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EFFECTS OF HYDROLOGIC REGIMES ON LIFETIME PRODUCTION AND NUTRIENT DYNAMICS OF SAWGRASS

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Effects of Hydrologic Regimes on Lifetime Production and Nutrient Dynamics of Sawgrass

By

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Environmental Sciences Division
Resource Planning Department
South Florida Water Management District

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EXECUTIVE SUMMARY

Assimilation of surface-water nutrients by Everglades plant communities should be an integral component of management strategies for the Water Conservation Areas. Although nutrient uptake and storage roles of wetlands are well established, the value of marsh plants as permanent nutrient sinks is ultimately dependent upon the fate of accumulated nutrients during death and decomposition of plant tissues. Results of this study indicate that nutrient storage capabilities of both aboveground and belowground components of sawgrass are greatly affected by hydrologic regimes.

Biomass production and associated nutrient uptake by sawgrass were greater in relatively constant, shallow water regimes than in stands subjected to predominantly deep, but widely fluctuating water levels. Differences in biomass production and nutrient uptake were linked to alternative growth and life history patterns which sawgrass adopts when exposed to these contrasting hydrologic conditions. Shallow water levels favor extended survival of culms and promote channeling of available resources into individual plant growth and biomass production (particularly leaf production). Widely fluctuating water level regimes lead to slower individual plant growth rates, high early mortality, and emphasis on new shoot production rather than biomass production.

Shallow and stable water level conditions also appeared to be more conducive to permanent storage (retention) of nutrients accumulated by sawgrass tissues, than deep, widely fluctuating stages. Due to slow decomposition rates in marsh soils, nutrients retained in belowground tissues of dead plants likely are trapped in the soil complex. Belowground plant parts accounted for 12% of total plant production and may retain up to 11% of nitrogen and phosphorus accumulated by sawgrass in shallow water. Moreover, due to high rates of leaf production in shallow water conditions, leaf litter may accumulate on the soil surface faster than leaf decomposition, and thereby bury a portion of the nutrients retained by dead leaf tissues. In contrast, where water levels are predominantly deep and widely fluctuating, sawgrass typically grows on tussocks on which all plant parts are perched above the soil surface. Although some evidence suggests that reproductive effort required by deep, fluctuating water level conditions is accomodated by greater internal recycling of nutrients, most stored nutrients in tussock sawgrass tissues are ultimately returned to either the surrounding water column or soil surface as plants die and decompose.

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ACKNOWLEDGEMENTS

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ABSTRACT

Nutrient storage capabilities of aboveground and belowground components of sawgrass were evaluated in Everglades habitats with contrasting hydrologic regimes. Biomass production, tissue nutrient concentrations, and nutrient storage potential were higher in sawgrass stands exposed to shallow, stable water levels than in stands growing in relatively deep and widely fluctuating water levels. Differences in production and nutrient uptake were linked to adaptive growth characteristics and life history strategies that sawgrass adopts when subjected to these water level regimes. Results indicate that belowground tissues may permanently retain 11% of nitrogen and phosphorus accumulated during a plant's lifetime, but the actual value of sawgrass as a nutrient sink is ultimately dependent upon nutrient flux associated with leaf production and leaf litter decomposition dynamics. Plant growth relationships established in this study provide a simple method for routinely evaluating sawgrass production and nutrient storage dynamics throughout the Everglades system.

Key Words: Sawgrass, Hydrology, Everglades, Nutrient Dynamics, Life History Strategies.

INTRODUCTION

Since much of the water presently flowing into the Water Conservation Areas (WCA's) consists of nutrient-laden runoff from agricultural areas, nutrient uptake and storage functions of Everglades plant communities should be key components of management strategies for the system. Nutrient uptake and storage roles of wetlands are well established (Howell et al., 1974; Tilton et al., 1976; Greeson et al., 1978) and several studies (Gleason et al., 1974; Davis and Harris, 1978; Swift, 1981; Davis, 1982, 1984) suggest that flora and soils of the WCA's quickly assimilate high nutrient loads carried by existing surface water inputs. However, it is not clear if Everglades plant communities form permanent nutrient sinks or merely temporarily intercept nutrients that are eventually returned to surface water as plants die and decompose. Moreover, relationships between nutrient dynamics of Everglades plant communities and hydrologic regimes resulting from usage of the WCA's for flood control and water storage have not been explored.

The effectiveness of wetland plants as nutrient sinks is largely dependent upon the fate of accumulated nutrients during death and decomposition of plant tissues. Nutrients remaining in dying aboveground plant tissues are either translocated and internally recycled (Hopkinson and Schubauer, 1984; Prentki et al., 1978) or returned to surface water during decomposition (Klopatek, 1975; Prentki et al., 1978; Twilley et al., 1977). Nutrients released from decomposing belowground plant components may be transported by groundwater, assimilated and recycled in new plant growth (Klopatek, 1975; Brinson and Davis, 1976; Prentki et al., 1978; de la Cruz and Hackney, 1977; Gallagher and Plumley, 1979; Barko and Smart, 1980; Hemond, 1983), or permanently stored in the soil complex (Schlesinger, 1981; Dolan et al., 1981). Thus, nutrient storage in belowground plant biomass is of critical importance when assessing the value of wetland plants as nutrient sinks.

Belowground plant parts form a major portion of total standing crop biomass in many wetland plant communities (Gallagher, 1974; Bristow, 1975; Shaver and Billings, 1975; Brinson and Davis, 1976; de la Cruz and Hackney, 1977; Gallagher and Plumley, 1979, Bernard et al., 1985). Accumulations of nutrients in belowground plant parts may even exceed nutrient stocks in aboveground tissues (Dykyjova and Hradecka, 1976; Dolan et al., 1981); however, nutrient distributions among plant parts commonly undergo periodic flux in association with seasonal growth and/or life history patterns (Klopatek, 1975; Dykyjova and Hradecka, 1976; Prentki et al., 1978; Twilley et al., 1977; Dolan et al., 1981; Gopal and Sharma, 1984). In fact, translocation of nutrients to belowground parts during plant senescence may be an important means by which plants conserve nutrients for use in subsequent new growth (Bayly and O'Neill, 1972; Hopkinson and Schubauer, 1984; Klopatek, 1975; Prentki et al., 1978; Twilley et al., 1977).

The importance of belowground plant components in nutrient storage within the Everglades has been largely unexplored, but several studies indicate that nutrient concentrations of roots and rhizomes of sawgrass, Cladium jamaicense (Miller, 1918; Parsons, 1977) and cattail, Typha spp. (Davis, 1984) are comparable to nutrient concentrations in live leaves of these species. Another study (Davis, in prep.) has investigated nutrient flux associated with sawgrass leaf production and decomposition at sites exposed to variable surface water nutrient loads. This study attempts to assess the nutrient storage potential of belowground components of sawgrass through (1) comparative measurements of production and nutrient accumulation by belowground and aboveground plant components and (2) estimates of nutrient release associated with plant or tissue death. These parameters are evaluated in Everglades habitats with altered hydrologic regimes.

PURPOSE AND SCOPE

Much of the original Everglades presently encompassed by the three Water Conservation Areas has been subjected to altered hydrologic and nutrient regimes. Implementation of management options such as backpumping, the Lake Okeechobee Interim Action Plan, and increased usage of the Water Conservation Areas for water storage would exacerbate these environmental modifications. Ongoing studies by Environmental Sciences Division staff are designed to evaluate effects of altered environmental conditions on Everglades plant communities. Much of this work focuses on the ability of wetland flora to remove surface water nutrients, and how environmental conditions, such as hydroperiod and nutrient loads, affect this function. Previous studies have analyzed nutrient flux associated with production and decomposition of aboveground plant parts. This study complements these efforts by evaluating effects of water levels on production and nutrient dynamics of belowground components of sawgrass - the dominant plant species in the Water Conservation Areas.

METHODS

Study Area

The study was conducted in Water Conservation Area 2A, Palm Beach and Broward Counties, Florida (Figure 1A). Nutrient enriched water enters this 547 km^2 marsh through three S-10 spillways in levee L-39, flows south over the marsh, and exits into WCA2B and 3A via culverts in levee L-35B and S-11 spillways in levee L-38 (Figure 1B).

Two sampling sites with contrasting hydrologic characteristics were chosen. Site NLS was located 50 m south of levee L-39, approximately 2.6 km northwest of structure S-10D. It was characterized by an elliptically shaped (approximately 75 m x 50 m) sawgrass stand which was completely surrounded by a mixed cattail (Typha sp.) and arrowhead (Sagittaria lancifolia) community. Due to high ground elevations, water levels in this section of WCA-2A are generally shallow throughout the year. Site SLS was located about 150 m north of levee L-35B and culvert S-145; all sampling was conducted along the west border of the slough opposite S-145. Due to "ponding" behind L-38 and L-35B, high water levels prevail in this section of WCA-2A when S-11 spillways are closed. However, this site undergoes rapid drainage through sloughs and peripheral canals when spillways are open. Thus, monospecific sawgrass marsh throughout this region is typically exposed to widely fluctuating water levels.

Plant Sampling

Effects of hydrologic regimes on sawgrass growth characteristics and nutrient storage were evaluated through site comparisons of densities, growth rates, lifetime production, and nutrient accumulation and flux in individual culms. Sawgrass densities were measured by counting live culms within contiguous 0.5 m^2 quadrats along a 16m transect at NLS and a 14m transect at SLS. To compare growth rates, stock lengths (Figure 2) of marked new shoots were measured after 11 months of growth at each site. Stock lengths provide a measure of plant growth because sawgrass stocks elongate as new leaves develop at the shoot apex (Conway, 1936). Sawgrass stock lengths were also used as an indicator of the physiological age (sensu Bates, 1971) of individual culms in site comparisons of lifetime production and nutrient flux.

Nutrient storage by sawgrass was evaluated at NLS and SLS in September-October 1982 and January-February, April-May, July-August, and September-October 1983. Four samples were obtained at each site (two samples/week for two consecutive weeks) during each sampling period.

A sample was obtained by enclosing a clump of sawgrass culms within either a 55 cm (NLS) or 87 cm (SLS) high, 55 cm diameter polyethylene cylinder. To insure that entire root systems of all enclosed culms were obtained, samples were selected so that culms were not positioned against the inside edge of the cylinder. While carefully digging around its outside periphery with a long-bladed (root-pruning) shovel, the cylinder was gradually pushed into the soil to a depth of about 40 cm. Using a knife, the bottom plane of the enclosed core was cleaved from the soil below, allowing the cylinder and solid core to be lifted en masse from the substrate.

Each sample contained culms representing different life history stages, including new shoots, mature culms, and at least one centrally located flowering culm. Since a sawgrass culm dies soon after it flowers, the fate of accumulated nutrients in plant tissues could be tracked at known intervals after death by sampling culms that flowered during the summer preceding the initial sampling period. Thus, each sample contained at least one culm that flowered during summer 1982 and died within the next several months. To facilitate identification of culms that flowered in 1982 during later sampling periods, approximately 50 of these culms were tagged at each site in November 1982. However, during subsequent sampling periods through October 1983, culms that flowered in 1982 were easily identified by their dead,

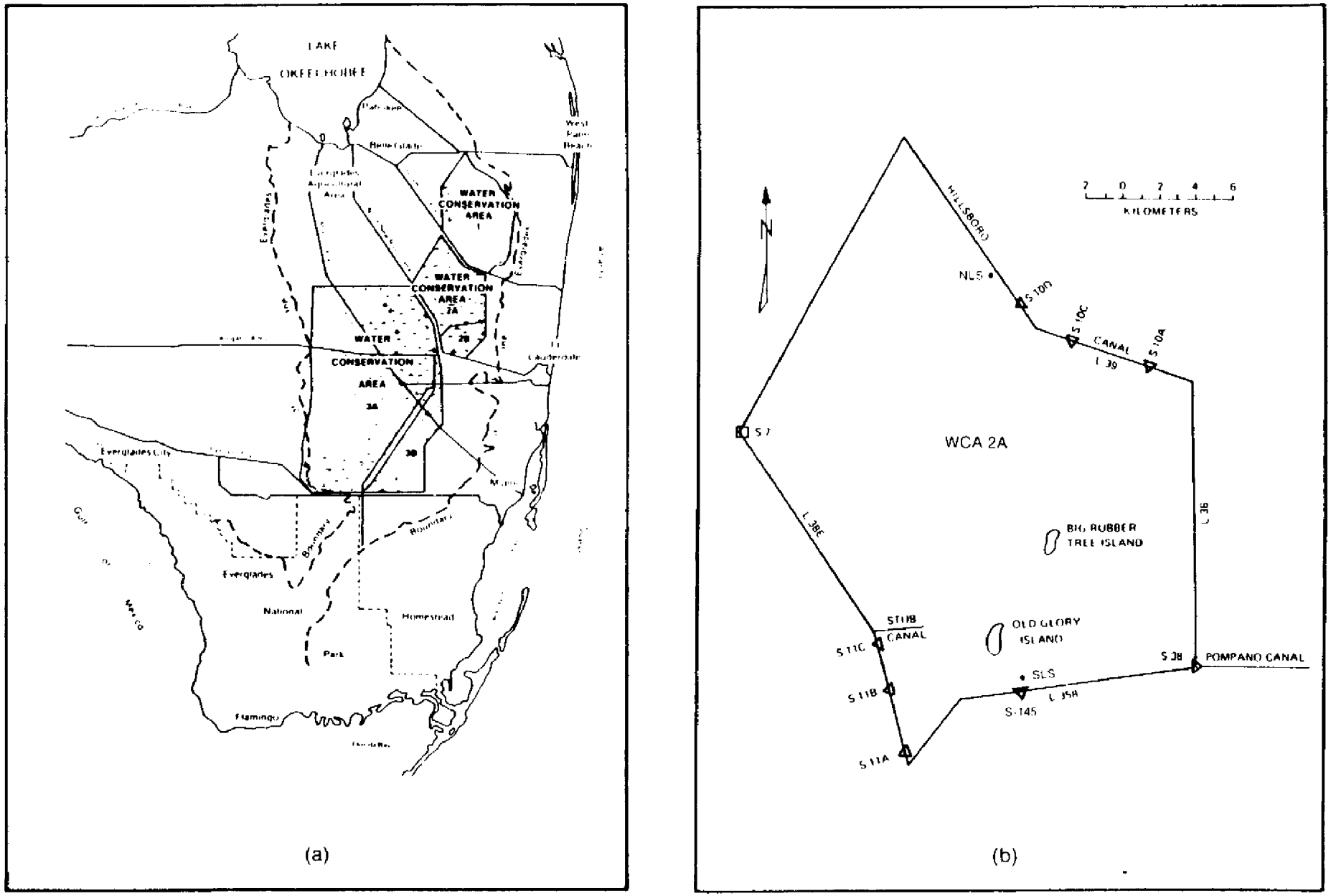


FIGURE 1. **Location of sawgrass sample sites. (a) Map of south Florida showing Water Conservation Areas; (b) Water Conservation Area 2A showing locations of sample sites NLS and SLS.**

