survival throughout the study with a decrease from the first to the second harvest, an increase from the second to the third harvests and finally a slight decrease from the third to final harvests.

Sagittaria had a 100% survival during the first and second harvests (Figure 2-2). At the third harvest (week 15), inundated high nutrient plants maintained 100% survival, while saturated high nutrient plants decreased to 66% survival.

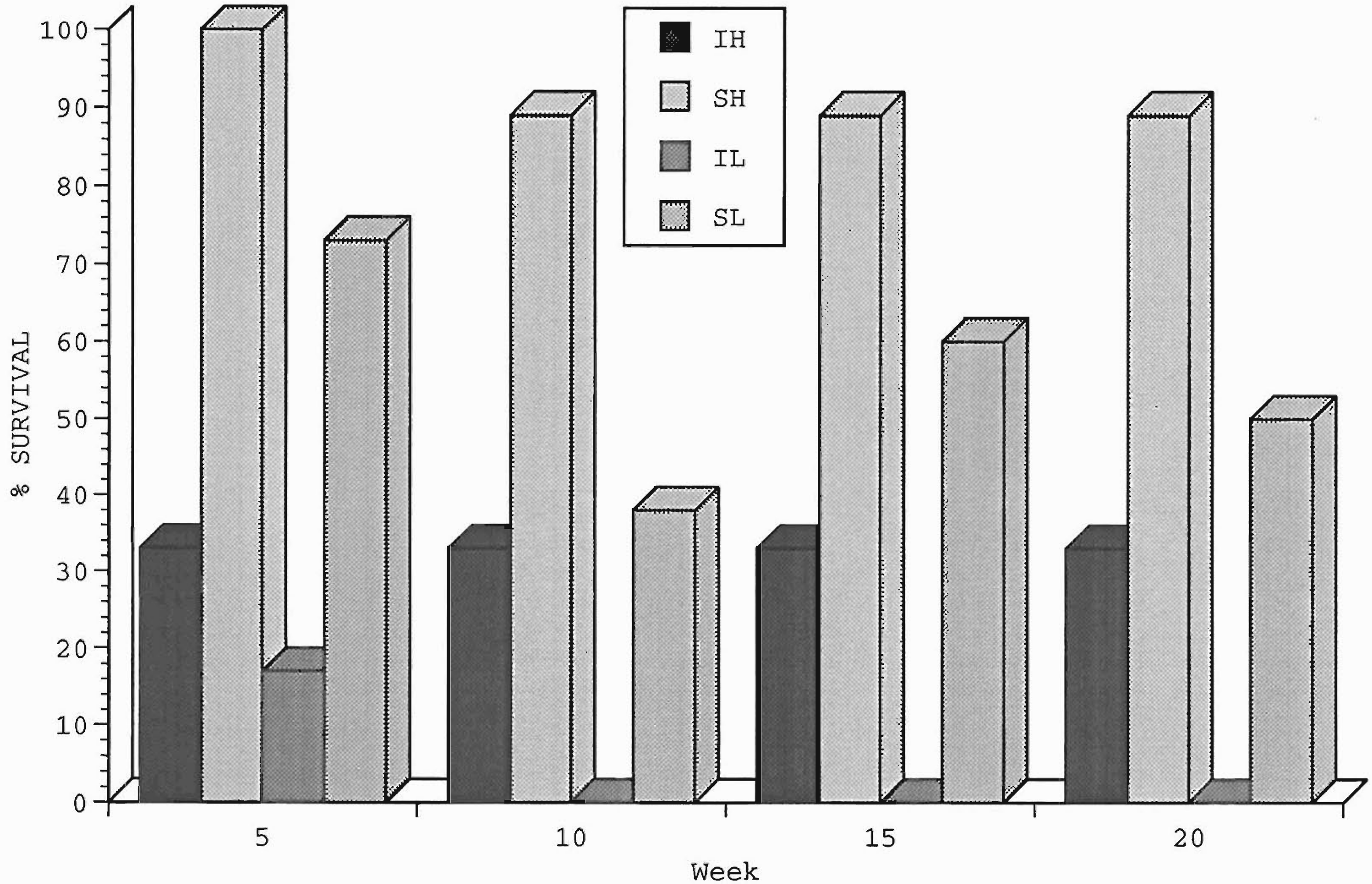

Figure 1. Percent survival of remaining plants of *Sambucus canadensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms after the 5, 10, 15, and 20 week harvests.

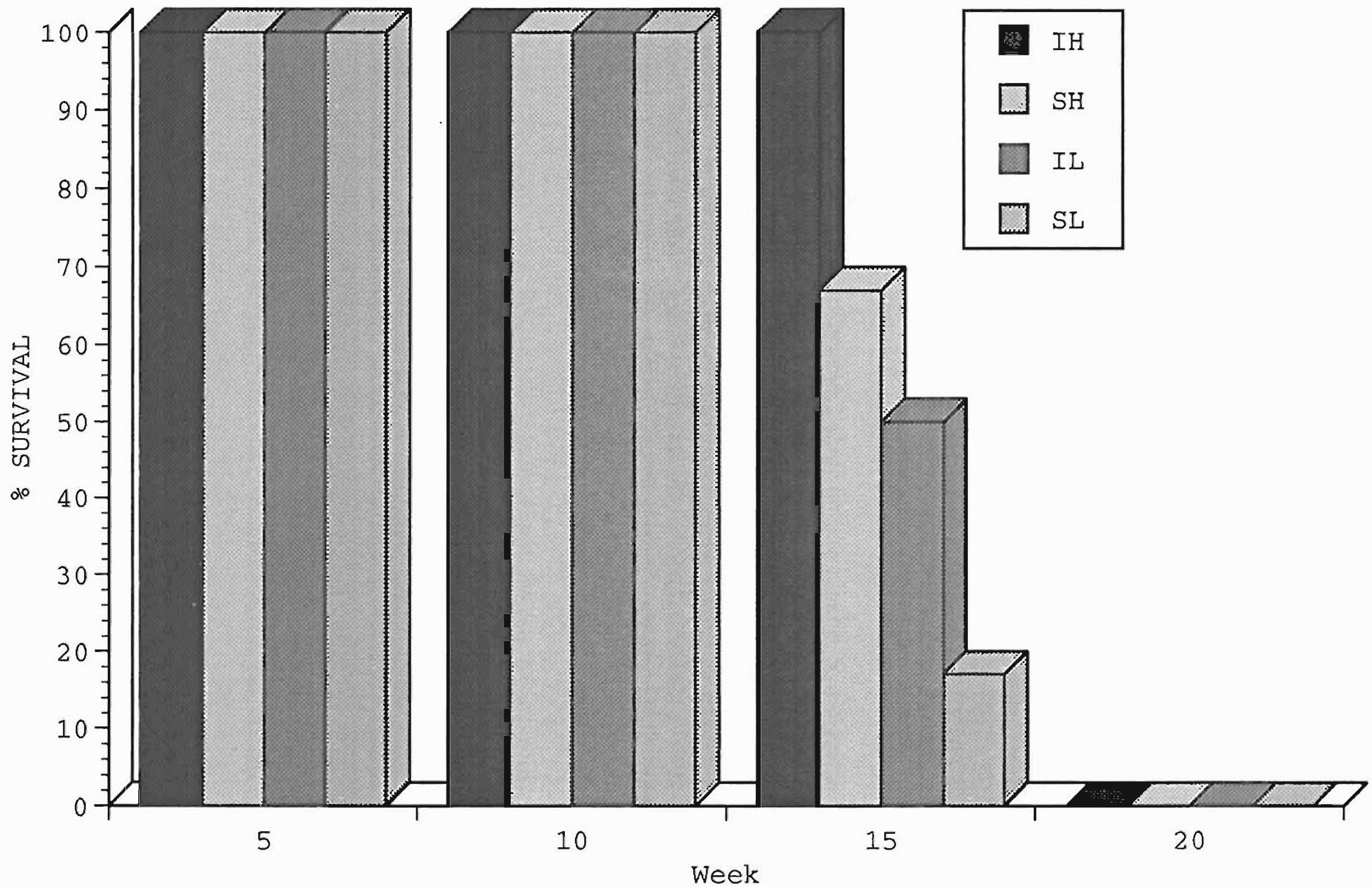

Figure 2. Percent survival of remaining plants of *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms after the 5, 10, 15, and 20 week harvests.

Low nutrient inundated and saturated individuals had survival percentages of 50% and 18%, respectively. By the third harvest (week 20), all *Sagittaria* individuals had died.

Height

The mean heights of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* varied conciderably. *Typha* individuals were significantly taller under inundated conditions versus saturated conditions in high nutrient microcosms over the 5 month study (Tables 2-1,A-1,A-2). No significant differences in height were evident for *Typha* in inundated low nutrient compared to saturated low nutrient conditions. *Typha* produced taller individuals in high nutrient inundated conditions as early as the 24-Aug-93 measurement date (Figure 2-3). A slight increase in mean height of saturated high nutrient plants was evident during the 13-Dec-93 and 28-Dec-93 measurements. Nutrient level had no significant effect on plant height for individuals grown in saturated conditions.

There were significant differences in height of *Sagittaria* grown in inundated versus saturated high nutrient conditions (Table 2-1). No significant differences in height were found in low nutrient inundated versus saturated, inundated high nutrient versus inundated low nutrient, nor saturated high nutrient versus saturated low nutrient. High nutrient inundated individuals exhibited increasing height to 100 cm by 30-Nov-93 (Figure 2-4). Rapid decreases in height

Table 1. Mean height (cm) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Comparison	*Typha*			*Sagittaria*			*Sambucus*			*Salix*		
IL vs SL	125		109	75		57	88		71	98		114
IH vs SH	151	*	122	94	*	59	65		62	148		132
IH vs IL	151	*	125	94		75	65		88	148	*	98
SH vs SL	122		109	59		57	62		71	132	*	114

* = significantly different (alpha level = .0125)

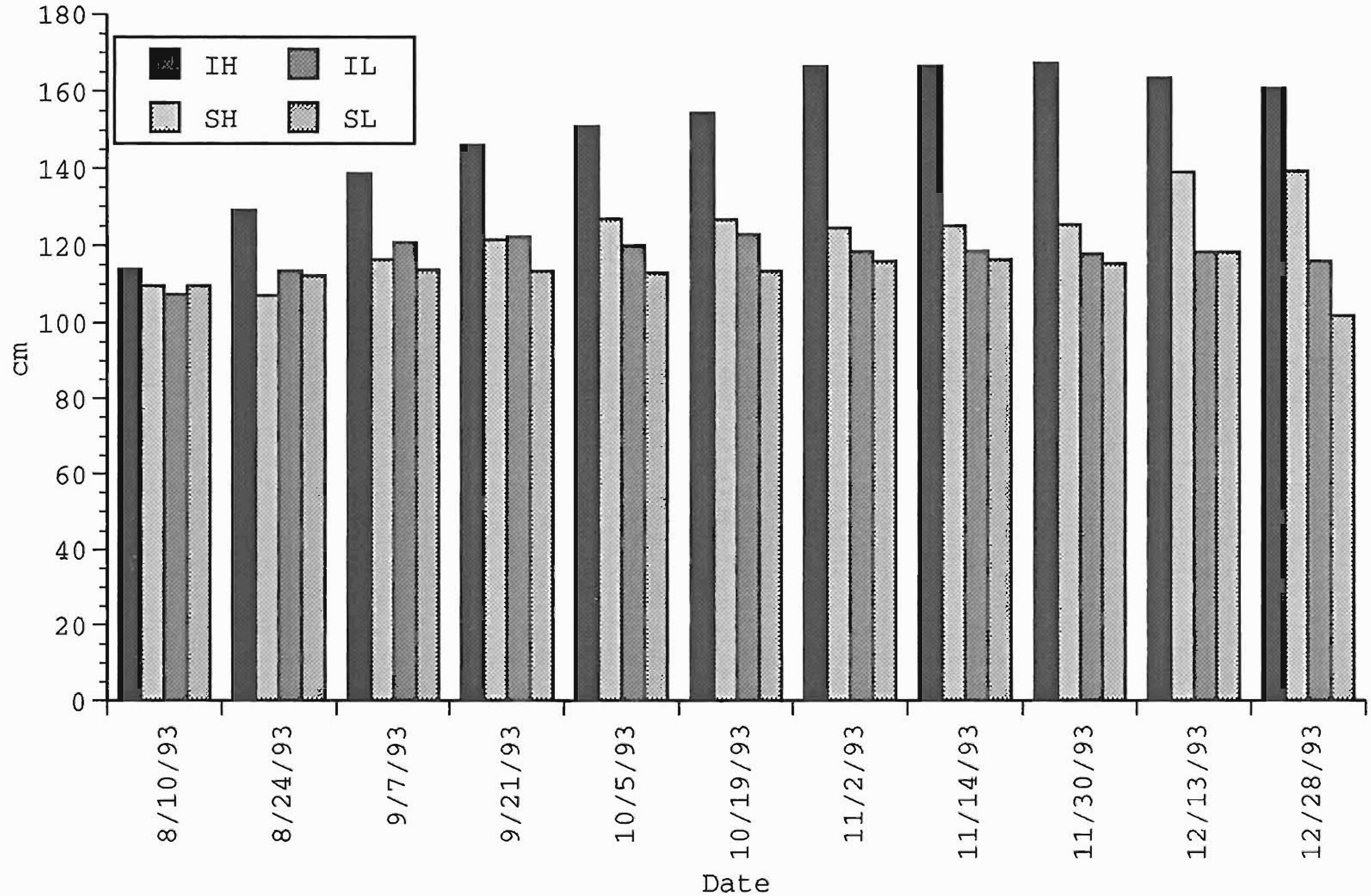

Figure 3. Mean height of *Typha domingensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms measured at biweekly intervals during the 5 month study period.

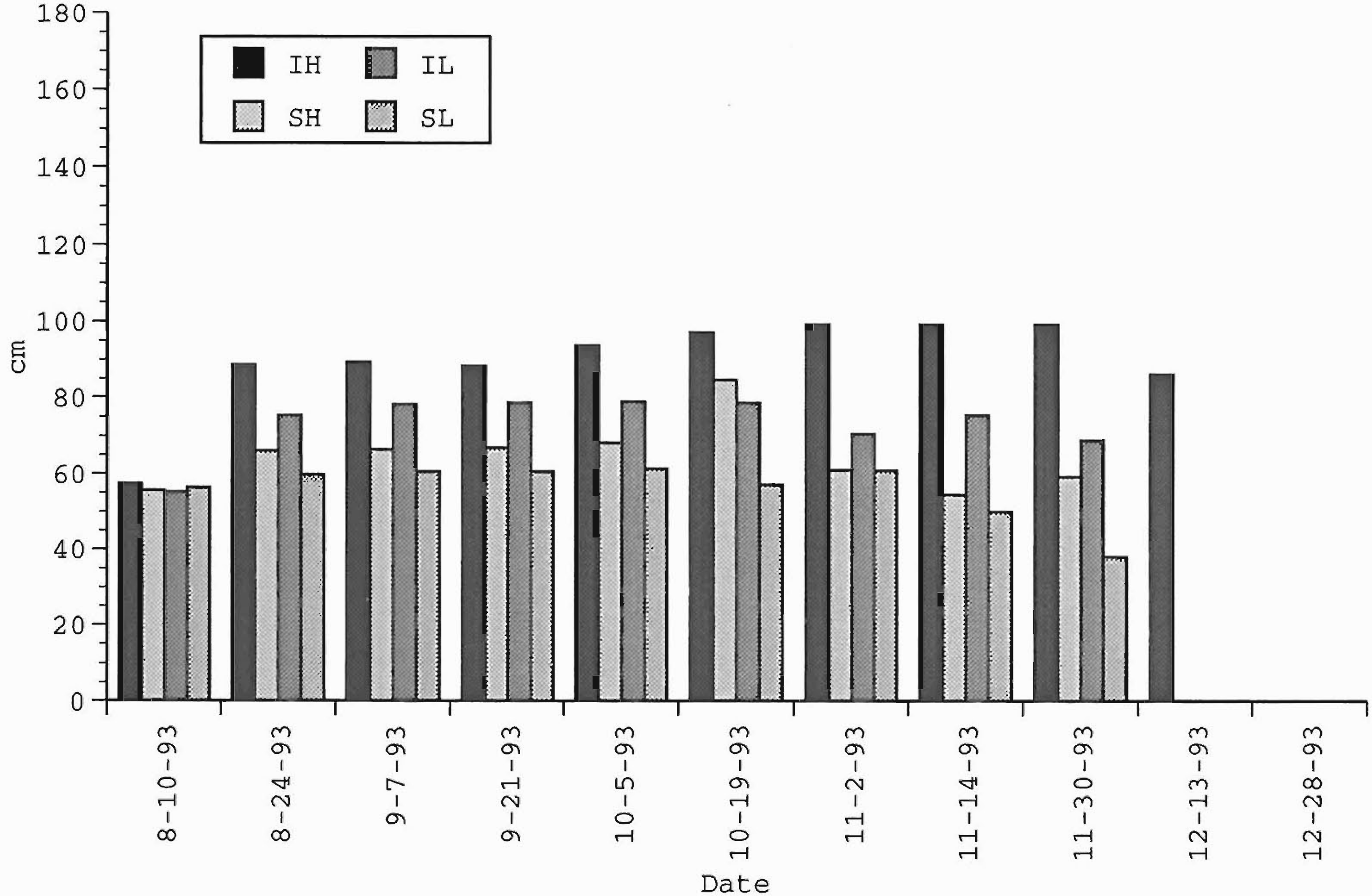

Figure 4. Mean height of *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms measured at biwweekly intervals during the 5 month study period.

after the 30-Nov-93 measurements were primarily due to end-of-growing season senescence. Saturated high nutrient plants reached a maximum mean height of 86 cm by the 19-Oct-93 measurement date and decreased in height thereafter. Inundated low nutrient individuals had peak mean heights of 80 cm between the 21-Sept-93 and 19-Oct-93 measurement dates. Saturated low nutrient plants exhibited maximum mean height during the 5-Oct-93 measurement date and began to decrease slowly in height after this measurement date.

Sambucus had no significant height differences for the nutrient and water combinations during this study (Table 2-1). A slight increase in mean height of saturated high nutrient plants was evident during the period of 10-Aug-93 to 21-Sept-93 prior to the death of these individuals (Figure 2-5). Plants in the other water and nutrient conditions showed no increases in mean height over the five month study.

Salix exhibited significant differences in height between inundated high nutrient and inundated low nutrient conditions (Table 2-1). Under saturated conditions, this species also had significant differences in mean height between high and low nutrient levels. There were no significant differences in height between inundated and saturated individuals in high or low nutrient conditions. Both inundated and saturated high nutrient individuals exhibited the greatest increases in height during the study (Figure 2-6).

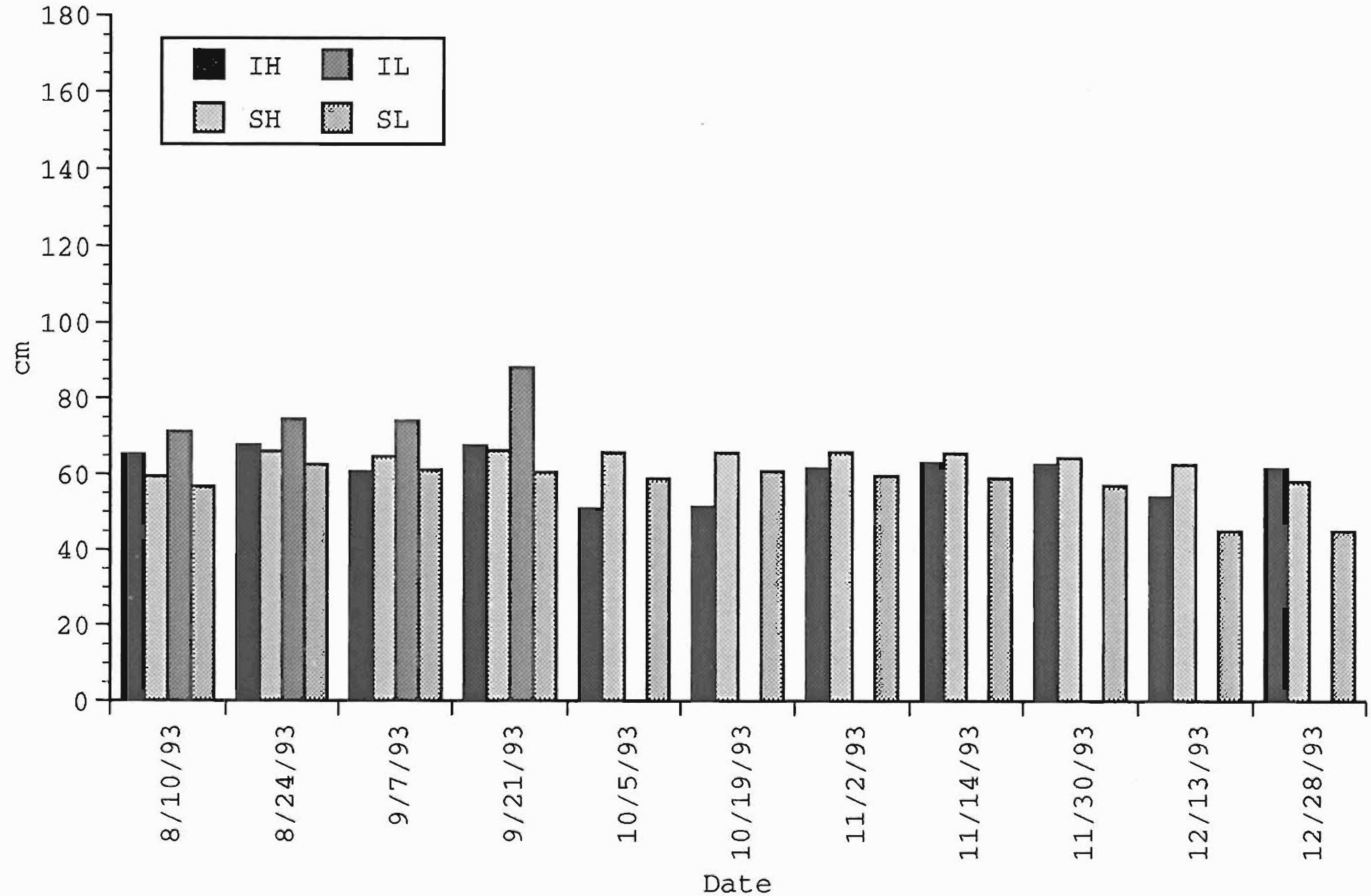

Figure 5. Mean height of *Sambucus canadensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms measured at biweekly intervals during the 5 month study period.

