ABOVEGROUND BIOMASS AND NET PRIMARY PRODUCTION ALONG A VIRGINIA BARRIER ISLAND DUNE CHRONOSEQUENCE

by

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ABSTRACT

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Aboveground biomass was examined along a chronosequence of dune communities on Hog Island, a Virginia Coast Reserve LTER site. The dominant species were Ammophila breviligulata and Spartina patens. Aboveground biomass was harvested monthly from ten quadrats on dunes 6, 24, 36, and 120 years old. Sampling was conducted from April to November 1993. Biomass values were greater for younger dunes. Total aboveground biomass decreased with increasing site age and ranged from 152 g m^{-2} on the 120 year old dune to 205 g m^{-2} on the 6 year old dune in October 1993. Spartina patens biomass was greater than Ammophila breviligulata for the 6, 24, and 36 year old dune ridges. It also showed a pattern of decreasing biomass with increasing dune age; in July it ranged from 72 g m^{-2} to 5 g m^{-2}. The same month showed less variation in Ammophila breviligulata; it increased from 17 g m^{-2} to 39 g m^{-2} across increasing dune age. Ammophila breviligulata had greater biomass for only the 120 year old dune. Net aboveground primary productivity did not vary greatly among different age dunes. There appeared to be a midsummer decline in biomass due to drought conditions. The aboveground net primary production (ANPP) from the sum of species peaks was 259 g m^{-2} yr^{-1} for the 6 year old dune, 226

g m^{-2} yr^{-1} for the 24 year old dune, 256 g m^{-2} yr^{-1} for the 36 year old dune and 274 g m^{-2} yr^{-1} for the 120 year old dune. Nitrogen and phosphorus concentrations in plant tissue were low. Biomass and nutrient values are reflective of production in a stressed environment. The variation in production of aboveground biomass across dune age may be controlled by moisture, microclimatic conditions and soil nitrogen levels.

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INTRODUCTION

The ecology of sand dune plants has been widely studied. The landmark work by Cowles (1899) on the vegetational and physiographic dynamics of the Lake Michigan dunes is considered the first thorough study of a complete successional series. Cowles accomplished this by assuming that the spatial dune series of Lake Michigan paralleled a temporal successional change. On a smaller scale, spatially and temporally, a similar time space dune arrangement exists on Hog Island, a National Science Foundation Long Term Ecological Research (LTER) site located along the eastern shore of Virginia. A large body of data has been gathered on aboveground production in natural grasslands; however, aboveground biomass and production in dune grass systems have not been as extensively studied. These estimates are important because natural dune systems are increasingly being altered and disturbed by humans (Dolan et al., 1973). Clampitt (1991) stated the maritime dunes at Seashore State Park in Virginia Beach, Virginia are degraded and small and active dune communities in Virginia are rare and declining. Shoreline stabilization is an area that has met only moderate success.

Although aboveground and belowground production data are necessary to fully understand total production, the bulk of vegetation data has focused on aboveground production. Belowground biomass has been studied on Hog Island dunes by Conn and Day (1993) and seasonal fine root production has been examined by Stevenson and Day (1993). The present study quantified aboveground biomass and production on Hog Island. Although numerous studies have examined dune vegetation on Hog Island (Dueser et al., 1976; Levy, 1990; McCaffrey and Dueser 1990a; 1990b), none have quantitatively followed growth for an entire growing season. Hall and Scurlock (1991) proposed there is still a critical need for more work on long-term primary productivity of natural grasslands. The present study is intended as the beginning of a long term evaluation of aboveground biomass, species composition and production of dune vegetation on Hog Island. These types of basic ecological measurements are fundamental for the NSF's Long Term Ecological Research Program (Franklin et al., 1990).

The environmental extremes that are associated with barrier islands provide an interesting framework for production studies. Zonation patterns on barrier islands appear to be controlled by many physical and chemical factors. Oosting and Billings (1942) and Oosting (1945) examined the effects of salt spray on vegetational zonation of coastal dunes and found that tolerance to wind born salt explained the zonal distribution of major dune species. Due to the highly leached sandy soils common to dune ecosystems, the soil NaCl does not accumulate to toxic levels on Hog Island dunes. The salt spray, however, greatly affects the vegetation. On Hog Island, overwash has an important influence on vegetation life history characteristics. Fahrig et al. (1993) found that on Hog Island perennials reproducing by clonal spreading are more common in areas of high overwash probability.

Island ecosystems are subject to other harsh environmental conditions that influence plant growth and reproduction. The effects of erosion, burial, water and nutrient loss, and pH fluctuations are prevalent in coastal systems. Van der Valk (1974) examined the dune sands in North Carolina and noted very low cation exchange capacities. He also found salt spray to account for a large annual input of nutrients and to substitute for the lack of an internal reservoir. Salt spray has been found to contain all necessary mineral ions for plant growth except nitrates and phosphates (Boyce, 1954). The constant deposition and leaching that Van der Valk measured in coastal foredune communities are characteristic of a very inefficient nutrient cycle. Odum (1969) and Vitousek and Reiners (1975) proposed this loose nutrient cycling is common in an early successional ecosystem.

The major questions addressed in the present study were: (1) How does aboveground production vary along a chronosequence of dunes? (2) How does species composition vary along a chronosequence of dunes? and (3) What are the seasonal dynamics of aboveground biomass and species composition? To examine these questions monthly sampling was conducted on the different age dunes on Hog Island to determine the relationship between dune age, biomass production and species richness.

SITE DESCRIPTION

Hog Island (37° 40'N, 75° 40'W) is a barrier island that is part of the Nature Conservancy's Virginia Coast Reserve, and is designated as a Long Term Ecological Research (LTER) site (Fig. 1). The island has a low-lying topography and is 11.3 km long with an average width of 0.8 km. It is located 14 km from the mainland with the long axis of the island oriented north-south, parallel to the Delmarva Peninsula (Fig. 2). Hog Island is one of 13 barrier islands located along the eastern shore of the Delmarva Peninsula in Accomack County, Virginia. The island is approximately 5000 years old (Hayden et al., 1991). From 1608 to 1700 it was used by the Accomac and Accohannock indian tribes (Hayden et al., 1991). Later the island was used as pasture with the last feral cows removed in the 1980's. Hog Island has a highly dynamic physical environment. The town of Broadwater was miles from shore on the southern end of Hog Island in 1603 (Hayden et al., 1991), but, by 1933 the shore was even with the town and presently the site of the town is several hundred meters offshore. Despite the scattered disturbances from man the island is presently free from anthropogenic disturbance.

Fig. 1. Study site location on Hog Island, Virginia. The chronosequence is illustrated by the transect on the northern end of the island.

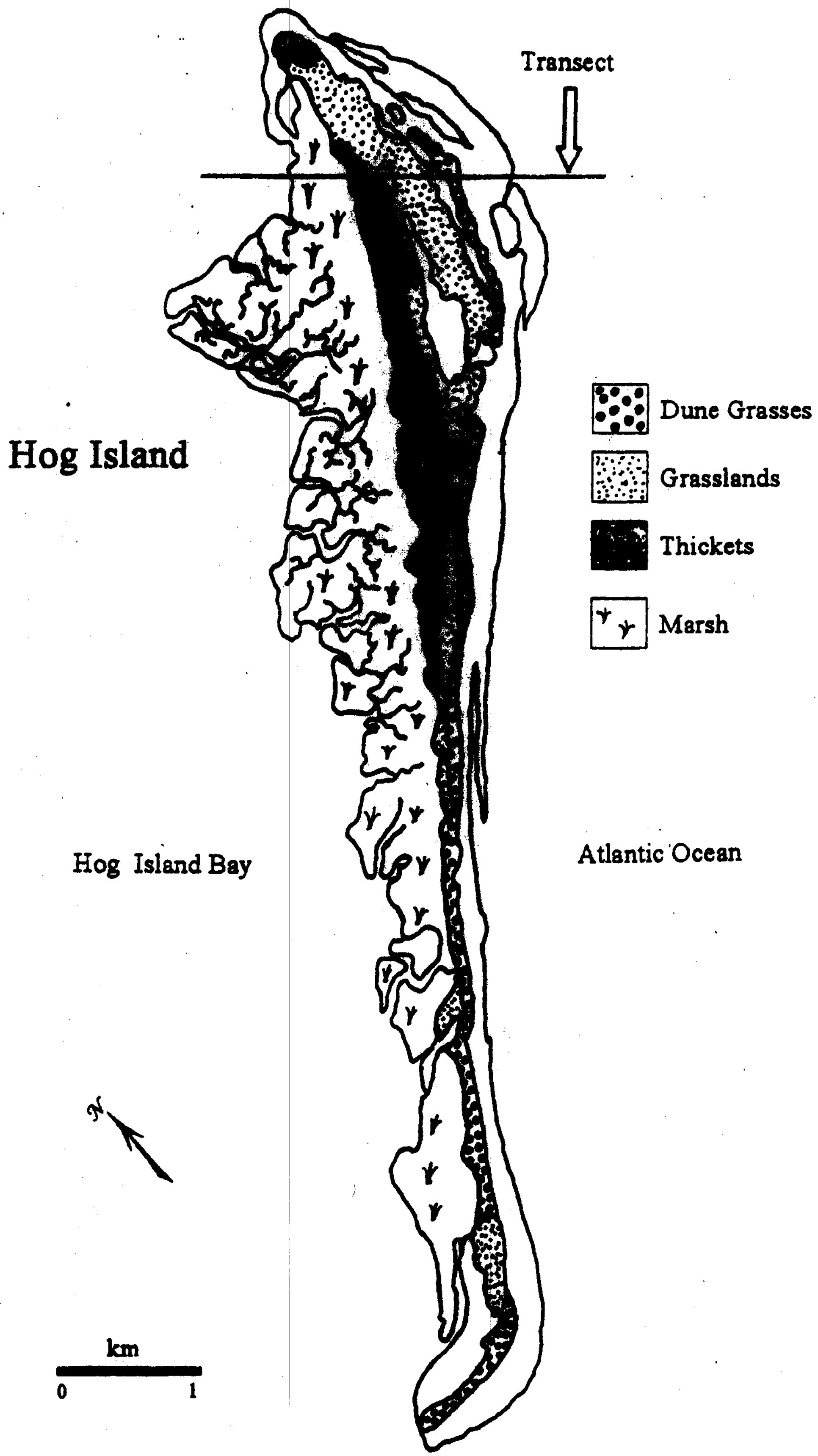
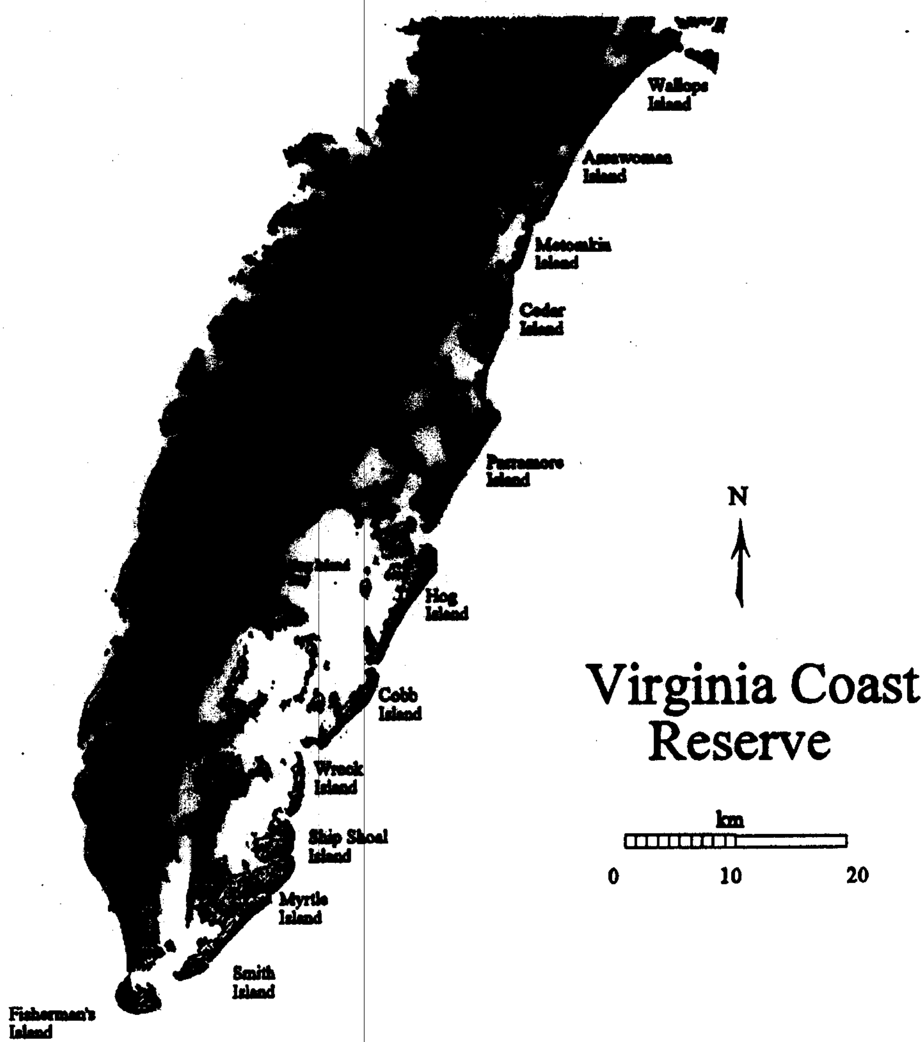

Transect
Dune Grasses
Grasslands
Thickets
Marsh
Hog Island
Hog Island Bay
Atlantic Ocean
N
km
0
1

Fig. 2. Hog Island in the Virginia Coast Reserve on the eastern shore of Virginia.