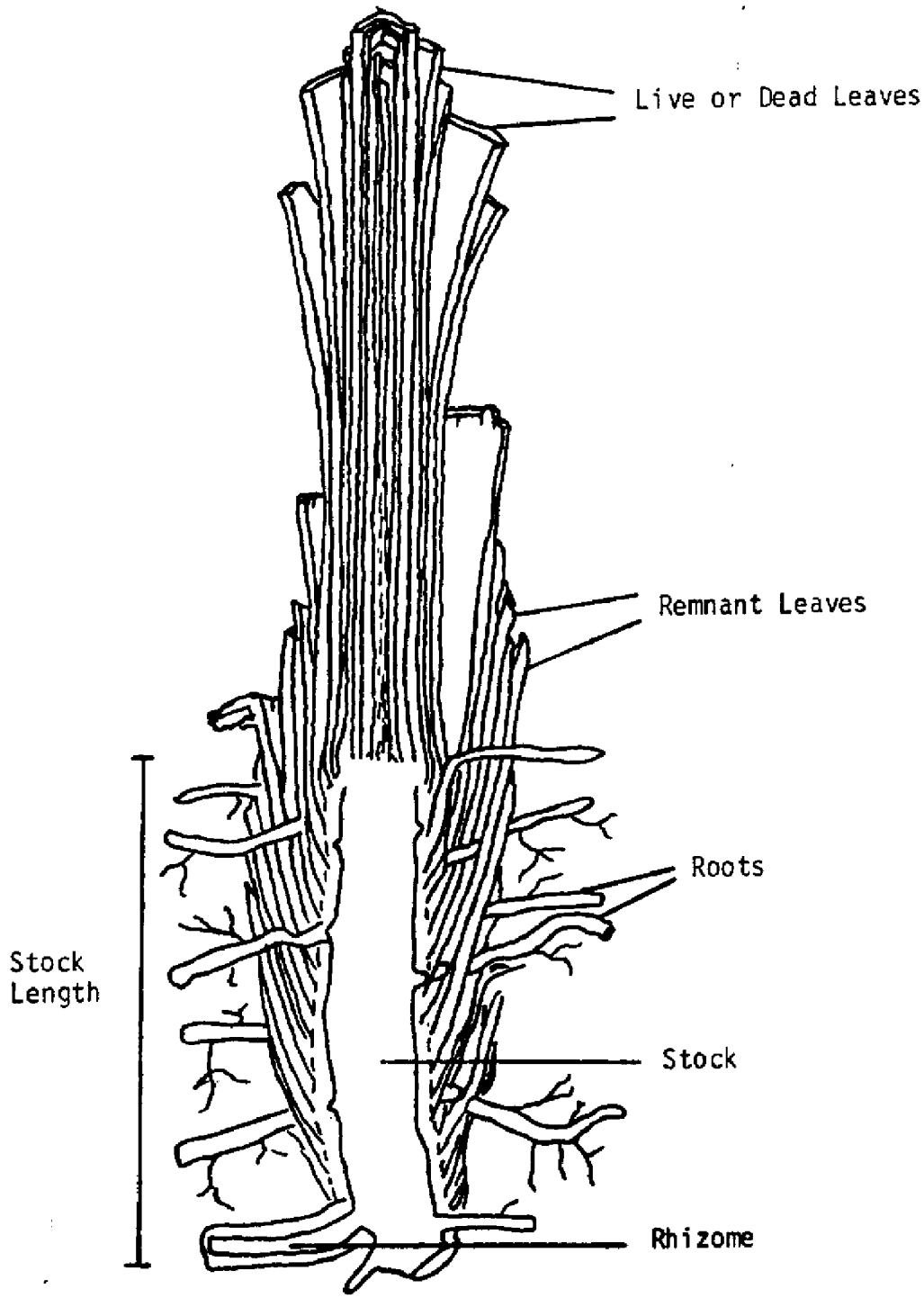


FIGURE 2. Schematic of a sawgrass culm (adapted from Conway, 1936).

brown flower stalk, which could be clearly differentiated from grey flower stalks of culms that flowered during the previous year.

All sawgrass culms within each sample were extracted and processed individually. First, loose soil was washed from the belowground portion of the sample until a sawgrass stock was exposed. Rhizomes and roots were then detached from the stock, carefully separated from soil, and rinsed free of adhering debris. Next, remnant leaves, the partially decomposed bases of dead leaves that were still attached to the stock, were removed. The stock and aerial parts of the culm were then separated from the sample and aboveground plant parts (i.e., live leaves, dead leaves, flower stalk, and inflorescences) were detached from the stock. Finally, any roots that were uncovered when remnant leaves were separated from the stock were clipped and added to previously removed roots. This process was repeated until all plants in the sample were separated. Each culm was categorized (S. Yates, 1974) as live, dead, remnant, live flower, dead flower, or remnant flower. Most live culms had green leaves; however, very young new shoots had only newly formed white leaves, and some live, but dying, flowering culms had only a green flower stalk. Dead culms possessed long (though sometimes broken), light brown dead leaves, while only partially decomposed, dark brown or black remnant leaves remained on remnant culms. Field observations indicated that individual dead leaves of both live and dead culms break off stocks within 2-3 months after each leaf dies. Thus, remnant culms generally had been dead longer and undergone greater decomposition than dead culms. In fact, many remnant culms were buried within the soil. Dead and remnant flowering culms both had at least part of their flower stalks still attached to the stock. Remnant flowering culms included only plants that flowered prior to 1982 (i.e., plants that had been dead at least one year).

Components of each culm were processed and analyzed separately. All live, dead, and remnant leaves of live culms were counted. Remnant leaves included brown, scale leaves that occur at the base of a newly formed shoot. After lengths of intact live leaves were measured (nearest 1.0 cm), dead portions were separated and combined with dead leaves. Lengths of stocks were also measured to the nearest 0.5 cm.

Each plant component was dried for four days at 90°C, weighed to the nearest 0.01 g, ground in a Wiley mill, and analyzed for nitrogen (N) and phosphorus (P) concentrations by the South Florida Water Management District Soil Chemistry Laboratory. Due to procedural limitations, plant component samples weighing less than 0.75 g were generally combined with other comparable samples (e.g., live leaves of two or more new shoots) prior to nutrient analysis. Plant tissue nutrient analyses were performed with a Technicon AutoAnalyzer II, after Kjeldahl digestion of N and P using a block digester (modified from Black, 1965).

Soil Sampling

Two replicate soil cores, 7 cm in diameter and 20 cm deep, were taken along the outside periphery of each sample (i.e., eight cores/site/sampling period). Soil cores were transported to the laboratory and frozen upright. Frozen cores were cut into 10 cm long sections, dried, ground in a Wiley mill, and analyzed for N and P concentration with the Technicon AutoAnalyzer II (see above).

Water Sampling

Two replicate 1.0 l water samples were collected on each sampling date (i.e., four samples/site/sampling period) and at monthly intervals (or more frequently) during interim periods. Water samples were analyzed (Standard Methods, 1971) for total dissolved phosphorus and nitrogen fractions using a Technicon AutoAnalyzer II by the South Florida Water Management District Water Chemistry Laboratory. Samples for total and total dissolved phosphorus analyses were digested using an autoclave. Samples for total and total dissolved nitrogen were digested by the Kjeldahl procedure using a block digester.

Surface water depths (nearest 0.1 cm), relative to mean ground elevation at each site, were recorded on each sampling date, and at monthly intervals (or more frequently) during interim periods.

RESULTS

Surface Water Depths and Nutrient Concentrations

Water stages at NLS and SLS during 1982-84 (Figure 3A) illustrate typical differences in surface water depths at these locations, as well as differential site responses to controlled drawdowns. Water depths at SLS were widely fluctuating and considerably higher than those at NLS during wet season months. Stages at NLS were characteristically stable, rising only briefly during periods of heavy rainfall. During drawdown periods, water depths at SLS fell below average ground elevation while stages at NLS were maintained above ground elevation by groundwater seepage from WCA 1 (i.e., beneath the L-39 levee, Figure 1).

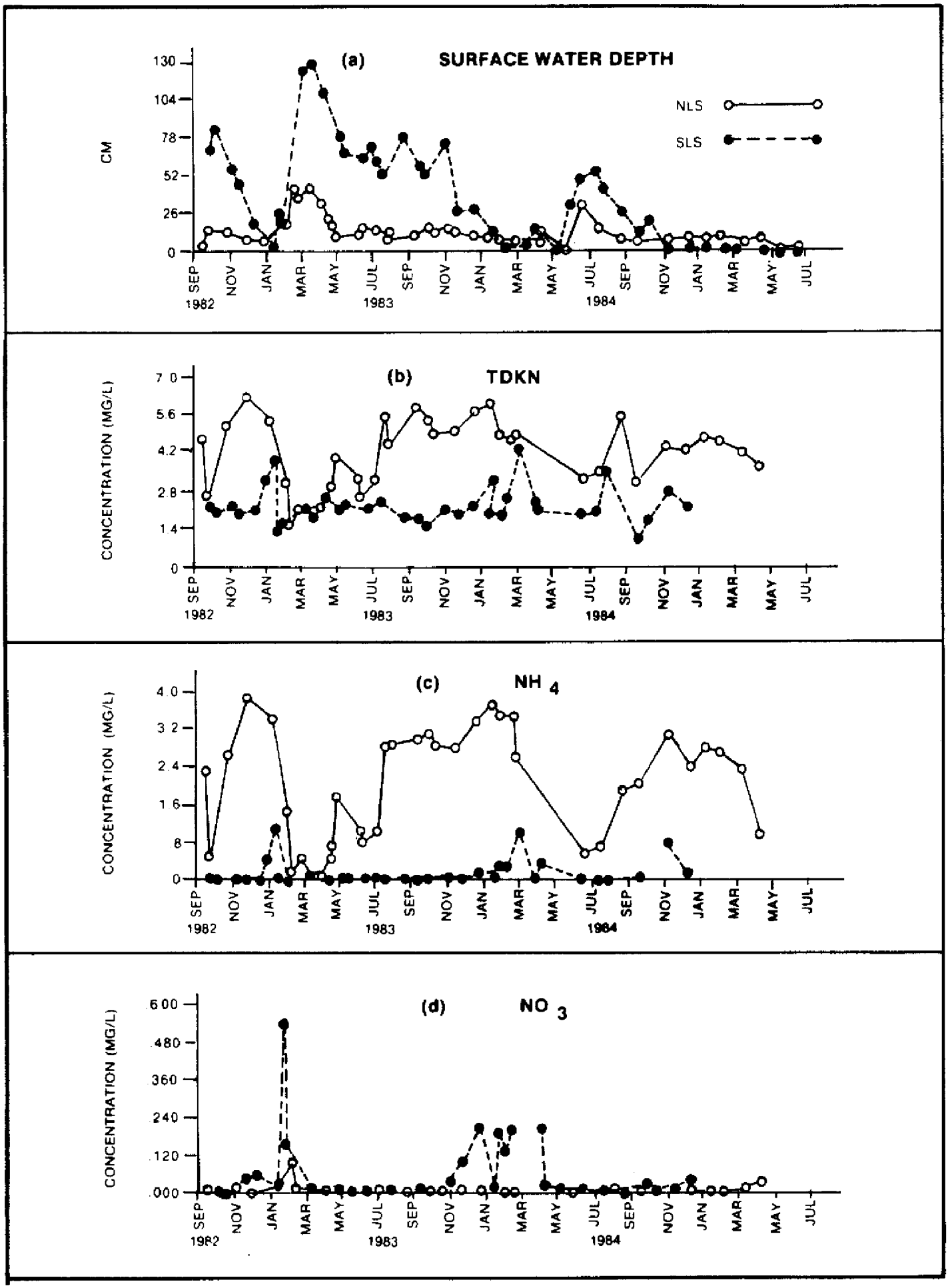


FIGURE 3. **Surface water depths and nutrient concentrations at NLS and SLS from September 1982-July 1985. (a) depth, (b) total dissolved kjeldahl nitrogen, (c) ammonia, (d) nitrate.**