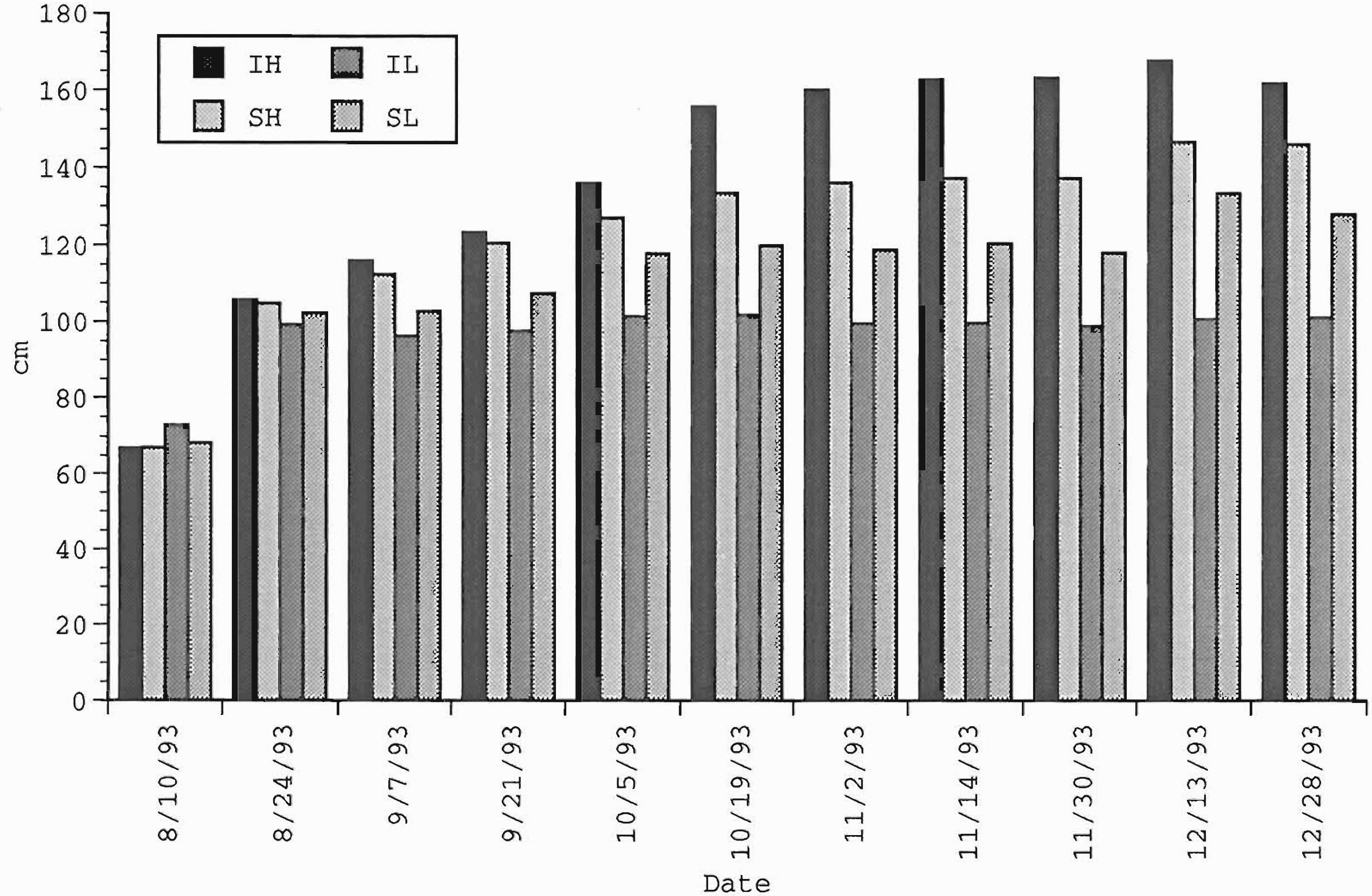

Figure 6. Mean height of *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms measured at biweekly intervals during the 5 month study period.

Aboveground Biomass

Mean aboveground biomass production (g dry wt/plant) is presented in Table 2-2,A-3,A-4. *Typha* exhibited significantly different aboveground biomass under inundated and saturated high nutrient conditions (Table 2-2). The greatest difference occurred at the third harvest (week 15) when the high nutrient inundated individuals had 68% more mean aboveground biomass than the saturated high nutrient individuals (Figure 2-7). Plants grown in inundated high nutrient conditions produced significantly more aboveground biomass than plants grown in inundated low nutrient conditions. Differences ranged from 45% at the first harvest (week 5) to 82% at the third harvest (week 15). Significant differences were also found for plants growing in saturated high nutrient conditions and saturated low nutrient conditions. Differences under these conditions ranged from 3% at week 5 to 72.3% at week 20. Over the entire study period, there was a 53% difference in plants grown in saturated high and saturated low nutrient conditions.

Sagittaria exhibited no significant differences among the four comparisons (Table 2-2). Compared with the other herbaceous species, *Typha*, *Sagittaria* produced less biomass under all water and nutrient conditions (Figure 2-8). Only slight differences in biomass occurred during the four harvest dates. *Sambucus* (Figure 2-9; Table 2-2) also exhibited no significant differences among the four

Table 2. Mean aboveground biomass (g dry wt/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Comparison	*Typha*			*Sagittaria*		*Sambucus*		*Salix*		
IL vs SL	14		14	4	2	8	6	33		36
IH vs SH	43	*	29	10	4	5	7	76	*	55
IH vs IL	43	*	14	10	4	5	8	76	*	33
SH vs SL	29	*	14	4	2	7	6	55	*	36

* = significantly different (alpha level = .0125)

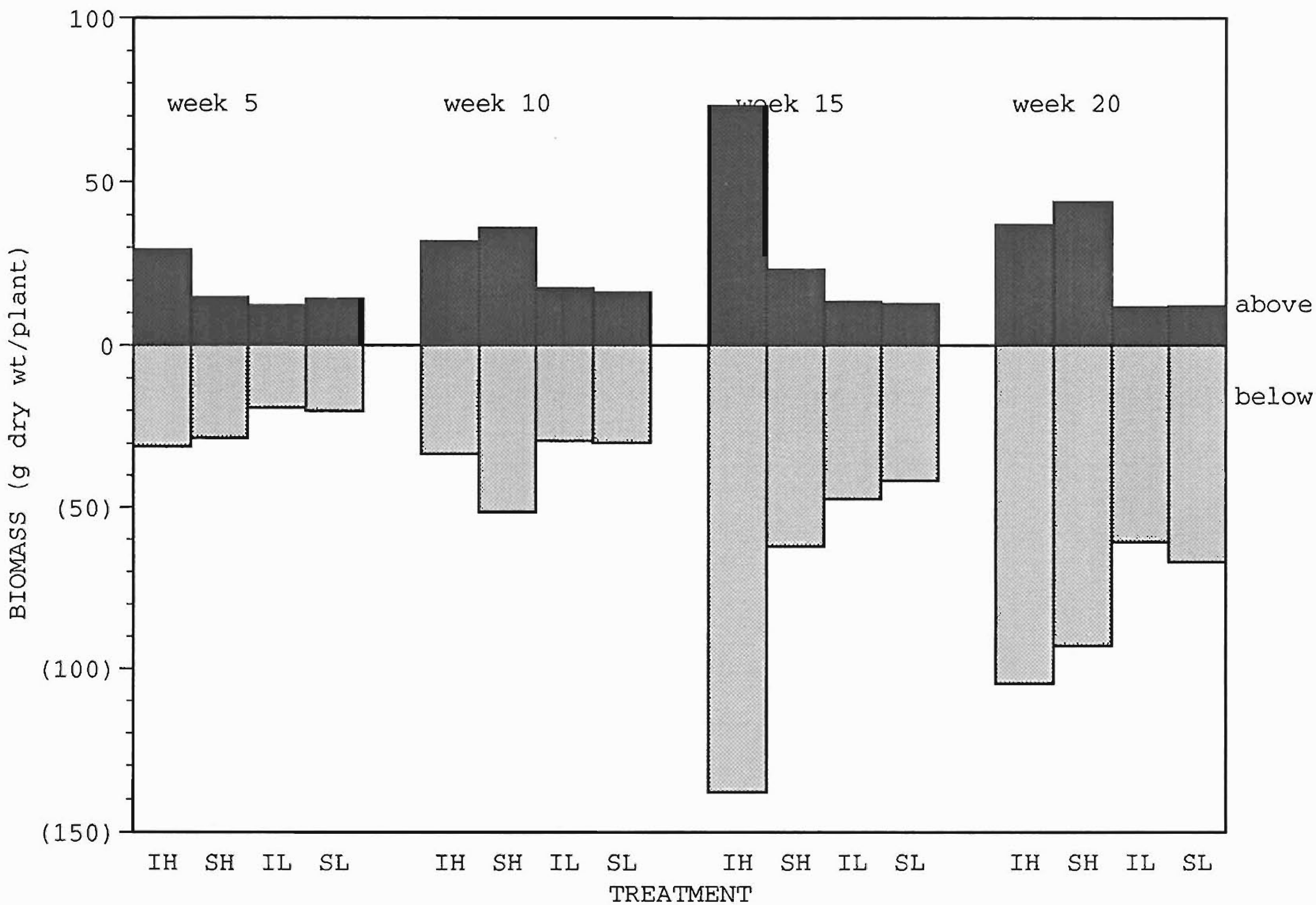

Figure 7. Mean aboveground and belowground biomass of *Typha domingensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

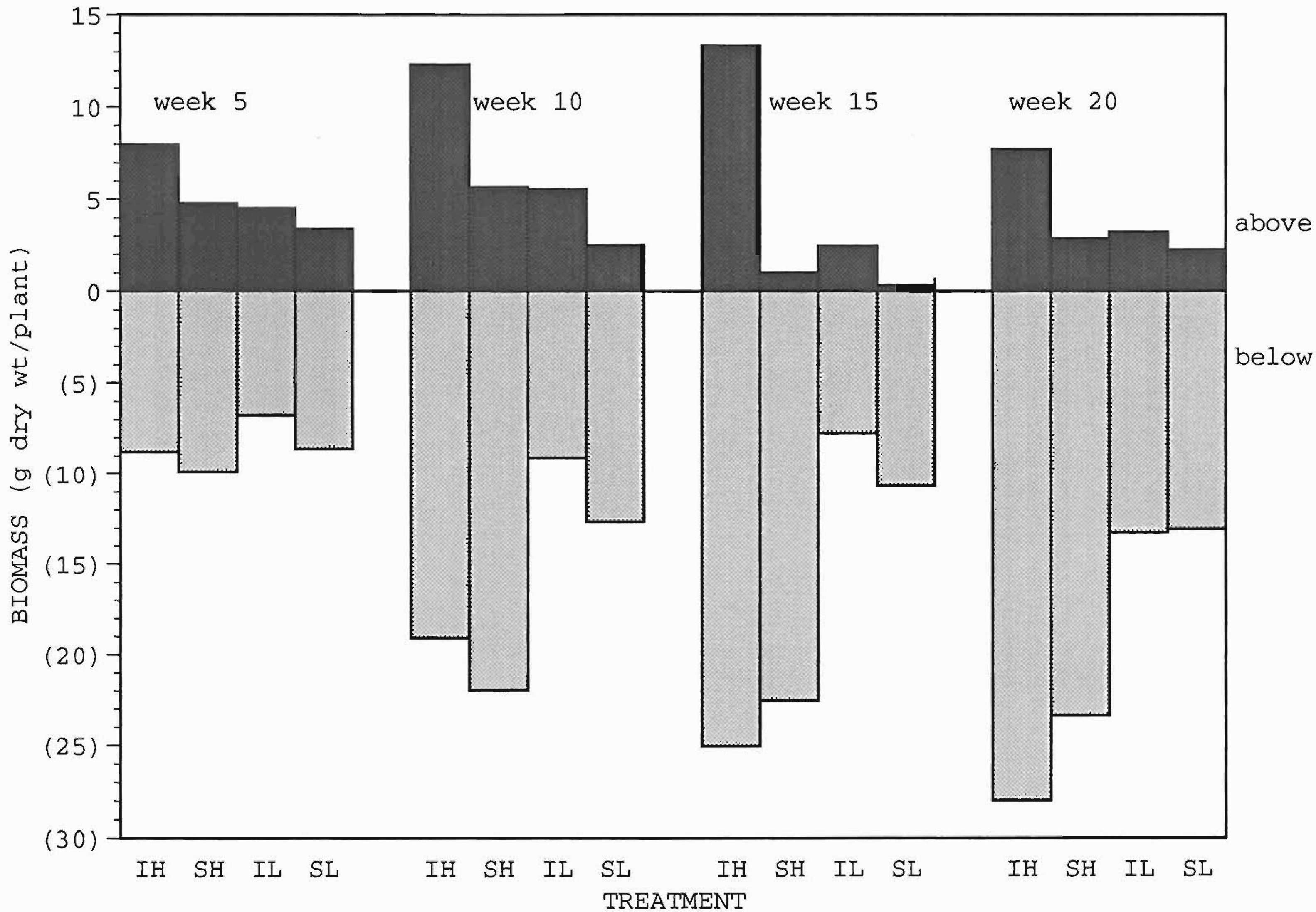

Figure 8. Mean aboveground and belowground biomass of *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

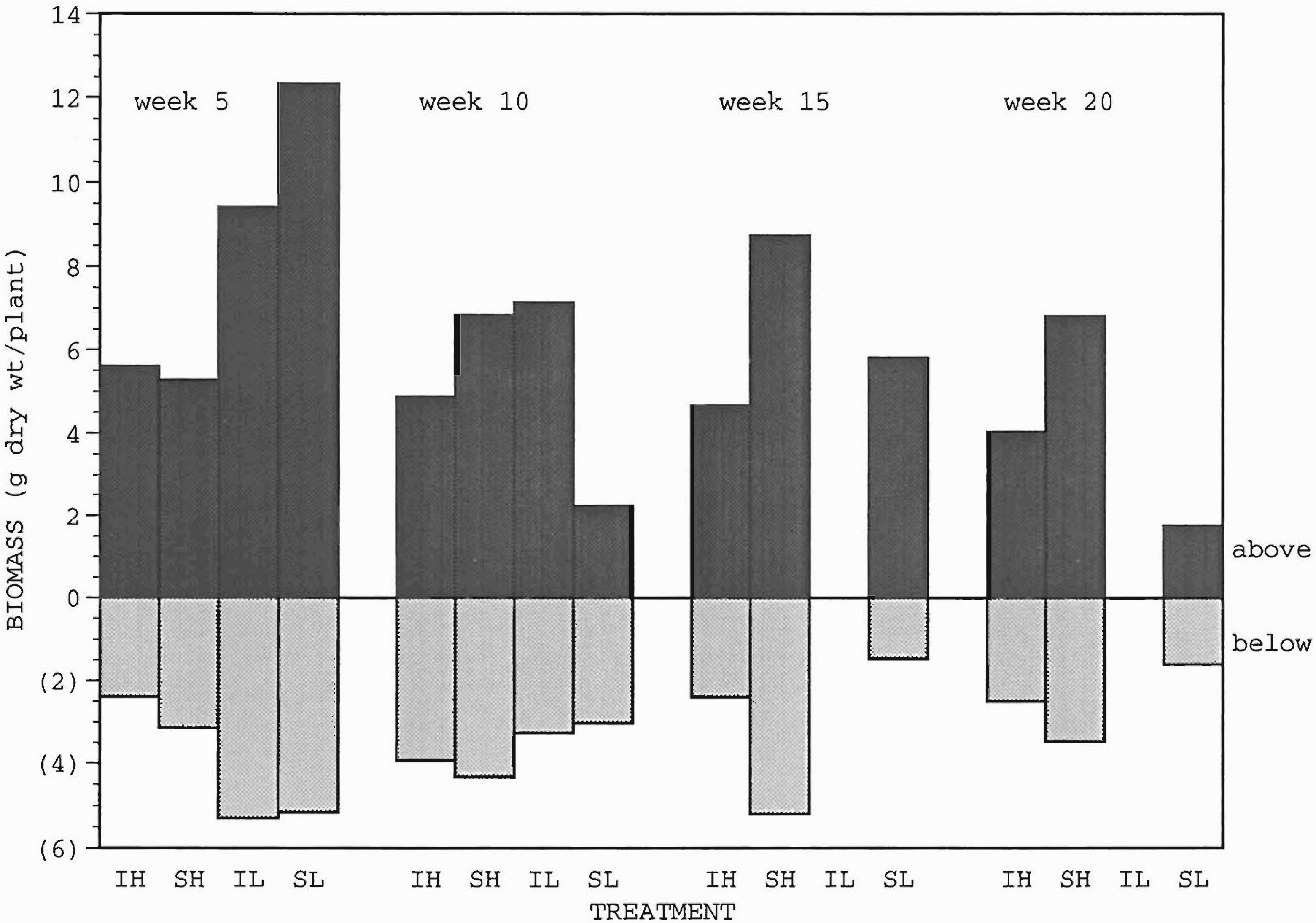

Figure 9. Mean aboveground and belowground biomass of *Sambucus canadensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

comparisons. Many of the individuals died during the study and the remaining live plants did not show increases in growth.

Salix had significant growth differences between all comparisons except inundated low nutrient conditions compared with saturated low nutrient conditions (Table 2-2; Figure 2-10). Inundated high nutrient conditions produced plants with mean aboveground biomass of 76.31±40.10 g dry wt/plant which significantly differed from the mean of 54.79±28.72 g dry wt/plant of individuals grown in saturated high nutrient conditions over the study period. Plants grown in inundated high nutrient conditions significantly produced 57% percent more biomass than plants grown in inundated low nutrient conditions. Under saturated conditions, plants grown in high nutrient conditions produced significantly more biomass than low nutrient conditions which produced mean aboveground biomass of 36.03±10.41 g dry wt/plant.

Belowground Biomass

The statistical analysis of belowground biomass was completed by harvest due to a time interaction in the model (Table 2-3,A-5,A-6). Belowground production of *Typha* greatly increased from week 10 to week 15 in inundated high nutrient conditions (Figure 2-7). There were no significant differences among the four comparisons for *Typha* at either week 5 or week 10. At week 15, *Typha* produced significantly more belowground biomass (137.93±18.81 g dry wt/plant) in inundated high nutrient conditions compared to belowground

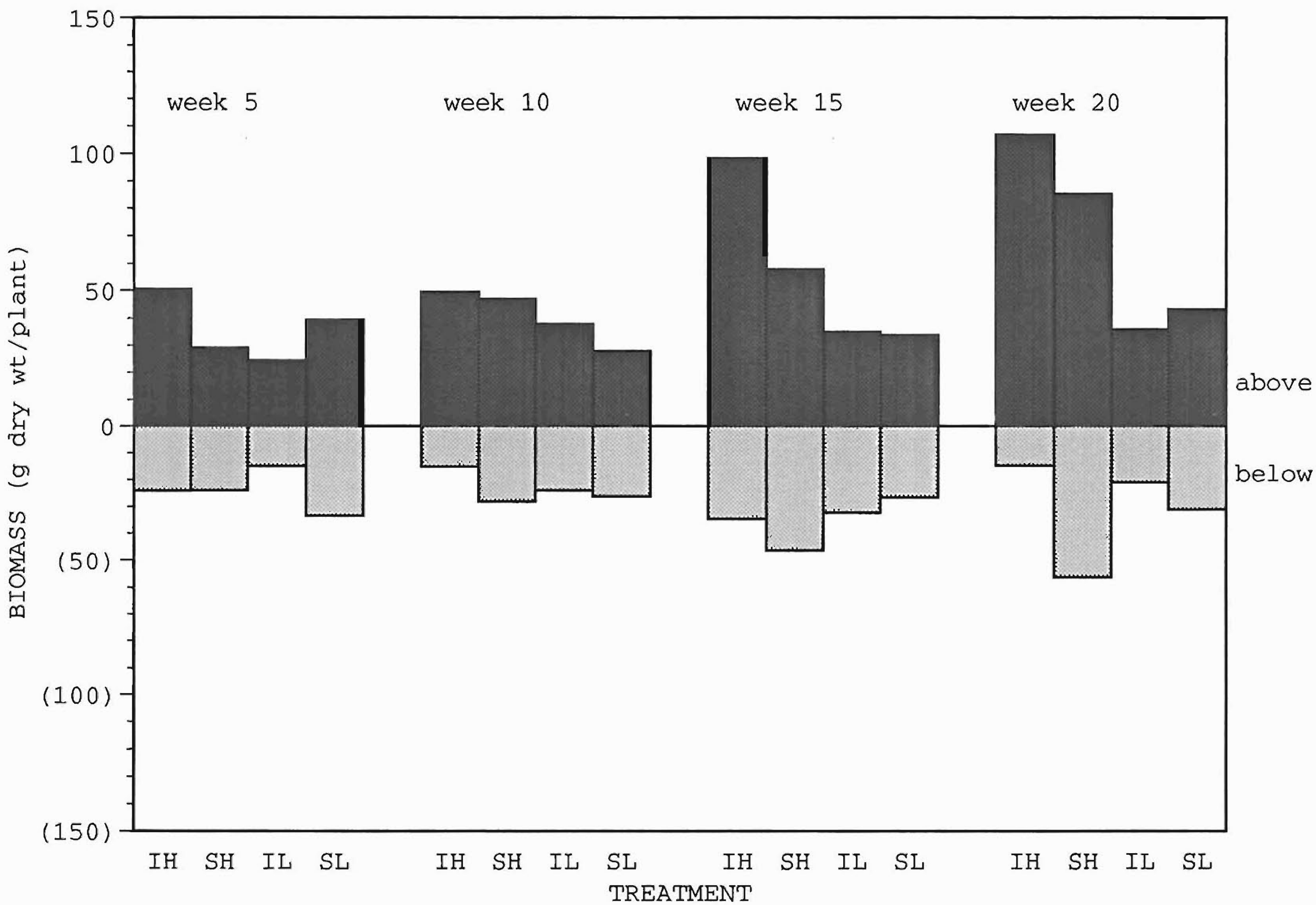

Figure 10. Mean aboveground and belowground biomass of *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

Table 3. Mean belowground biomass (g dry wt/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Comparison	*Typha*		*Sagittaria*		*Sambucus*		*Salix*	
IL vs SL(1)	19	20	7	9	5	5	15	33
IH vs SH(1)	31	28	9	10	2	3	24	24
IH vs IL(1)	31	19	9	7	2	5	24	15
SH vs SL(1)	28	20	10	9	3	5	24	33
IL vs SL(2)	29	30	9	13	3	3	24	26
IH vs SH(2)	33	51	19	22	4	4	15	28
IH vs IL(2)	33	29	19	9	4	3	15	24
SH vs SL(2)	51	30	22	13	4	3	28	26
IL vs SL(3)	47	42	8	11	*******		32	27
IH vs SH(3)	138	* 62	25	22	2	5	35	46
IH vs IL(3)	138	* 47	25	8	*******		35	32
SH vs SL(3)	62	42	22	11	5	1	46	27
IL vs SL(4)	61	68	13	13	*******		21	31
IH vs SH(4)	105	93	28	23	2	3	15	* 56
IH vs IL(4)	105	* 61	28	13	*******		15	21
SH vs SL(4)	93	* 67	23	13	3	2	56	* 31

* = significantly different (alpha level = .0031)
(1),(2),(3), and (4) = harvests.

biomass in saturated high nutrient conditions (62.17±6.86 g dry wt/plant). The plants grown in inundated high nutrient conditions also produced significantly more belowground biomass than plants grown in inundated low nutrient conditions (47.50±8.80 g dry wt/plant) (Table 2-3). There were no significant differences in belowground biomass of *Typha* grown in both saturated high and low nutrient conditions. At week 20, significant belowground biomass differences were evident between plants grown in inundated high nutrient conditions (104.67±36.45 g dry wt/plant) and plants grown in inundated low nutrient conditions (60.77±17.15 g dry wt/plant). Saturated high nutrient conditions also produced plants that had significantly greater belowground biomass (92.90±16.48 g dry wt/plant) than plants grown in saturated low nutrient conditions (66.97±3.56 g dry wt/plant).