Wallops Island
Assawoman Island
Metomkin Island
Cedar Island
Parramore Island
Hog Island
Cobb Island
Wreck Island
Ship Shoal Island
Myrtle Island
Smith Island
Fisherman's Island
N
Virginia Coast Reserve
km
0
10
20

The sites in this study were on the northern end of the island with an approximate maximum age of 130 years (Hayden et al., 1991) (Fig. 1, 3). The island was formed from deposited marine sands. Soils are of the well drained Newhan-Corolla complex (Dueser et al., 1976). The Newhan soils are mixed, thermic, typic Udipsamments and the Corolla sand is a thermic uncoated typic quartzpsamment. Hog Island is impacted by recurrent extratropical storms (northeasters), tropical storms and hurricanes (Dolan and Hayden 1981). Hog Island is heavily influenced by salt spray, overwash, and other marine influences. Previous measurements of soil organic matter, soil NO_2+NO_{3-}, soil NH_4, soil water NO_2+NO_{3-}, TKN and NH_4 and soil Eh and pH have been completed on these research sites (Table 1) (Day and Lakshmi, unpublished). Several environmental patterns were observed along the dune chronosequence. Soil NH_4 was lower on the 6 year old site than on the 24, 36, and 120 year old site (Table 1). Soil redox was significantly higher on the older dunes (Table 1). The oldest dune had significantly higher ($P<0.05$) soil organic matter (Table 1). There was also a pattern of increasing NO_2+NO_3^- with increasing dune age and of increasing available nitrogen with increasing dune age (Table 1).

A weather observatory is operated by the University of Virginia in an area adjacent to the oldest study site, near the interior of the island. Historical 50 year

Fig. 3. Hog Island dune chronosequence.

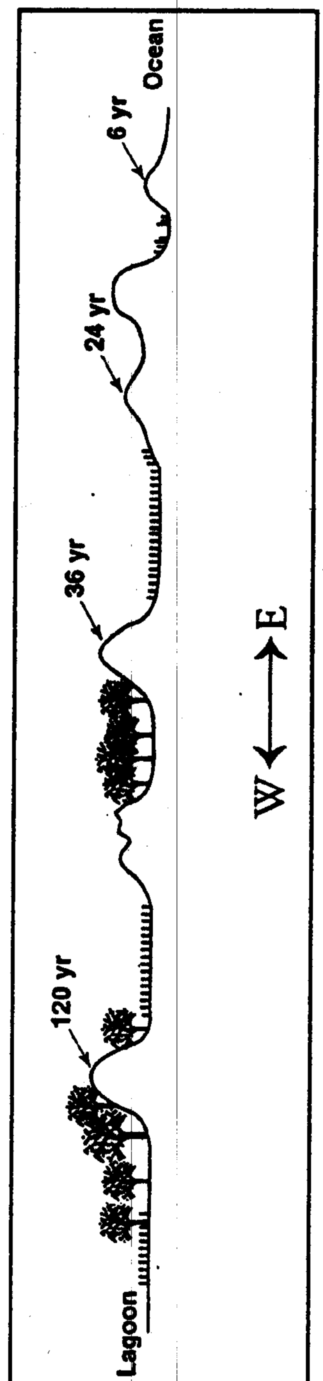

Lagoon
120 yr
36 yr
24 yr
6 yr
Ocean
W
E

Table 1. Environmental characteristics of Hog Island dunes. Values are annual means (1991) with one standard error in parentheses (Day and Lakshmi unpublished).

	Dune age			
	6 yr	24 yr	36 yr	120 yr
Soil Eh(mv)		488(5)	529(5)	541(5)
Soil pH		6.2(0.1)	5.9(0.1)	5.7(0.1)
Soil temp(°C)		22(1)	24(1)	23(1)
Ground water level(cm)		-92	-97	-116
Groundwater range (cm)		-116 to -48	-134 to -39	-137 to -78
Soil Organic Matter(%)		0.51(0.05)	0.42(0.01)	0.60(0.08)
PO_4, Soil water (mg/l)		0.02(0.004)	0.02(0.004)	0.02(0.006)
Total P, Soil Water (mg/l)		0.07(0.01)	0.07(0.01)	0.09(0.02)
N-Mineralization rate ($gm^{-2}\ yr^{-1}$)		0.20	0.02	0.19
Mineralization ($mg\ kg^{-1}\ day^{-1}$)	0.008	0.053	0.015	0.047
Nitrate+ Nitrite-N ($mg\ kg^{-1}$)	0.30	0.17	0.29	0.44
Ammonium-N ($mg\ kg^{-1}$)	0.88	2.09	2.53	2.37

precipitation records indicate a range of 85 to 140 cm per year. The 1993 precipitation totaled 70.5 cm. This is slightly lower than the yearly range; however, during the 1993 growing season precipitation was 50% below average for July, August, and September (Table 2). Mean daily temperature for this region ranges from -1 to 10° C in January and 18 to 30° C in July (Dueser et al., 1976).

The northern end of Hog Island is accreting 5 m per year. This has resulted in a chronosequence of dunes of increasing age extending east to west. This time-space cross-section of the island has been determined through detailed analysis of historical aerial photographs and survey charts (Hayden et al., 1991). A shoreline growth of almost a km has been observed on the northern end since 1871. The study sites, four dune ridges (6, 24, 36, and 120 years old), represented the chronosequence across the island (Fig. 3). The six-year-old dune is the most unprotected site with greatest maritime influence. The older dunes are greater distances from the ocean and thus less influenced by salt spray and wind. <u>Spartina patens</u> (Aiton) Muhl. and <u>Distichlis spicata</u> (L.) Greene dominate the marsh swale communities west of the 6 and 24 year old dunes. <u>Myrica cerifera</u> L., an actinorhizal nitrogen fixing shrub, dominates the swales west of the 36 and 120 year old dunes.

The plant species composition on Hog Island varies significantly with topographic position. The dune

Table 2. Average monthly temperature and rainfall, Hog Island, 1993. * (Krovetz and Porter, 1993)

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
°C	6	3	6	11	19	23	27	24	22	16	11	5
PPT mm	107	55	144	62	97	62	36	22	82	84	28	68

* Data from on site or nearest weather station

vegetation of Hog Island is conspicuously patchy with clear zonation and sharp transition between patches (Dueser et al., 1976). The plants dominant on the dunes are Ammophila breviligulata Fern., Spartina patens, Panicum amarum Ell., and Aristida tuberculosa Nuttall. Only one frequently occurring dune species is introduced. Fernald (1950) described Rumex acetosella L. as a species introduced to the island. In this study two species rare in the state of Virginia were encountered. The scale used by The Virginia Natural Heritage Program to rank plant rarity ranges from S1 to S5, with S1 being an endangered species; Aristida tuberculosa Nutt. was found to be S1S2 and Euphorbia ammanoides HBK to be S1 (Virginia Natural Heritage Program, 1989).

METHODS

Measurement of aboveground biomass of vascular plants was completed within 10 0.25 m^2 plots randomly located on each of the four dunes. Sampling was conducted once a month from April 1993 to October 1993. Plots were harvested of all live vegetation as close to the soil surface as possible. Biomass here refers to live vegetation only. The vegetation was then sorted by species and placed into labeled paper bags. Nomenclature follows Radford, Ahles, and Bell (1968). Plots were flagged in the center to prevent duplicate sampling during the growing season. Plant material was oven dried at 70° C for 48 hours and the mass determined on an analytical balance. The dried Ammophila breviligulata and Spartina patens samples were ground in a Wiley mill to 40 mesh size, acid digested and analyzed colorimetrically on a Scientific Instruments AP-200 autoanalyzer using the molybdate blue method for phosphorus and the total Kjeldahl method for nitrogen (Technicon Instruments, 1977). Ammophilia breviligulata and Spartina patens samples were bulked by site replicates on each date to get seasonal nutrient values for each species. Each replicate for each species in September, a peak biomass month, was individually analyzed to test for significant differences in nutrient concentrations between sites.

The peak biomass method was used to calculate net aboveground production from the harvests. The minimum monthly aboveground biomass was subtracted from the maximum monthly aboveground biomass for each species (Stroud, 1976). Dickerman et al. (1986) compared peak biomass values to other harvest methods of measuring production and found it to give consistently conservative estimates; thus, these data represent minimum estimates of net aboveground primary production. Total net aboveground production was determined by the summation of individual species. This is necessary because at the time of community peak biomass all of the species may not be at their individual peak biomass.

Herbivory was not considered because previous work along the dune chronosequence found no significant difference in growth between screened plots and unscreened plots (Day, unpublished).

Groundwater levels were continuously measured in wells equipped with Stevens recorders on the 24, 36 and 120 year old dunes. Eight hour means were averaged for daily well values. Hydrographs were generated from two week means.

Data were statistically analyzed using SAS version 6.01 on an IBM 3090 mainframe computer. A two way analysis of variance (ANOVA) was used to test for significant differences in total, _Spartina patens_, and _Ammophila breviligulata_ aboveground biomass among dune sites and dates and for a site*date interaction. Total biomass and _Spartina patens_ data were square root transformed to satisfy the normality assumption of the analysis. Site means of total, _Spartina patens_, and _Ammophila breviligulata_ aboveground biomass values were compared using the REGWF multiple comparison procedure. The average species richness values were analyzed by a two way analysis of variance (ANOVA) to test for a significant site*date interaction. Site means of average species richness were compared using the REGWF multiple comparison procedure. The nutrient concentration values were analyzed by a one way analysis of variance (ANOVA) to test for a significant site difference for nitrogen and phosphorus in both _Ammophila breviligulata_ and

Spartina patens and for a species*site interaction. TUKEYS standardized range test was used to compare all possible pairs of means for nitrogen and phosphorus concentration in both species and for differences in species means for all sites.

RESULTS

ABOVEGROUND BIOMASS

Total aboveground biomass was highest on the 6 year old dune and ranged from 152 g m^{-2} on the 120 year old dune to 205 g m^{-2} on the 6 year old dune in October 1993. Total biomass increased after April, peaked in August, September and October, and declined thereafter (Fig. 4). There was no significant site*date interaction in total aboveground biomass (2-way ANOVA, F=0.81, p=0.7091). Dune total aboveground biomass differed significantly among sites (2-way ANOVA, F=5.10, p=0.0019). Biomass for the two youngest dune sites, 6 years old and 24 years old, did not significantly differ, and means for the three oldest dune sites, 24, 36 and 120 years old, did not significantly differ (REGWF, p<0.05)(Fig. 5). These results indicate a general pattern of decreasing total aboveground biomass with increasing dune age.