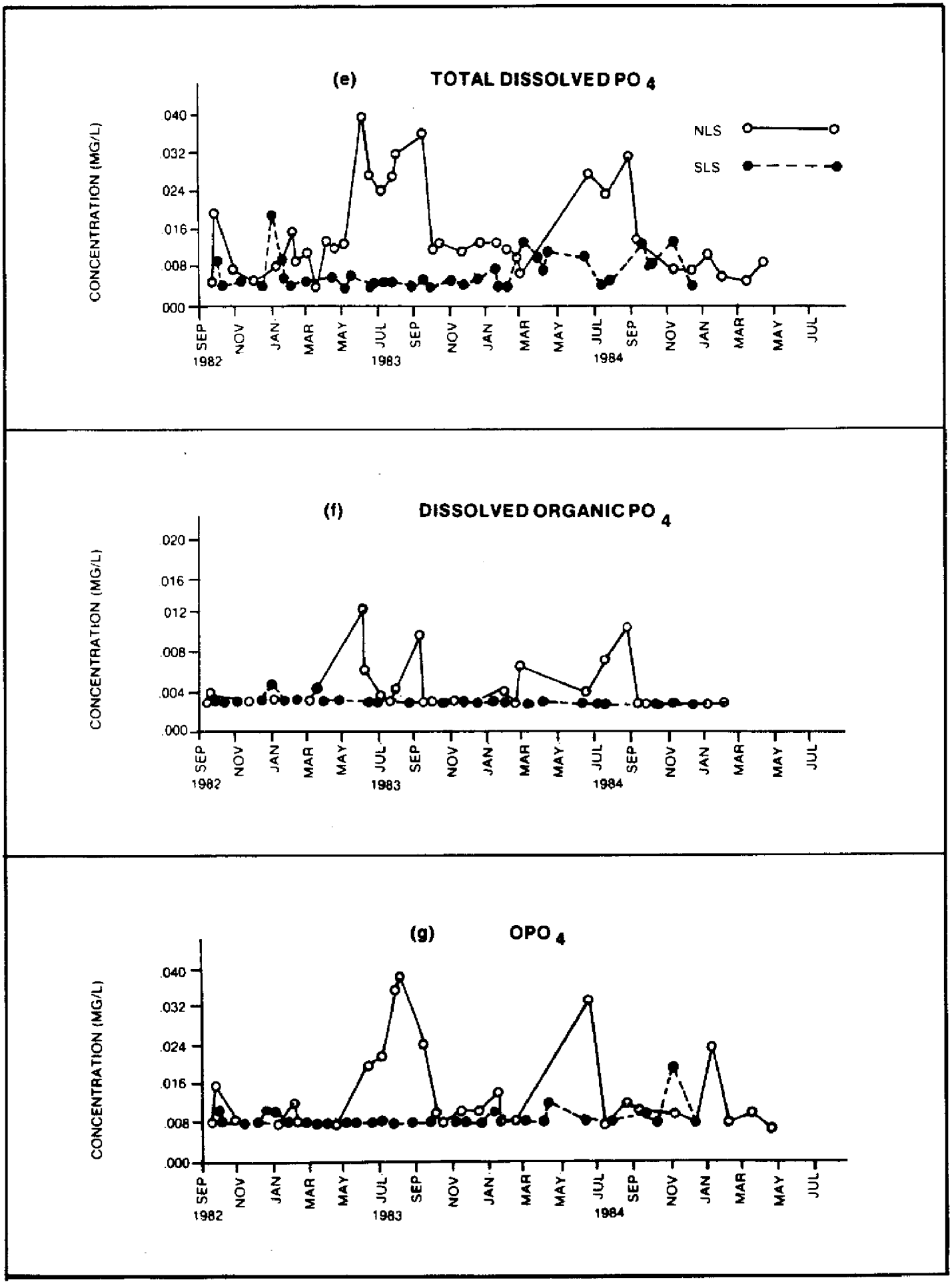


FIGURE 3. **Contd. (e) total dissolved phosphate, (f) dissolved organic phosphate, (g) orthophosphate.**

Surface water concentrations of dissolved nitrogen (TDKN) and phosphorus ($TDPO_4$) tended to be higher at NLS than SLS (Figure 3B,E), but neither site experienced nutrient "enrichment" typical of areas influenced by agricultural surface water runoff (Davis, 1984). Differences in dissolved phosphorus concentrations at the two sites were most pronounced during spring, summer, and fall months when levels of dissolved organic phosphate increased to 0.018 - 0.029 mg/l (Figure 3F) and inorganic (OPO_4) phosphate rose to 0.010 - 0.020 mg/l (Figure 3G) at NLS. Higher dissolved nitrogen concentrations at NLS were due to higher concentrations of ammonia (NH4). Ammonia concentrations commonly exceeding 1.5 mg/l at NLS probably resulted from incomplete decomposition (i.e., negligible nitrification) in the stagnant, low dissolved oxygen conditions that are typical at this site. Relatively high ammonia concentrations were characteristic of average water level conditions at NLS, but fell to levels comparable to concentrations found at SLS when stages rose during heavy rains (e.g., February-April 1983). Ammonia and nitrate (NO_3) concentrations at SLS were low during high stages, but increased sharply as water depths fell. Similar increases in ammonia and nitrate concentrations during falling water levels at other interior marsh sites in WCA's 1, 2A, and 3A have been attributed to release of these ions during decomposition of organic matter (Swift and Nicholas, 1985). During low stages at SLS, nitrate concentrations at this site exceeded levels found in surface water at NLS.

Soil Nutrient Concentrations

Soil nitrogen (TKN) and phosphorus concentrations showed significant (two-way ANOVA: $p(F) < 0.05$) differences among sampling dates as well as between soil depths and sampling sites (Table 1). Differences in soil nitrogen and phosphorus concentrations among sampling dates did not display any distinct seasonal pattern or appear to be correlated with changes in surface water depths or nutrient concentrations. Nitrogen concentrations of soil at NLS increased with depth and were significantly lower than concentrations of comparable soil layers at SLS. In contrast, phosphorus levels declined with depth at both sites and were significantly higher in soils at NLS.

Stand Characteristics

Prevailing hydroperiods and water stages at NLS and SLS appear to have resulted in distinct differences in sawgrass growth characteristics at these locations. In areas like SLS, where water levels are relatively deep most of the year, sawgrass typically forms "tussocks" on which all plant components, including stocks, rhizomes, and roots are perched

TABLE 1. Mean nitrogen and phosphorus concentrations (% dry weight) of soil samples. Except as noted, all "main effect" factors were significant ($p(F) < 0.05$) and all interaction terms were non-significant ($p(F) > 0.05$).

Site	Depth (cm)	Fall 82	Winter 83	Spring 83	Summer 83	Fall 83
				Nitrogen		
NLS+	0-10	2.62	2.80	2.66	2.67	2.63
	10-20	2.74	2.93	2.77	2.95	2.93
SLS	0-10++	2.74	3.13	2.93	3.07	3.13
	10-20	2.75	3.02	3.02	3.15	3.13
				Phosphorus		
NLS	0-10*	0.080	0.077	0.079	0.073	0.060
	10-20**	0.035	0.056	0.052	0.035	0.021
SLS	0-10*	0.036	0.035	0.025	0.029	0.024
	10-20**	0.025	0.020	0.014	0.019	0.011

\+ Date factor not significant in Date x Depth ANOVA of NLS soils
++ Depth factor not significant in Date x Depth ANOVA of SLS soils
* Date factor not significant in Date x Site ANOVA of 0-10 cm soil layer
** Significant interaction term in Date x Site ANOVA of 10-20 cm soil layer

above the soil surface. Tussock formation permits growth of photosynthetic tissues of new sawgrass shoots above prevailing high water levels. Tussocks at SLS were anchored by sawgrass roots that grew down through the water column to approximately 20 cm beneath the soil surface. Tussocks consisted of densely packed culms that were interconnected by rhizomes and/or grew off stocks of parent plants. Spacing of individual tussocks resulted in a clumped distribution of sawgrass culms at this site. At NLS, where water levels were shallow and predominately stable throughout the year, sawgrass stocks, rhizomes, and roots developed primarily below the soil surface and individual culms tended to be more evenly distributed. Sawgrass roots at NLS penetrated as deep as 40-50 cm below the soil surface.

Sawgrass growth rates also appeared to differ at NLS and SLS. After 11 months of growth, stock lengths of marked new shoots (i.e., plants with stock lengths ≤ 2.0 cm) averaged 5.0 ± 0.8 (std. dev.) cm at NLS and only 2.7 ± 1.0 cm at SLS. Because rates of stock elongation in relation to leaf production (i.e., slopes of linear regressions in Figure 4) were similar at NLS and SLS (ANCOVA, $p(F) > 0.20$), comparable increases in stock length reflect equivalent increments of plant growth at these sites. Thus, sawgrass growth rates appeared to be slower at SLS.

Leaves of culms at NLS also grew taller than at SLS (Figure 5). Live leaf lengths of young shoots increased asymptotically with plant growth at both sites, but reached an average maximum of about 300 cm at NLS and only 210 cm at SLS. Live leaf length-weight relationships (Figure 6) were not significantly different at NLS and SLS (ANCOVA, $p(F) > 0.20$). Leaf growth characteristics and individual culm distribution patterns resulted in a densely shaded stand at NLS and a comparatively open canopy at SLS.

Stock length frequency distributions of harvested plants (Figures 7 and 8) suggest that rates of new shoot production and mortality schedules also vary at the two sites. For example, culms with stock lengths ≤ 2.0 cm accounted for an average of about 43% of both live and dead shoots in SLS samples and only 26% of live plants and 16% of dead plants collected at NLS. Higher frequencies of young live and dead culms in SLS samples indicate that rates of new shoot production and early mortality are greater at this site than at NLS. High frequencies of live culms with root stock lengths ≤ 2.0 cm may also reflect slower growth rates at SLS. Live plant root stock length frequency distributions at each site were generally consistent among sampling periods; however, a higher frequency of young live culms was found at NLS during summer and fall 1983. This increase in new shoot production appeared to have been accomodated by high plant mortality (see Figure 8) resulting from an infestation by stem-boring Lepidopteran larvae during summer 1983.

Due to spacing of tussocks at SLS, sample densities did not reflect overall culm densities at the two sites. Although sample densities were considerably higher at SLS (Figure 7), mean live plant density at this site (28.3 culms/m^2) was not significantly different ($0.20 < p(t) < 0.50$) than at NLS (32.1 culms/m^2).

Production

High correlations between total leaf production and stock length (Figure 4) provide a basis for estimates of cumulative leaf biomass production (CLP) in relation to plant growth.

$$CLP(s) = \sum_{i=0.5}^{x} Y(i) * (MLW(YMAX(i)) \quad (1)$$

where

x = stock length

s = site

Y(i) = number of leaves produced by individual culms at site(s) during the interval in which their stock lengths increased from i - 0.5 to i (based on linear regressions shown in Figure 4).

YMAX(i) = mean maximum live leaf length of plants at site(s) with stock lengths = i when $i \leq 3.0$. Mean maximum live leaf length of all culms at site(s) with stock lengths > 3.0 was used when $i > 3.0$.

MLW(i) = computed weight of YMAX(i) (based on regressions shown in Figure 6).

Due primarily to taller, more robust leaf growth at NLS, estimates of cumulative leaf biomass production at the two sites diverge shortly after new shoots are established (i.e., when stocks of culms have grown to about 3.0 cm) (Figure 9A). These estimates are comparable to more rigorous measurements of cumulative aboveground production at other sites in WCA2A (Davis, unpubl., Figure 9B).

Standing crop biomass of stocks, rhizomes, and roots of individual live culms provided a direct measurement of cumulative production of these plant parts (assuming sloughing of these tissues was minimal). Stock and root production were highly correlated with plant growth (i.e, stock length) at both sites (Figure 10), and stock production was significantly greater (ANCOVA, $p(F) < 0.05$) at NLS than among comparable growth stages at SLS.

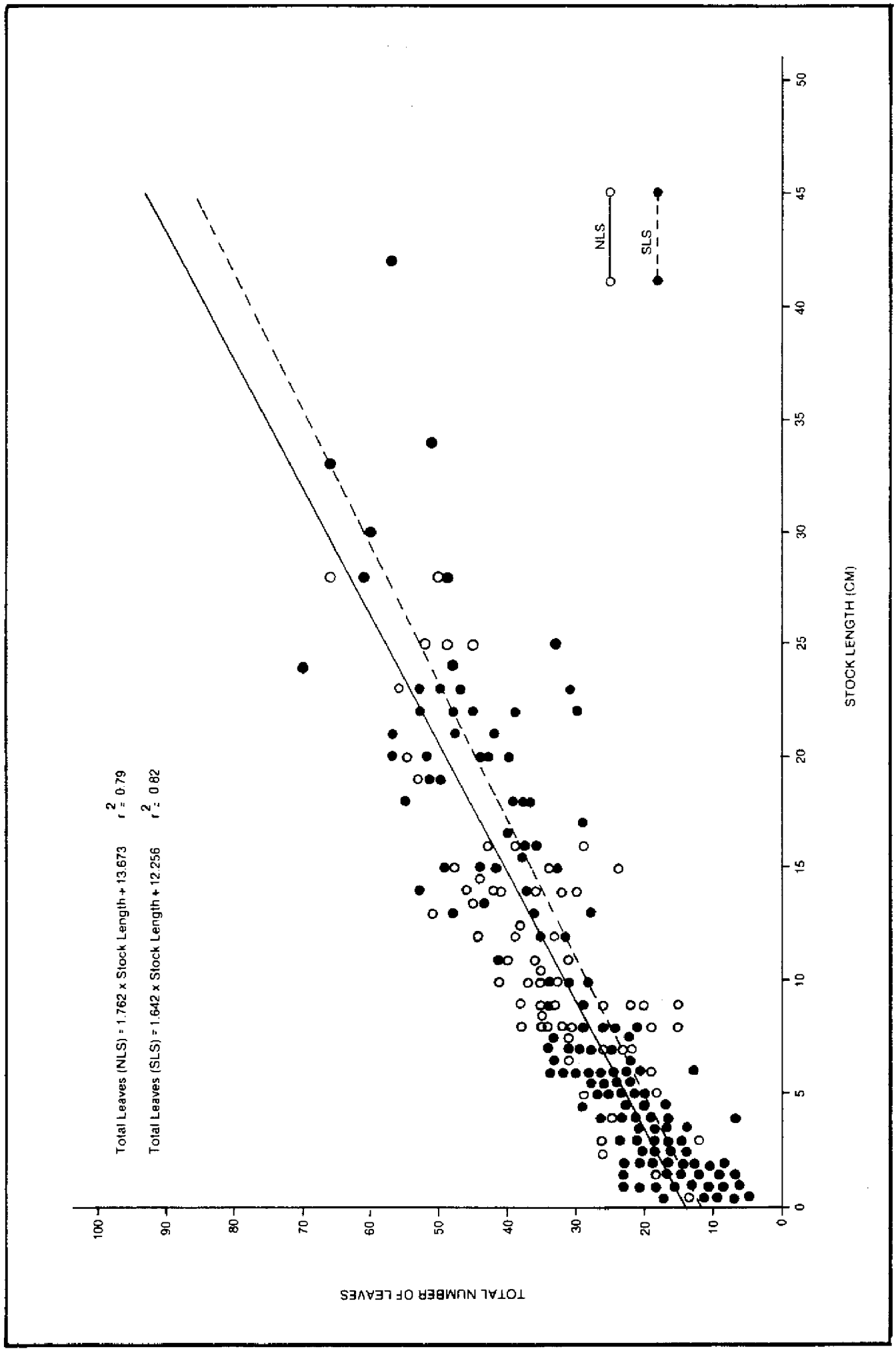


FIGURE 4. Relationships between stock lengths and the total number of leaves produced by harvested live culms at NLS and SLS.