Belowground biomass production of *Sagittaria* showed no significant differences among comparisons between water and nutrient levels (Figure 2-8). Some increase in belowground biomass in inundated and saturated high nutrient conditions is evident from the figure but not statistically supported.

Sambucus also did not produce significant differences in below ground biomass under varying nutrient and water conditions. Any trends in belowground biomass production on a five week harvest schedule were not evident from the information presented (Figure 2-9). *Salix* did not produce significant differences among the comparisons during week 5, week 10 or week 15 harvests (Table 2-3; Figure 2-10). Belowground biomass of *Salix* at the week 20 harvest did exhibit significant differences among two comparisons. Plants grown in inundated high and saturated high nutrients had significantly different mean belowground biomass (14.83±3.58 g dry wt/plant and 56.43±17.54 g dry wt/plant, respectively). Significant differences were also found between belowground biomass of plants grown in saturated high nutrient conditions and plants grown in saturated low nutrient conditions (31.20±9.60 g dry wt/plant).

Nutrient Assimilation

Nitrogen

Total nitrogen was statistically analyzed and presented as a mean dry weight N (mg/g/plant). The mean percentages were also multiplied by the associated mean biomass to obtain mean mg N/plant and are also graphically presented.

Typha produced no significant differences in aboveground N among the four statistical comparisons (Table 2-4,A-7,A-8; Figure 2-11). Mean aboveground N ranged from 7.4±2.7 mg/g/plant N for plants grown in inundated high nutrient conditions to 9.3±3.1 mg/g/plant N for plants grown in saturated high nutrient conditions (Table 2-4). A downward sloping trend was evident in mean N from the week 10 harvest to the week 20 harvest (Figure 2-11). Mean TN (mg N/plant) shows no trends in TN assimilation for aboveground *Typha* (Figure 2-12).

Table 4. Mean aboveground N (mg/g/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Comparison	*Typha*		*Sagittaria*		*Sambucus*		*Salix*	
IL vs SL	8	7	12 *	15	8 *	11	7	8
IH vs SH	7	9	11	12	8 *	12	8	8
IH vs IL	7	8	11	12	8	8	8	7
SH vs SL	9	7	12 *	15	12	11	8	8

* = significantly different (alpha level = .0125)

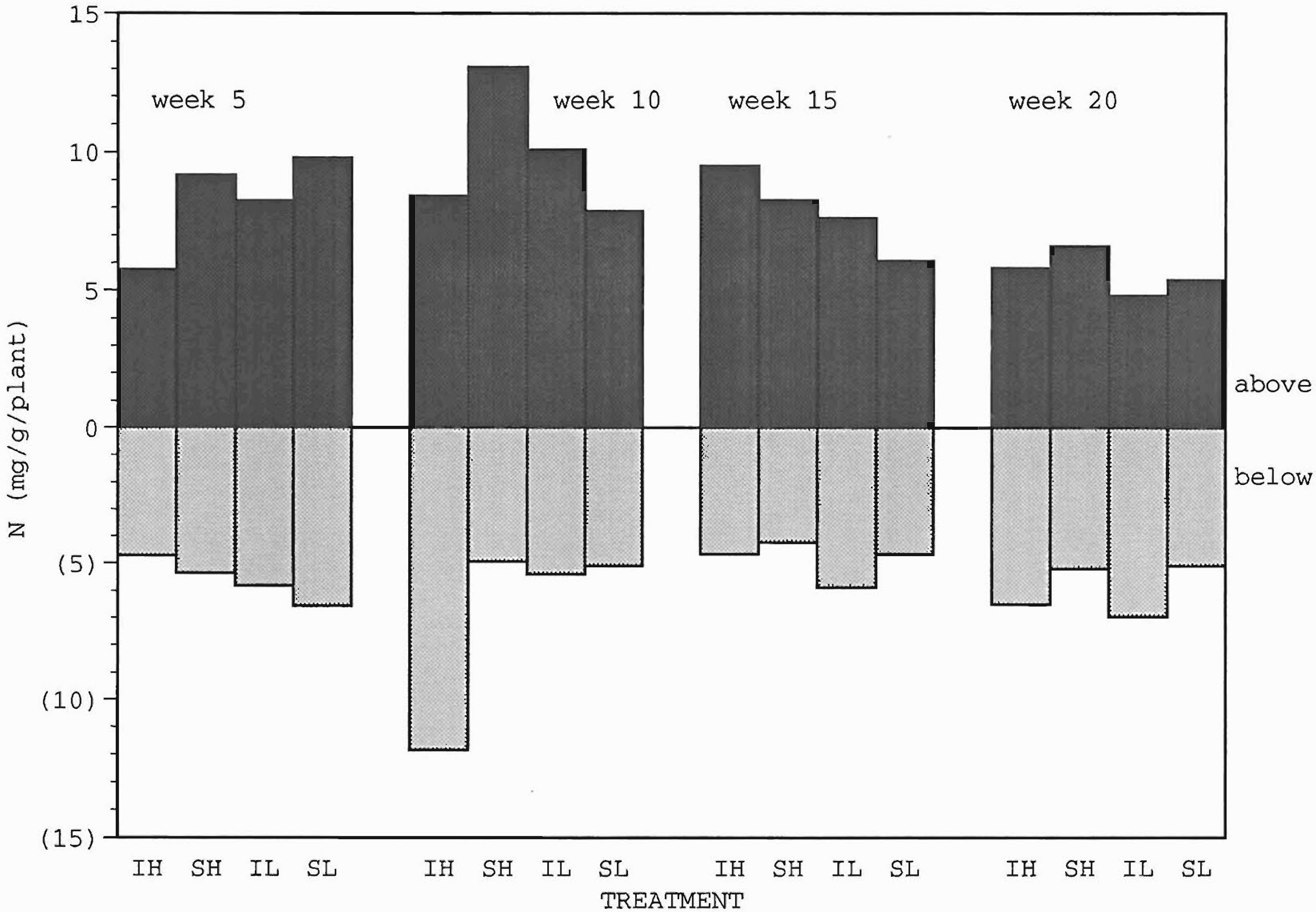

Figure 11. Mean aboveground and belowground N (mg/g/plant) of *Typha domingensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

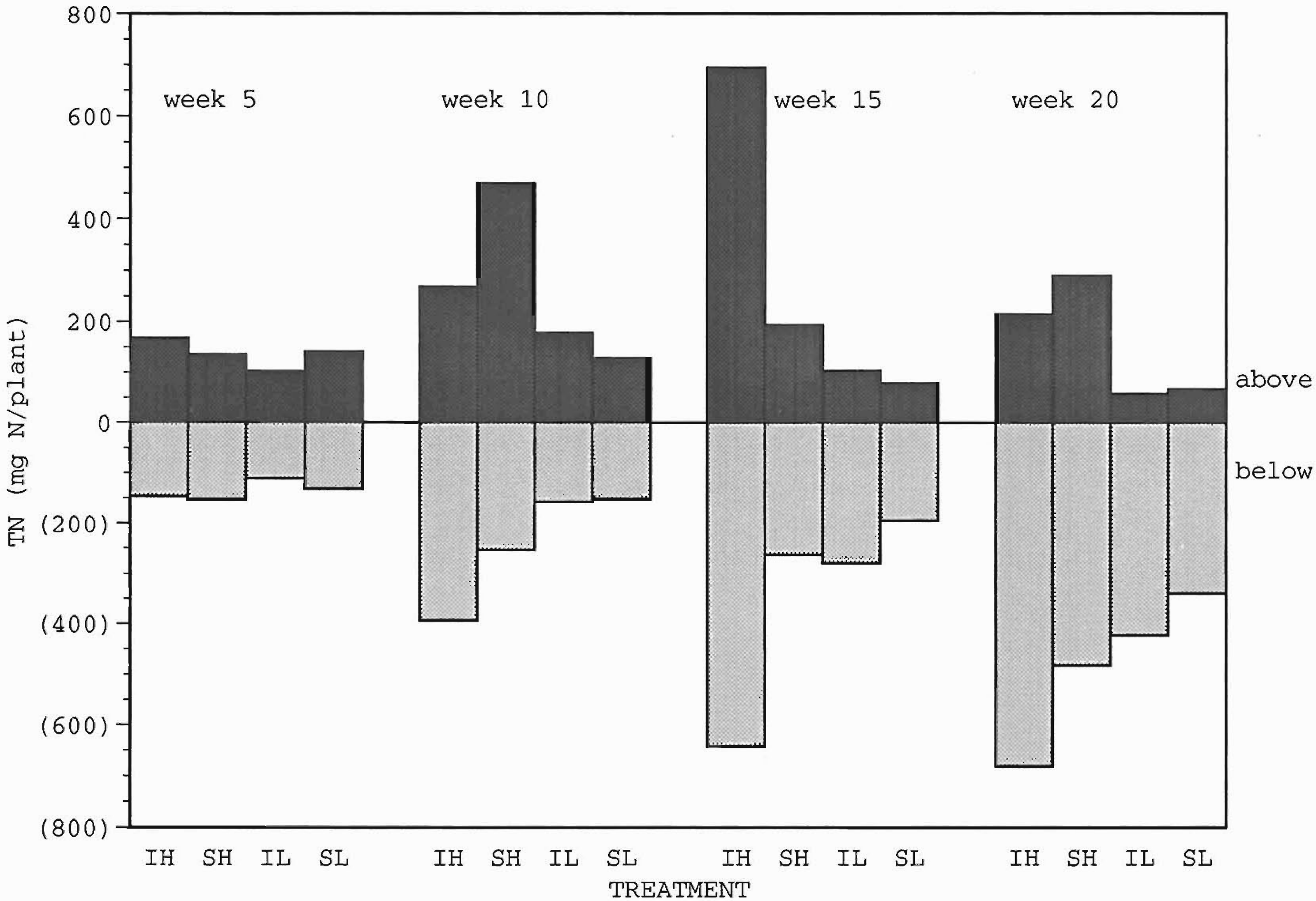

Figure 12. Mean aboveground and belowground TN (mg N/plant) of *Typha domingensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

Table 5. Mean belowground N (mg/g/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Comparison	*Typha*	*Sagittaria*	*Sambucus*	*Salix*
IL vs SL	6 5	14 12	7 * 10	8 9
IH vs SH	5 5	11 12	6 * 11	9 9
IH vs IL	5 6	11 * 14	6 7	9 8
SH vs SL	5 5	12 12	11 10	9 9

* = significantly different (alpha level = .0125)

Belowground N (mg/g/plant) also produced no significant differences among the four statistical comparisons (Table 2-5). Belowground N ranged from 4.9±1.1 mg/g/plant for plants grown in saturated high nutrients and 5.9±1.1 mg/g/plant for plants grown in inundated low nutrients (Table A-7). Figure 2-11 supports the lack of differing belowground N with no increase over time. Figure 2-11 does show an increase over time in belowground N especially in the inundated high nutrient conditions. Week 20 harvest exhibits a trend of increasing N in all water and nutrient conditions.

Mean N of aboveground *Sagittaria* ranged from a low of 11.1±2.3 for plants grown in inundated high nutrient conditions to 14.5±4.0 for plants grown in saturated low nutrient conditions (Table 2-4). A significant difference was evident between plants grown in inundated low nutrient conditions and plants grown in saturated low nutrient conditions (Table 2-4). The week 15 harvest showed a large difference in N for plants grown in these conditions (Figure 2-13). Plants grown in saturated high nutrient conditions had a significantly higher mean N than *Sagittaria* plants grown in saturated low nutrient conditions. Overall, N levels remained fairly constant throughout the study. TN remained constant throughout all harvests except for plants grown in the inundated high nutrient condition (Figure 2-14). There was a difference by the week 10 harvest possibly due to an increased aboveground biomass of *Sagittaria* in the inundated high nutrient condition.

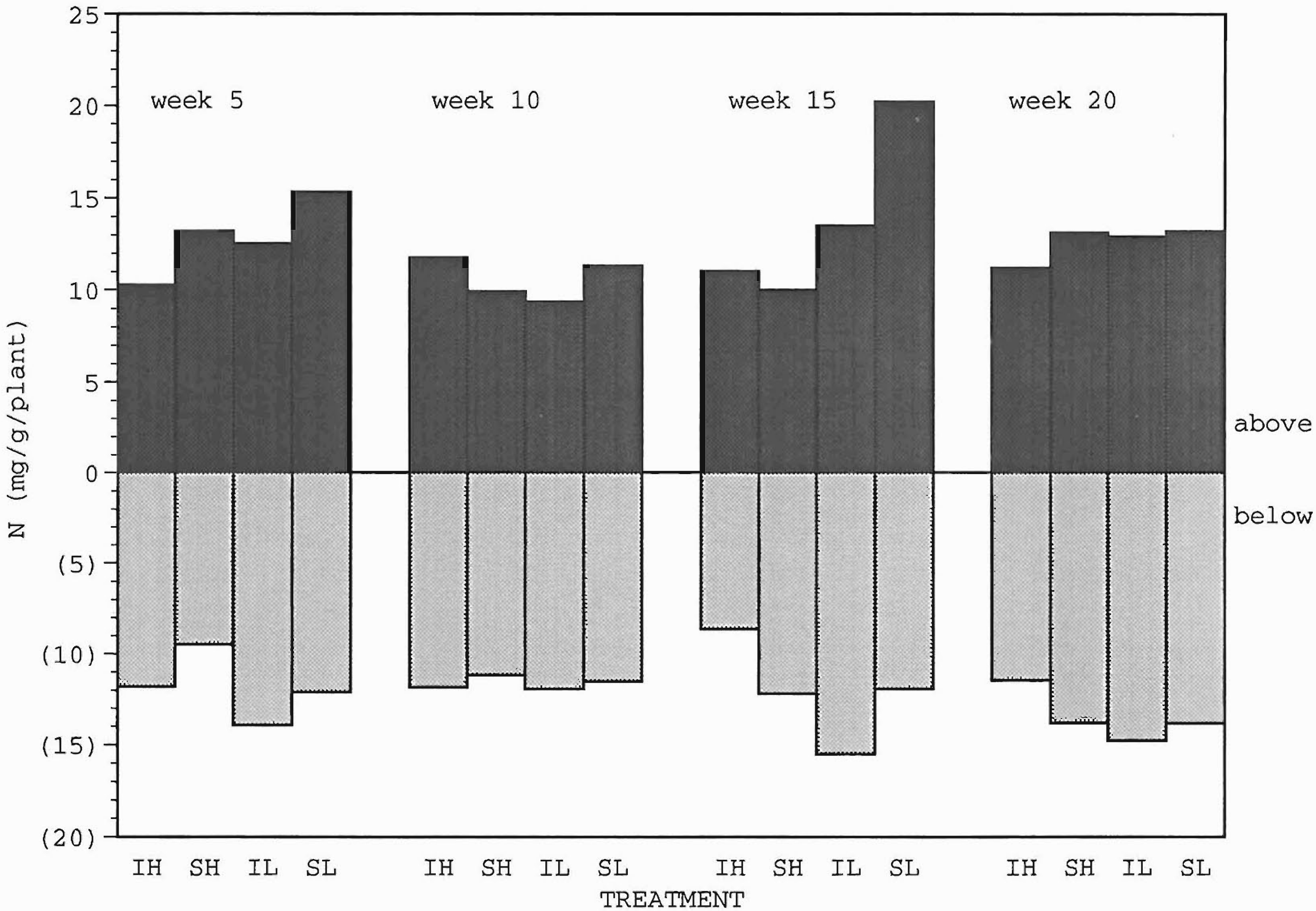

Figure 13. Mean aboveground and belowground N (mg/g/plant) of *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

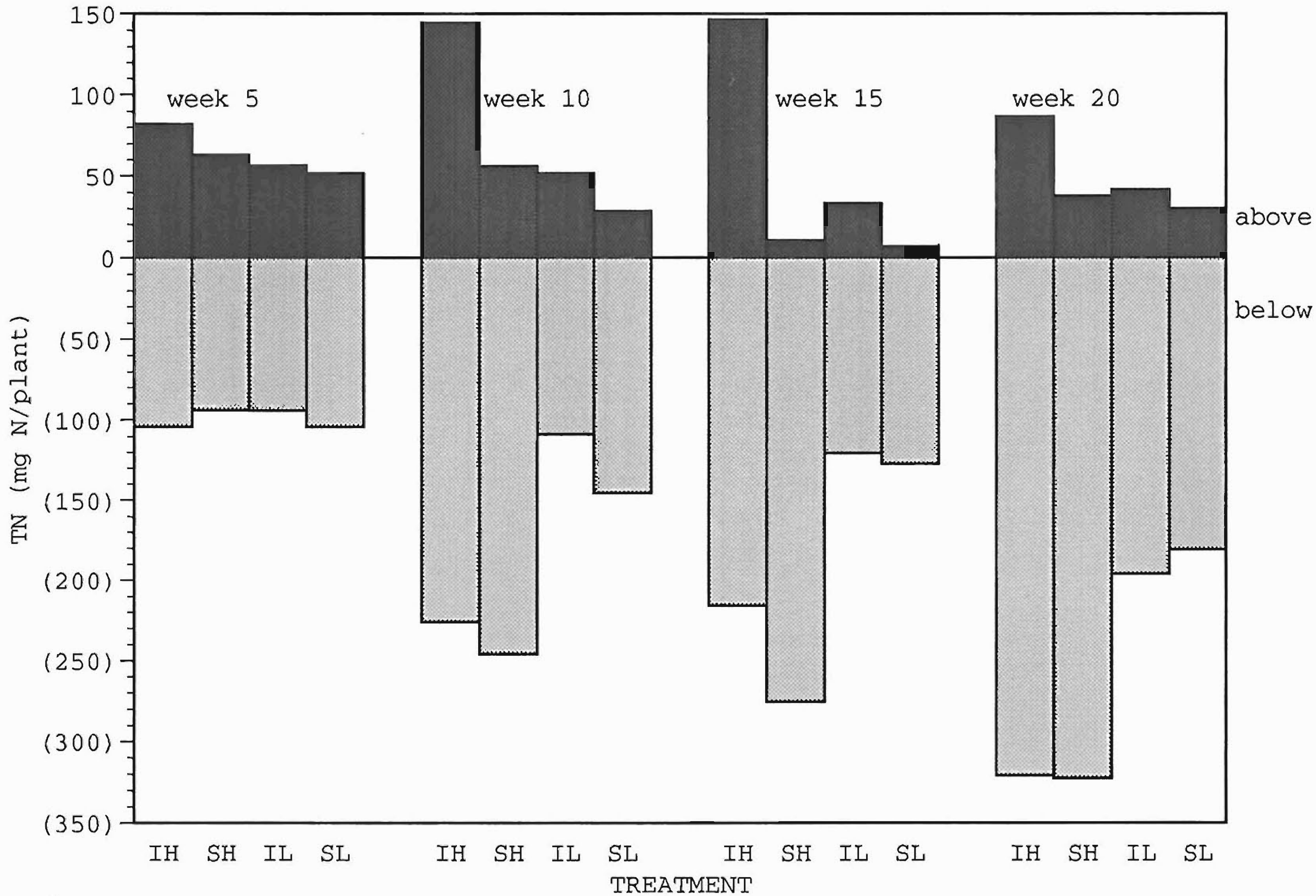

Figure 14. Mean aboveground and belowground TN (mg N/plant) of *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

The inundated high nutrient condition significantly influenced plant belowground N over plants grown in the inundated low nutrient condition (Table 2-5). All other comparisons showed no significant differences in belowground N. An increase by harvest in belowground N was evident for all conditions except inundated high nutrient conditions. A distinct increase of N in inundated and saturated high nutrient conditions was evident at week 10, week 15 and week 20 (Figure 2-13).