Graminoid contribution to aboveground biomass was 92% on the 120 year old dune, 95% on the 36 year old dune, 95%

Fig. 4. Seasonal total aboveground biomass for the dune chronosequence through the 1993 growing season. Error bars equal one standard error. N=10.

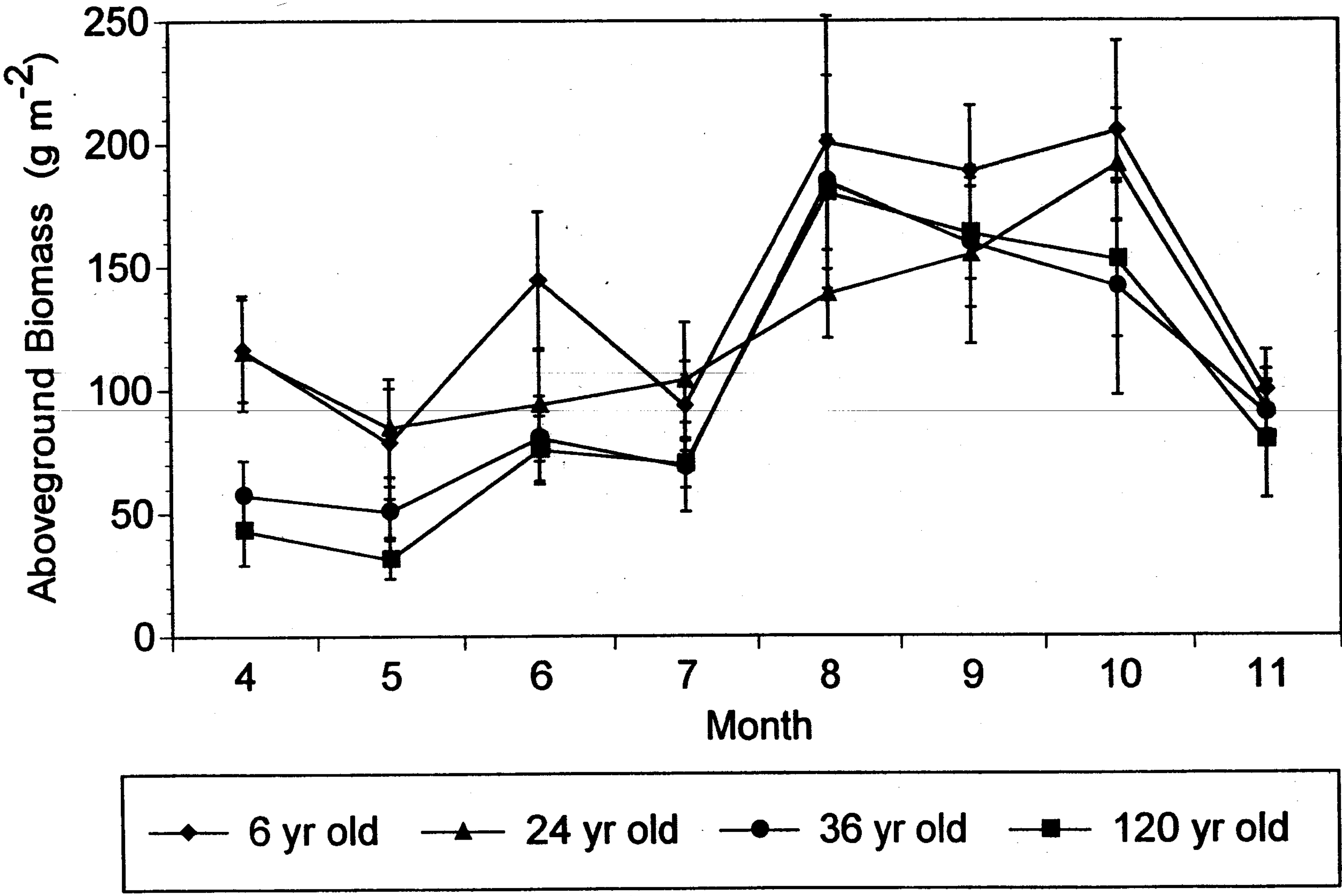
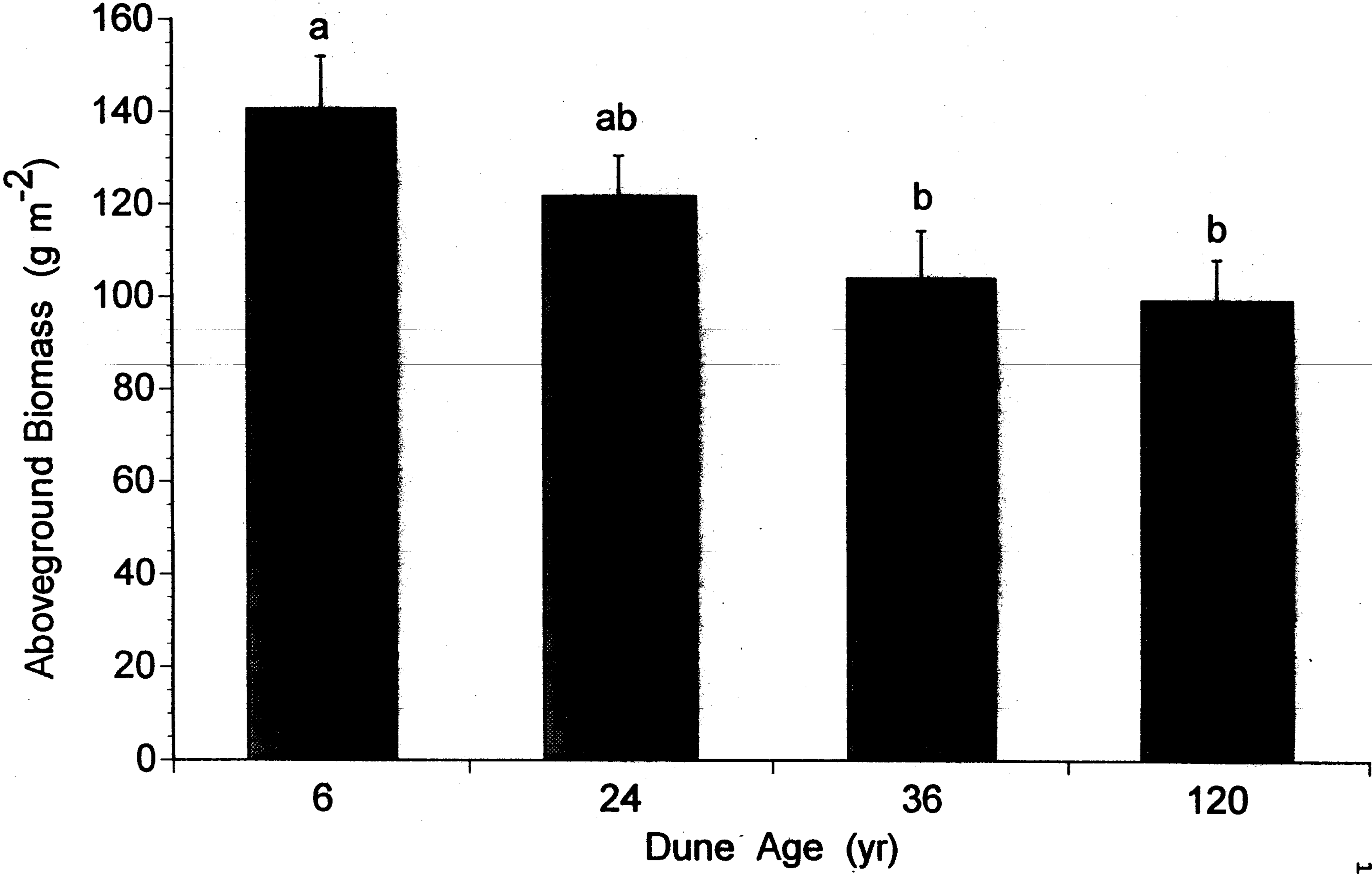

Aboveground Biomass (g m-2)
250
200
150
100
50
0
4
5
6
7
8
9
10
11
Month
6 yr old
24 yr old
36 yr old
120 yr old

Fig. 5. Total aboveground biomass along the dune chronosequence. Error bars are one standard error. Different lower case letters indicate significant differences among sites (REGWF $p<0.05$). N=80.



Aboveground Biomass (g m-2)
160
140
120
100
80
60
40
20
0
a
ab
b
b
6
24
36
120
Dune Age (yr)

on the 24 year old dune, and 97% on the 6 year old dune. The two dominant species found on the dunes are Spartina patens and Ammophila breviligulata. The 120 year old dune site was the only site with higher Ammophila breviligulata values than Spartina patens. There was a clear pattern of decreasing Spartina patens biomass with increasing dune age (Fig. 6). There was no significant site*date interaction for Spartina patens aboveground biomass (2-way ANOVA, F=0.87, p=0.6328). Spartina patens aboveground biomass on the six-year-old dune differed significantly (2-way ANOVA, F=25.28, p=0.0001) from the other dunes. The 24 year old and the 36 year old dunes were significantly different from the other dunes. The oldest dune, the 120 year old, was significantly different from the other dunes (REGWF, p<0.05)(Fig. 6). These results indicate a pattern of decreasing Spartina patens aboveground biomass with increasing dune age similar to the total aboveground biomass pattern (Fig. 5). Seasonally, Spartina patens aboveground biomass varied considerably (Fig. 7). The 120 year old dune had the lowest Spartina patens aboveground biomass consistently throughout the growing season. Spartina patens aboveground biomass peaked in August for both the 6 and 36 year old dunes and peaked in October on the 24 year old dune (Fig. 7).

Ammophila breviligulata had a slight increase in biomass with increasing dune age (Fig. 8). Ammophila

Fig. 6 Spartina patens aboveground biomass along the dune chronosequence. Error bars are one standard error. Different lower case letters indicate significant differences among sites (REGWF $p<0.05$). $N=80$.