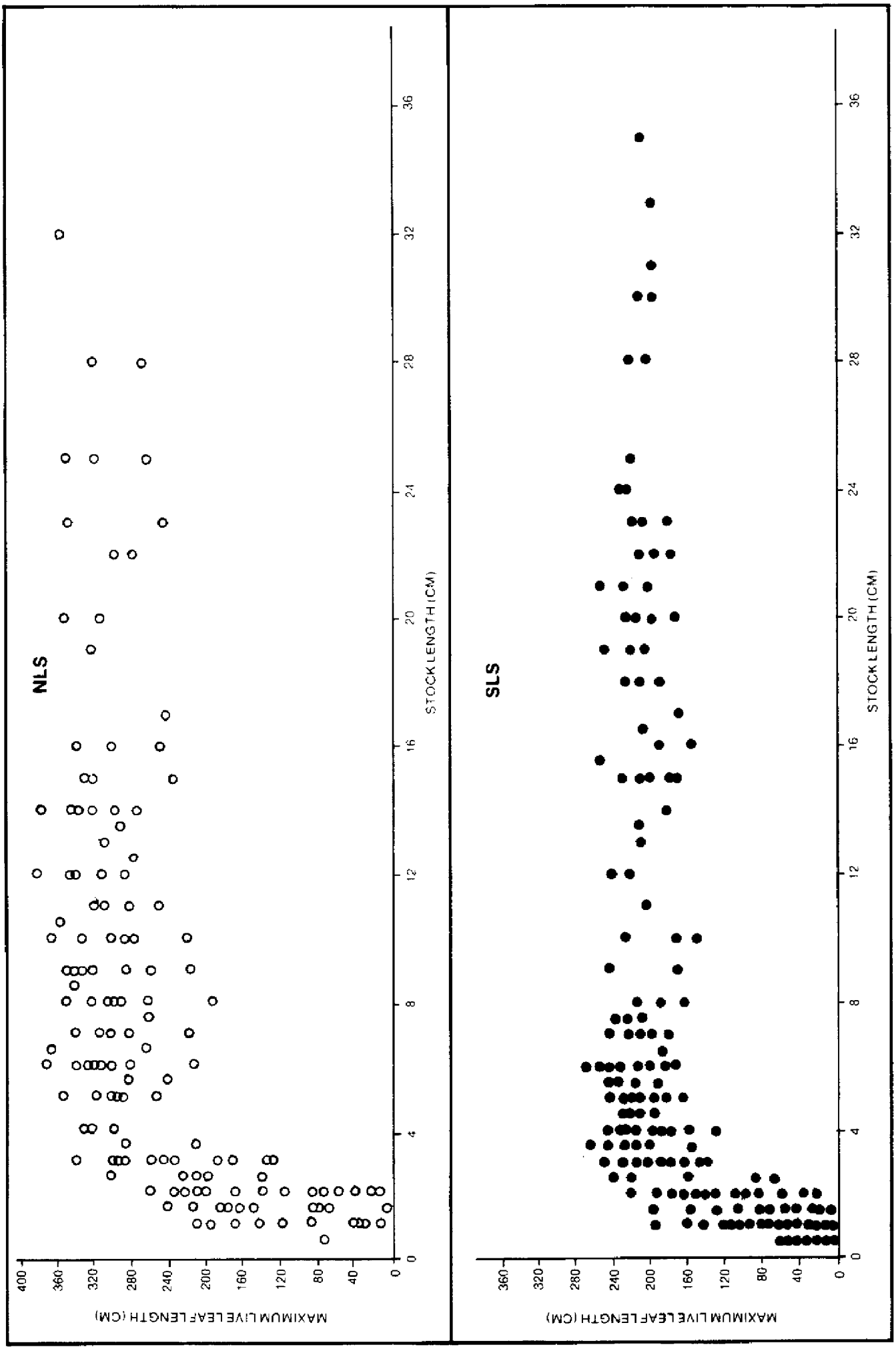


FIGURE 5. Maximum live leaf lengths in relation to stock lengths of harvested culms at NLS and SLS.

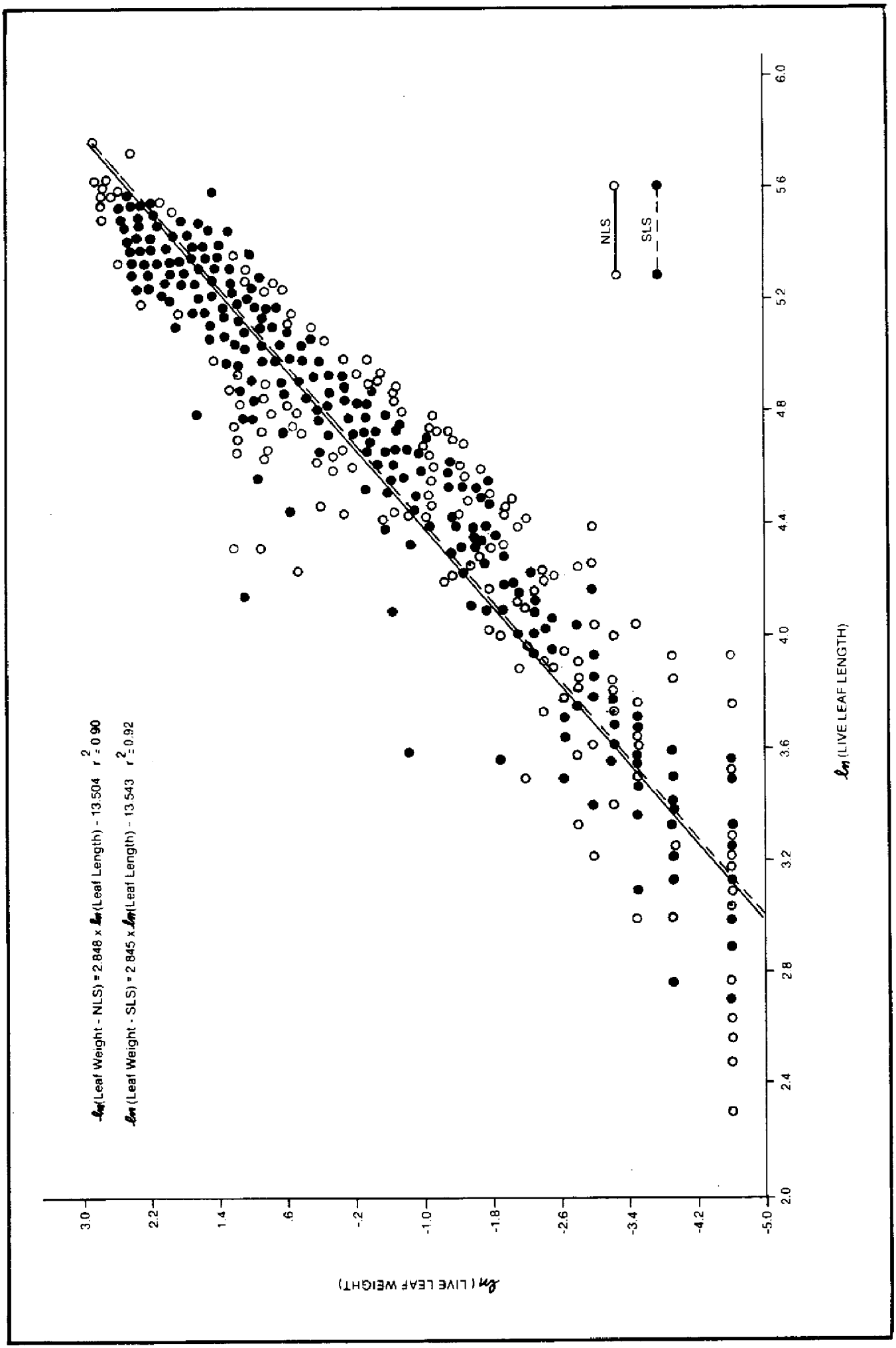
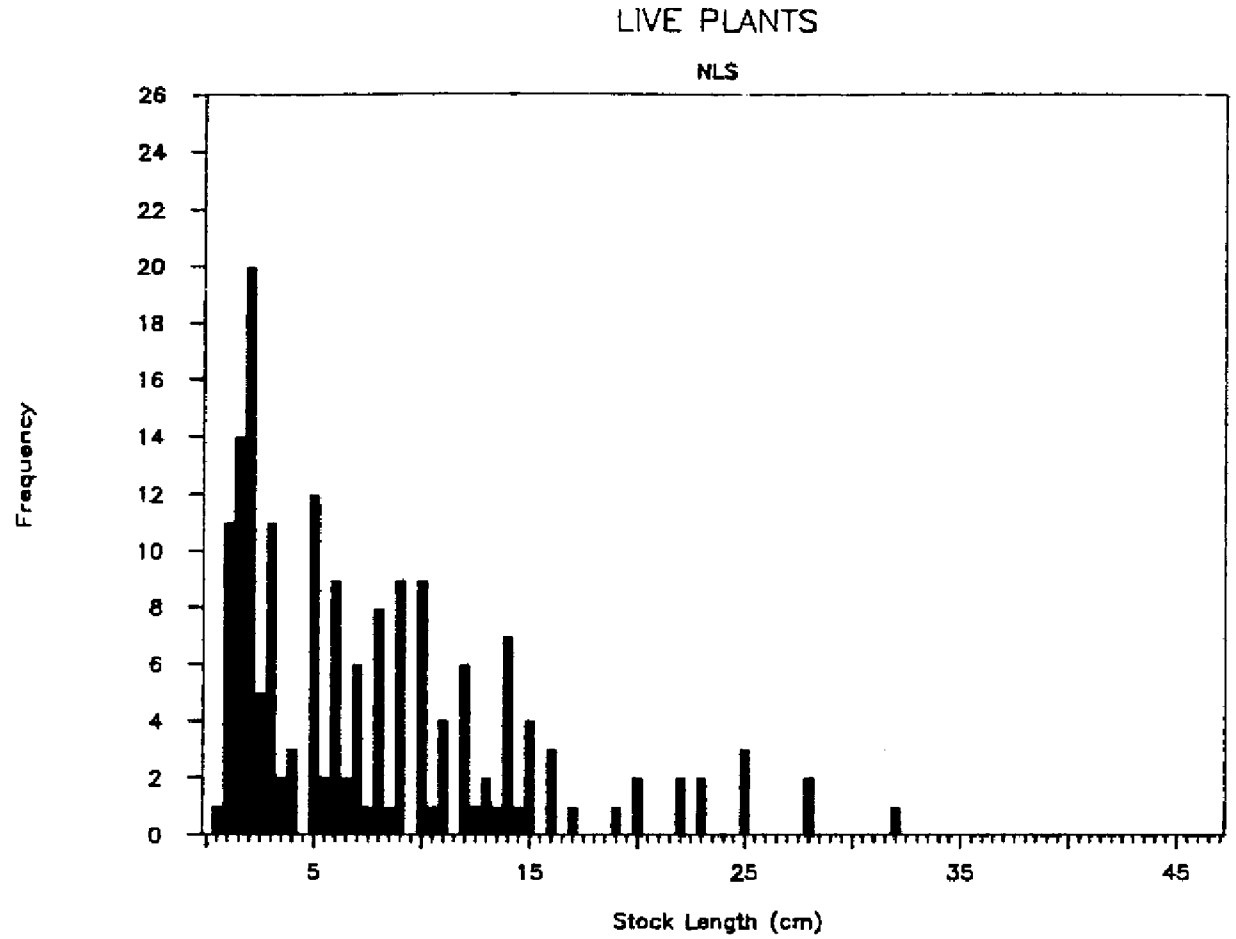


FIGURE 6. **Log $_e$ - log $_e$ relationships between live leaf lengths and weights at NLS and SLS.**