Sambucus aboveground N ranged from 8.3±4.1 for plants grown in inundated high nutrient conditions to 11.5±3.0 for plants grown in saturated high nutrient conditions (Table 2-4,A-7). Plants grown in inundated low nutrient conditions significantly differed in aboveground N from plants grown in saturated low nutrient conditions. Percent N for inundated and saturated low nutrient conditions was 7.7±2.5 and 10.9±2.8, respectively. The other comparisons of inundated high versus low nutrient conditions and saturated high versus low nutrient conditions did not differ significantly (Figures 2-15,2-16). Belowground N ranged from 6.3±2.5 for plants in inundated high nutrient conditions to 10.7±2.3 for plants in saturated high nutrient conditions (Table 2-5). Significant differences in plant below-ground N were found for comparisons between inundated low nutrient and saturated low nutrient conditions and for inundated and saturated high nutrient conditions. These significant differences along

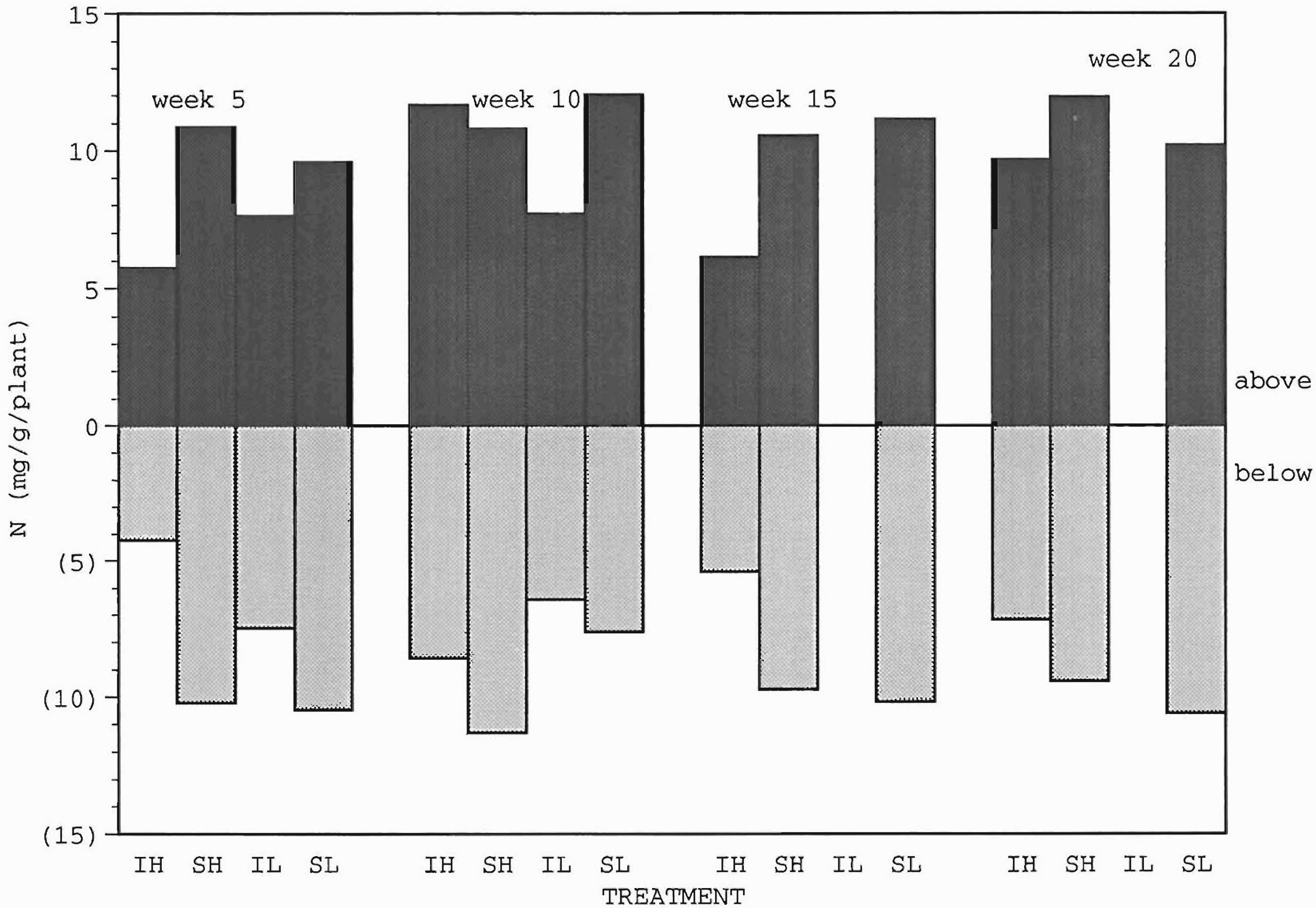

Figure 15. Mean aboveground and belowground N (mg/g/plant) of *Sambucus canadensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

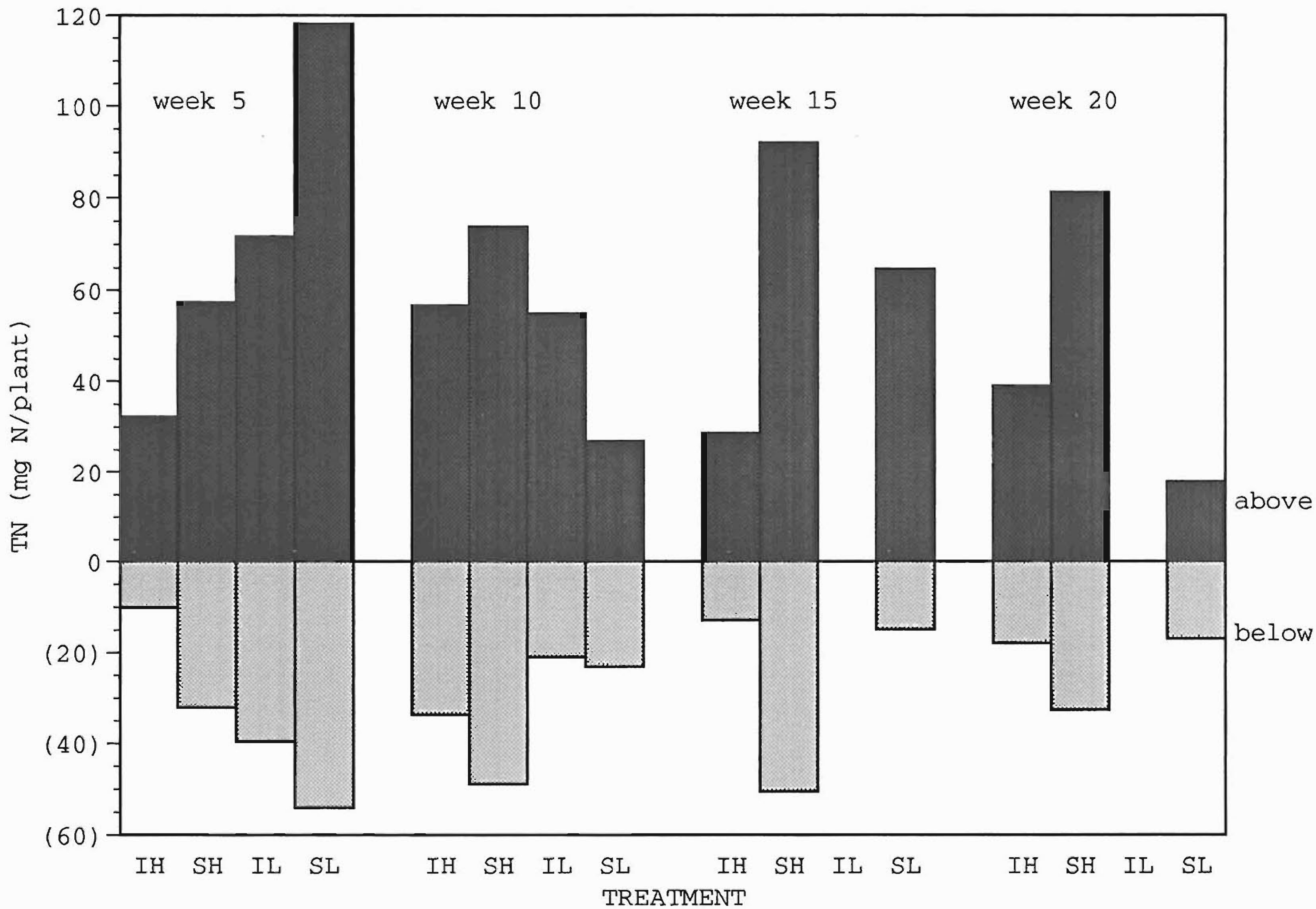

Figure 16. Mean aboveground and belowground TN (mg N/plant) of *Sambucus canadensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

with comparison the mean N by harvest (Figure 2-15) suggested that *Sambucus* is very intolerant to flooding. TN calculations (Figure 2-16) for each harvest exhibit no definite trends during the study period. Missing plants in inundated low nutrient conditions was due to complete mortality of these individuals.

All statistical comparisons of nutrient and water conditions exhibit no significant differences for *Salix*. Mean N ranges from 6.7±0.8 for plants grown in inundated low nutrient conditions to 8.2±2.2 for plants grown in inundated high nutrient conditions (Table 2-4). General aboveground nitrogen assimilation trends are similar to aboveground biomass production trends for *Salix* (Figure 2-17). Increasing mean aboveground TN (mg N/plant) with time is evident over the five month study period (Figure 2-18). This increase is a direct effect of continually increasing biomass production of *Salix*, especially in both inundated and saturated high nutrient conditions with N remaining constant. Belowground N comparisons showed no significant differences between conditions studied (Table 2-5). Mean belowground N of *Salix* ranged from 7.7±1.2 for plants in inundated low nutrient conditions to 9.0±1.6 for plants in saturated high nutrient conditions. Mean N of belowground *Salix* did exhibit an increasing trend over the four harvests (Figure 2-17). Plants grown in saturated high nutrient conditions had higher TN than other water and nutrient conditions (Figure 2-18).

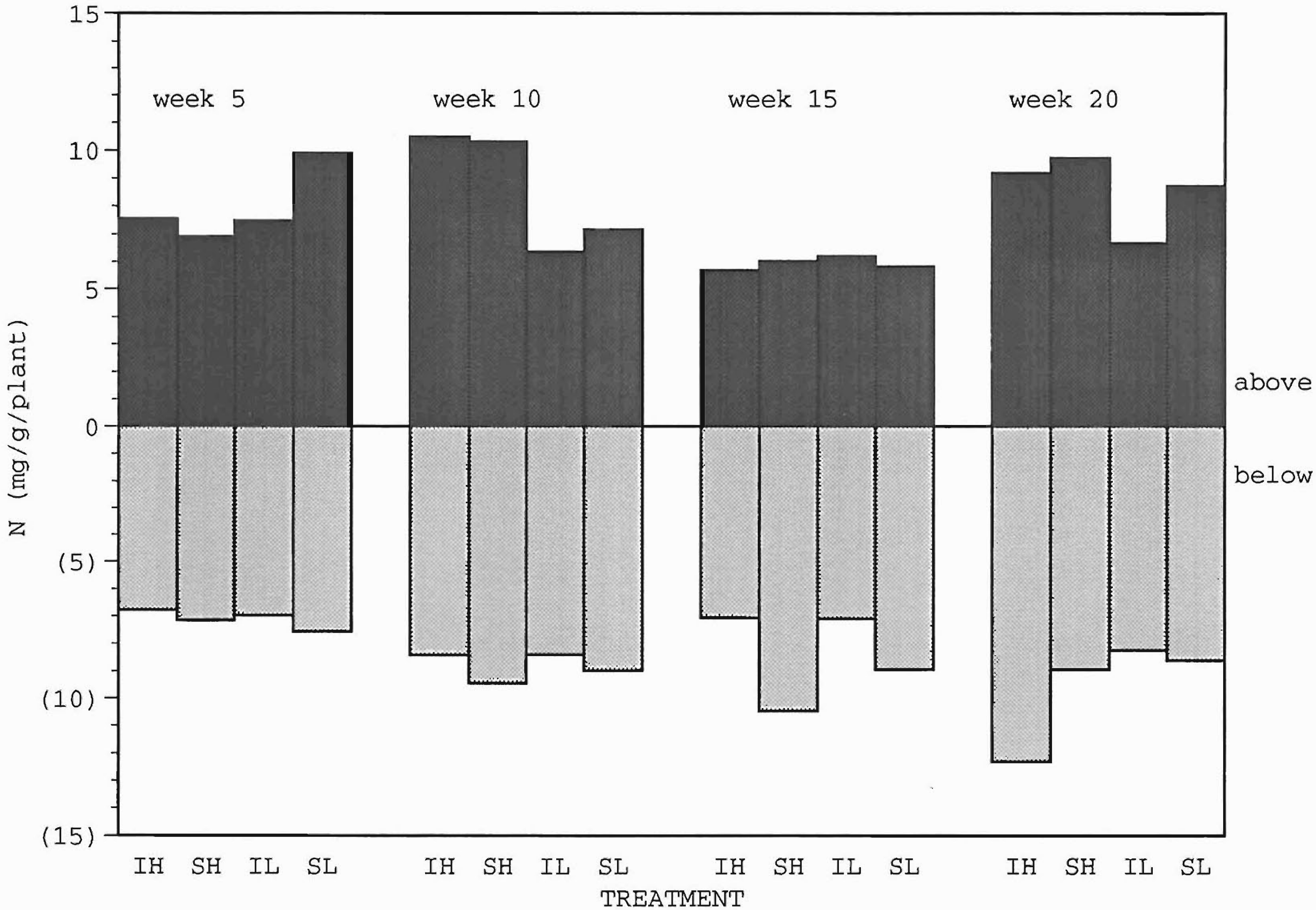

Figure 17. Mean aboveground and belowground N (mg/g/plant) of *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

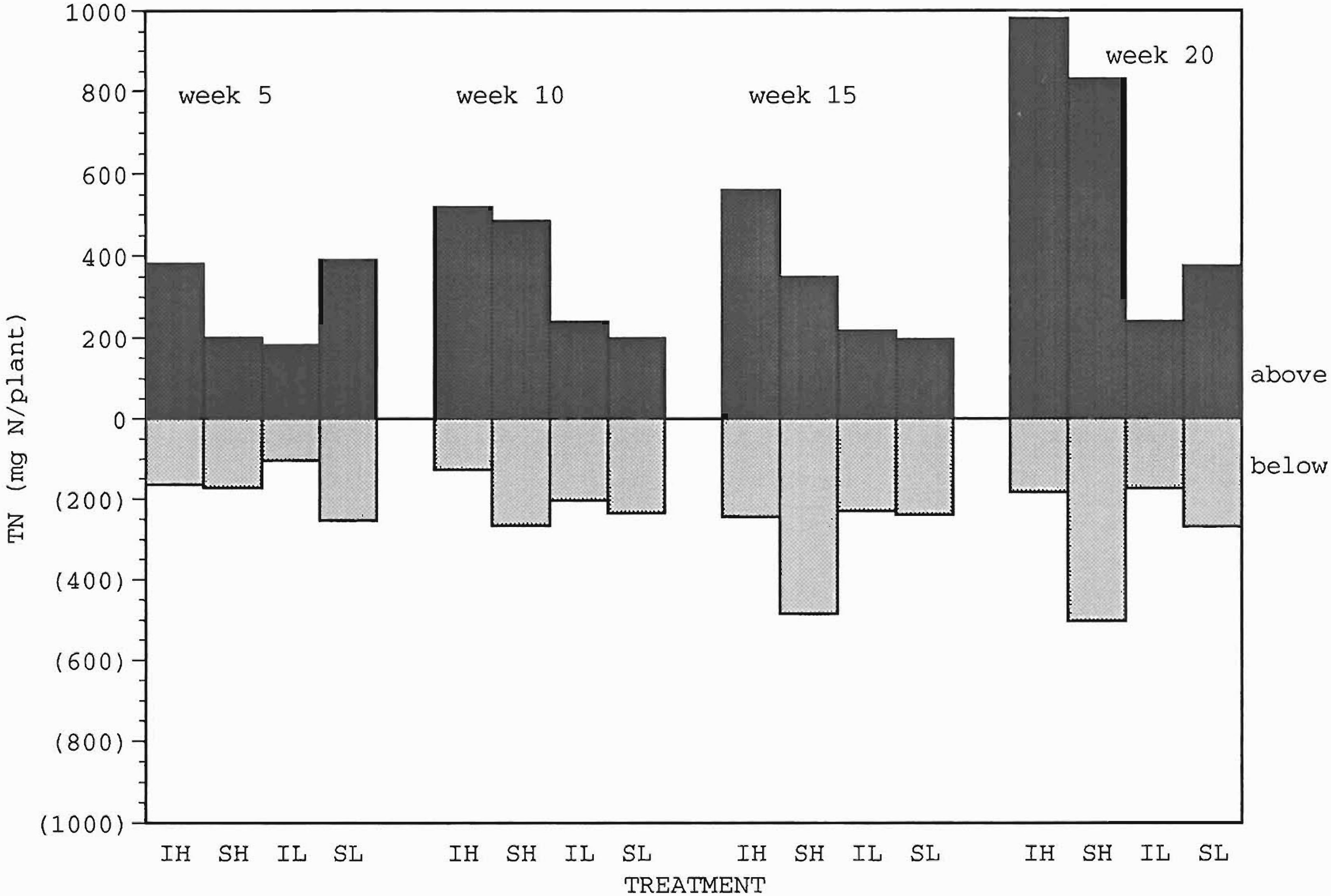

Figure 18. Mean aboveground and belowground TN (mg N/plant) of *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

Phosphorus

Mean aboveground P for *Typha* ranged from 1.1±0.8 in saturated low nutrient conditions to 1.3±0.8 in inundated low nutrient and saturated high nutrient conditions (Table 2-6,A-11,A-12). Because all water-nutrient levels had similar aboveground P levels, statistical comparisons did not differ significantly (Table 2-6). Aboveground P for *Typha* plants in inundated and saturated high nutrient conditions increased from week 5 to week 10 and decreased from week 10 to a low at the final harvest in week 20 (Figure 2-19). P was at a maximum concentration at week 5 for plants in inundated and saturated low nutrient conditions. These peak concentrations decreased during the following three harvests to a low at week 20. TP increased to a maximum amount at week 15 in plants grown in inundated high nutrient conditions (Figure 2-20). The high aboveground biomass during this period of the study explains the relatively high TP (mg P/plant) at week 15 harvest. Belowground P (mg/g/plant) (Figure 2-19) narrowly ranged from 1.3±0.3 to 1.6±0.6 under saturated low nutrient and inundated and saturated high nutrient conditions, respectively (Table 2-7). No significant conclusions of differences in the statistical comparisons can be drawn from these results. Again, saturated and inundated low nutrient conditions produced the highest mean P at the week 5 harvest. These levels consistently decreased from week 5 to a low at week 20.

Table 6. Mean aboveground P (mg/g/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Comparison	*Typha*		*Sagittaria*			*Sambucus*		*Salix*		
IL vs SL	1.3	1.2	1.5		1.5	1.0	1.4	1.0		1.0
IH vs SH	1.2	1.3	1.9		1.5	1.1	1.5	1.5		1.3
IH vs IL	1.2	1.3	1.9	*	1.5	1.1	1.0	1.5	*	1.0
SH vs SL	1.3	1.1	1.5		1.5	1.5	1.4	1.3		1.0

* = significantly different (alpha level = .0125)

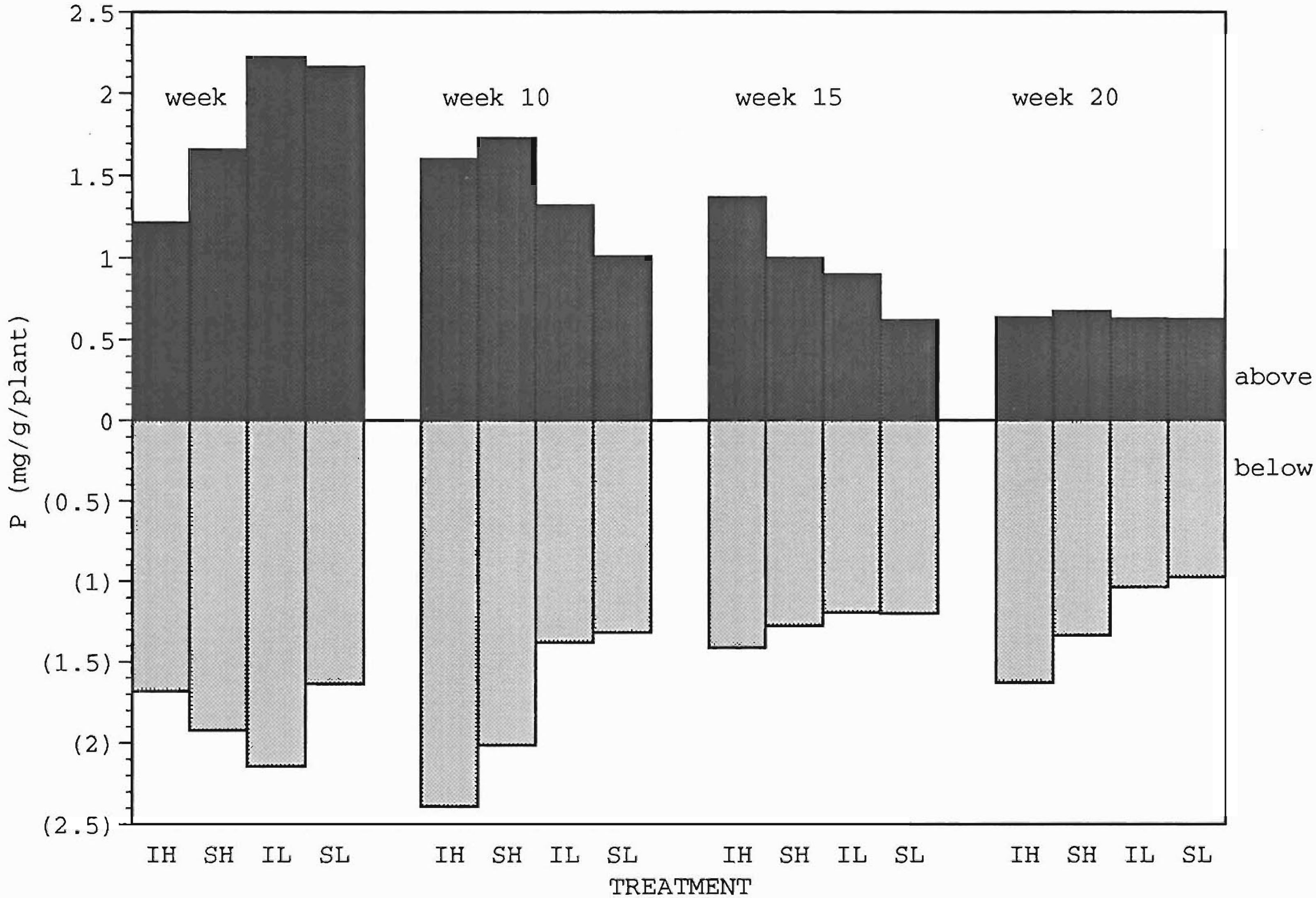

Figure 19. Mean aboveground and belowground P (mg/g/plant) of *Typha domingensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

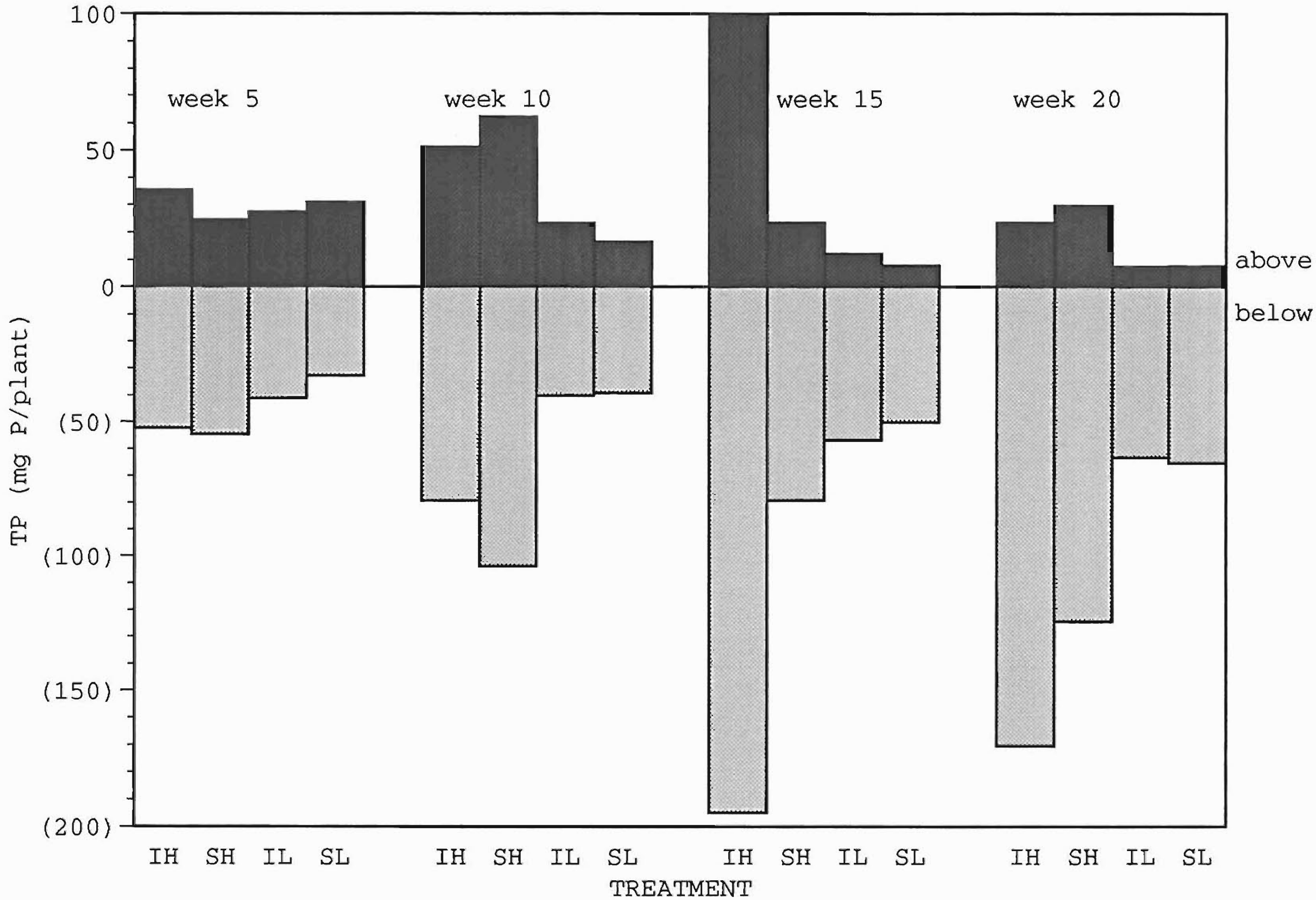

Figure 20. Mean aboveground and belowground TP (mg P/plant) of *Typha domingensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

Table 7. Mean belowground P (mg/g/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Comparison	*Typha*			*Sagittaria*			*Sambucus*			*Salix*	
IL vs SL	1.5		1.3	2.8	*	2.1	0.4		1.0	1.0	1.0
IH vs SH	1.6		1.6	2.0		2.3	0.4	*	1.1	1.3	1.2
IH vs IL	1.6		1.5	2.0	*	2.8	0.4		0.4	1.3	1.0
SH vs SL	1.6		1.3	2.3		2.1	1.1		1.0	1.2	1.0

* = significantly different (alpha level = .0125)

Saturated and inundated high nutrient conditions produced plants with mean P that increased from week 5 to week 10 and substantially decreased to week 15 with a slight increase again at week 20. High TP (mg P/plant) was evident from plants grown in inundated and saturated conditions from week 10 to the end of the study.