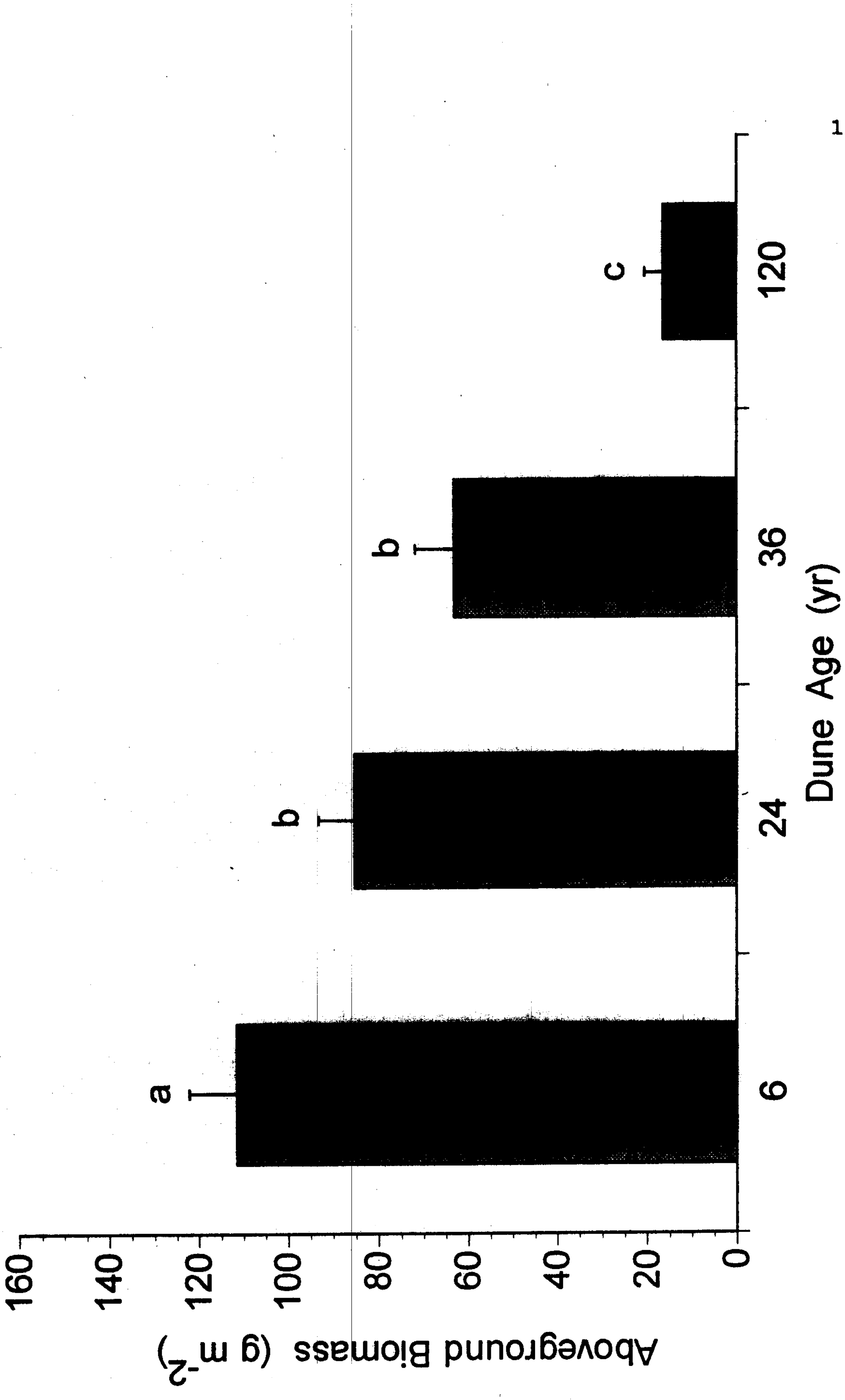
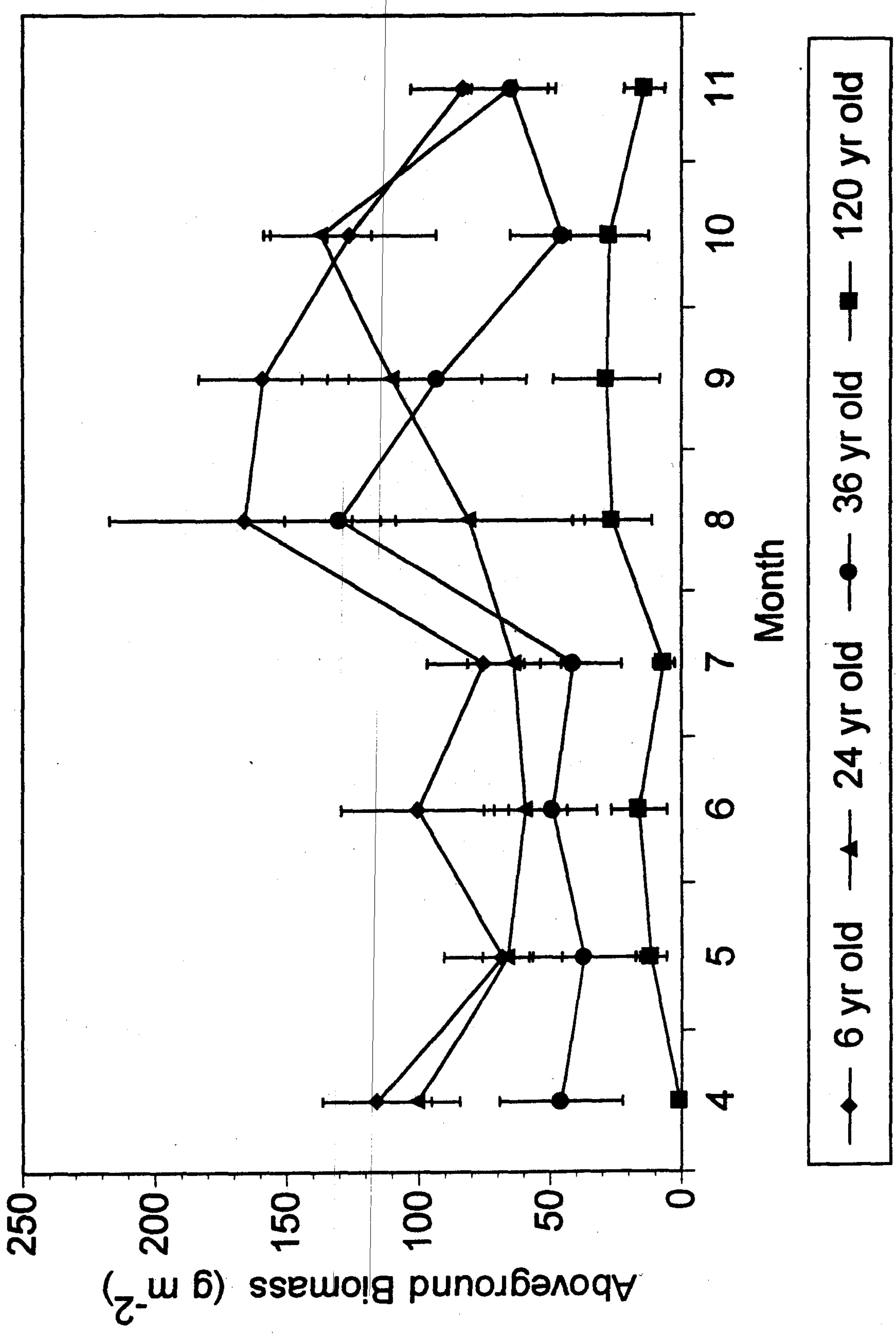
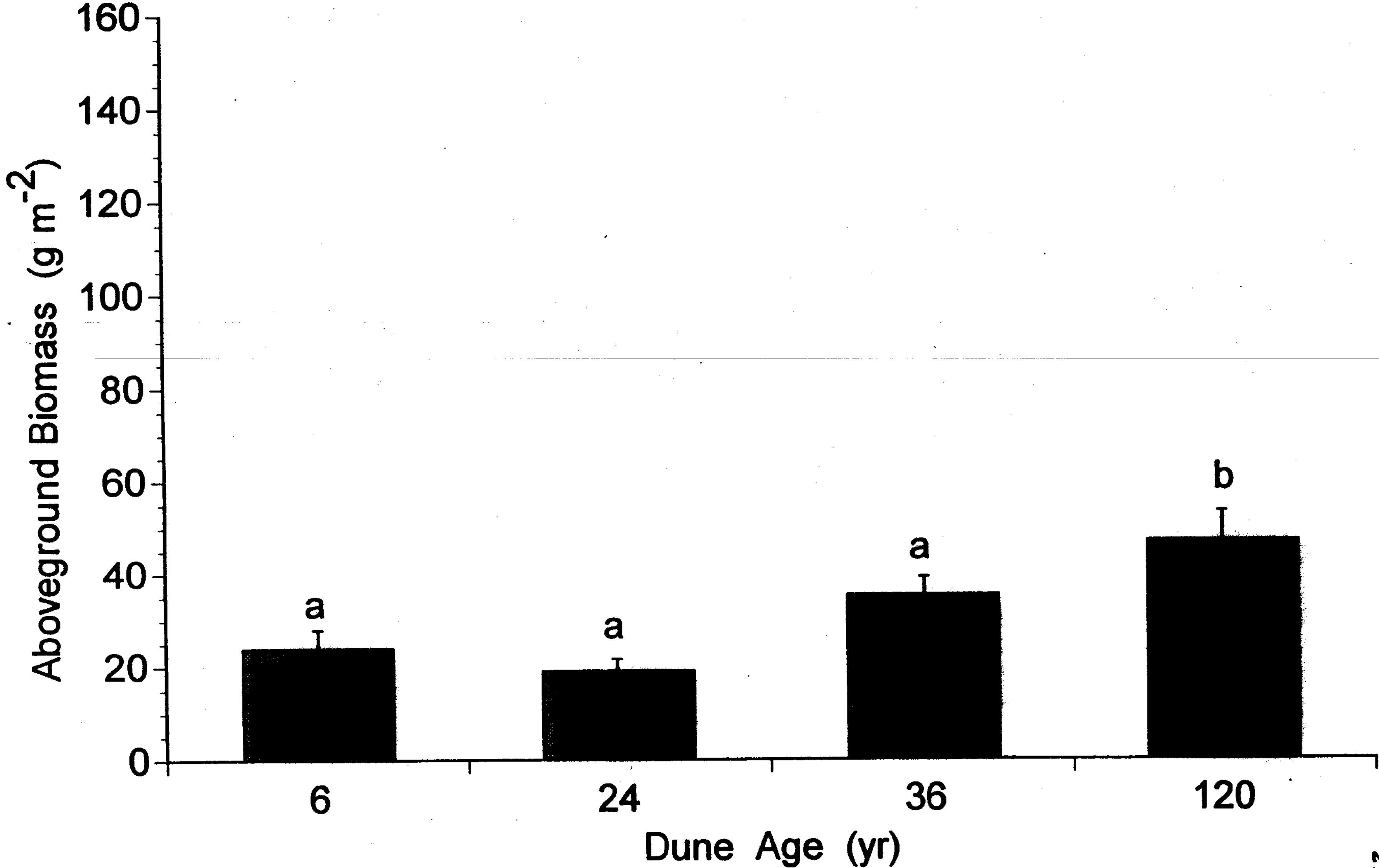

Aboveground Biomass (g m-2)
0
20
40
60
80
100
120
140
160
Dune Age (yr)
6
24
36
120
a
b
b
c

Fig. 7. Seasonal *Spartina patens* aboveground biomass for the dune chronosequence through the 1993 growing season. Error bars equal one standard error. N=10



Aboveground Biomass (g m-2)
250
200
150
100
50
0
4
5
6
7
8
9
10
11
Month
6 yr old
24 yr old
36 yr old
120 yr old

Fig. 8. *Ammophila breviligulata* aboveground biomass along the dune chronosequence. Different lower case letters indicate significant differences among sites (REGWF $p<0.05$). Error bars equal one standard error. N=80.

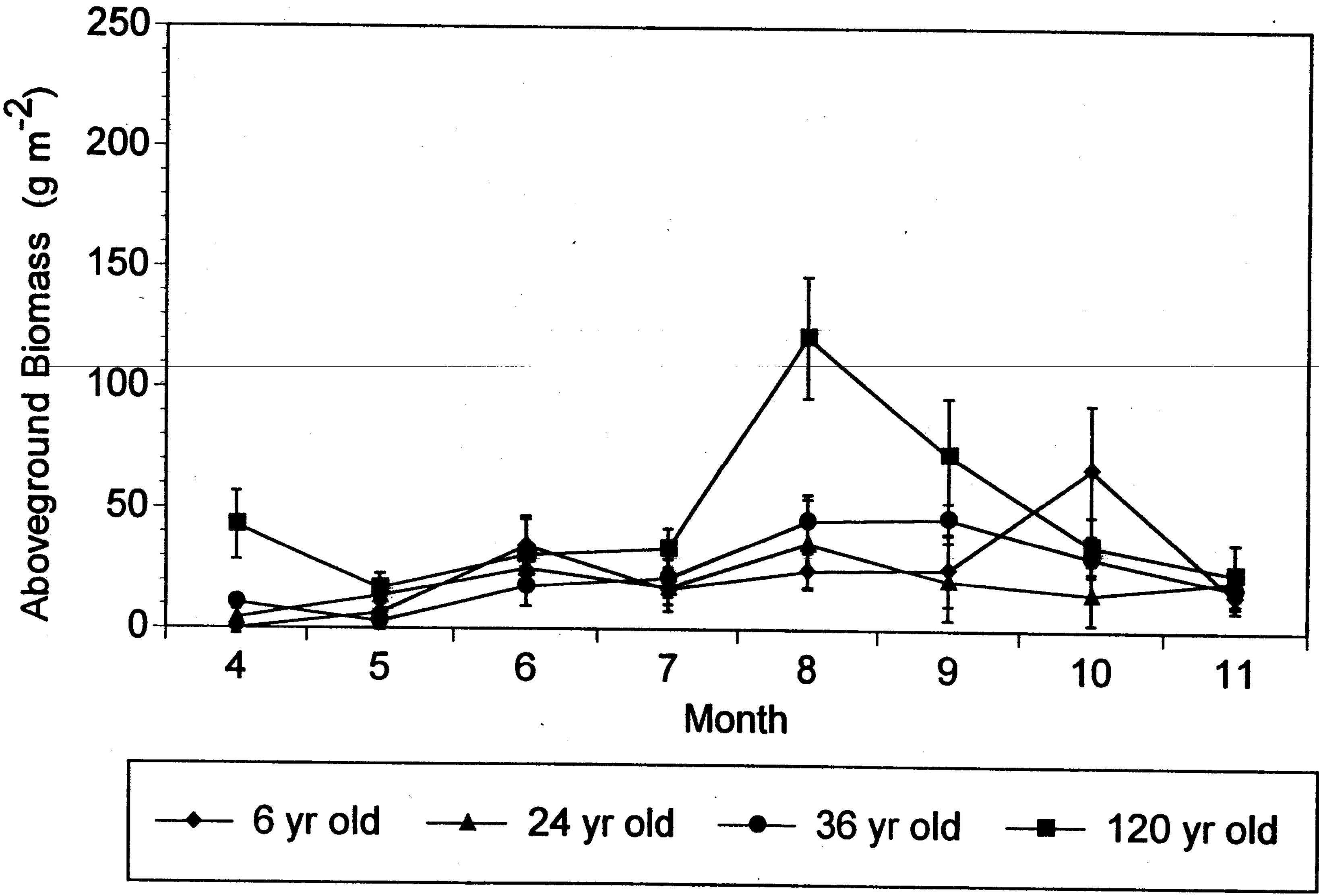

160
140
120
100
80
60
40
20
0
Aboveground Biomass (g m-2)
a
a
a
b
6
24
36
120
Dune Age (yr)