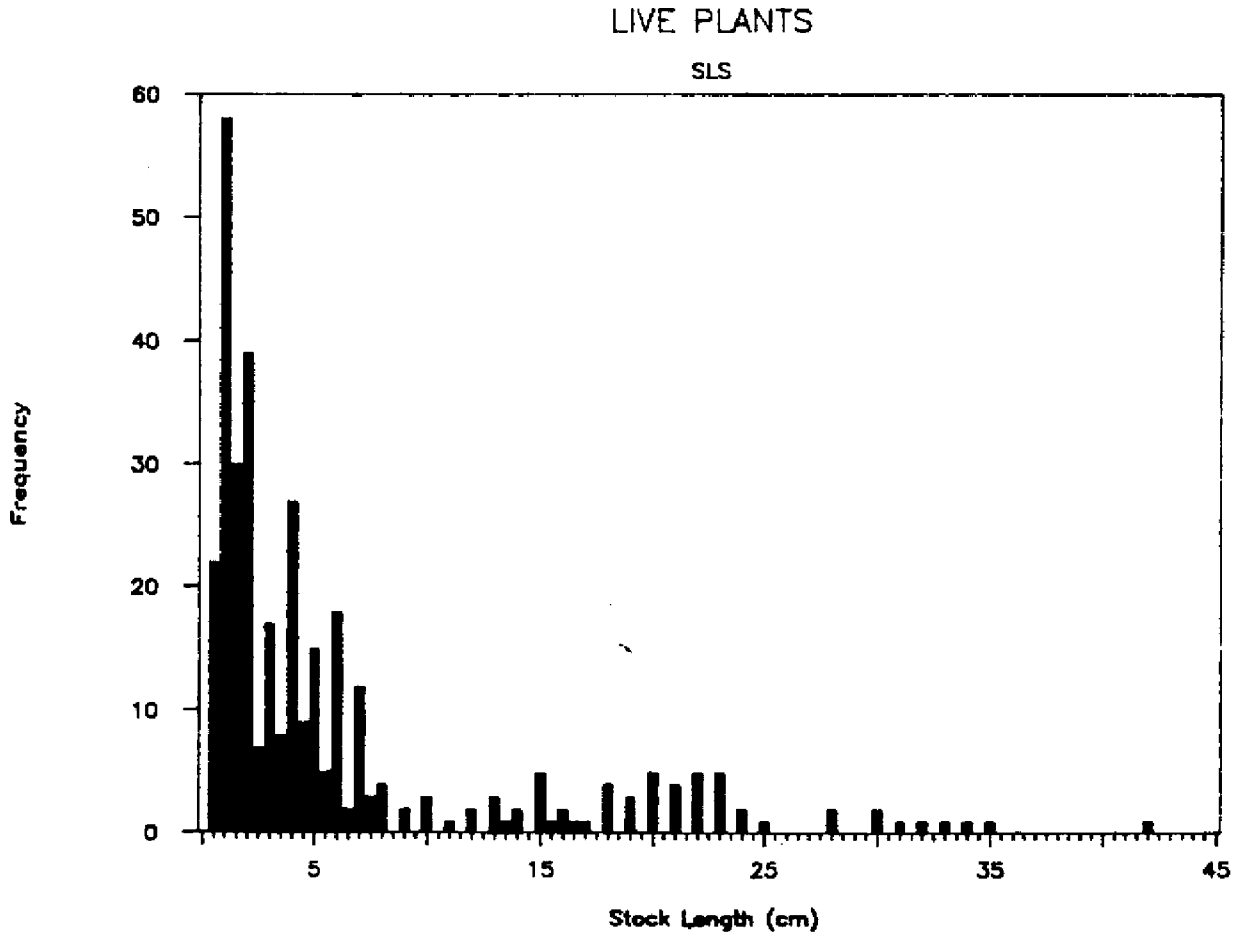
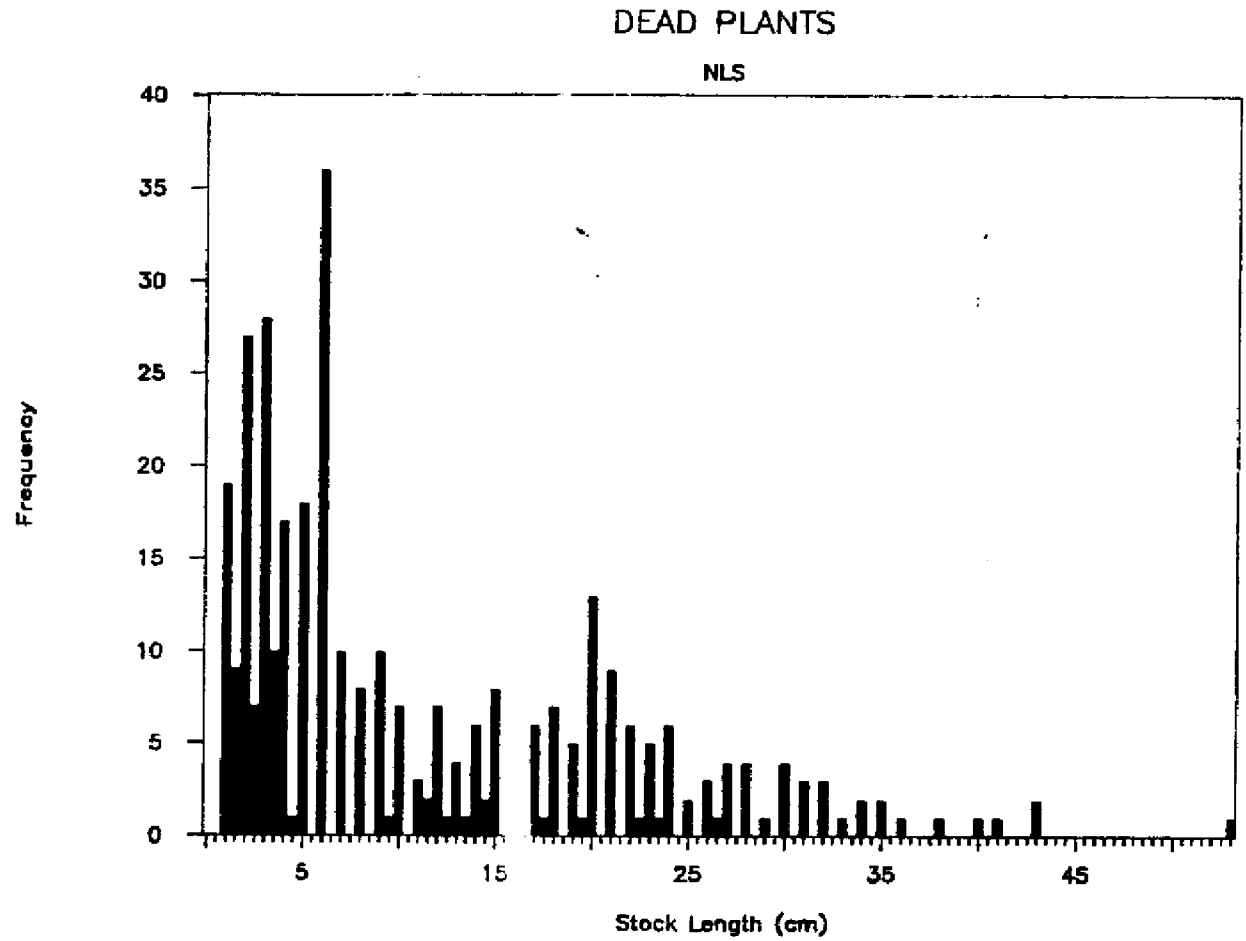


FIGURE 7. Stock length - frequency distributions of harvested live culms at NLS and SLS.



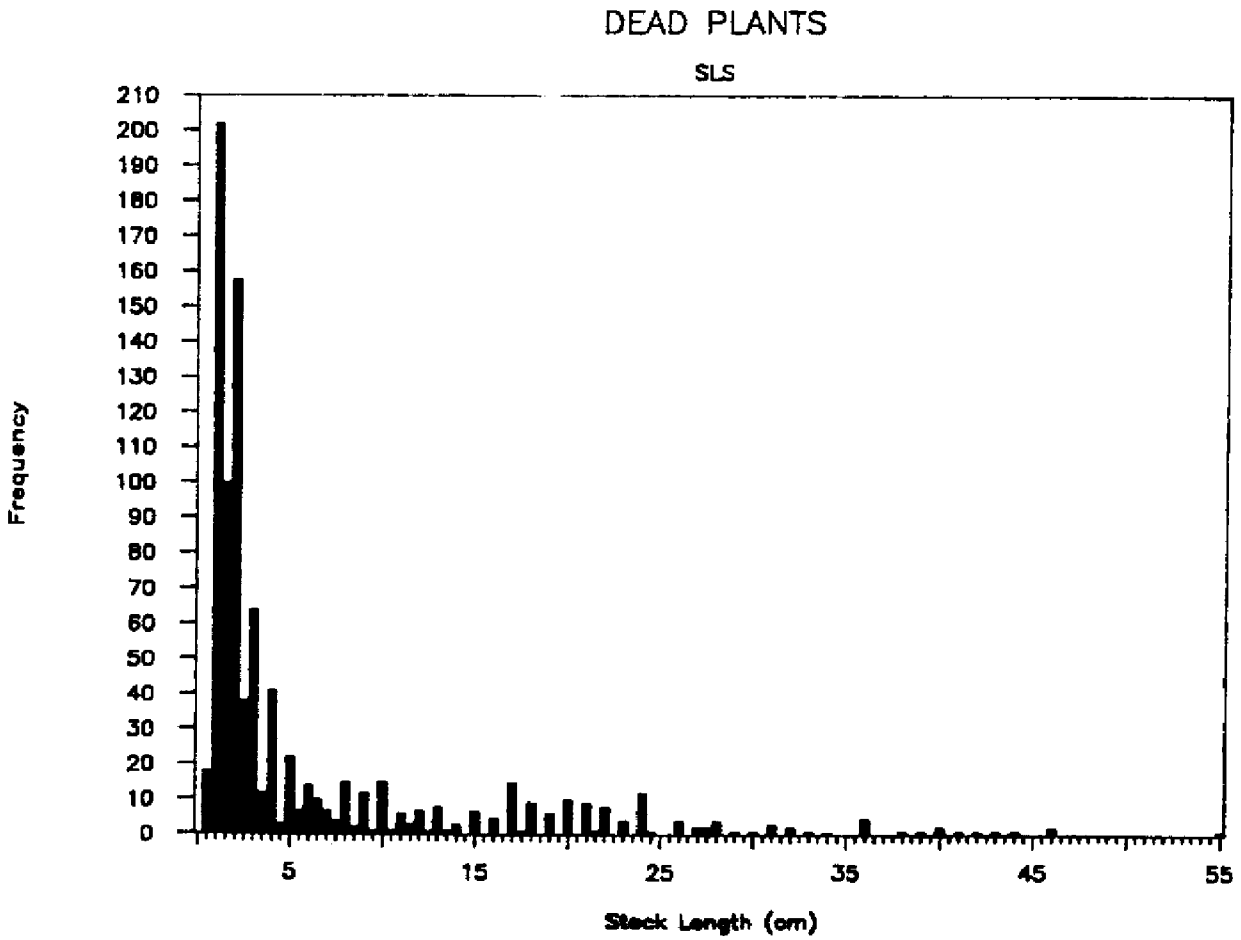


FIGURE 8. Stock length - frequency distributions of harvested dead culms at NLS and SLS.

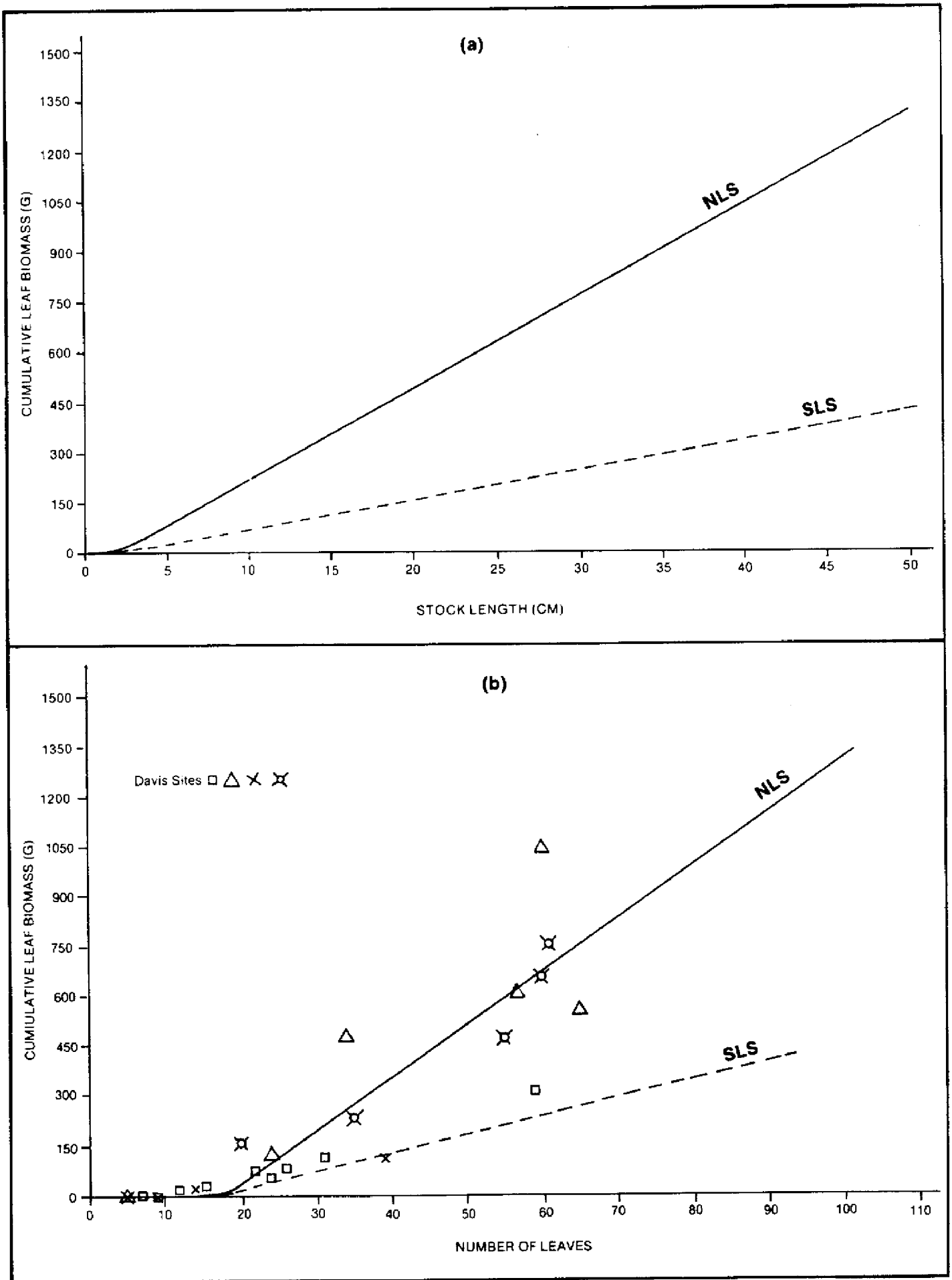


FIGURE 9. **Cumulative (lifetime) leaf biomass production at NLS and SLS, based upon equation (1); (a) Relationships between lifetime leaf biomass production and stock length; (b) relationships between leaf biomass production and cumulative number of leaves produced during lifetimes of culms. Davis' (unpubl.) measurements of lifetime leaf biomass production at four other locations in Water Conservation Areas 2A are also shown.**

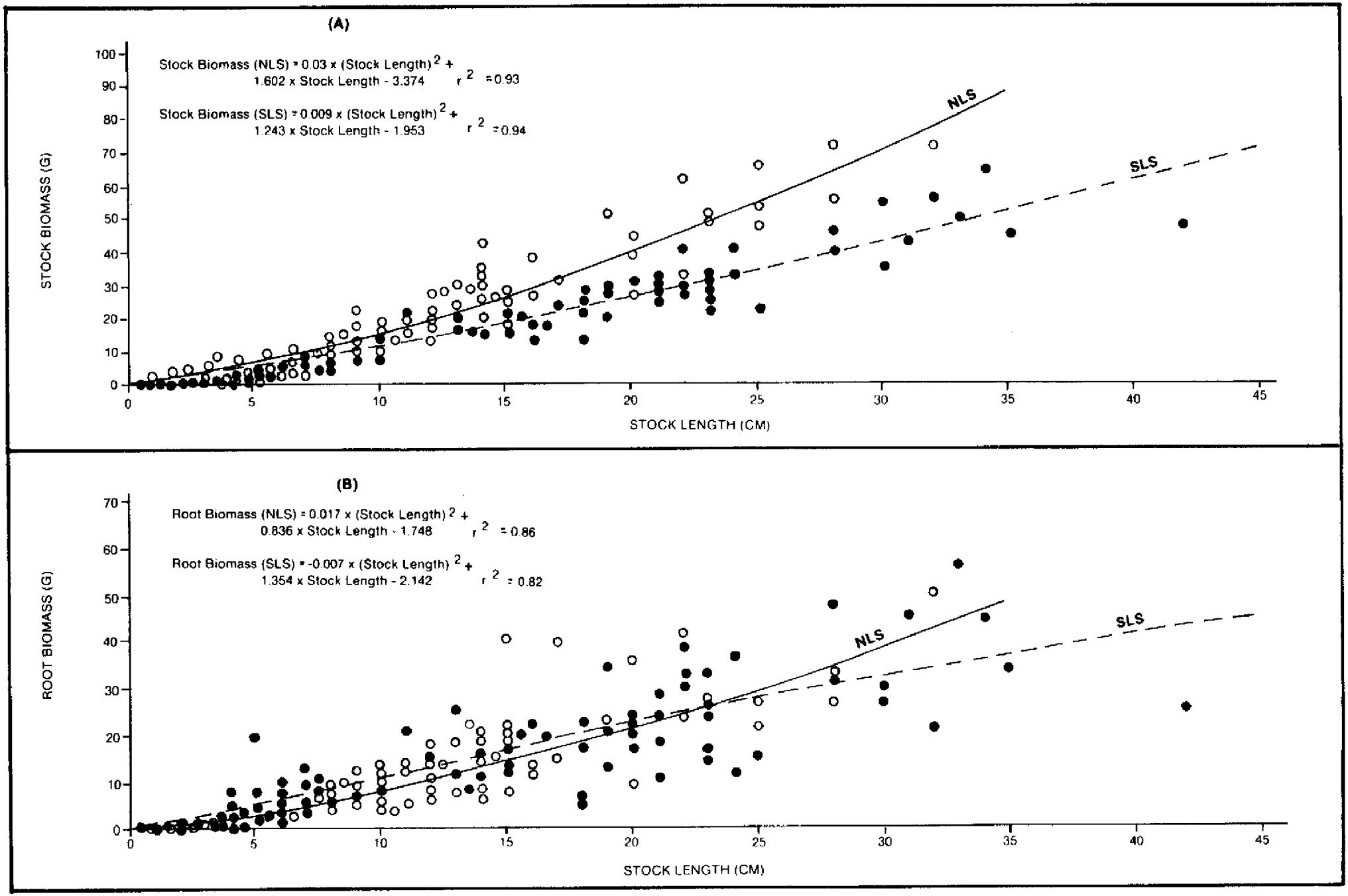


FIGURE 10. **Lifetime stock and root biomass production at NLS and SLS.**
(a) Cumulative stock biomass production; (b) cumulative root biomass production.