Sagittaria exhibited a significant difference in aboveground P of plants grown in inundated high nutrient conditions compared to plants grown in inundated low nutrient conditions. Mean P of aboveground structures of plants grown in saturated high nutrient, inundated low nutrient, and saturated low nutrient was 1.5 mg/g/plant P. Inundated high nutrient conditions produced a plant P mean of 1.9±0.6 (Table 2-6). An overall decline in P of plants grown in saturated high nutrient, inundated low nutrient, and saturated low nutrient conditions is evident in Figure 2-21. Plants grown in inundated high nutrient conditions maintained a constant P from week 5 harvest to week 15 harvest and decreased at the week 20 harvest. Plant TP (Figure 2-22) showed only a slight trend of increasing TP among plants in inundated high nutrient conditions from week 5 to week 15 which paralleled results found in the P analysis. Belowground mean P (Table 2-7; Figure 2-21) ranged from 0.4±0.2 in inundated high and low nutrient conditions to 1.1±0.4 for plants in saturated high nutrient conditions. A significant difference (Table 2-7) was found for *Sambucus* in inundated high

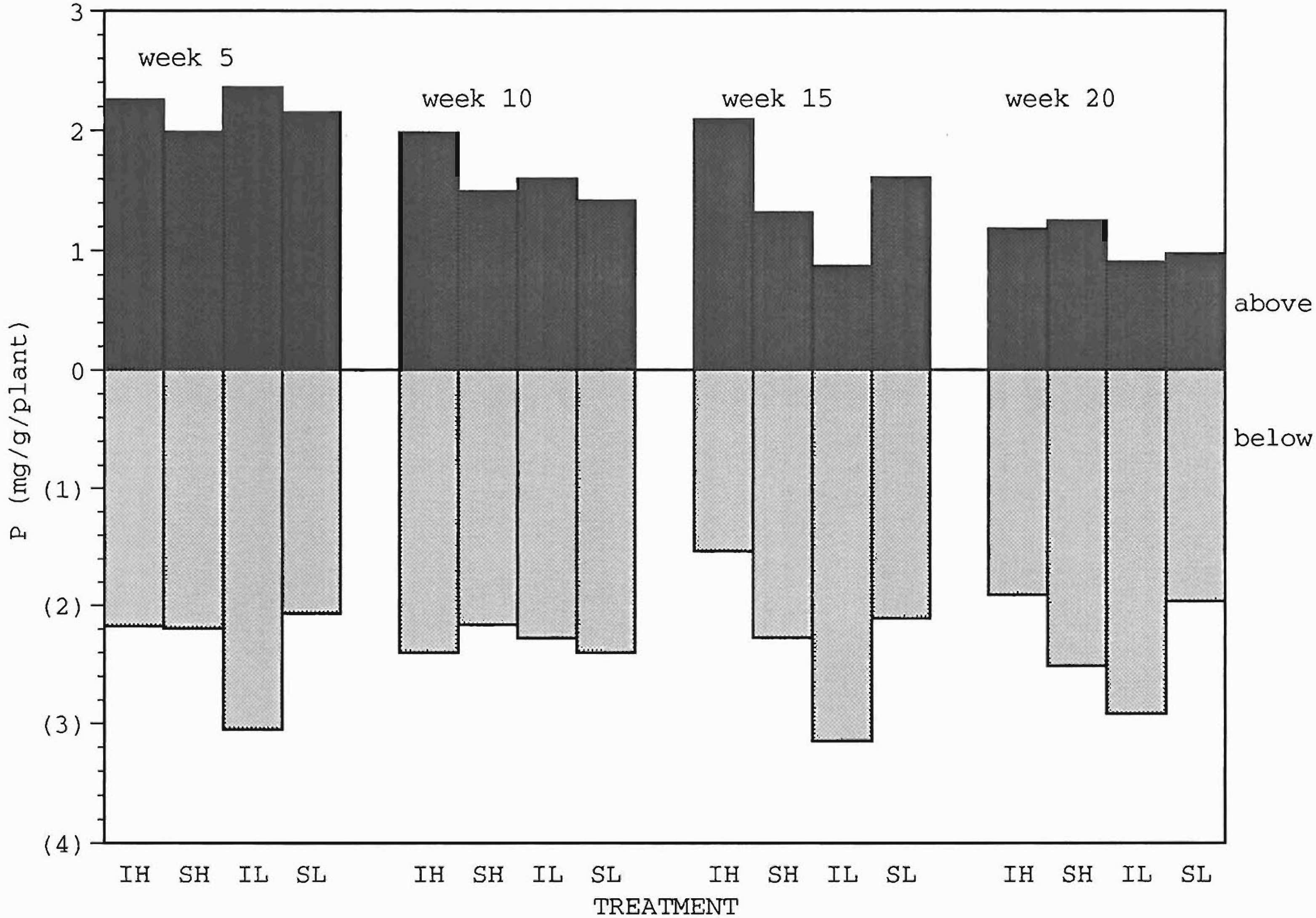

Figure 21. Mean aboveground and belowground P (mg/g/plant) of *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

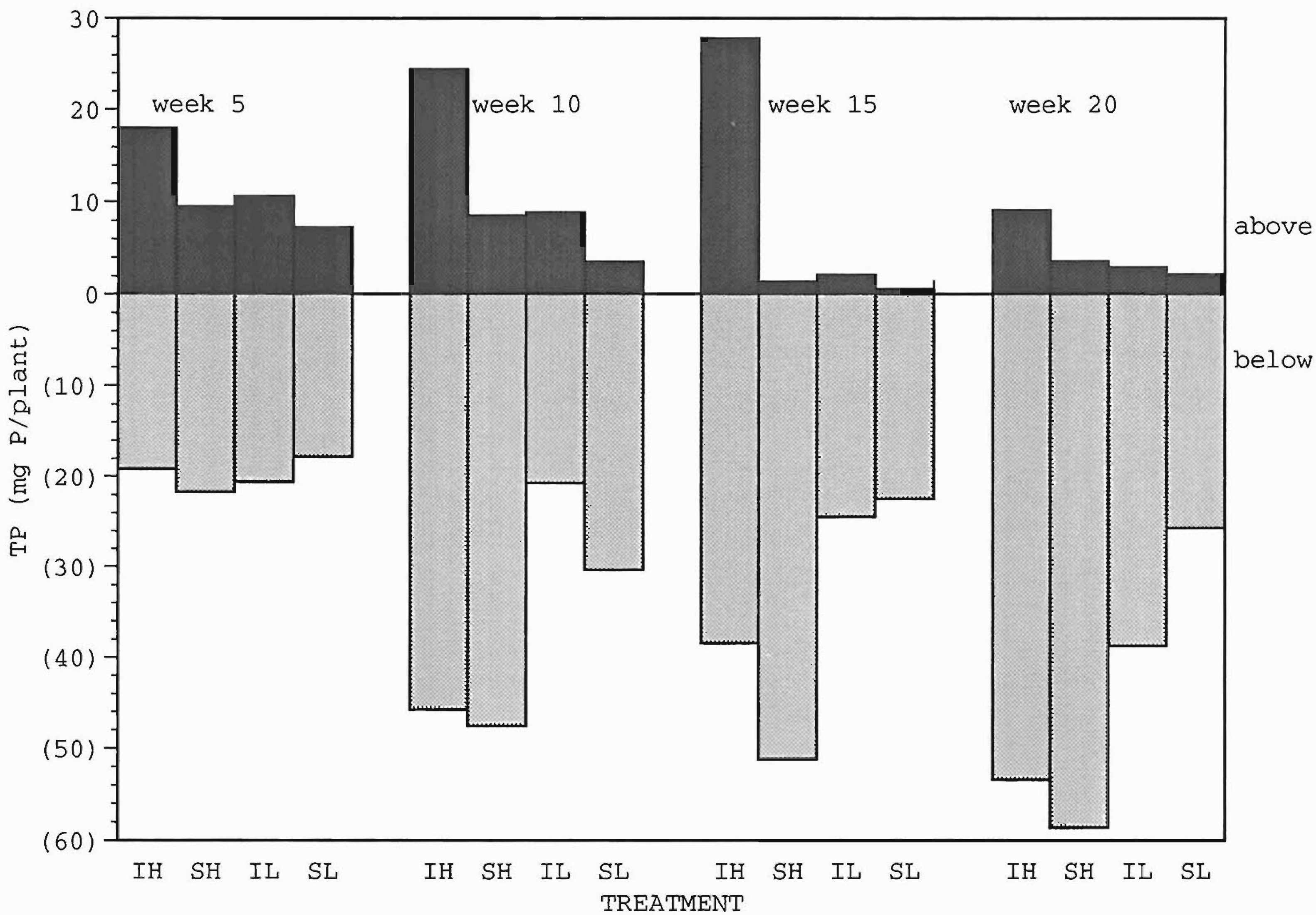

Figure 22. Mean aboveground and belowground TP (mg P/plant) of *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

nutrient compared to plants in saturated high nutrient conditions. P assimilation was 64% greater in plants in saturated high nutrient conditions compared to those plants in inundated high nutrient conditions. Varying P concentrations under all water-nutrient conditions is evident, but a overall increase in the saturated plants over the inundated individuals may be present (Table 2-6). No trends were found for *Sambucus* P above or belowground (Tables 2-6,2-7; Figure 2-23). Limited growth of *Sambucus* negatively influenced TP assimilation (Figure 2-24). Again, the stresses of flooding could not be overcome by this species.

Salix aboveground P concentration (Table 2-6) ranged from 1.0±0.2 in low nutrient, inundated or saturated conditions to 1.5±0.5 for plants grown in inundated high nutrient conditions. No significant differences (Table 2-6) were found for individuals in inundated and saturated low nutrient conditions nor for plants in inundated and saturated high nutrient conditions. Significant differences were also not found for plants grown in saturated high nutrient conditions compared to plants in saturated low nutrient conditions. Significant differences were found for plants grown in inundated high nutrient conditions compared with plants in inundated low nutrient conditions. A trend of higher P concentrations in plants grown in high nutrient conditions was evident, especially individuals in inundated high nutrient conditions (Figure 2-25). Since plants in the

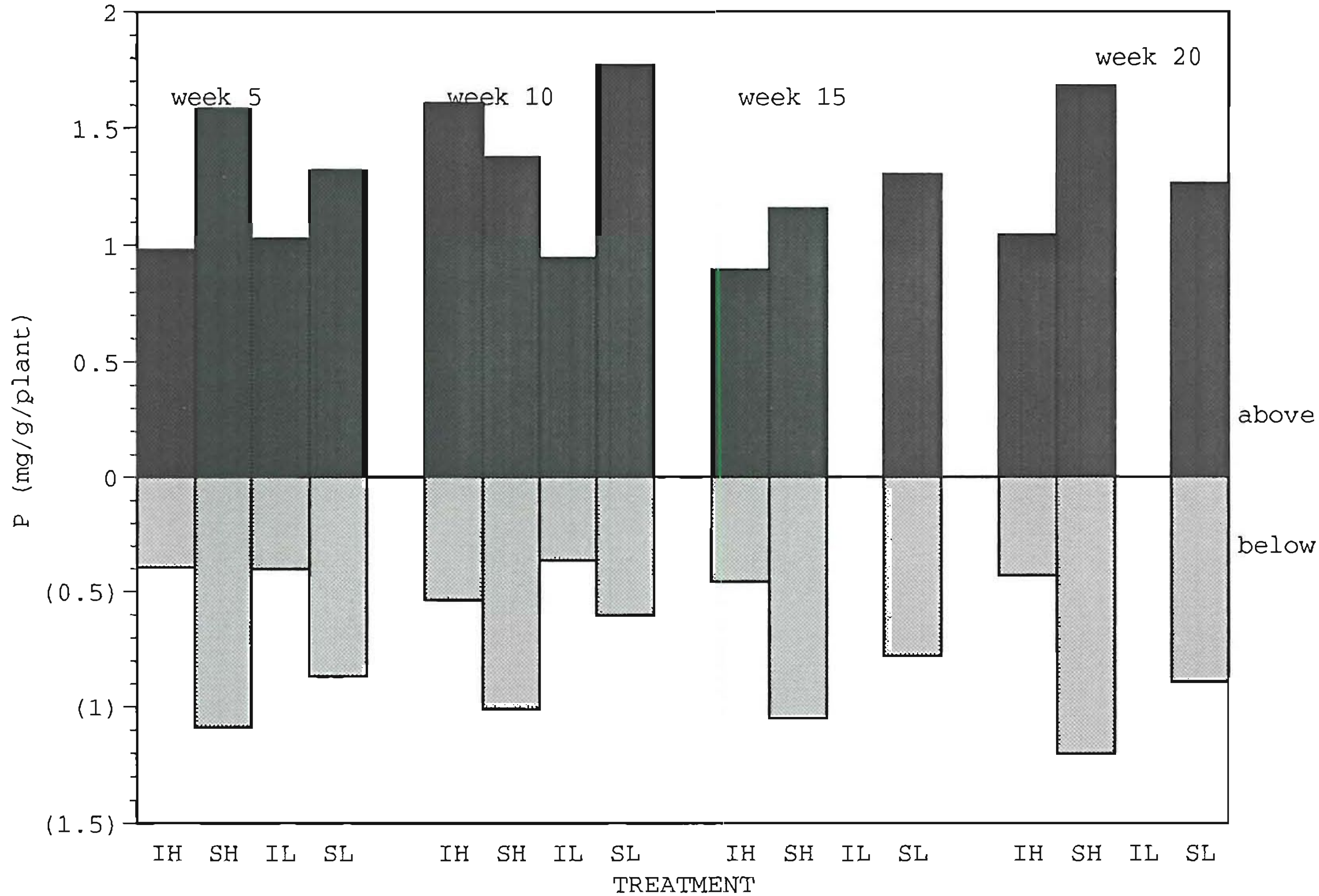

Figure 23. Mean aboveground and belowground P (mg/g/plant) of *Sambucus canadensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

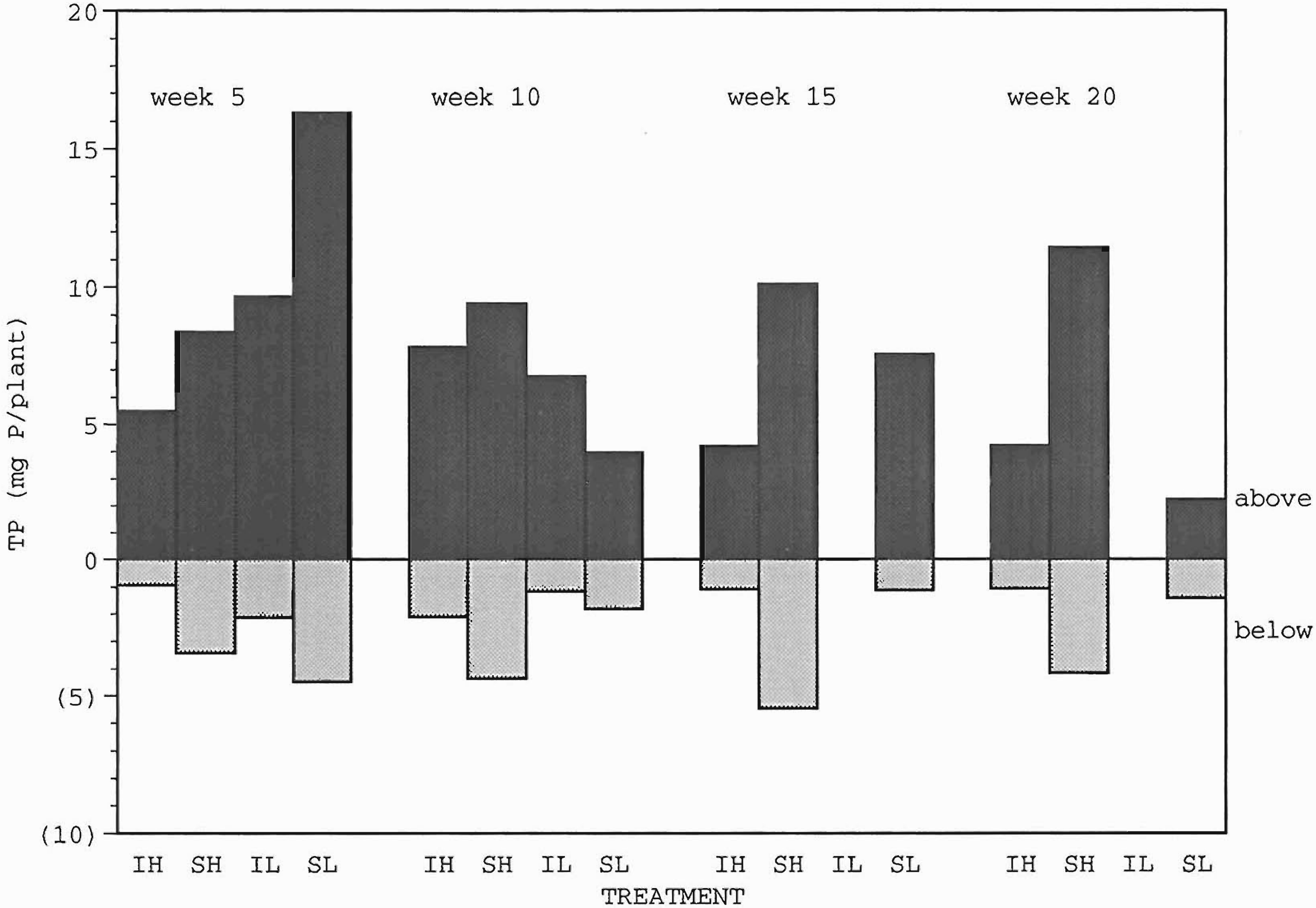

Figure 24. Mean aboveground and belowground TP (mg P/plant) of *Sambucus canadensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

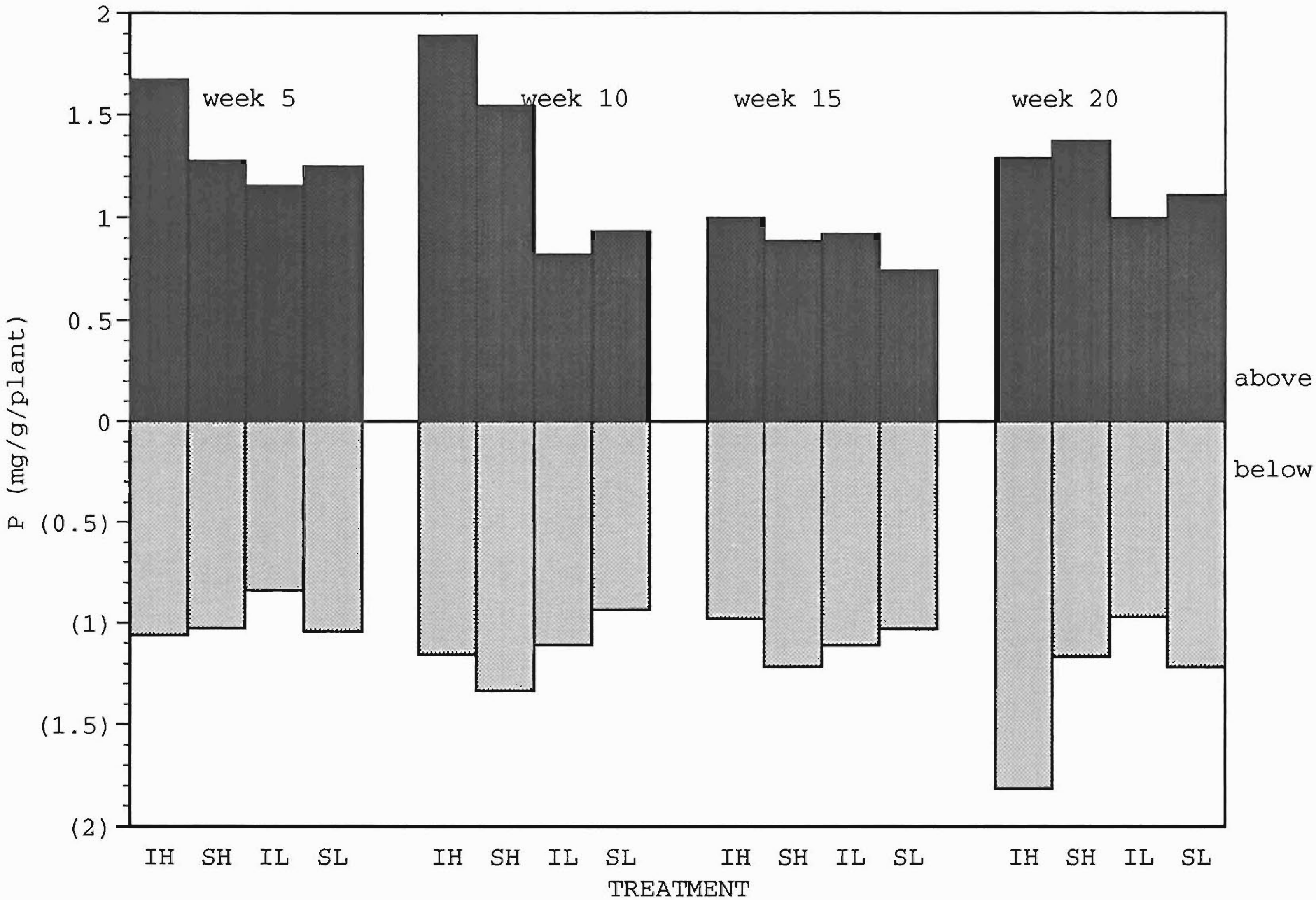

Figure 25. Mean aboveground and belowground P (mg/g/plant) of *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

inundated high nutrient conditions had a significant advantage in P assimilation compared with plants in inundated low nutrient conditions, overall biomass production was greater thus maximizing TP assimilation for this species (Figure 2-26). Belowground mean P for *Salix* and statistical analysis are presented in Tables A-13 and A-14. Belowground P concentration ranged from 1.0±0.1 in both low nutrient conditions to 1.3±0.4 in inundated high nutrient conditions (Table 2-7). No statistically significant differences existed among the four comparisons of this study. General trends can be interpreted from Figure 2-25. All water-nutrient conditions remained relatively constant with regard to P throughout the study. A slow, progressive increase in TP was evident in individuals growing in saturated high nutrient conditions (Figure 2-26). The other conditions again remained constant throughout the study.