breviligulata had a significant site*date interaction (2-way ANOVA, F=2.20, p=0.0022). *Ammophila breviligulata* aboveground biomass on the dunes differed significantly (2-way ANOVA, F=8.78, p=0.0001). The oldest dune, the 120 year old, was significantly different from the other dunes (REGWF, $p<0.05$)(Fig 8). Seasonally, *Ammophila breviligulata* aboveground biomass peaked in August on the 120 year old dune (Fig. 9). The 6 year old dune showed a small peak in October. The 24 and 36 year old dunes had more uniform biomass values throughout the 1993 season.

ABOVEGROUND NET PRIMARY PRODUCTION

Aboveground biomass was collected from 19 species on the 120 year old dune, 17 species on the 36 year old dune, 11 species on the 24 year old dune, and 12 species on the 6 year old dune. The aboveground net primary production (ANPP) from the sum of species peaks was 259 g m^{-2} yr^{-1} for the 6 year old dune, 226 g m^{2} yr^{-1} for the 24 year old dune, 256 g m^{-2} yr^{-1} for the 36 year old dune and 274 g m^{-2} yr^{-1} for the 120 year old dune (Table 3). No patterns were apparent in ANPP data across sites. The peak community biomass was

Fig. 9. Seasonal *Ammophila breviligulata* aboveground biomass for the dune chronosequence through the 1993 growing season. Error bars equal one standard error. N=10



250
200
150
100
50
0
Aboveground Biomass (g m-2)
4
5
6
7
8
9
10
11
Month
6 yr old
24 yr old
36 yr old
120 yr old

Table 3. Contribution of species to total net aboveground primary production (g m^{-2} yr^{-1}) on Hog Island dunes, 1993.

Species	Site age (yr)			
	6	24	36	120
Spartina patens (Aiton)Muhl.	165.6	136.9	129.6	28.3
Ammophila breviligulata Fernald	67.0	35.9	46.3	121.3
Andropogon scoparius Michaux	0	0	37.0	39.2
Panicum amarum Ell.	4.4	36.4	4.4	9.0
Aristida tuberculosa Nuttall	6.7	0	18.1	30.1
Carduus spinosissimus Walter	2.7	6.8	8.7	8.7
Triplasis purpurea (Walt.)Chapman	0.1	0	0.1	8.7
Panicum lanuginosum Ell.	0	0.4	2.1	5.9
Eragrostis spectabilis (Pursh)Steudel	4.6	5.0	0.6	5.6
Eupatorium hyssopifolium L.	0	0	0	4.4
Erigeron canadensis L.	4.3	0.6	0.5	1.0
Rumex acetosella L.	1.5	1.3	1.8	3.3
Juncus dichotomus Ell.	0	0	2.6	1.3
Monarda punctata L.	0	0	0	2.5
Juncus canadensis J. Gay ex La Harpe	0	0	2.4	0
Festuca sciurea Nuttall	2.3	0.6	0	0.4
Solanum carolinense L.	0	1.5	1.5	0
Festuca rubra L.	0	0	0.7	0.2
Linaria canadensis (L.)Dumont	0.2	0	0.2	0.7
Gnaphilium purpureum L.	0.04	0.3	0.2	0.5
Parthenocissus quinquefolia (L)Planchon	0	0	0	0.2
Total	259.4	225.6	256.9	274.

respectively, for 6, 24, 36, and 120 year old dunes. This pattern of increasing difference in these two methods of production calculation can be attributed to the higher species richness of the older dunes.

SPECIES RICHNESS

Twenty-one species contributed to aboveground production along the entire dune chronosequence. All plants collected in this study are listed in Table 3. Species richness data are based on the total number of species found in all plots for each site (Table 4). Species richness was also calculated by calculating mean species number for all replicates (Fig. 10). No significant site*date interaction was found (2-way ANOVA, $F=1.38$, $p=0.1288$); however, species richness differed among the dune sites (2-way ANOVA, $F=5.13$, $p=0.0018$)(Fig. 10). Species richness was significantly lower in the 6 year old dune site than in the 24, 36, and 120 year old dune sites (REGWF, $p<0.05$).

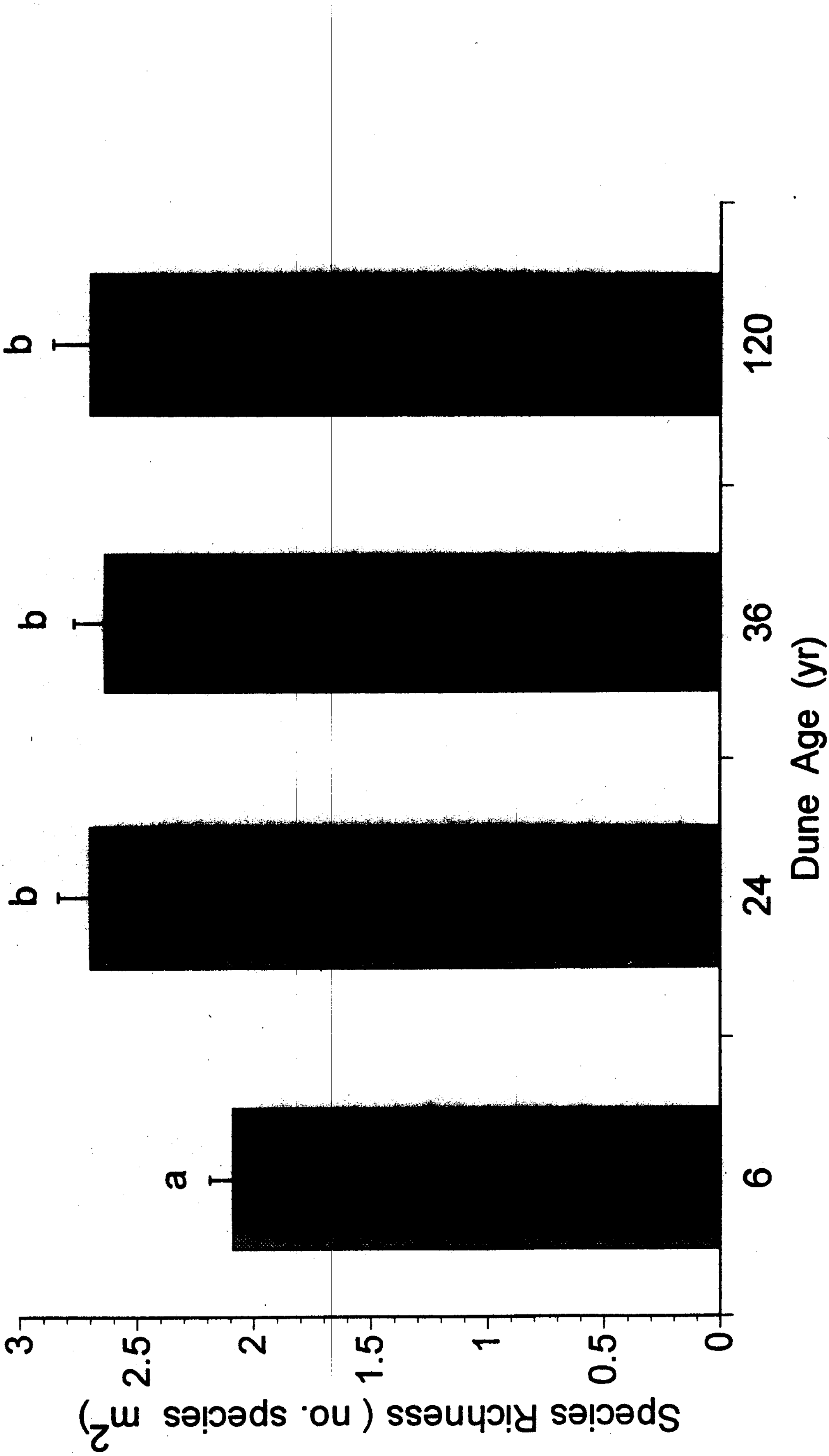
FOLIAR N AND P

Nitrogen and phosphorus nutrient concentrations in aboveground <u>Spartina patens</u> and <u>Ammophila breviligulata</u> were compared between species and sites for the month of August 1993 (Fig. 11 and 12). An inter-species comparison found significantly higher concentrations of nitrogen and phosphorus in <u>Ammophila breviligulata</u> aboveground tissue

Table 4. Species richness (total number of species in 10 sample plots) across Hog Island chronosequence, 1993.

Site Age (yr)	April	May	June	July	Aug	Sept	Oct	Nov
6	4	5	7	4	5	4	5	4
24	5	6	7	9	9	8	8	6
36	3	5	10	9	11	7	10	5
120	2	7	14	9	13	10	11	8

Fig. 10. Species richness per site(mean number of species in 10 sample plots). Error bars are one standard error. Different lower case letters indicate significant differences among sites (TUKEY p<0.05). N=80



Species Richness (no. species m^{-2})
0
0.5
1
1.5
2
2.5
3
a
b
b
b
6
24
36
120
Dune Age (yr)

Fig. 11. TKN in aboveground biomass of the two dominant species. Error bars are one standard error. Different lower case letters indicate significant differences among sites (TUKEY $p<0.05$). N=4-10