Relationships between rhizome biomass and plant growth (Figure 11A, B) were more variable, particularly at NLS ($r = 0.61$). Since rhizomes were frequently severed during the sampling process (i.e., when they extended outside the enclosed sample area), rhizome biomass was probably underestimated. However, an equally poor correlation ($r = 0.63$) between the rate of rhizome formation (i.e, number produced) and stock length at NLS (Figure 11C), suggests that rhizome production changes very little with plant growth at this site. In contrast, plants at SLS appear to continuously produce new rhizomes (Figure 11D).

Combined stock, rhizome, and root biomass of individual live plants at NLS was slightly higher (ANCOVA, $p(F) < 0.05$) than among comparable growth stages at SLS (Figure 12). Based upon frequency distributions of live plant growth stages during each sampling period, these plant parts accounted for an average of $12.2 \pm 0.1\%$ (std. dev.) of total lifetime biomass production of sawgrass at NLS and $27.9 \pm 0.6\%$ of total biomass production during lifespans of plants at SLS. These differences were due primarily to higher cumulative leaf biomass production at NLS than SLS.

Nutrient Concentrations in Live Plant Tissues

Since nutrient concentrations in new shoot tissues tend to be diluted as young plants grow (Ulrich, 1952; Smith, 1962; Steward and Ornes, 1975; Shaver and Melillo, 1984), divisive cluster analyses[1] were utilized to differentiate young and mature plant growth categories. Based upon these analyses, young culms included shoots with stock lengths ≤ 3.0 cm while mature culms had stock lengths ≥ 3.5 cm.

Nutrient concentrations of most live plant components of young shoots at both sites were significantly higher ($p(F \text{ or } t) < 0.05$) than comparable plant parts in mature culms (Table 2). Nutrient concentrations of most live plant tissues were significantly ($p(F \text{ or } t) < 0.05$) higher at NLS than SLS (Table 2); however, nitrogen concentrations in stocks and rhizomes of mature culms were higher at SLS. Stocks generally had the highest nutrient concentrations of live plant components at both sites. Mean nitrogen concentrations of stocks of young and mature culms ranged from 0.9 -1.8% at NLS and 1.1 - 1.4% at SLS, while phosphorus levels averaged 0.09 - 0.30% at NLS and 0.06 - 0.13% at SLS. Nutrient concentrations of roots at NLS and live leaves of culms at both sites were intermediate between concen-trations in stocks and all other live plant parts at NLS and SLS. Although nutrient concentrations of all live plant components at both sites varied significantly (ANOVA $p(F) < 0.05$) among sampling periods (Appendix 1), there was no evidence of temporal translocation of nutrients between live plant parts at either site.

Nutrient Concentrations in Dead Plant Tissues

As leaves died, 28-37% of accumulated nitrogen and 58-65% of accumulated phosphorus was released from leaf tissues (Tables 2 and 3). Subsequent increases in TKN concentrations of remnant leaves suggests that nitrogen remaining in dead leaf tissues was incorporated in associated microbial (decomposer) biomass as matter was lost during leaf decomposition (Enwezor, 1976). In contrast, comparable phosphorus concentrations in dead and remnant leaves indicate that phosphorus release during decomposition occurred in direct proportion to the rate of leaf breakdown (i.e, weight loss). Phosphorus concentrations remaining in both dead and remnant leaves were significantly higher (p (F or t) < 0.05) at NLS, while nitrogen levels in dead and decomposing leaf tissues were similar at the two sites.

Stocks of dead culms also exhibited significant losses of nitrogen and phosphorus (Tables 2 and 3). Dead and decomposing stock tissues of young culms, for example, appeared to lose 42-51% of accumulated nitrogen and about 84% of stored phosphorus. Dead and remnant stocks of young and mature culms at NLS retained significantly higher phosphorus concentrations than stocks of dead culms at SLS, while stocks of mature culms at SLS maintained higher TKN levels.

Differences in nutrient concentrations among rhizomes and roots of live, dead and remnant culms (Tables 2 and 3) were not as explicit as those displayed by leaves and stocks. Rhizomes and roots of dead and remnant culms at NLS maintained higher phosphorus levels than comparable components of dead culms at SLS, while dead and decomposing rhizome tissues at SLS retained significantly higher nitrogen concentrations. Nitrogen concentrations ultimately

[1] Separate analyses were conducted on standardized TKN and P concentrations of individual plant components, based upon Euclidean distance between each case and the mean (center) of all cases in the cluster. Nutrient concentrations were standardized (divided by standard deviations) to eliminate bias resulting from difference in scale associated with TKN and P measurements.

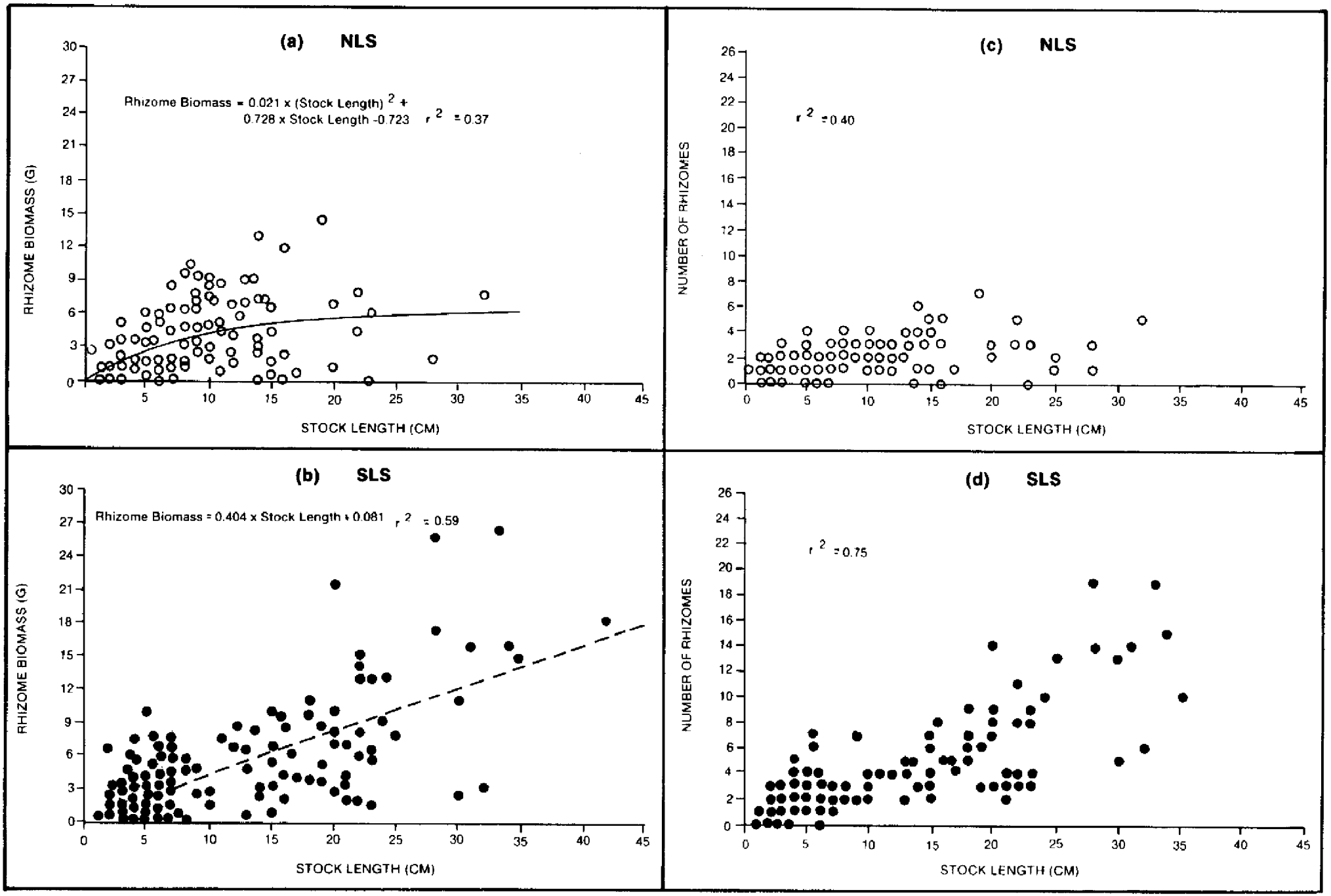


FIGURE 11. **Relationships between culm growth (stock length) and cumulative rhizome biomass production (a,b) and total numbers of rhizomes produced during culm lifetimes (c,d).**

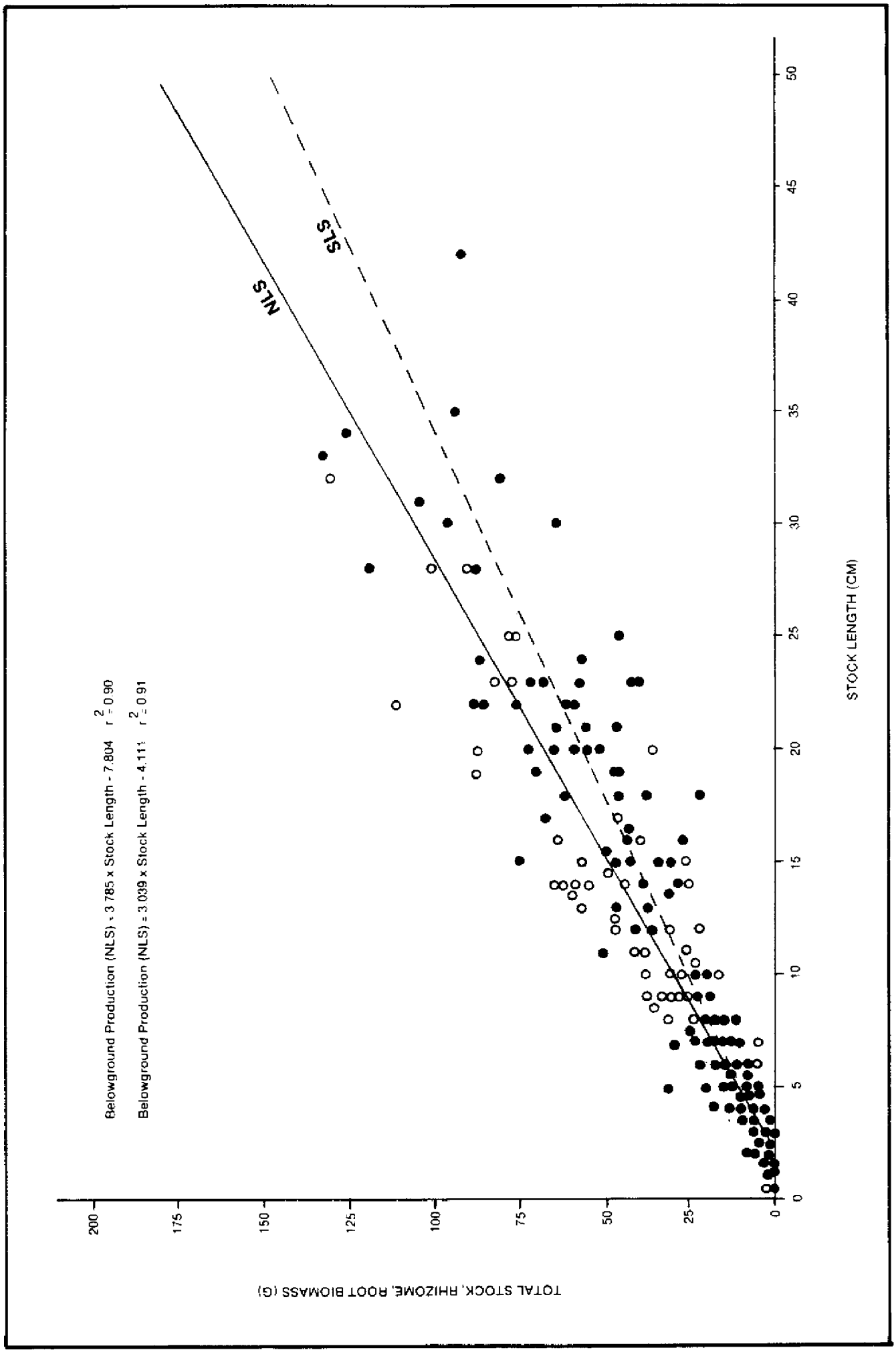


FIGURE 12. Cumulative (lifetime) stock, rhizome, and root biomass production in relation to culm growth at NLS and SLS.

retained by dead and decomposing root tissues were equivalent at the two sites.