Litter Dynamics

Litter is defined in this study as fallen or standing dead plant material. The two woody species, *Sambucus* and *Salix* produced negligible amounts of litter throughout the study. Both *Typha* and *Sagittaria* began to produce collectable amounts of litter between the week 5 harvest and the week 10 harvest. Litter was collected at the biweekly measurement dates and analysis was completed at the time of the plant harvest.

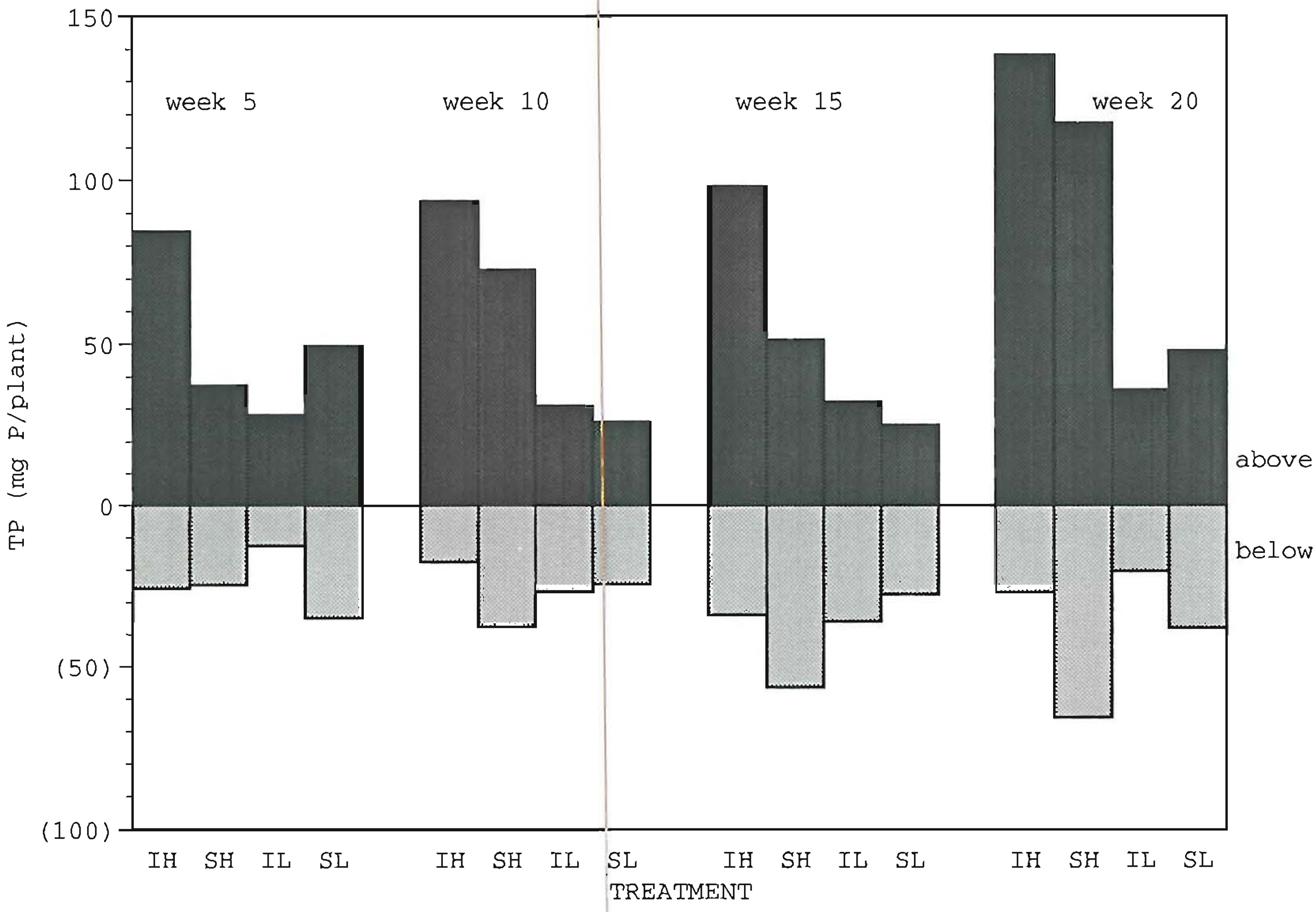

Figure 26. Mean aboveground and belowground TP (mg P/plant) of *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 5, 10, 15, and 20 week harvests.

Aboveground Litter Production

Typha litter production (Table 2-8,A-15,A-16) ranged from 7.24±5.81 g dry wt/plant in saturated low nutrient conditions to 13.48±6.77 g dry wt/plant in inundated high nutrient conditions. Plants in inundated high nutrient conditions produced significantly more litter than did plants in saturated high nutrient conditions (Table 2-8). Plants in inundated high nutrient conditions also produced significantly more litter than plants in inundated low nutrient conditions. Steady increases in litter production were evident from week 10 harvest to the week 20 harvest (Figure 2-27). Plants in inundated high nutrient conditions produced significantly more litter between week 10 harvest and the week 15 harvest and decreased litter production from week 15 harvest to week 20 harvest.

Sagittaria mean litter production ranged from 1.27±.41 g dry wt/plant in inundated low nutrient conditions to 3.17±.96 g dry wt/plant in inundated high nutrient conditions (Table 2-8). There were no significant differences in litter production among individuals grown in the various water-nutrient manipulations. Figure 2-28 does show that inundated and saturated low nutrient plants produced relatively constant amounts of litter throughout the study. Inundated and saturated high nutrient individuals increased in litter production between the week 10 harvest and the week 15 harvest and decreased thereafter. Overall, there were no noticeable trends in litter production of *Sagittaria*.

Table 8. Mean aboveground litter (g dry wt/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Comparison	*Typha*			*Sagittaria*	
IL vs SL	9		7	1	2
IH vs SH	13	*	9	2	3
IH vs IL	13	*	9	2	1
SH vs SL	9		7	3	2

* = significantly different (alpha level = .0125)

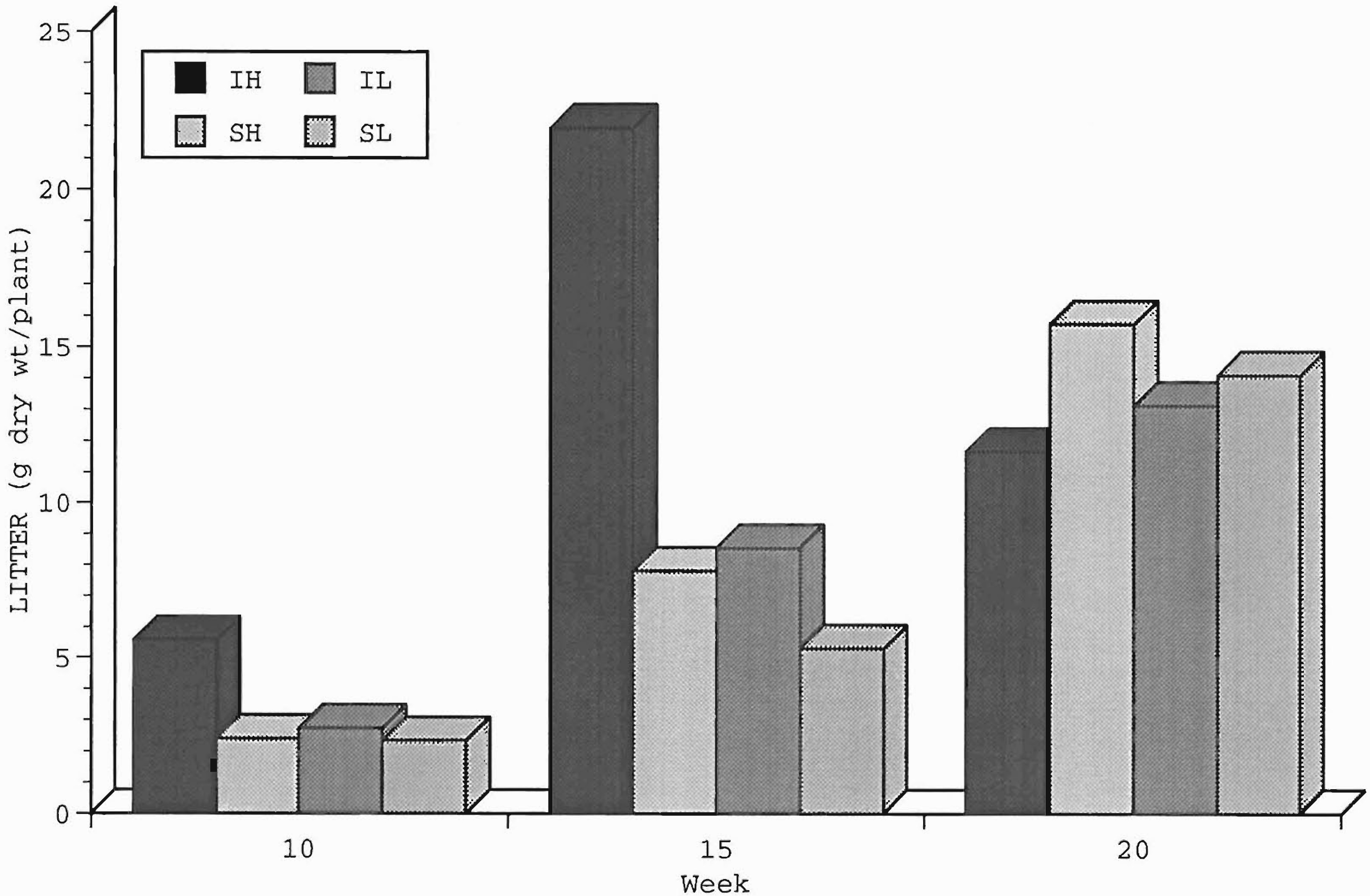

Figure 27. Mean aboveground litter (g dry wt/plant) of *Typha domingensis* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms collected during the 10, 15, and 20 week harvests.

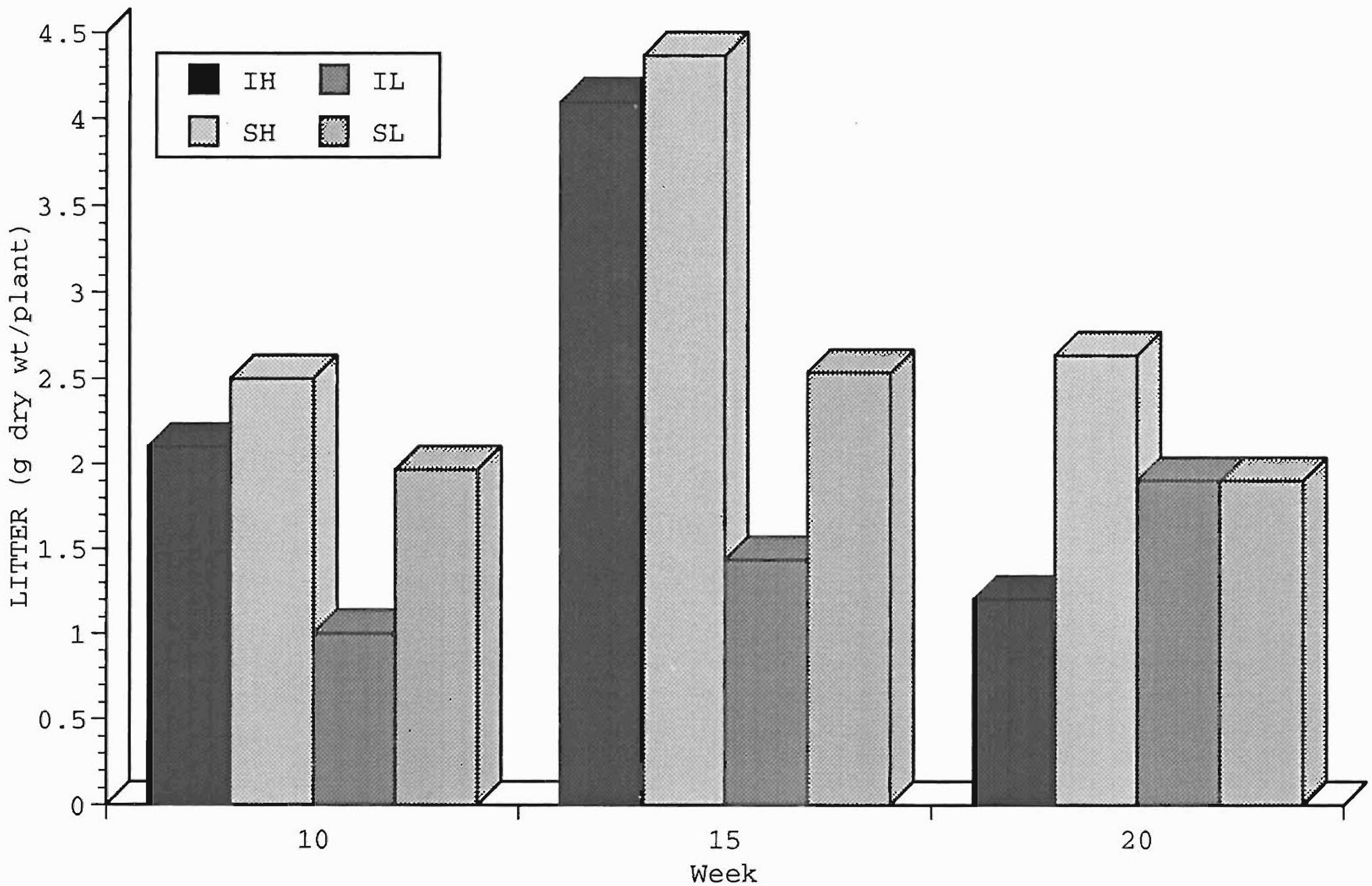

Figure 28. Mean aboveground litter (g dry wt/plant) of *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms collected during the 10, 15, and 20 week harvests.

Nutrient Assimilation

Mean N of *Typha* litter ranged from 4.9±0.7 % for plants in the saturated low nutrient conditions to 6.4±1.3 % for plants in inundated high nutrient conditions (Table 2-9). There were no significant differences in the statistical comparisons in Table 2-9. Mean N in litter of *Typha* decreased in every water-nutrient condition, except for plants in the inundated low nutrient condition, from the week 10 harvest to the week 20 harvest. Plants in the inundated low nutrient condition increased mean N in the produced litter during the week 10 harvest to the week 15 harvest and subsequently decreased in mean litter N from the week 15 harvest to the week 20 harvest (Figure 2-29).

Mean litter N for *Sagittaria* ranged from 9.9 mg/g/plant in inundated and saturated low nutrient conditions to 12.2±2.6 in inundated high nutrient conditions (Table 2-9). Plants grown in inundated high nutrient conditions had a significantly greater percent concentration of N in the litter than plants grown in inundated low nutrient conditions. Likewise, plants in saturated high nutrient conditions had significantly greater percent concentration of N in the litter produced than plants in saturated low nutrient conditions (Table 2-9). Plants in both inundated and saturated high nutrient conditions declined in litter N concentration from the week 10 harvest to the week 20 harvest. Individuals in inundated low nutrient conditions

Table 9. Mean litter N (mg/g/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Comparison	*Typha*		*Sagittaria*		
IL vs SL	6	5	10		10
IH vs SH	6	5	12		11
IH vs IL	6	6	12	*	10
SH vs SL	5	5	11	*	10

* = significantly different (alpha level = .0125)

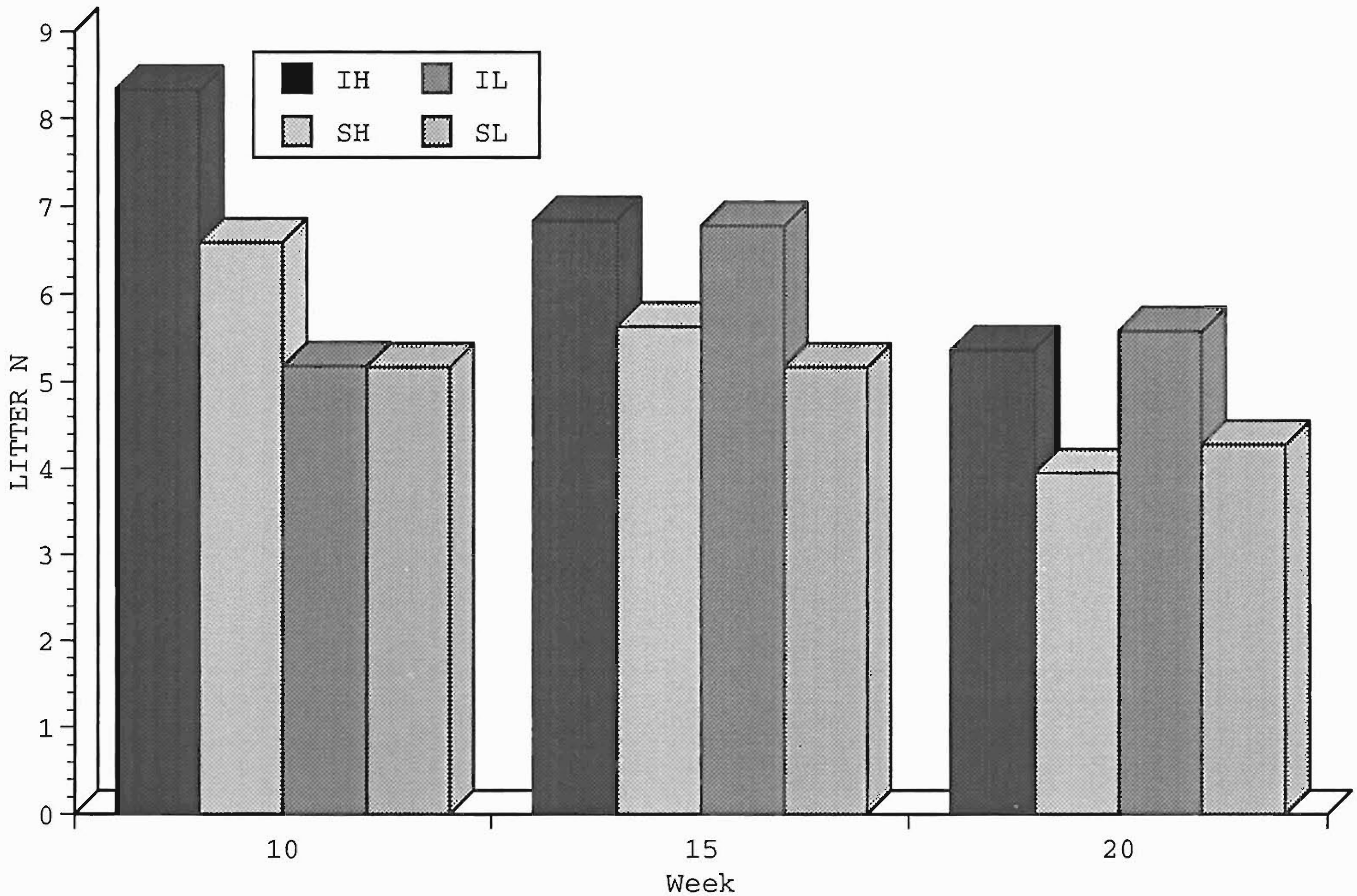

Figure 29. Mean N (mg/g/plant) of *Typha domingensis* aboveground litter grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated high nutrient microcosms during the 10, 15 and 20 week harvests.

increased in litter N concentration from the week 10 harvest to the week 15 harvest and subsequently decreased thereafter. Individuals in saturated low nutrient conditions remained constant from the week 10 harvest to the week 15 harvest, and decreased by the week 20 harvest (Figure 2-30).

Tables A-19 and A-20 summarize the statistical analysis of the results of the litter P concentration of *Typha* and *Sagittaria*. *Typha* ranged from 0.6 P in both inundated and saturated low nutrient conditions to 1.1±0.6 P in inundated high nutrient conditions (Table 2-10). Plants in the inundated high nutrient condition had significantly greater P concentration than plants in the inundated low nutrient condition. All individuals, except those in the inundated low nutrient condition, exhibited a decline in litter P concentration from the week 10 harvest to the week 20 harvest (Figure 2-31). *Sagittaria* ranged from 0.6 P in inundated and saturated low nutrient conditions to 1.0±0.3 P in saturated high nutrient conditions (Table 2-10). Individuals grown in saturated high nutrient conditions assimilated significantly greater quantities of P in their litter than did individuals grown in saturated low nutrient conditions. All plants in the four water-nutrient conditions increased in mean litter P concentration between the week 10 harvest and the week 20 harvest (Figure 2-32) . A decrease in mean litter P concentration for all nutrient-water conditions was apparent by the week 20 harvest.

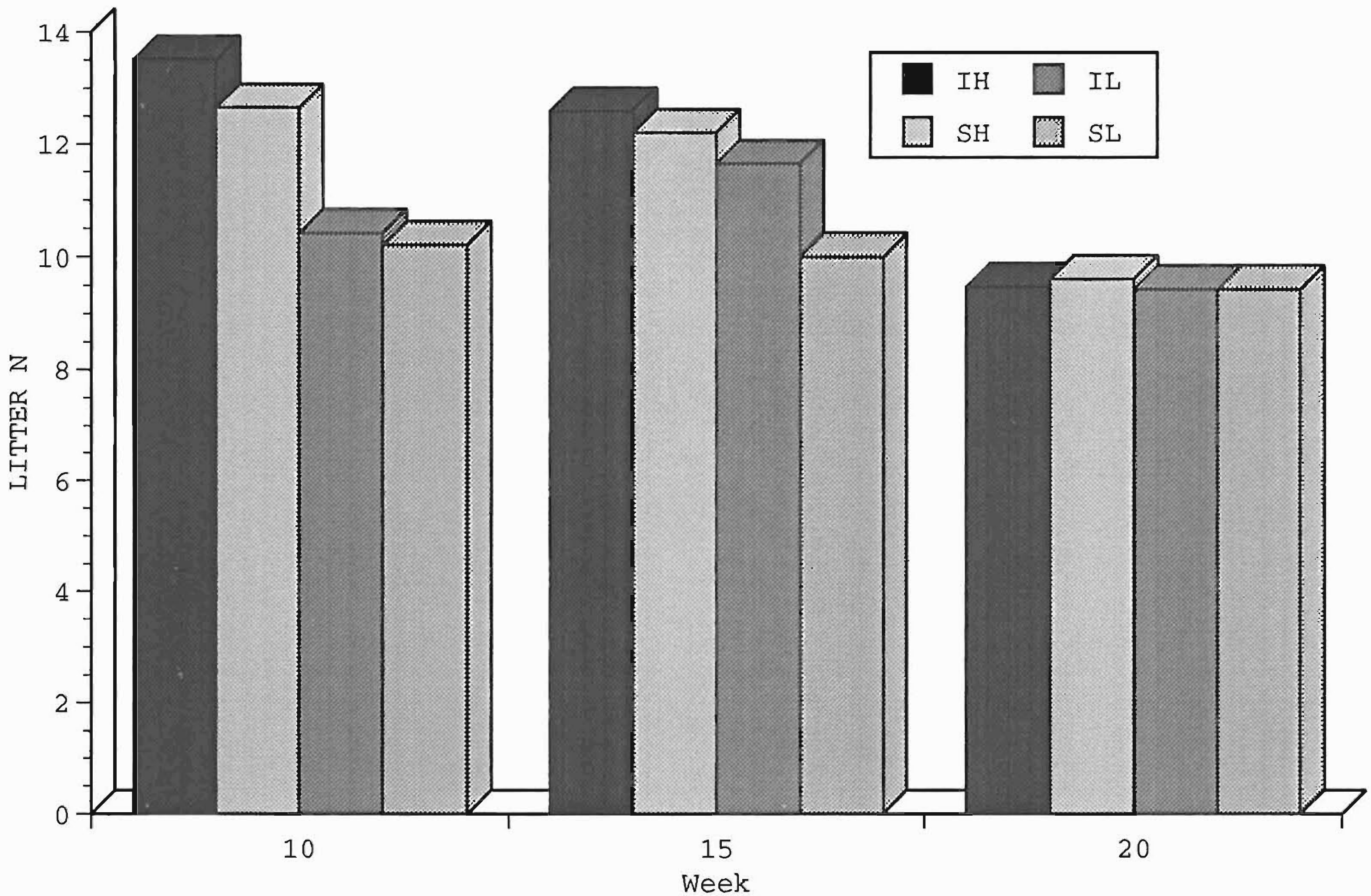

Figure 30. Mean N (mg/g/plant) of *Sagittaria latifolia* aboveground litter grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 10, 15, and 20 week harvests.