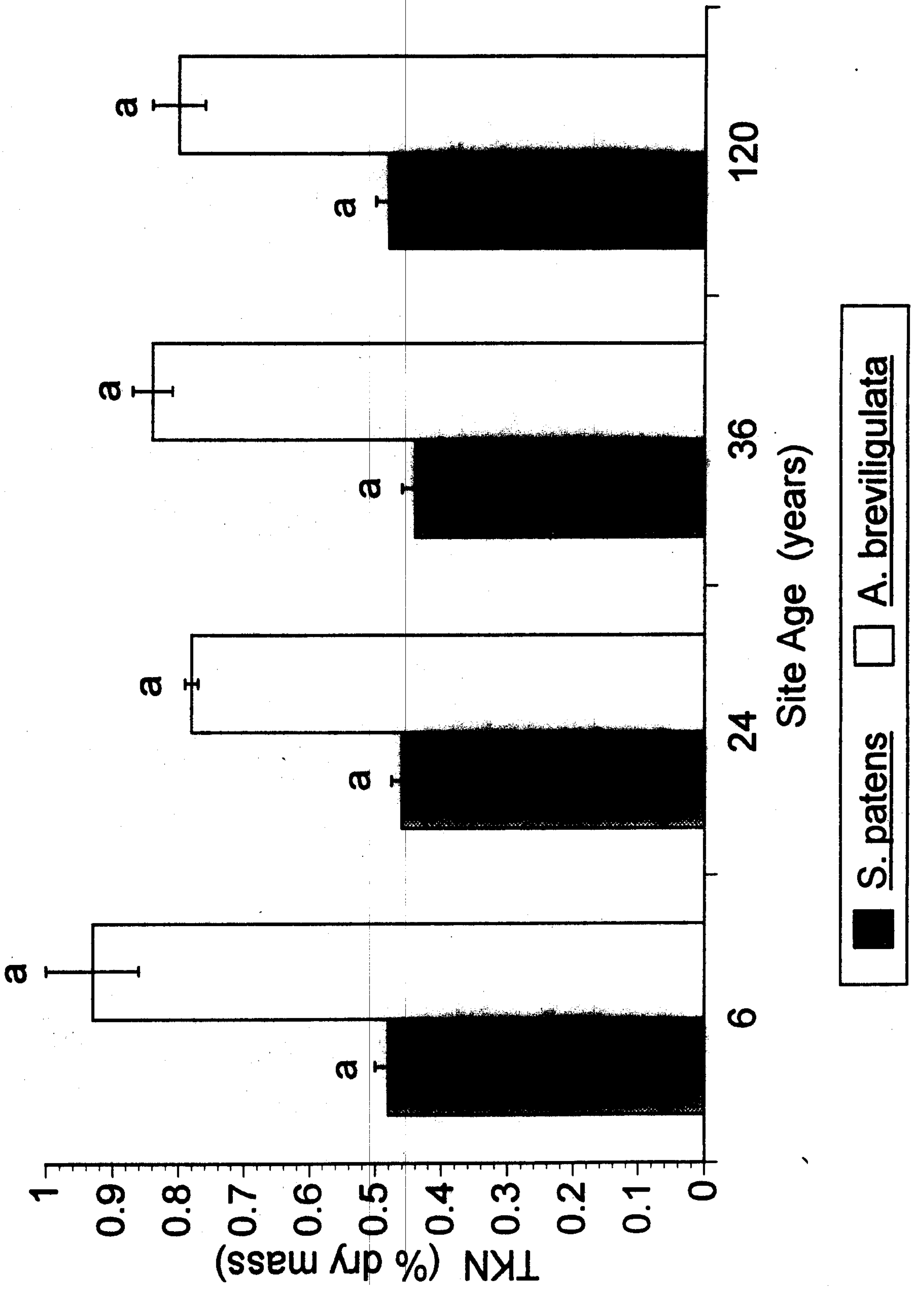
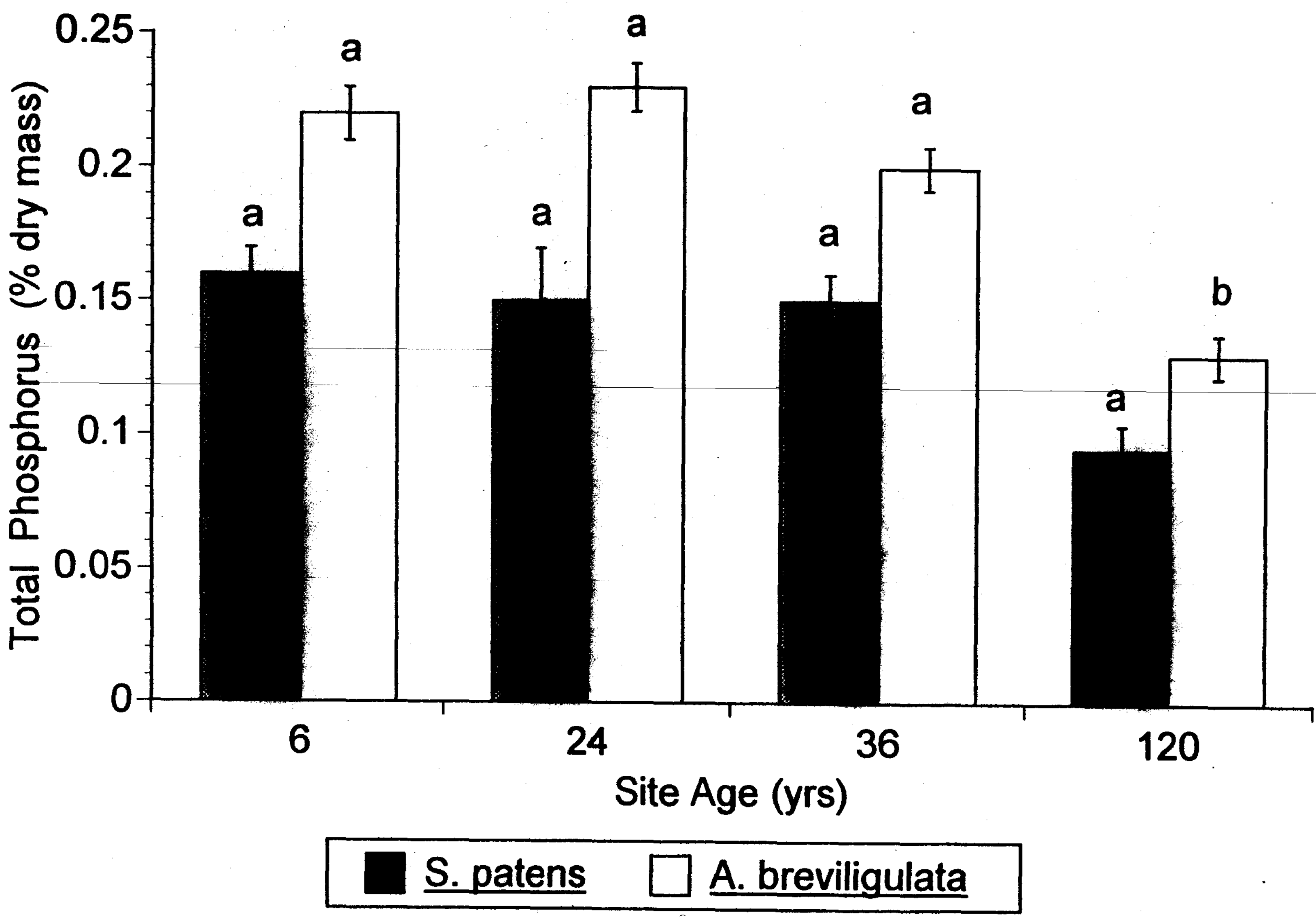

TKN (% dry mass)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
a
6
24
36
120
Site Age (years)
S. patens
A. breviligulata

Fig. 12. Total phosphorus in aboveground biomass of the two dominant species. Error bars are one standard error. Different lower case letters indicate significant differences among sites (TUKEY $p<0.05$). N=6-8

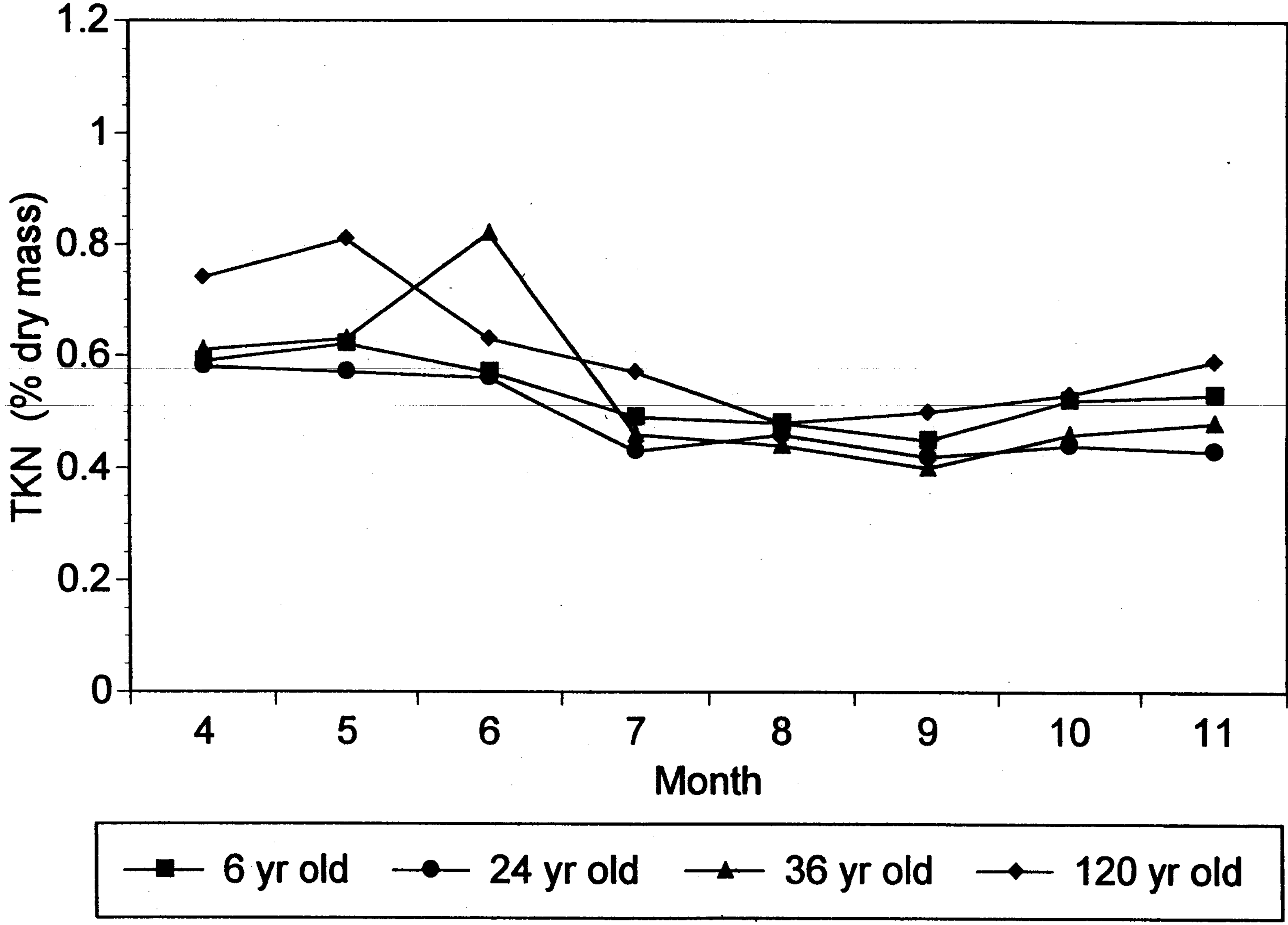

0.25
0.2
0.15
0.1
0.05
0
Total Phosphorus (% dry mass)
a
a
a
a
a
a
a
b
6
24
36
120
Site Age (yrs)
S. patens
A. breviligulata

than *Spartina patens* for all sites ($p<0.01$)(TUKEY, $p<0.05$).

Nitrogen concentration did not vary significantly ($p<0.01$) among sites for either species (Fig. 11). Nitrogen concentrations in *Spartina patens* remained stable throughout the growing season for all sites with a slight peak for the 36 year old dune in June and with the oldest site remaining higher than the other sites throughout the year (Fig. 13). In *Ammophila breviligulata* nitrogen concentrations were slightly higher in the first few months for the two older sites but later in the growing season the values were more similar (Fig. 14).