Nutrient concentrations of flowering plant parts provide additional evidence of high nutrient losses during plant death, but suggest that nitrogen and phosphorus concentrations in dead plant tissues subsequently remain relatively constant (Table 4). For example, nutrient concentrations of leaves, stocks, rhizomes, and roots of culms that died during late fall 1982 did not appear to change from January-October 1983.

TABLE 2. Mean Nitrogen (TKN) and phosphorus concentrations (% dry weight of of live plant components. Means were derived from mean nutrient concentrations during each sampling period. Except as noted, all nutrient concentrations were significantly different (p[F or t]) <0.05 between age classes and sites.

NLS

	TKN (%)		P (%)	
	Young	Mature	Young	Mature
Live Leaves	0.95	0.71	0.077	0.036
Dead Leaves	0.67	0.46	0.041	0.015
Remnant Leaves	0.46	0.57+	0.020 *	0.021
Root Stocks	1.80	0.86	0.296	0.094
Rhizomes	0.62++	0.47++	0.033++	0.020
Roots	0.98	0.81	0.047	0.028

SLS

	TKN (%)		P (%)	
	Young	Mature	Young	Mature
Live Leaves	0.79	0.60	0.046	0.024
Dead Leaves	0.46	0.38	0.014	0.009
Remnant Leaves	0.38	0.56+	0.016	0.010
Root Stocks	1.44	1.10	0.131	0.064
Rhizomes	0.64++	0.54++	0.025++	0.014
Roots	0.59 *	0.59	0.015	0.011

*Concentrations not significantly different (Date x Age ANOVA) between young and mature plants
+TKN concentrations of remnant leaves of mature plants not significantly different (Date x Site ANOVA) between sites.
++TKN and P concentrations of rhizomes of young plants (t-tests) and TKN concentrations of rhizomes of mature plants (Date x Site ANOVA) not significantly different between sites.

TABLE 3 Mean nitrogen (TKN) and phosphorus (P) concentrations (% dry weight) of dead and remnant plant components. Means were derived from mean nutrient concentrations during each sampling period.

NLS

	TKN (%)				P (%)			
	Dead Plants		Remnant Plants		Dead Plants		Remnant Plants	
	Young	Mature	Young	Mature	Young	Mature	Young	Mature
Dead Leaves	0.64	0.49	--	--	0.028	0.016	--	--
Remnant Leaves	0.56	0.62	0.63	0.66	0.025	0.024	0.025	0.024
Root Stocks	1.11	0.66	0.80	0.64	0.084	0.050	0.041	0.030
Rhizomes	0.72	0.49	0.49	0.47	0.026	0.016	0.021	0.017
Roots	0.73	0.70	0.73	0.62	0.030	0.016	0.026	0.021

SLS

	TKN (%)				P (%)			
	Dead Plants		Remnant Plants		Dead Plants		Remnant Plants	
	Young	Mature	Young	Mature	Young	Mature	Young	Mature
Dead Leaves	0.57	0.49	--	--	0.016	0.011	--	--
Remnant Leaves	0.51	0.60	0.64	0.76	0.012	0.012	0.013	0.014
Root Stocks	1.08	0.94	0.83	0.79	0.049	0.031	0.021	0.014
Rhizomes	0.62	0.51	0.58	0.61	0.015	0.012	0.017	0.011
Roots	0.56	0.56	0.60	0.65	0.011	0.010	0.011	0.012

TABLE 4. **Mean nitrogen (TKN) and phosphorus (P) concentrations (% dry weight) of components of sawgrass culms that flowered during Summer 1982 and died between Fall 1982 and Winter 1983 sampling periods.**

	Fall 1982	Winter 1983	Spring 1983	Summer 1983	Fall 1983
			NLS (TKN Concentrations)		
Live Leaves	0.92	---	---	---	---
Dead Leaves	0.68	0.52	0.48	0.39	0.52
Remnant Leaves	0.86	0.57	0.65	0.65	0.65
Root Stocks	0.81	0.44	0.51	0.52	0.49
Rhizomes	0.53	0.37	0.46	0.49	0.52
Roots	0.86	0.66	0.69	0.71	0.61
			NLS (P Concentrations)		
Live Leaves	0.032	---	---	---	---
Dead Leaves	0.020	0.016	0.015	0.014	0.014
Remnant Leaves	0.028	0.020	0.026	0.024	0.023
Root Stocks	0.032	0.024	0.018	0.033	0.016
Rhizomes	0.022	0.014	0.017	0.013	0.012
Roots	0.021	0.018	0.018	0.019	0.013
			SLS (TKN Concentrations)		
Live Leaves	0.65	---	---	---	---
Dead Leaves	0.50	0.47	0.39	0.38	0.39
Remnant Leaves	0.69	0.64	0.55	0.60	0.60
Root Stocks	1.11	0.93	1.12	0.86	0.87
Rhizomes	0.72	0.55	0.47	0.46	0.53
Roots	0.78	0.60	0.57	0.54	0.56
			SLS (P Concentrations)		
Live Leaves	0.018	---	---	---	---
Dead Leaves	0.010	0.008	0.008	0.008	0.008
Remnant Leaves	0.011	0.010	0.008	0.011	0.011
Root Stocks	0.022	0.015	0.026	0.044	0.024
Rhizomes	0.013	0.009	0.008	0.011	0.009
Roots	0.013	0.009	0.009	0.009	0.009

late fall 1982 did not appear to change from January-October 1983.

Cumulative Nutrient Uptake and Flux in Plant Tissues

Due to higher biomass production and tissue nutrient concentrations, live culms at NLS accumulated more nitrogen and phosphorus than comparable growth stages at SLS (Figure 13). Site differences in nutrient accumulation were greatest in leaf tissues, and nutrient dynamics associated with leaf production was the dominant uptake pathway during the lifetime of plants. Based upon frequency distributions of live plant growth stages during each sampling period, stocks, rhizomes, and roots stored only 13% of nitrogen and 19% of phosphorus accumulated by live culms at NLS and 34-35% of the nitrogen and phosphorus accumulated by sawgrass tissues at SLS (Figure 14).

Based upon differences in nutrient concentrations between live and dead plant tissues, dying culms released an average of 29-34% of nitrogen and 57% of phosphorus accumulated during the lifespan of culms at each site (Figure 14). Dying leaves accounted for the greatest nutrient losses; stocks, rhizomes, and roots released only 3-4% of total accumulated nitrogen and 9-16% of total accumulated phosphorus. Moreover, relative to nutrient accumulation by each plant component, nutrient retention was greater in dead stocks, rhizomes, and roots than in dead leaves (Figure 15). Nutrient retention by dead stocks, rhizomes, and roots represented 30% of nitrogen and 19% of phosphorus accumulated by live culms at SLS, and 11% of total nitrogen and phosphorus accumulated by sawgrass at NLS (Figure 14).

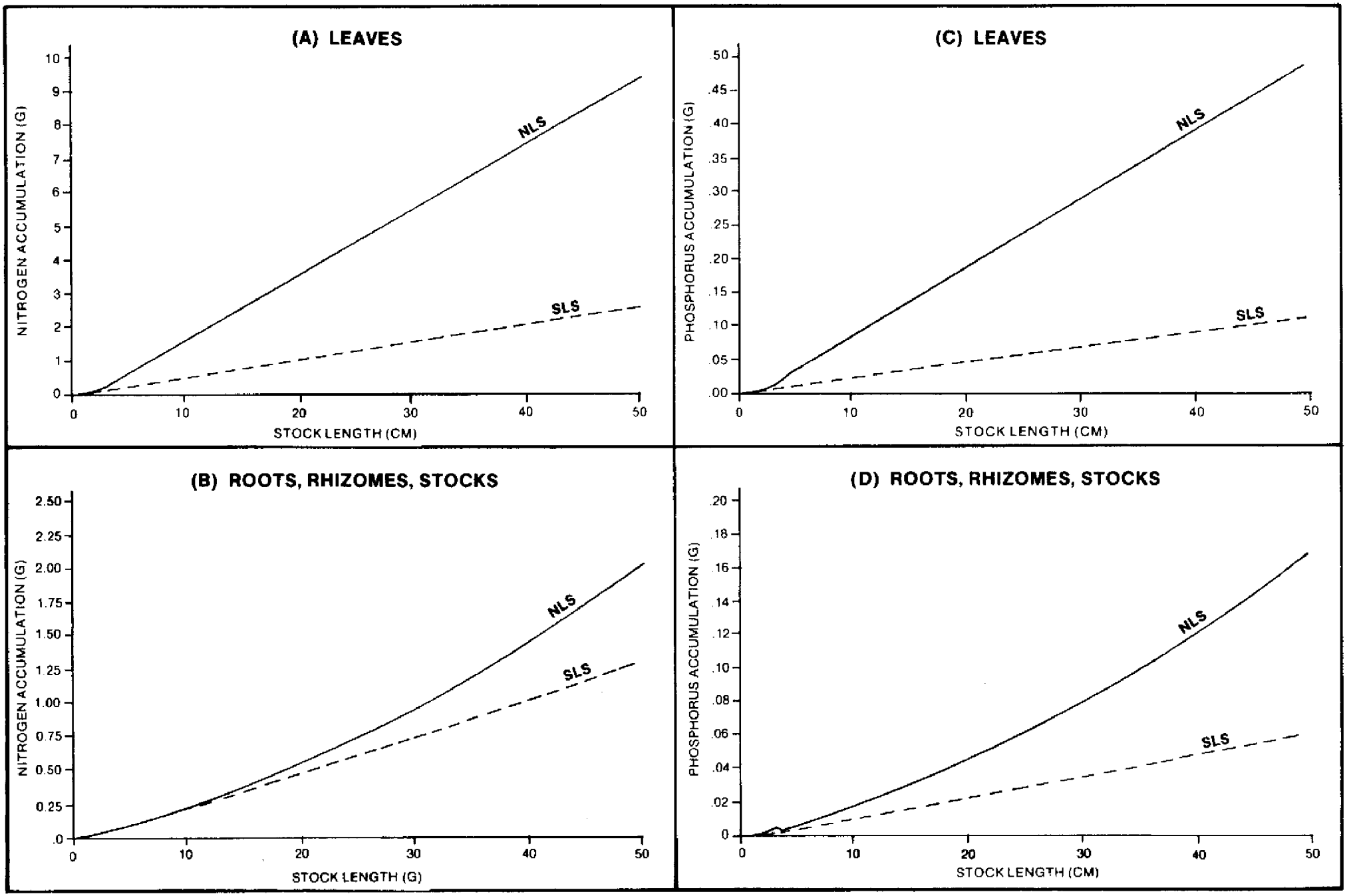


FIGURE 13. **Lifetime nutrient accumulation by sawgrass tissues at NLS and SLS; (a) Lifetime nitrogen accumulation by leaves; (b) lifetime nitrogen accumulation by stocks, rhizomes and roots; (c) lifetime phosphorus accumulation by leaves; (d) lifetime phosphorus accumulation by stocks, rhizomes and roots.**

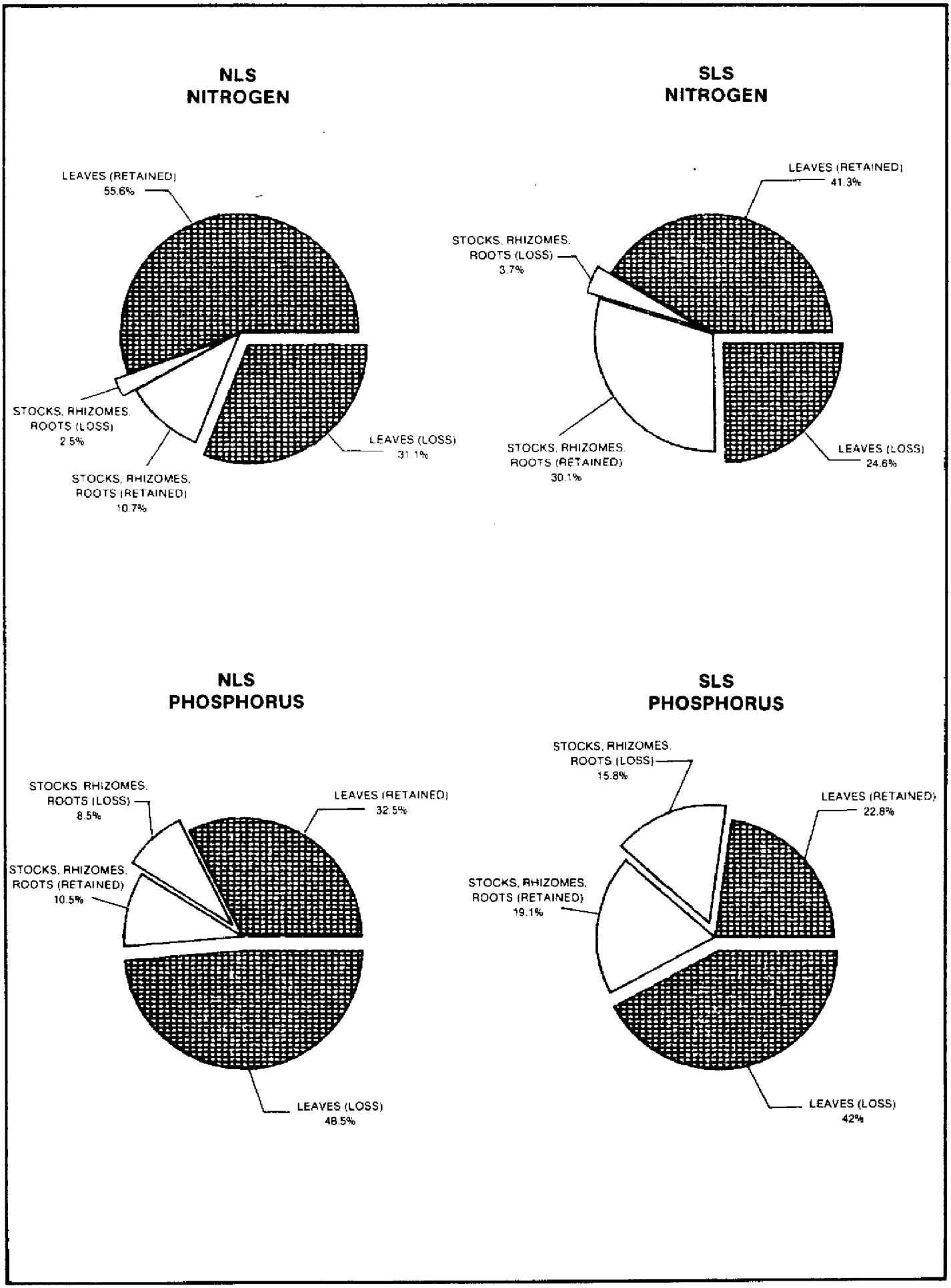


FIGURE 14. **Lifetime nutrient losses and retention by sawgrass tissues relative to total nutrient accumulation by <u>all</u> plant components.**