Table 10. Mean litter P (mg/g/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Comparison	*Typha*			*Sagittaria*		
IL vs SL	0.6		0.6	0.6		0.6
IH vs SH	1.1		0.9	0.8		1.0
IH vs IL	1.1	*	0.6	0.8		0.6
SH vs SL	0.9		0.6	1.0	*	0.6

* = significantly different (alpha level = .0125)

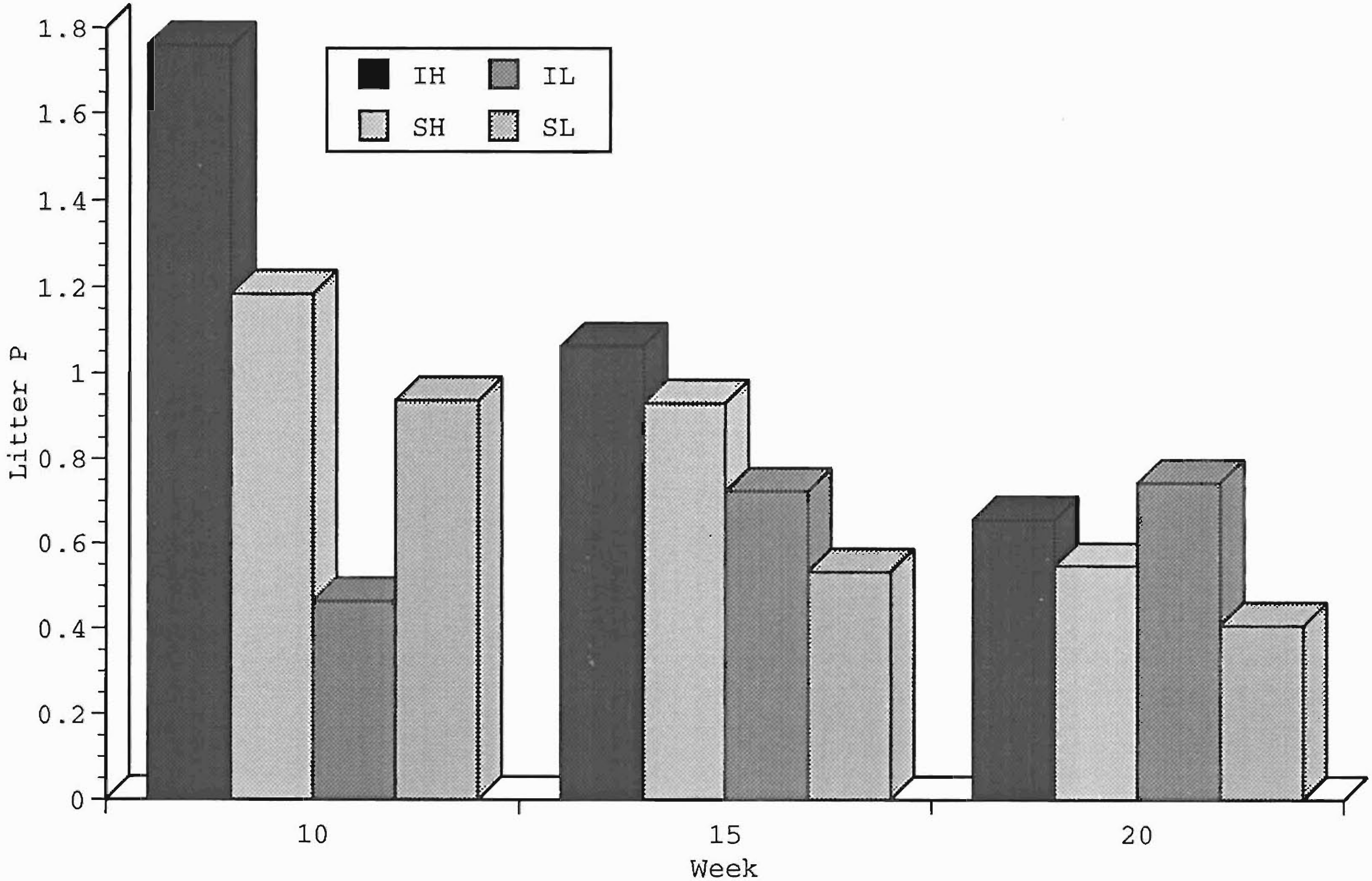

Figure 31. Mean P (mg/g/plant) of *Typha domingensis* aboveground litter grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 10, 15, and 20 week harvests.

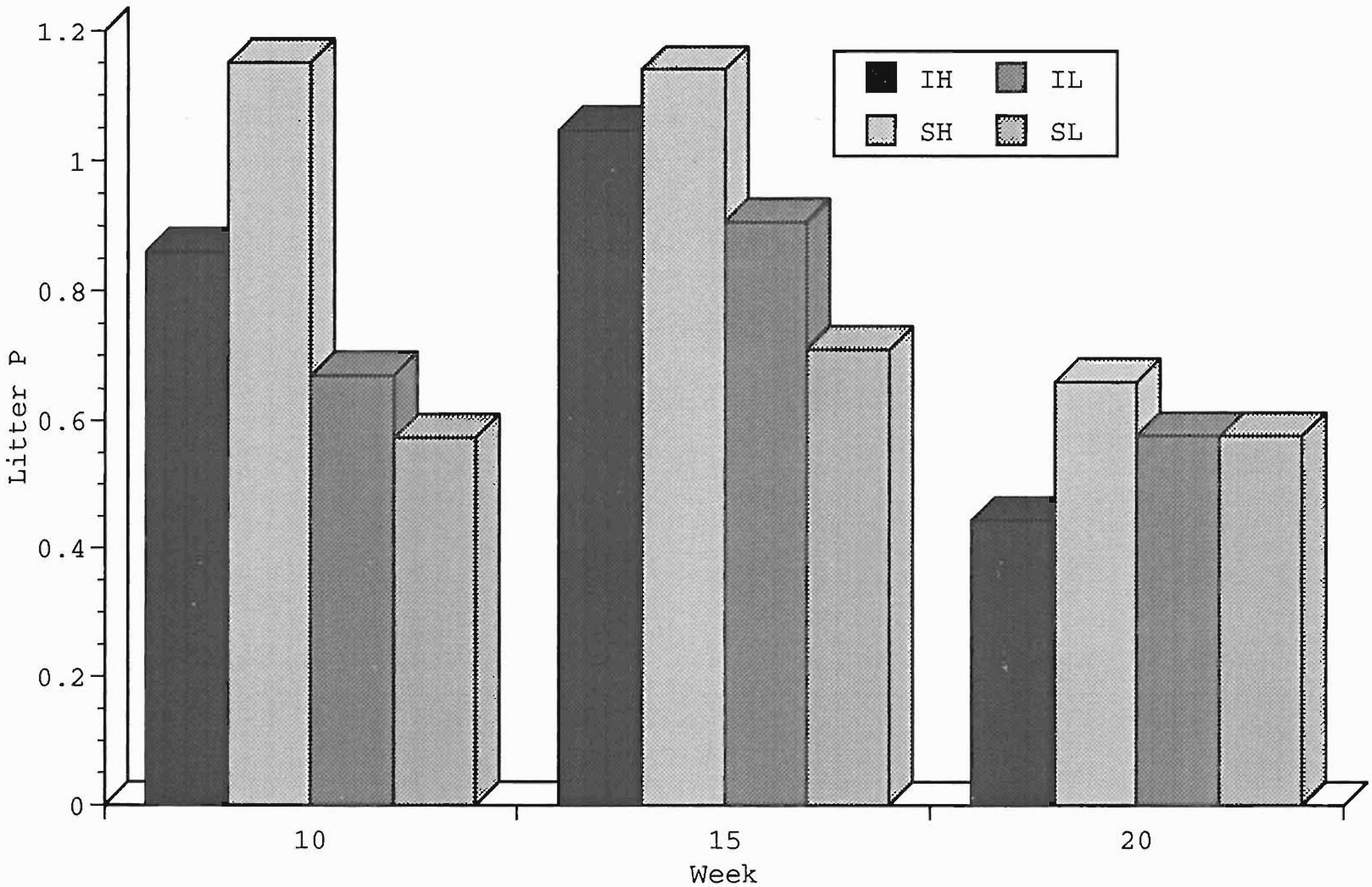

Figure 32. Mean P (mg/g/plant) of *Sagittaria latifolia* aboveground litter grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms during the 10, 15, and 20 week harvests.

DISCUSSION AND CONCLUSIONS

Survival

The successful survival of *Typha* and *Salix* is primarily due to the fact that both of these species are highly adapted to wetland ecosystems. *Typha*, *Salix*, and *Sagittaria* are listed as obligate hydrophytes in Florida (Reed, 1988). *Sagittaria*'s high mortality during the week 15 and week 20 harvests was explained by the fact that this herbaceous macrophyte naturally senesced at the end of a artificially extended growing season. Photoperiod probably dictates when senescence initiates in this species. *Sambucus* simply could not tolerate the stresses of flooding and soil waterlogging. The species had some success in the high nutrient conditions only if the individuals were able to produce adventitious roots. All belowground structures were reduced to a supportive framework only, and adventitious roots were necessary to continue physiological activities.

Typha produced significantly taller shoots only in inundated high nutrient conditions. *Typha domingensis* has been found to grow better in deeper water than *T. latifolia*, a similar species (Grace, 1988). Grace (1989) also found that *Typha domingensis* had a greater ability to oxidize its rhizosphere compared to T. latifolia. If this is the case, plants under inundated high nutrient conditions would have a greater ability to overcome the stresses of anoxia and take advantage of nutrients present in the anoxic sediments. Light limitation may also be a factor in extended heights of both *Typha* and *Sagittaria* in this study. Both herbaceous species *Typha* and *Sagittaria* produced abovewater heights equal to plants grown in saturated conditions. This may be a competitive advantage for plants growing in deeper microenvironments. The literature also suggests that this response to flooding may be necessary for the plant to maintain a positive gas exchange ability. Both *Typha* and *Sagittaria* are able to oxidize their rhizosphere and maintain a positive carbon balance.

Sambucus produced no variation in height during the study. *Sambucus* struggled to overcome the stresses of waterlogged and inundated conditions. As with survival, any increases in growth of *Sambucus* was a direct result of substantial adventitious root formation. Plants that did not produce adventitious roots exhibited no increase in height or growth in general. Individuals that did not produce adventitious roots became chlorotic and eventually lost most of their leaves. Individuals that did produce adventitious roots continued to photosynthesize until harvested. These plants did not necessary overcome the effects of flooding but were able temporarily overcome the immediate stresses during the study.

Changes in height among individuals of *Salix* in the various water-nutrient conditions were directly correlated with nutrient level. Plants grown in high nutrient conditions were taller than plants grown in low nutrient conditions independent of water level. Growth of *Salix* was directly correlated to nutrient level. Both inundated and saturated individuals in high nutrient conditions were taller than individuals in low nutrient conditions. Plants in high nutrient inundated conditions produced extensive systems of adventitious roots that formed right below the water level. Plants grown in inundated low nutrient conditions did not produce the extensive adventitious roots that the high nutrient plants produced. Both inundated and saturated low nutrient plants became chlorotic around the midpoint of the study. Obvious differences in height and growth were evident after four weeks into the study. Both *Sambucus* and *Salix* were not able to maintain substantial root growth belowground. Decreased root function initiated adventitious root formation for survival and growth. The ability of *Salix* to produce adventitious roots readily makes this plant a highly adaptive woody species in wetland systems.

Biomass

Inundated high nutrient individuals of *Typha* produced the greatest amounts of biomass in all four water-nutrient conditions. Plants in inundated high nutrient conditions produced more shoots than saturated high nutrient plants. Significant increases in height among these individuals supported greater biomass. Underwater aboveground structures may not be photosynthetically active but increase total aboveground biomass due to supportive structures needed in these conditions. Both saturated and inundated high and low nutrient individuals produced a secondary root mat at the soil-water interface. This root mat was a additive root structure which presumably increased water and nutrient assimilation from the water column. Davis (1990) suggested that *Typha* is a high nutrient status plant and can be highly competitive under nutrient enriched conditions. The significant differences of both inundated and saturated high nutrient individuals compared with inundated and saturated low nutrient individuals supported this conclusion. Belowground biomass production was significantly similar to aboveground biomass production for this species. High nutrient inundated individuals produced the most belowground production. The root mat formed on most individuals was included in the belowground biomass estimates. *Typha* produced extensive rhizomes and associated roots in all water-nutrient conditions.

Sagittaria had no significant differences in biomass between any of the four comparisons. These plants did have significant differences in height between inundated and saturated high nutrient conditions but produced no biomass differences because the supportive structures of the increases stem lengths were constituted of aerachymous tissue. This air-filled tissue sufficiently supported the taller plants and increased air movement to the anoxic root zone. This adaptation was completed without the necessity of increasing aboveground biomass. *Sagittaria* did not significantly differ in belowground biomass production in any of the water-nutrient conditions. Individuals were, for the most part, unaffected by nutrient and water manipulations. Tuber production increased among individuals in the high nutrient conditions. *Sagittaria* also produced a rhizome system with associated secondary and primary roots.

Sambucus again could not overcome the stresses of flooding to increase aboveground biomass significantly. Some leaf production was evident in saturated high nutrient conditions but stem production was not evident. Belowground biomass of *Sambucus* exhibited no significant differences among statistical comparisons. No new root formation was evident on any harvested plants during this study. *Sambucus* has a complete intolerance to root flooding which affects overall growth and survival of this species.

Aboveground biomass production followed the same trends of height in *Salix*. This species had the highest aboveground production in inundated high nutrient conditions. Again, this was due to the ability of the species to overcome the anoxic conditions of flooding by producing adventitious roots. Belowground biomass was significantly less for individuals grown in inundated high nutrient conditions. It must be noted that adventitious roots were assumed to be aboveground biomass in this study. Some secondary root formation was evident on saturated species. All new root formation ceased for individuals grown in inundated conditions. This shift from belowground root production to adventitious root production explained the significantly low belowground biomass production for inundated individuals of *Salix*.

Nutrient Assimilation

Nitrogen assimilation by *Typha* did not significantly differ among water-nutrient treatments. Percent N concentrations remained relatively constant for above and belowground plant structures. TN (mg N/plant) increased proportionately with increases in biomass of individuals in high nutrient water. *Sagittaria* increased concentrations of percent N in high nutrient conditions. Belowground percent N also exhibited increases in inundated plants in high nutrient conditions. Clark and Clay (1989) suggested that *Sagittaria* species grow better in inundated conditions than low water conditions. *Sagittaria* optimized nutrient uptake of N in both aboveground and belowground biomass in the inundated state. *Sambucus* exhibited significantly greater increases in percent N in inundated low nutrient aboveground biomass compared to saturated low nutrient aboveground biomass. Again, levels of N in above and below ground plant tissues of *Sambucus* suggested that this species cannot adjust morphologically or physiologically to the stresses of flooding. Like the other highly productive plant, *Typha*, *Salix* actually did not exhibit any differences in % N concentration in above or belowground plant structures.

Phosphorus assimilation mimicked assimilation of nitrogen in *Typha*. Again, concentrations followed the same pattern of nitrogen assimilation. TP assimilation increased proportionately with above and belowground biomass production. *Sagittaria* had a slightly greater percent P concentration among plants grown in inundated high nutrient conditions compared to plants grown in low nutrient inundated conditions. Both *Sambucus* and *Salix* exhibited no significant differences in percent P or TP concentrations among the four comparisons. *Salix* individuals grown in inundated high nutrient conditions had a significantly greater percent P concentration than plants grown in inundated low nutrient conditions. Coupled with high biomass production of these individuals, overall TP assimilation abilities of *Salix* were quite high.

Litter dynamics

Typha and *Sagittaria* were the only litter producing species in this study. The two woody species did not produce significant amounts of litter. Typha plants grown in inundated high nutrient conditions had the greatest amounts of litter compared to plants in all other conditions. The litter response of *Typha* correlates directly with overall aboveground biomass production. *Sagittaria* exhibited no trends in litter production in any of the water nutrient conditions. This response also reflected results found in the aboveground biomass production for Sagittaria.

Litter percent N for *Typha* was lower than aboveground biomass percent N. No significant differences were found among any of the comparisons for litter percent N. *Sagittaria* litter percent N showed no trends in differences compared to aboveground biomass percent N. Plants grown in the high nutrient conditions had significantly higher amounts of N than plants grown in low nutrient conditions. This supported the response that plants grown in highly nutrified waters may maintain greater amounts of nitrogen in litter than plants grown in less nutrified water.

Both species exhibited high percent P concentration in plants grown in the high nutrient conditions. *Typha* only produced a significant difference amoung plants grown in inundated high versus low nutrient conditions. Percent P concentration of litter found in plants grown in the high nutrient conditions resembled amounts found throughout all conditions in aboveground percent P concentration of living biomass throughout the study.

Sagittaria also produced greater amounts of P in litter of plants grown in high nutrient conditions. Plants grown in saturated high nutrient conditions had significantly greater amounts of P in litter than plants in low nutrient conditions. Litter produced by plants grown in saturated high nutrient conditions had higher P concentrations than aboveground biomass of plants grown in inundated high nutrient conditions.

Implications for competition

Growth and nutrient assimilation performance of plant species presents an idea of how well a species may be suited in a competitive environment. The performance of species based on height, above and belowground biomass, nitrogen and phosphorus assimilation, and litter production and nutrient content may give an insight to which factors influence competitive advantages of certain species.

Height of plants influences the amount of light the plant can receive for photosynthesis, the basis for plant production and survival. Among the herbaceous species, *Typha* produced the tallest individuals. Although *Sagittaria* produced shorter plants, a broad leaf morphology allowed this species to use available light more efficiently than *Typha* which has very narrow leaves. *Salix* exhibited the ability to produce taller individuals than *Sambucus*. Under all nutrient-water conditions, *Salix* produced taller individuals than *Sambucus*. *Salix* was also able to produce individuals with numerous branches. *Sambucus* could not overcome the stresses of flooding and did not increase in height. With limited leaf and stem elongation or production, *Sambucus* did not exhibit an ability to compete for available light.

Higher nutrient water levels seemed to increase aboveground and belowground biomass production in both herbaceous species. Greater biomass production increases the species competitive advantage for space. Great differences in *Typha* aboveground and belowground production existed between high and low nutrient conditions. This suggested that *Typha* is a high nutrient status plant which may become highly competitive for space in high nutrient conditions. *Sagittaria* did especially well in high nutrient inundated conditions which supported the conclusion that *Sagittaria* is dependent on flooded conditions to maintain a competitive edge. *Salix*, another high nutrient status plant, produced biomass much like *Typha*. Under both inundated and saturated flooding conditions, *Salix* produced greater amounts of biomass in high nutrient conditions. This species also seemed directly dependent on nutrients rather than water level to become highly competitive in such environments. *Sambucus* again was unable to overcome the stresses of inundation or saturation to produce significant amounts of biomass in any nutrient-water condition. *Sambucus* is a very poor competitor for space in wetland systems under saturated or inundated hydrologic regimes.

Nutrient assimilation (nitrogen and phosphorus) mimicked biomass production for the high nutrient status plants. Tissue nitrogen and phosphorus were greater in individuals of *Salix* grown in high nutrient conditions. This response supported the fact that this species is a nutrient dependent plant for competitive strategies. This response may also suggest that *Salix* can initiate and maintain luxury uptake of nutrients. *Typha* produced relatively constant nitrogen and phosphorus concentrations in plants grown in all nutrient and water conditions. Limited ability to have a luxury uptake of nutrients in individuals of *Typha* was evident during the study. *Sagittaria* produced greater concentrations of nitrogen and phosphorus in individuals grown in both low nutrient conditions. This is probably a direct result of "nutrient dilution" in species grown in the high nutrient conditions which had greater biomass than species grown in low nutrient conditions. This response suggested that *Sagittaria* is not a species that exhibits a luxury uptake of nutrients. *Sambucus* did exhibit increases in nutrient concentrations in individuals grown in both saturated conditions. Again, limited grown was evident, but the plants grown in saturated conditions maintained some root structure and were able to assimilate nutrients. This response again suggested that *Sambucus* would have limited competitive ability in most wetland conditions and is controlled primarily by water level.

Litter production relates similarly to aboveground production for the study species. Litter nutrient retention is an important factor for competitive evaluation of a species. Decreased nutrient loss may increase a species competitive advantage by not relinquishing the assimilated nutrients back to the water column for other species to utilize. The woody species have the decisive advantage in this case since neither *Sambucus* nor *Salix* produced noticeable amounts of litter during the study. Both *Typha* and *Sagittaria* lose most of their aboveground structures to end-of-growing-season senescence, this loss of nutrients may be a factor in competitive advantages. Both *Typha* and *Sagittaria* lost more nutrients from litter produced in plants grown in high nutrient conditions than plants in low nutrient conditions. Thus, neither species was able to retain the gain in nutrient assimilation once senescence begins. Prior to senescence, translocation ,in many instances, becomes a mechanism for herbaceous species to utilize the assimilated nutrients from one growing season to the next. Both *Sagittaria* and *Typha* exhibited some level of translocation of biomass and nutrients from aboveground to belowground plant structures. *Typha* seemed to translocate more constituents than *Sagittaria*, again a response of a high nutrient status plant.