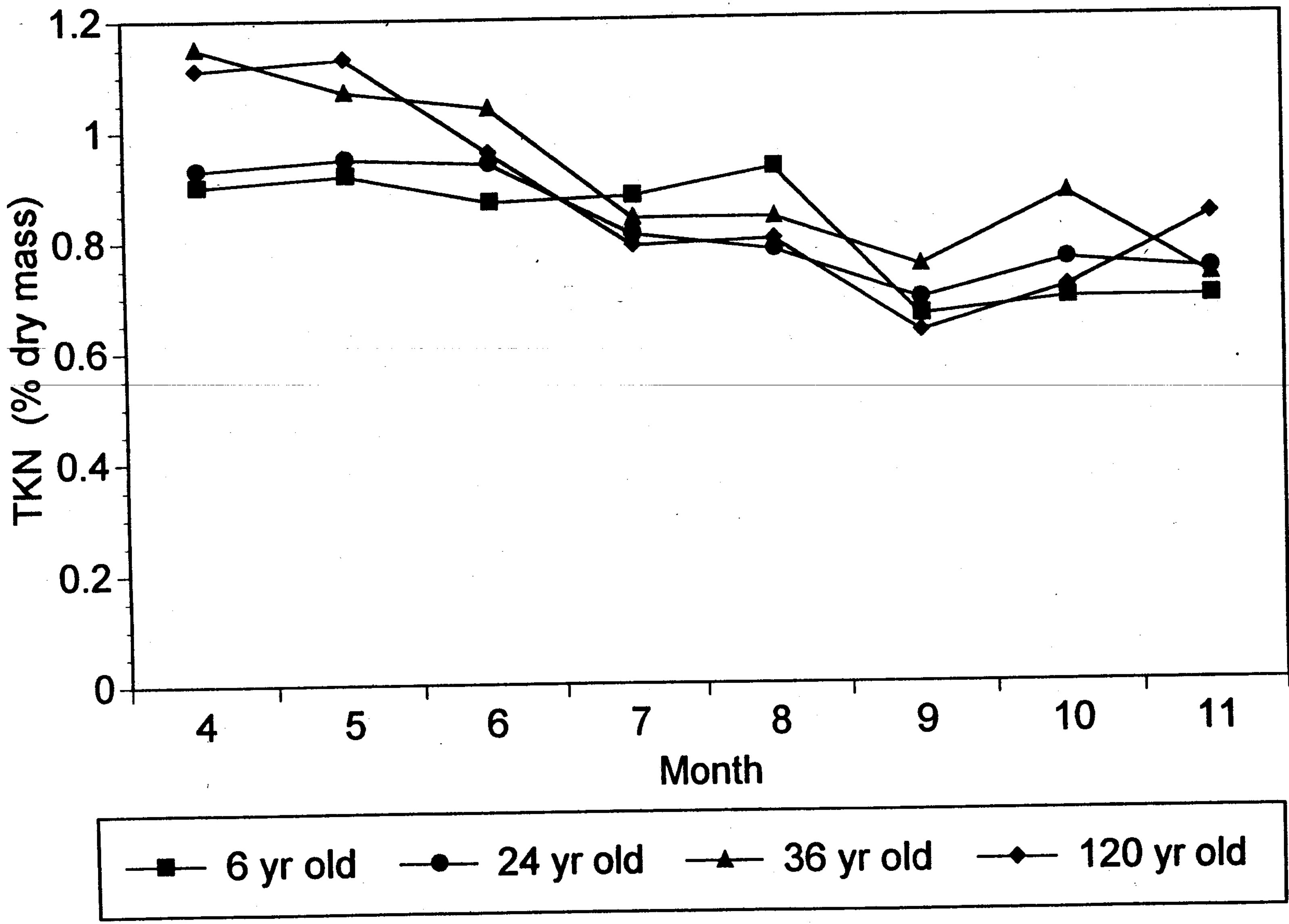
Spartina patens phosphorus concentration did not vary significantly among sites (TUKEY, $p<0.05$)(Fig. 12). *Spartina patens* phosphorus concentration peaked in May for the 36 year old dune, peaked in June for the 6 and 24 year old dune and remained stable and lower throughout the season for the 120 year old dune (Fig. 15). The 120 year old dune had the lowest *Spartina patens* phosphorus concentrations for most of the year. In *Ammophila breviligulata*, phosphorus concentration ranged from 13% to 22.5% (Fig. 16), and the 6, 24, and 36 year old dunes significantly differed from the 120 year old site (TUKEY, $p<0.05$) but did not significantly differ from each other. *Ammophila breviligulata* phosphorus concentration peaked in July for the 6 year old dune, and in June for the 24, 36, and 120 year old dunes (Fig. 16). The 120 year old dune had the lowest *Ammophila breviligulata*

Fig. 13. Seasonal TKN in aboveground Spartina patens by dune site.



1.2
1
0.8
0.6
0.4
0.2
0
TKN (% dry mass)
4
5
6
7
8
9
10
11
Month
6 yr old
24 yr old
36 yr old
120 yr old

Fig. 14. Seasonal TKN in aboveground *Ammophila breviligulata* by dune site.



1.2
1
0.8
0.6
0.4
0.2
0
TKN (% dry mass)
4
5
6
7
8
9
10
11
Month
6 yr old
24 yr old
36 yr old
120 yr old

Fig. 15. Seasonal total phosphorus in aboveground *Spartina patens* by dune site.

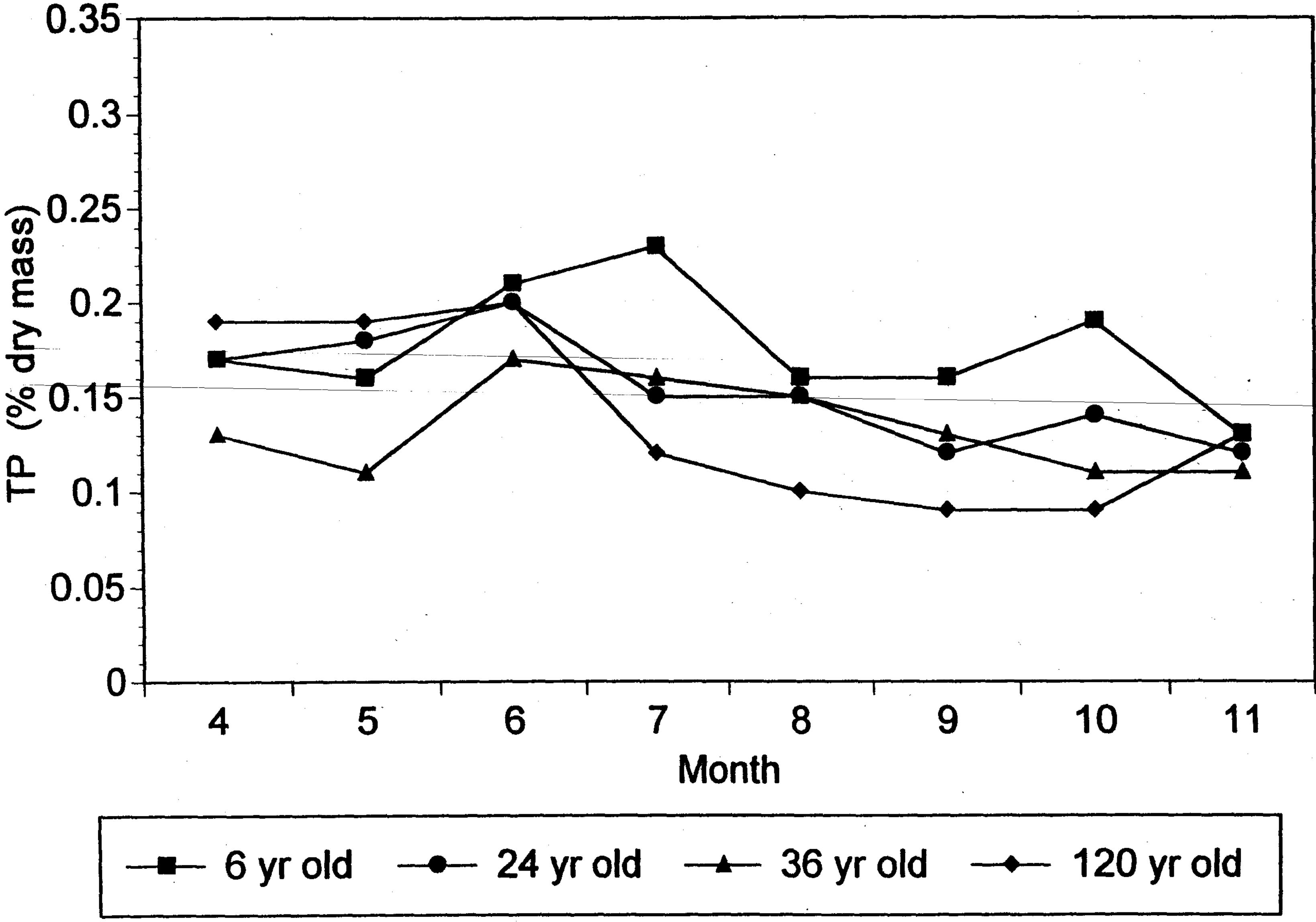
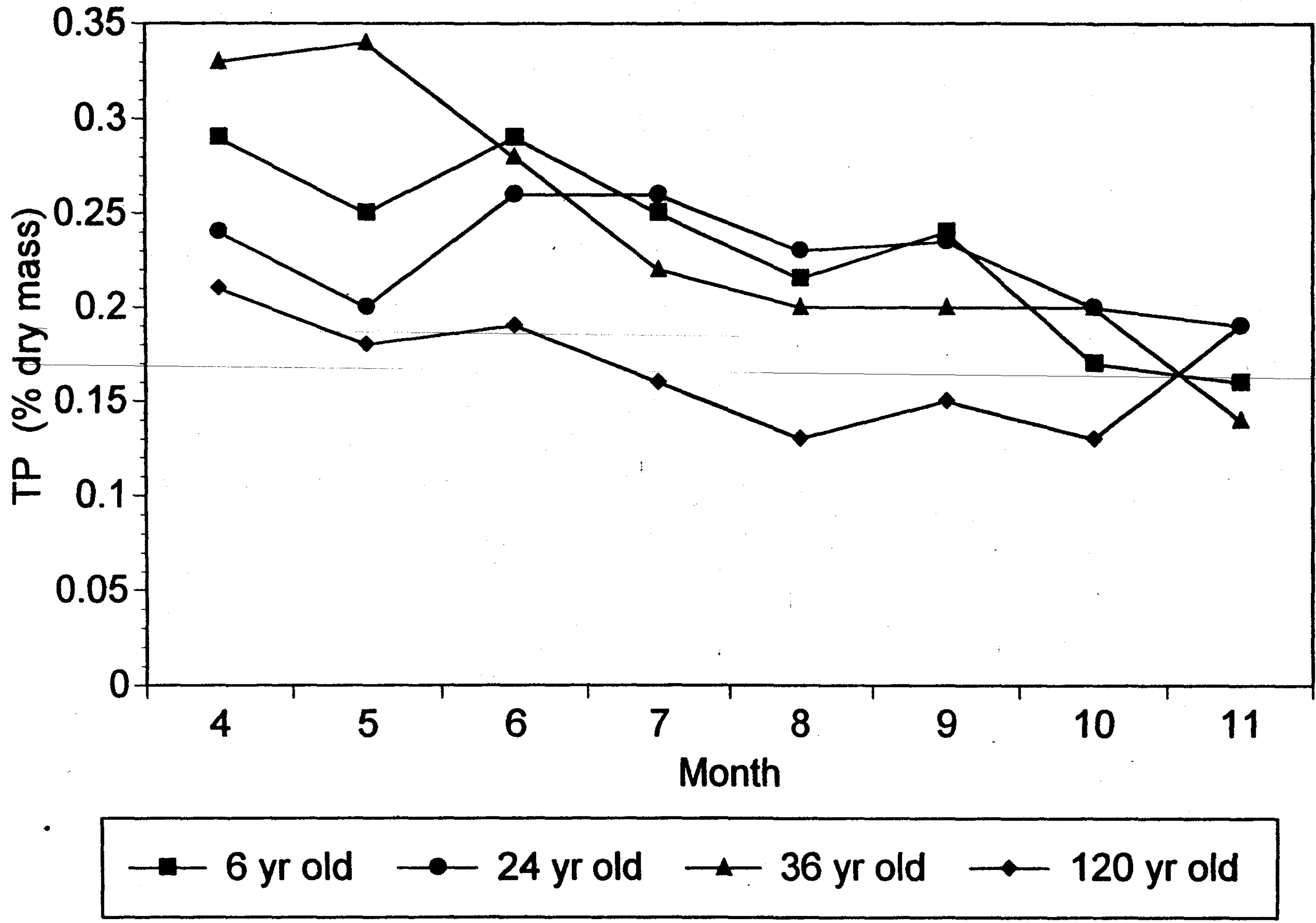

0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
TP (% dry mass)
4
5
6
7
8
9
10
11
Month
6 yr old
24 yr old
36 yr old
120 yr old

Fig. 16. Seasonal total phosphorus in aboveground *Ammophila breviligulata* by dune site.