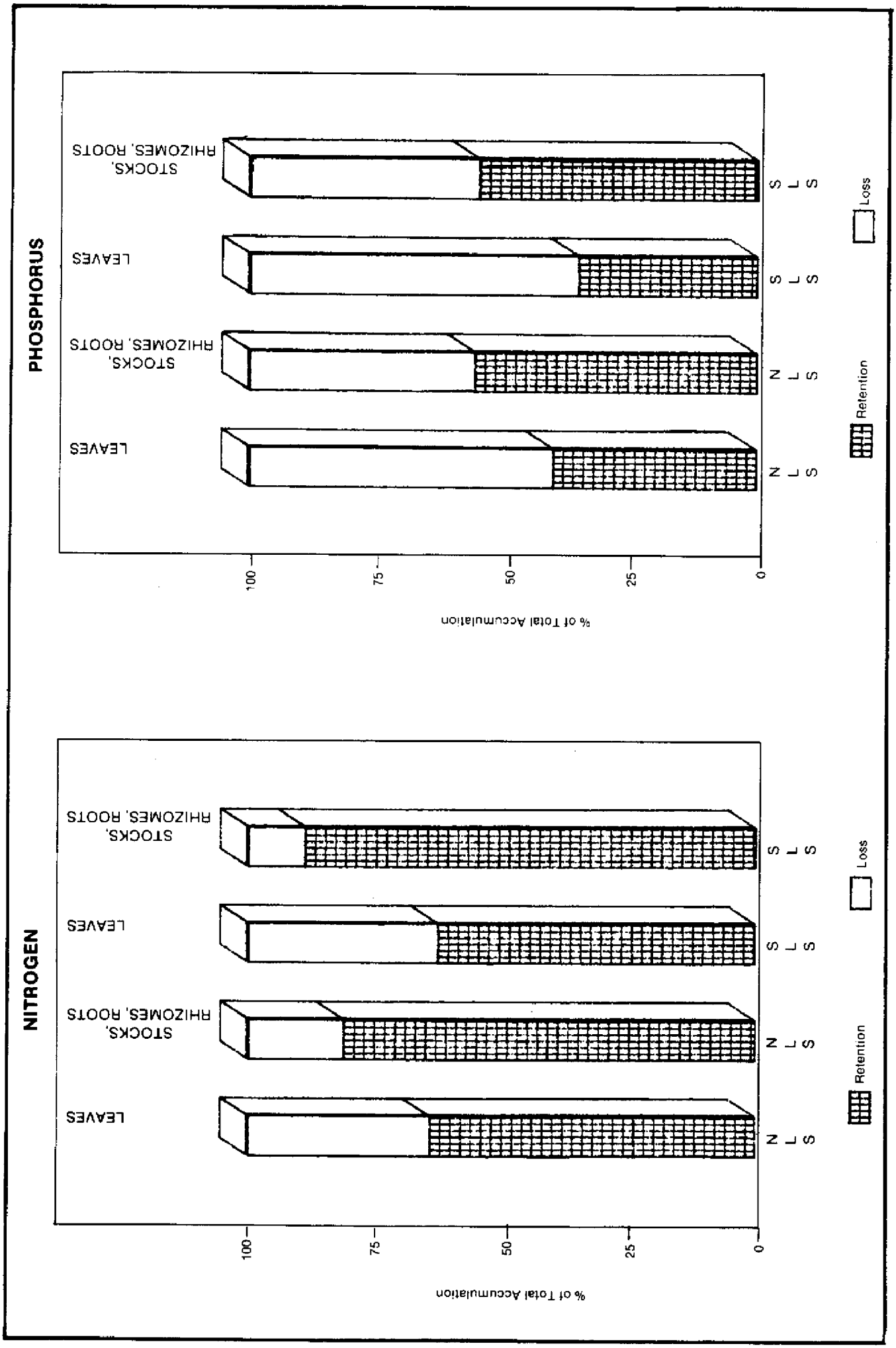


FIGURE 15. Lifetime nutrient losses and retention by sawgrass tissues relative to total nutrient accumulation by each plant component.

DISCUSSION

Hydrologic factors greatly influence the biology of sawgrass and its functional role in the Everglades ecosystem. Results of this study indicate that water regimes may directly affect sawgrass growth rates and mortality schedules and lead to adaptive growth characteristics and life history strategies. Tussock formation, slow plant growth rates, and heavy early mortality coupled with high rates of new shoot production appear to be characteristics of sawgrass subjected to stresses associated with deep and widely fluctuating water levels. In contrast, where water levels are shallow and stable throughout the year, rapid growth rates and extended survival of sawgrass culms result in densely shaded stands in which new shoot development is limited. These alternative life history patterns appear to represent a tradeoff between reproductive effort and individual plant growth. Maximum reproductive effort (e.g., rate of new shoot production) is adaptive when plants are exposed to hydrologic conditions where the probability of extended survival is low, while favorable water level regimes appear to produce selection pressures which promote channeling of available resources into individual plant growth (Giesel, 1976).

Hydrologic regimes also indirectly affect lifetime biomass production of sawgrass. As a result of taller leaf growth and greater frequencies of older growth stages at NLS, cumulative leaf production at this site appeared to be higher than at SLS. Water level regimes clearly regulated frequency distributions of growth stages at NLS and SLS and may have also contributed to site differences in leaf length. Conway (1938) found that leaf extension by Cladium mariscus was greatest when this species grew in continuously waterlogged soils like those that occur at NLS. Nutrient concentrations of most plant tissues reflected differences in surface water nutrient levels at the two sites, but it is not known if higher surface water nutrient concentrations at NLS led to "luxury consumption" and/or a simultaneous increase in tissue nutrient concentrations and plant production (Smith, 1962). However, higher nitrogen concentrations in stocks and rhizomes at SLS provides evidence indicating that acquired nutrients may be distributed among plant tissues such that reproduction rather than individual plant biomass production is promoted. Thus, site differences in leaf growth also may have been influenced by life history strategies that sawgrass adopts when exposed to contrasting hydrologic conditions.

Interactions between hydrologic regimes and sawgrass growth, production and life history patterns extend to nutrient uptake and storage dynamics. Site differences in nutrient uptake were primarily associated with cumulative leaf production and probably involve contrasting nutrient recycling pathways. Nutrients accumulated by sawgrass leaves may be recycled directly, through translocation, or reabsorbed after release from dead and decomposing leaf tissues. Translocation appears to be the most effective means of accomodating reproductive effort required by prevailing hydrologic conditions at SLS because nutrients released by dead tissues are generally greatly diluted by the predominately deep water levels that occur at this site, and are subject to uptake by more efficient competitors, like free-living algae and periphyton (Whittaker, 1975), which thrive under the open canopy. In contrast, dense leaf foliage at NLS appears to inhibit development of understory algal communities as well as new sawgrass shoots (Conway, 1938). Thus, nutrients released from decomposing leaf litter at NLS are readily available for recycling by existing sawgrass culms. In fact, plant decomposition processes appear to account for the high surface water nitrogen concentrations that were encountered at this site (i.e., relative to SLS). Although nutrient recycling pathways appear to complement sawgrass growth and life history characteristics, recycling is not an efficient mechanism for permanent removal of nutrients from surface waters, particularly when nutrient loads are high (Shaver and Melillo, 1984).

A potentially important means by which sawgrass may act as a nutrient sink involves burial of dead plant tissues below the zone of nutrient uptake before stored nutrients are released by decomposition processes. Decomposition rates in marsh soils are typically slow (Hackney and de la Cruz, 1980), so considerable organic matter accumulation may occur before sawgrass tissues completely break down and stored nutrients are released. At NLS and SLS, intact remnant plants with attached roots, rhizomes and some remnant leaves were found as deep as 40 cm below the soil surface. Moreover, results of a radiophosphorus study (Davis, 1982) suggest that nutrient uptake by sawgrass roots occurs primarily in the surface litter layer. Thus, nutrient uptake and storage by sawgrass tissues can be a significant means by which limited inputs of nutrients are permanently removed from Everglades surface waters. However,

due to differences in sawgrass growth characteristics, this function is probably more effective in stands like NLS than SLS. As a result of lower plant growth rates and leaf production at SLS, the rate of organic matter deposition is lower at this site than at NLS. Furthermore, in contrast to NLS, where roots, rhizomes and stocks of sawgrass grow belowground, all plant parts at SLS are perched above the soil surface. Consequently, most nutrients that are released as plant tissues at SLS die and decompose are returned to surface water, where they are probably recycled. At NLS, nutrients that are stored in leaves also are subject to recycling, but nutrients that are released by slow decomposition of roots, rhizomes and stocks are likely trapped in the soil. Although retention of nutrients in belowground tissues may permanently remove up to 11% of nitrogen and phosphorus accumulated by plants at NLS, the definitive value of sawgrass as a nutrient sink appears to be largely dependent upon the ultimate fate of nutrients associated with plant tissues that are deposited on the soil surface.

In summary, while roots, rhizomes and stocks may account for as much as 28% of total sawgrass biomass production, and stocks are the principal sawgrass nutrient storage organ, the importance of these plant tissues in nutrient flux in Everglades surface waters is subordinate to leaf production and associated nutrient recycling dynamics. Thus, investigations that track the ultimate fate of nutrients stored in decomposing leaf litter (Davis, in prep.) are needed to define precisely the value of sawgrass as a nutrient sink. However, water regimes such as those at SLS clearly lead to stands with growth characteristics that are incompatible with management goals regarding nutrient retention in the Water Conservation Areas.

Plant growth relationships established in this study provide a simple method for evaluating sawgrass production and nutrient storage at other locations in the Everglades system.

CONCLUSIONS AND RECOMMENDATIONS

1. Biomass production, tissue nutrient concentrations, and nutrient storage potential of sawgrass is higher in stands exposed to shallow water levels than in stands where water levels are predominately deep and undergo unnatural fluctuations.

2. In both water level regimes, nutrient uptake and retention by belowground sawgrass tissues is of minor import compared to nutrient flux associated with aboveground production and decomposition of plant litter on the soil surface.

3. Results of this study should be integrated with other Environmental Sciences Division research dealing with ecological implications of current and proposed water management practices in the Water Conservation Areas. These studies provide the environmental basis for the formulation of management guidelines that can be used in the decision making process to insure the integrity of the Everglades ecosystem.

4. Because predominately deep water level regimes appear to provide unfavorable conditions for growth and survival of sawgrass, and interfere with the ability of this species to permanently remove surface water nutrients, management options leading to excessive depths in the Water Conservation Areas should be avoided. Measures such as the newly implemented water regulation schedule should continue to be taken to alleviate high water level conditions in Water Conservation Area 2A.

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APPENDIX 1. **Mean Nitrogen and Phosphorus Concentrations (% Dry Weight) of Live Plant Components during each Sampling Period.**

	Fall 1982	Winter 1983	Spring 1983	Summer 1983	Fall 1983
		TKN Concentrations-Young Plants (NLS)			
Live Leaves	0.95	0.92	0.89	1.05	0.96
Dead Leaves	0.82	0.54	0.66	0.75	0.65
Remnant Leaves	0.53	0.58	0.38	0.42	0.44
Root Stocks	2.23	1.69	1.69	1.56	1.76
		TKN Concentrations-Mature Plants (NLS)			
Live Leaves	0.94	0.73	0.69	0.67	0.60
Dead Leaves	0.58	0.46	0.42	0.45	0.43
Remnant Leaves	0.74	0.52	0.58	0.56	0.55
Root Stocks	1.00	0.85	0.70	0.95	0.86
Rhizomes	0.49	0.46	0.45	0.48	0.47
Roots	0.98	0.76	0.81	0.84	0.76
		P Concentrations-Young Plants (NLS)			
Live Leaves	0.052	0.063	0.064	0.105	0.088
Dead Leaves	0.035	0.026	0.036	0.077	0.043
Remnant Leaves	0.019	0.024	0.017	0.025	0.019
Root Stocks	0.248	0.201	0.235	0.293	0.382
		P Concentrations-Mature Plants (NLS)			
Live Leaves	0.038	0.037	0.035	0.038	0.032
Dead Leaves	0.018	0.017	0.012	0.017	0.014
Remnant Leaves	0.023	0.020	0.021	0.021	0.019
Root Stocks	0.045	0.096	0.066	0.140	0.011
Rhizomes	0.019	0.024	0.018	0.023	0.015
Roots	0.023	0.026	0.027	0.036	0.028
		TKN Concentrations-Young Plants (SLS)			
Live Leaves	0.88	1.00	0.78	0.66	0.65
Dead Leaves	0.49	0.49	0.46	0.45	0.44
Remnant Leaves	0.45	0.47	0.31	0.37	0.37
Root Stocks	1.25	1.54	1.29	1.37	1.65
Rhizomes	0.63	0.70	0.66	0.58	0.55
Roots	0.71	0.65	0.54	0.56	0.58
		TKN Concentrations-Mature Plants (SLS)			
Live Leaves	0.73	0.66	0.57	0.55	0.54
Dead Leaves	0.44	0.38	0.35	0.36	0.38
Remnant Leaves	0.62	0.64	0.52	0.51	0.55
Root Stocks	1.15	1.10	1.10	1.06	1.12
Rhizomes	0.65	0.65	0.48	0.47	0.52
Roots	0.73	0.63	0.57	0.57	0.56
		P Concentrations-Young Plants (SLS)			
Live Leaves	0.041	0.074	0.044	0.032	0.035
Dead Leaves	0.017	0.016	0.016	0.011	0.011
Remnant Leaves	0.012	0.034	0.009	0.008	0.009
Root Stocks	0.077	0.074	0.122	0.196	0.162
Rhizomes	0.021	0.029	0.021	0.023	0.038
Roots	0.016	0.026	0.012	0.013	0.013
		P Concentrations-Mature Plants (SLS)			
Live Leaves	0.024	0.027	0.024	0.021	0.024
Dead Leaves	0.010	0.009	0.008	0.008	0.008
Remnant Leaves	0.012	0.010	0.009	0.011	0.010
Root Stocks	0.032	0.032	0.063	0.091	0.093
Rhizomes	0.014	0.014	0.014	0.014	0.014
Roots	0.014	0.011	0.011	0.011	0.010