APPENDIX
STATISTICAL SUMMARY TABLES

Table A-1. Mean heights (cm) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Species	Water-nutrient level	*n*	Mean±SD (cm)
Typha domingensis	IH	12	150.92±25.77
	SH	12	122.04±25.51
	IL	12	125.13±10.81
	SL	12	108.83±8.02
Sagittaria latifolia	IH	12	93.72±9.44
	SH	12	58.94±7.09
	IL	12	75.08±2.06
	SL	12	56.67±2.58
Sambucus canadensis	IH	12	64.63±22.76
	SH	12	61.55±16.64
	IL	6	88.00±##
	SL	11	71.20±26.97
Salix caroliniana	IH	12	147.50±32.89
	SH	12	132.33±23.57
	IL	12	98.29±18.08
	SL	12	113.83±30.66

Table A-2. Results of height comparisons of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period (MSE = 378.58, error DF = 111, alpha = 0.0125).

Species	Comparison	Conf. Interval	Conclusion
T. domingensis	IL vs SL	(-1.50, 34.08)	NS
	IH vs SH	(11.08, 46.67)	S
	IH vs IL	(8.00, 43.58)	S
	SH vs SL	(-31.00, 4.58)	NS
S. latifolia	IL vs SL	(-6.75, 43.58)	NS
	IH vs SH	(14.23, 55.32)	S
	IH vs IL	(-4.33, 41.61)	NS
	SH vs SL	(-25.25, 20.69)	NS
S. canadensis	IL vs SL	(-30.94, 64.54)	NS
	IH vs SH	(-22.37, 28.53)	NS
	IH vs IL	(-72.10, 25.35)	NS
	SH vs SL	(-13.85, 33.16)	NS
S. caroliniana	IL vs SL	(-33.33, 2.25)	NS
	IH vs SH	(-2.63, 32.96)	NS
	IH vs IL	(31.42, 67.00)	S
	SH vs SL	(-36.29, -0.70)	S

S = significantly different, NS = not significantly different

Table A-3. Mean aboveground biomass (g dry wt/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Species	Water-nutrient level	*n*	Mean±SD (g dry wt/plant)
Typha domingensis	IH	12	42.73±21.62
	SH	12	29.48±20.94
	IL	12	13.83±3.11
	SL	12	13.88±3.80
Sagittaria latifolia	IH	12	10.32±3.72
	SH	12	3.58±2.03
	IL	12	3.93±1.57
	SL	12	2.12±1.37
Sambucus canadensis	IH	12	4.79±2.73
	SH	12	6.88±3.43
	IL	6	8.27±4.73
	SL	11	5.87±5.66
Salix caroliniana	IH	12	76.31±40.10
	SH	12	54.79±28.72
	IL	12	33.22±10.66
	SL	12	36.03±10.41

Table A-4. Results of aboveground biomass comparisons of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period (MSE = 165.08, error DF = 139, alpha = 0.0125).

Species	Comparison	Conf. Interval	Conclusion
T. domingensis	IL vs SL	(-11.80, 11.70)	NS
	IH vs SH	(1.49, 24.99)	S
	IH vs IL	(17.14, 40.64)	S
	SH vs SL	(-27.35, -3.85)	S
S. latifolia	IL vs SL	(-9.93, 13.57)	NS
	IH vs SH	(-5.02, 18.48)	NS
	IH vs IL	(-5.37, 18.13)	NS
	SH vs SL	(-13.22, 10.28)	NS
S. canadensis	IL vs SL	(-12.21, 17.00)	NS
	IH vs SH	(-13.84, 9.66)	NS
	IH vs IL	(-17.86, 10.92)	NS
	SH vs SL	(-13.02, 11.00)	NS
S. caroliniana	IL vs SL	(-14.56, 8.94)	NS
	IH vs SH	(9.77, 33.27)	S
	IH vs IL	(31.34, 54.84)	S
	SH vs SL	(-30.52, -7.02)	S

S = significantly different, NS = not significantly different

Table A-5. Mean belowground biomass (g dry wt/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms at each harvest over the five month study period.

Species	(Harvest)Water-nutrient level	*n*	Mean±SD (g dry wt/plant)
Typha domingensis	(1)IH	3	31.07±9.85
	(1)SH	3	28.43±6.74
	(1)IL	3	19.20±3.08
	(1)SL	3	20.10±3.35
	(2)IH	3	33.27±5.80
	(2)SH	3	51.53±11.24
	(2)IL	3	29.17±2.61
	(2)SL	3	29.83±3.95
	(3)IH	3	137.93±18.81
	(3)SH	3	62.17±6.86
	(3)IL	3	47.50±8.80
	(3)SL	3	41.77±3.72
	(4)IH	3	104.67±36.45
	(4)SH	3	92.90±16.48
	(4)IL	3	60.77±17.15
	(4)SL	3	66.97±3.56
Sagittaria latifolia	(1)IH	3	8.80±1.45
	(1)SH	3	9.90±1.70
	(1)IL	3	6.77±2.00
	(1)SL	3	8.60±1.02
	(2)IH	3	19.07±1.47
	(2)SH	3	21.97±2.08
	(2)IL	3	9.10±1.45
	(2)SL	3	12.63±.59
	(3)IH	3	25.03±2.02
	(3)SH	3	22.53±.83
	(3)IL	3	7.76±.40
	(3)SL	3	10.67±1.27
	(4)IH	3	27.96±4.14
	(4)SH	3	23.33±5.39
	(4)IL	3	13.26±1.31
	(4)SL	3	13.06±1.05
Sambucus canadensis	(1)IH	3	2.40±1.02
	(1)SH	3	3.15±2.57
	(1)IL	3	5.30±3.64
	(1)SL	3	5.16±1.39

Table A-5. Cont.

	(2)IH	3	3.93±2.11
	(2)SH	3	4.33±2.34
	(2)IL	3	3.26±1.35
	(2)SL	3	3.03±2.01
	(3)IH	3	2.40±1.13
	(3)SH	3	5.20±.93
	(3)IL	0	********
	(3)SL	3	1.46±.73
	(4)IH	3	2.50±.86
	(4)SH	3	3.46±.50
	(4)IL	0	********
	(4)SL	2	1.60±.80
Salix caroliniana	(1)IH	3	24.33±7.12
	(1)SH	3	24.13±8.95
	(1)IL	3	14.93±5.46
	(1)SL	3	33.53±6.91
	(2)IH	3	15.16±4.88
	(2)SH	3	28.26±5.88
	(2)IL	3	24.23±14.36
	(2)SL	3	26.23±8.01
	(3)IH	3	34.73±13.70
	(3)SH	3	46.37±11.67
	(3)IL	3	32.40±9.10
	(3)SL	3	26.77±7.12
	(4)IH	3	14.83±3.58
	(4)SH	3	56.43±17.54
	(4)IL	3	21.07±2.88
	(4)SL	3	31.20±9.60

Table A-6. Results of belowground biomass comparisons of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period (MSE = 104.33, error DF = 123, alpha = 0.0031).

Species	Comparison	Conf. Interval	Conclusion
T. domingensis	(1)IL vs SL	(-24.75, 22.95)	NS
	(1)IH vs SH	(-21.22, 26.48)	NS
	(1)IH vs IL	(-11.98, 35.72)	NS
	(1)SH vs SL	(-32.18, 15.52)	NS
	(2)IL vs SL	(-24.52, 23.18)	NS
	(2)IH vs SH	(-42.12, 5.58)	NS
	(2)IH vs IL	(-19.75, 27.95)	NS
	(2)SH vs SL	(-45.55, 2.15)	NS
	(3)IL vs SL	(-18.12, 29.59)	NS
	(3)IH vs SH	(51.91, 99.62)	S
	(3)IH vs IL	(66.58, 114.28)	S
	(3)SH vs SL	(-44.25, 3.45)	NS
	(4)IL vs SL	(-30.05, 17.65)	NS
	(4)IH vs SH	(-12.08, 35.62)	NS
	(4)IH vs IL	(20.05, 67.75)	S
	(4)SH vs SL	(-49.78, -2.08)	S
S. latifolia	(1)IL vs SL	(-25.68, 22.02)	NS
	(1)IH vs SH	(-24.95, 22.75)	NS
	(1)IH vs IL	(-21.82, 25.88)	NS
	(1)SH vs SL	(-25.15, 22.55)	NS
	(2)IL vs SL	(-27.38, 20.32)	NS
	(2)IH vs SH	(-26.75, 20.95)	NS
	(2)IH vs IL	(-13.88, 33.82)	NS
	(2)SH vs SL	(-33.18, 14.52)	NS
	(3)IL vs SL	(-26.75, 20.95)	NS
	(3)IH vs SH	(-21.35, 26.35)	NS
	(3)IH vs IL	(-6.58, 41.12)	NS
	(3)SH vs SL	(-35.72, 11.98)	NS

Table A-6.
cont.

	(4)IL vs SL	(-23.65, 24.05)	NS
	(4)IH vs SH	(-19.22, 28.48)	NS
	(4)IH vs IL	(-9.15, 38.55)	NS
	(4)SH vs SL	(-34.12, 13.58)	NS
S. canadensis	(1)IL vs SL	(-23.72, 23.98)	NS
	(1)IH vs SH	(-24.85, 22.85)	NS
	(1)IH vs IL	(-26.75, 20.95)	NS
	(1)SH vs SL	(-22.08, 25.62)	NS
	(2)IL vs SL	(-23.62, 24.08)	NS
	(2)IH vs SH	(-24.25, 23.45)	NS
	(2)IH vs IL	(-23.18, 24.52)	NS
	(2)SH vs SL	(-25.15, 22.55)	NS
	(3)IL vs SL	(********)	**
	(3)IH vs SH	(-26.65, 21.05)	NS
	(3)IH vs IL	(********)	**
	(3)SH vs SL	(-27.58, 20.12)	NS
	(4)IL vs SL	(********)	**
	(4)IH vs SH	(-24.82, 22.88)	NS
	(4)IH vs IL	(********)	**
	(4)SH vs SL	(-28.53, 24.80)	NS
S. caroliniana	(1)IL vs SL	(-42.45, 5.25)	NS
	(1)IH vs SH	(-23.65, 24.05)	NS
	(1)IH vs IL	(-14.45, 33.25)	NS
	(1)SH vs SL	(-14.45, 33.25)	NS
	(2)IL vs SL	(-25.85, 21.85)	NS
	(2)IH vs SH	(-36.95, 10.75)	NS
	(2)IH vs IL	(-32.92, 14.78)	NS
	(2)SH vs SL	(-25.88, 21.82)	NS
	(3)IL vs SL	(-18.22, 29.48)	NS
	(3)IH vs SH	(-35.48, 12.22)	NS
	(3)IH vs IL	(-21.52, 26.18)	NS
	(3)SH vs SL	(-43.45, 4.25)	NS
	(4)IL vs SL	(-33.98, 13.72)	NS
	(4)IH vs SH	(-65.45, -17.74)	S
	(4)IH vs IL	(-30.08, 17.62)	NS
	(4)SH vs SL	(-49.08, -1.38)	S

S = significantly different, NS = not significantly different

Table A-7. Mean aboveground N (mg/g/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Species	Water-nutrient level	*n*	Mean±SD (mg/g)
Typha domingensis	IH	12	7.4±2.7
	SH	12	9.3±3.1
	IL	12	7.7±2.5
	SL	12	7.3±2.7
Sagittaria latifolia	IH	12	11.1±2.3
	SH	12	11.6±2.9
	IL	12	12.0±2.0
	SL	12	14.5±4.0
Sambucus canadensis	IH	12	8.3±4.1
	SH	12	11.5±3.0
	IL	6	7.7±2.5
	SL	11	10.9±2.8
Salix caroliniana	IH	12	8.2±2.2
	SH	12	8.1±2.4
	IL	12	6.7±0.8
	SL	12	7.7±1.8

Table A-8. Results of aboveground N comparisons of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period (MSE = 113.748, error DF = 144, alpha = 0.0125).

Species	Comparison	Conf. Interval	Conclusion
T. domingensis	IL vs SL	(-1.8, 2.6)	NS
	IH vs SH	(-4.1, 0.3)	NS
	IH vs IL	(-2.6, 1.9)	NS
	SH vs SL	(-4.2, 0.3)	NS
S. latifolia	IL vs SL	(-4.8, -0.3)	S
	IH vs SH	(-2.7, 1.8)	NS
	IH vs IL	(-3.2, 1.3)	NS
	SH vs SL	(0.7, 6.2)	S
S. canadensis	IL vs SL	(-6.0, -0.4)	S
	IH vs SH	(-5.4, -0.9)	S
	IH vs IL	(-2.1, 3.4)	NS
	SH vs SL	(-2.8, 1.7)	NS
S. caroliniana	IL vs SL	(-3.3, 1.2)	NS
	IH vs SH	(-2.1, 2.4)	NS
	IH vs IL	(-0.7, 3.8)	NS
	SH vs SL	(-2.6, 1.9)	NS

S = significantly different, NS = not significantly different

Table A-9. Mean belowground N (mg/g/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Species	Water-nutrient level	*n*	Mean±SD (mg/g)
Typha domingensis	IH	12	5.3±2.4
	SH	12	4.9±1.1
	IL	12	5.9±1.1
	SL	12	5.3±1.3
Sagittaria latifolia	IH	12	10.9±3.9
	SH	12	11.7±2.1
	IL	12	13.9±2.0
	SL	12	12.4±1.9
Sambucus canadensis	IH	12	6.3±2.5
	SH	12	10.7±2.3
	IL	6	7.0±2.4
	SL	11	9.6±2.5
Salix caroliniana	IH	12	8.6±2.6
	SH	12	9.0±1.6
	IL	12	7.7±1.2
	SL	12	8.5±0.9

Table A-10. Results of belowground N comparisons of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period (MSE = 181.953, error DF = 139, alpha = 0.0125).

Species	Comparison	Conf. Interval	Conclusion
T. domingensis	IL vs SL	(-1.3, 2.5)	NS
	IH vs SH	(-1.5, 2.2)	NS
	IH vs IL	(-2.5, 1.2)	NS
	SH vs SL	(-1.5, 2.3)	NS
S. latifolia	IL vs SL	(-0.4, 3.4)	NS
	IH vs SH	(-2.7, 1.1)	NS
	IH vs IL	(-4.9, -1.2)	S
	SH vs SL	(-1.2, 2.6)	NS
S. canadensis	IL vs SL	(-5.0, -0.3)	S
	IH vs SH	(-6.2, -2.4)	S
	IH vs IL	(-2.9, 1.7)	NS
	SH vs SL	(-2.9, 0.9)	NS
S. caroliniana	IL vs SL	(-2.6, 1.1)	NS
	IH vs SH	(-2.2, 1.5)	NS
	IH vs IL	(-0.9, 2.8)	NS
	SH vs SL	(-2.4, 1.3)	NS

S = significantly different, NS = not significantly different

Table A-11. Mean aboveground P (mg/g/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Species	Water-nutrient level	*n*	Mean±SD (mg/g)
Typha domingensis	IH	12	1.2±0.5
	SH	12	1.3±0.5
	IL	12	1.3±0.8
	SL	12	1.1±0.8
Sagittaria latifolia	IH	12	1.9±0.6
	SH	12	1.5±0.4
	IL	12	1.5±0.8
	SL	12	1.5±0.7
Sambucus canadensis	IH	12	1.1±0.5
	SH	12	1.5±0.5
	IL	6	1.0±0.2
	SL	11	1.4±0.5
Salix caroliniana	IH	12	1.5±0.5
	SH	12	1.3±0.3
	IL	12	1.0±0.2
	SL	12	1.0±0.2

Table A-12. Results of aboveground P comparisons of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period (MSE = 17.287, error DF = 144, alpha = 0.0125).

Species	Comparison	Conf. Interval	Conclusion
T. domingensis	IL vs SL	(-0.2, 0.5)	NS
	IH vs SH	(-0.4, 0.3)	NS
	IH vs IL	(-0.4, 0.3)	NS
	SH vs SL	(-0.5, 0.2)	NS
S. latifolia	IL vs SL	(-0.4, 0.3)	NS
	IH vs SH	(-0.1, 0.8)	NS
	IH vs IL	(0.1, 0.8)	S
	SH vs SL	(-0.4, 0.4)	NS
S. canadensis	IL vs SL	(-0.9, 0.1)	NS
	IH vs SH	(-0.8, 0.1)	NS
	IH vs IL	(-0.3, 0.6)	NS
	SH vs SL	(-0.4, 0.3)	NS
S. caroliniana	IL vs SL	(-0.4, 0.4)	NS
	IH vs SH	(-0.2, 0.6)	NS
	IH vs IL	(0.1, 0.9)	S
	SH vs SL	(-0.6, 0.1)	NS

S = significantly different, NS = not significantly different

Table A-13. Mean belowground P (mg/g/plant) of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Species	Water-nutrient level	*n*	Mean±SD (mg/g)
Typha domingensis	IH	12	1.6±0.6
	SH	12	1.6±0.5
	IL	12	1.5±0.5
	SL	12	1.3±0.3
Sagittaria latifolia	IH	12	2.0±0.7
	SH	12	2.3±0.4
	IL	12	2.8±0.4
	SL	12	2.1±0.8
Sambucus canadensis	IH	12	0.4±0.2
	SH	12	1.1±0.4
	IL	6	0.4±0.2
	SL	11	1.0±0.2
Salix caroliniana	IH	12	1.3±0.4
	SH	12	1.2±0.2
	IL	12	1.0±0.2
	SL	12	1.0±0.1

Table A-14. Results of belowground P comparisons of *Typha domingensis*, *Sagittaria latifolia*, *Sambucus canadensis*, and *Salix caroliniana* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period (MSE = 5.739, error DF = 139, alpha = 0.0125).

Species	Comparison	Conf. Interval	Conclusion
T. domingensis	IL vs SL	(-0.2, 0.6)	NS
	IH vs SH	(-0.4, 0.3)	NS
	IH vs IL	(-0.3, 0.5)	NS
	SH vs SL	(-0.7, 0.1)	NS
S. latifolia	IL vs SL	(0.3, 1.0)	S
	IH vs SH	(-0.7, 0.1)	NS
	IH vs IL	(-1.2, -0.4)	S
	SH vs SL	(-0.5, 0.2)	NS
S. canadensis	IL vs SL	(-0.9, 0.1)	NS
	IH vs SH	(-1.1, -0.3)	S
	IH vs IL	(-0.4, 0.5)	NS
	SH vs SL	(-0.8, 0.1)	NS
S. caroliniana	IL vs SL	(-0.4, 0.4)	NS
	IH vs SH	(-0.3, 0.4)	NS
	IH vs IL	(-0.1, 0.6)	NS
	SH vs SL	(-0.5, 0.3)	NS

S = significantly different, NS = not significantly different

Table A-15. Mean aboveground litter (g dry wt/plant) of *Typha domingensis* and *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Species	Water-nutrient level	*n*	Mean±SD (g dry wt/plant)
Typha domingensis	IH	6	13.48±6.77
	SH	8	9.43±5.72
	IL	6	8.78±6.34
	SL	9	7.24±5.81
Sagittaria latifolia	IH	6	2.47±1.20
	SH	9	3.17±.96
	IL	6	1.27±.41
	SL	9	2.13±.40

Table A-16. Results of aboveground litter comparisons of *Typha domingensis* and *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period (MSE = 5.07, error DF = 41, alpha = 0.0125).

Species	Comparison	Conf. Interval	Conclusion
T. domingensis	IL vs SL	(-1.12, 4.20)	NS
	IH vs SH	(1.33, 6.78)	S
	IH vs IL	(1.79, 7.61)	S
	SH vs SL	(-4.63, .27)	NS
S. latifolia	IL vs SL	(-3.52, 1.79)	NS
	IH vs SH	(-3.36, 1.96)	NS
	IH vs IL	(-1.71, 4.11)	NS
	SH vs SL	(-3.41, 1.34)	NS

S = significantly different, NS = not significantly different

Table A-17. Mean litter N (mg/g/plant) of *Typha domingensis* and *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Species	Water-nutrient level	*n*	Mean±SD (mg/g)
Typha domingensis	IH	6	6.4±1.3
	SH	8	5.3±1.4
	IL	6	5.6±1.9
	SL	9	4.9±0.7
Sagittaria latifolia	IH	6	12.2±2.6
	SH	9	11.4±1.8
	IL	6	9.9±1.5
	SL	9	9.9±0.9

Table A-18. Results of litter N comparisons of *Typha domingensis* and *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period (MSE = .0122, error DF = 40, alpha = 0.0125).

Species	Comparison	Conf. Interval	Conclusion
T. domingensis	IL vs SL	(-0.5, 2.0)	NS
	IH vs SH	(-0.2, 2.5)	NS
	IH vs IL	(-0.6, 2.2)	NS
	SH vs SL	(-1.6, 0.8)	NS
S. latifolia	IL vs SL	(-1.3, 1.3)	NS
	IH vs SH	(-0.4, 2.2)	NS
	IH vs IL	(0.9, 3.8)	S
	SH vs SL	(-2.6, -0.3)	S

S = significantly different, NS = not significantly different

Table A-19. Mean litter P (mg/g/plant) of *Typha domingensis* and *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period.

Species	Water-nutrient level	*n*	Mean±SD (mg/g)
Typha domingensis	IH	6	1.1±0.6
	SH	8	0.9±0.4
	IL	6	0.6±0.2
	SL	9	0.6±0.3
Sagittaria latifolia	IH	6	0.8±0.4
	SH	9	1.0±0.3
	IL	6	0.6±0.3
	SL	9	0.6±0.1

Table A-20. Results of litter P comparisons of *Typha domingensis* and *Sagittaria latifolia* grown in (IH) inundated high nutrient, (SH) saturated high nutrient, (IL) inundated low nutrient, and (SL) saturated low nutrient microcosms over the five month study period (MSE = .00066, error DF = 40, alpha = 0.0125).

Species	Comparison	Conf. Interval	Conclusion
T. domingensis	IL vs SL	(-0.4, 0.2)	NS
	IH vs SH	(-0.1, 0.5)	NS
	IH vs IL	(0.2, 0.8)	S
	SH vs SL	(-0.5, 0.1)	NS
S. latifolia	IL vs SL	(-0.3, 0.3)	NS
	IH vs SH	(-0.4, 0.1)	NS
	IH vs IL	(-0.1, 0.6)	NS
	SH vs SL	(-0.6, -0.1)	S

S = significantly different, NS = not significantly different

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BIOGRAPHICAL SKETCH

Robert Ernest Borer was born on August 27, 1968, in Rochester, New York. He graduated from Portville Central High School, Portville, New York, in June 1987. In August 1987 he entered Allegheny College, Meadville, Pennsylvania, then transfered to Clarion University of Pennsylvania, Clarion, Pennsylvania, in August 1988 where he received a Bachelor of Science degree in biology, cum laude, in April 1991. He entered into graduate studies at the University of Florida, Gainesville, Florida, Department of Environmental Engineering Sciences through a research assistantship at the Center for Wetlands and Water Resources, in August 1991. At the Univerity of Florida, he fell in love with and married, Kerry Kristine Signorella. He is a member of the Society of Wetland Scientists. His parents are Mr. Ernest Nelson Borer and Mrs. Barbara Ellen Engle Borer of Portville, New York. He has accepted a position with the South Florida Water Management District, West Palm Beach, Florida.