0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
TP (% dry mass)
4
5
6
7
8
9
10
11
Month
6 yr old
24 yr old
36 yr old
120 yr old

phosphorus concentrations for most of the year (Fig. 16).

HYDROLOGY

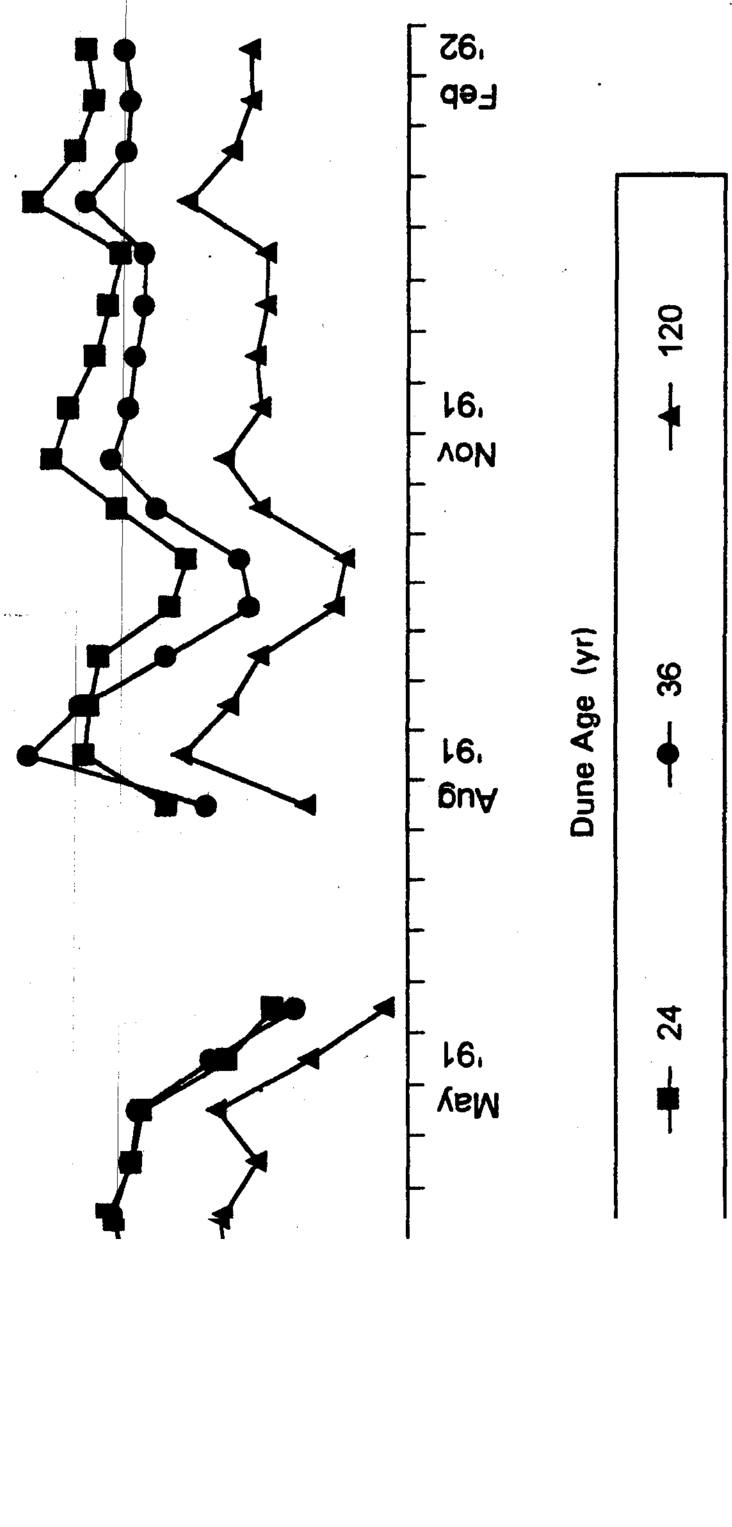
Hydrology measurements from 1991 (two years prior to the study year) showed throughout the year that the 120 year old dune had a greater depth to groundwater (Fig. 17). The 36 year old dune had the next greatest depth to groundwater for most of the year. The 24 year old dune, however, had groundwater levels similar to the 36 year old dune from February to May and was even lower than the 36 year old dune for one week in August. Due to drier than average conditions during the study year, the wells on all three sites went dry mid-summer and remained so until fall (Fig. 18). In the functioning months of well operation in 1993 a pattern was observed similar to 1991 data in which the older dunes had greater depth to ground water with ground water annual means of -92 cm for the 24 yr old dune, -97 cm for the 36 year old dune, and -116 cm for the 120 year old dune.

DISCUSSION

ABOVEGROUND BIOMASS

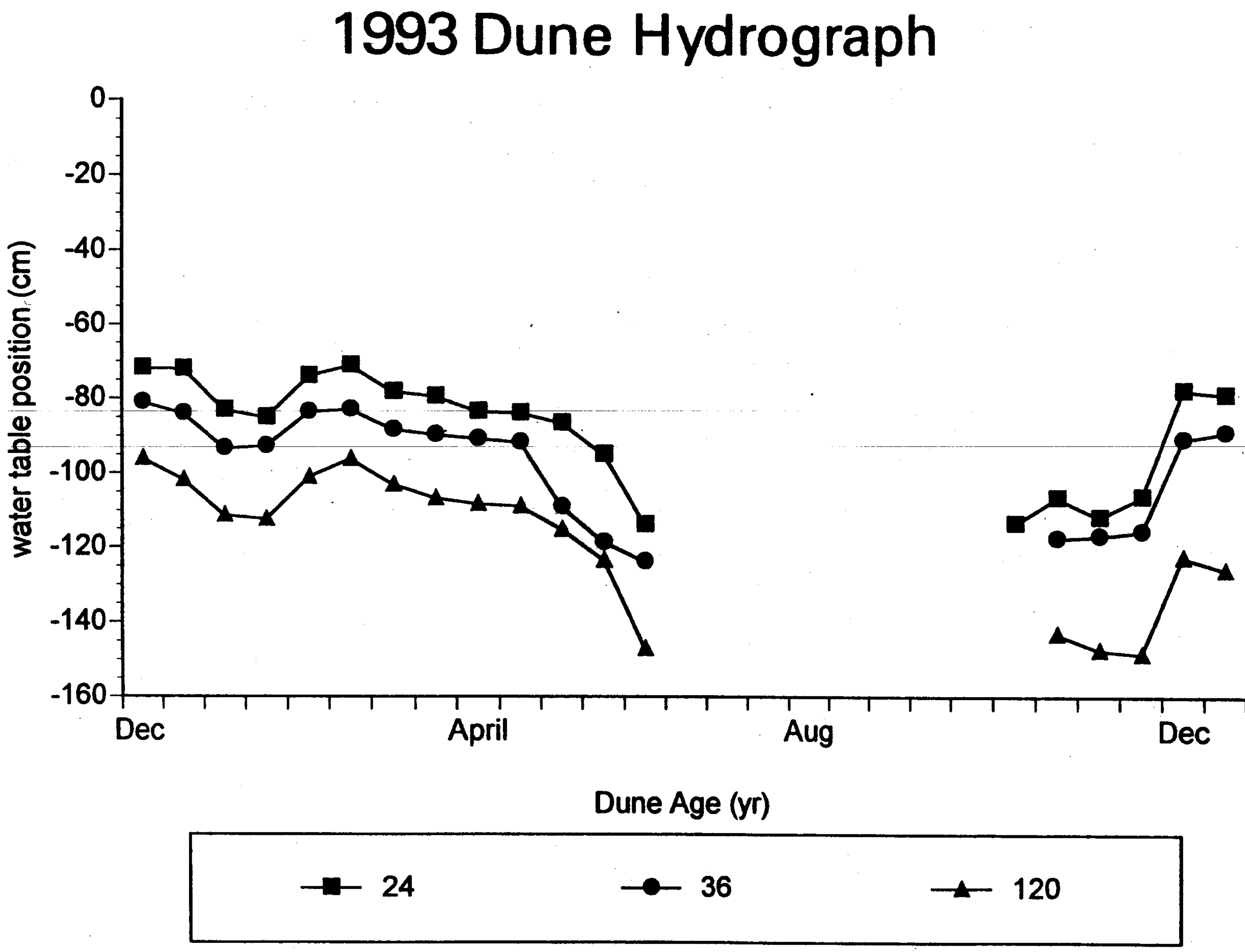
The aboveground biomass values for Spartina patens and Ammophila breviligulata for the 24, 36, and 120 year old dunes are consistent with earlier data from Day (1993). Values reported by Day (1993) were obtained in a single end of growing season harvest (November, 1991). The present

Fig. 17. Hydrographs from continuously recording wells located on the dune chronosequence on Hog Island. Graphs are based on two week means of data digitized daily from February 1991 to February 1992.



May '91
Aug '91
Nov '91
Feb '92
Dune Age (yr)
24
36
120

Fig. 18. Hydrographs from continuously recording wells located on the dune chronosequence on Hog Island. Graphs are based on two week means of data digitized daily from December 1993 to January 1993. Missing values represent periods wells were dry.



1993 Dune Hydrograph
water table position (cm)
0
-20
-40
-60
-80
-100
-120
-140
-160
Dec
April
Aug
Dec
Dune Age (yr)
24
36
120

data represent the most complete production study on the Hog Island dune chronosequence to date. The spatial variability on the dunes was high and the biomass values were generally low, indicating a resource limited system. The most pronounced spatial pattern in these data was the decrease of total biomass with increasing dune age. This contrasts with the greater biomass values expected for the higher nutrient levels and more developed soils of the older sites (Crocker and Major, 1955). Gleeson and Tilman (1990) found an increase in biomass along a 60 year successional chronosequence with root biomass showing greater increases than shoot biomass. Aplet and Vitousek (1994) also measured an increase in biomass with substrate age in a study of Hawaiian rain-forest succession. Despite increasing soil nitrogen with increasing dune age, nitrogen values throughout the chronosequence were low. Moisture along the chronosequence may be more limiting. Well recorders indicated the 120 year old dune may be under more water stress than the other sites. Well data indicated greater depth to ground water with increasing age. This could be a more important factor in controlling production along the dune chronosequence than any developmental benefits on the older dune sites (i.e., higher soil nitrogen and protection from wind and overwash).

Biomass production is correlated with the phenological development of plant species. There was a mid-summer decline in total aboveground biomass on every dune but the 24 year old dune in July. This decline may be attributed to the moisture and temperature stress of an unseasonably hot and dry June and early July. Spartina patens also had a mid-summer decline in total aboveground biomass in July on every dune but the 24 year old dune. The total aboveground biomass peak of the 24 year old dune in October, the Spartina patens aboveground biomass peak of the 24 year old dune in October and the Ammophila breviligulata aboveground biomass August peak of the 120 year old dune may be due to more favorable moisture and temperature conditions during these periods.

Ammophila breviligulata is considered the primary dune binding grass on the east coast north of Virginia Beach, Virginia (Seliskar and Huetre, 1993). This study found it was not dominant on the youngest dune ridge. The pattern of increasing Ammophila breviligulata aboveground biomass with increasing dune age was the reverse of the total aboveground biomass pattern. Spartina patens exceeded Ammophila breviligulata in aboveground biomass for the youngest dune site for every month sampled. This lack of Ammophila breviligulata's dominance could be the result of Hog Islands depositional environment. Since the sample area is rapidly accreting it is unlike the erosional environment found on the majority of east coast shoreline habitats of Ammophila breviligulata (Seliskar and Huetre, 1993; Seliskar, 1994).

Ammophila breviligulata is found on primary dunes and is less common inland where it is typically less competitive than other vegetation (Wallen, 1980). It is commonly assumed that _Ammophila breviligulata_ biomass decreases with dune age (Wallen, 1980). Higher biomass in _Ammophila breviligulata_ has been linked to sand accretion (Seliskar, 1994). Numerous studies have linked this decline in vigor to the lack of new root production (Seliskar, 1994). Old roots have been shown to be less efficient in the uptake of nutrients in _Ammophila breviligulata_ (Seliskar and Huetre, 1993). The beach on the north end of Hog Island may be growing at such a rapid rate that the young dunes lack a highly depositional environment due to their unusually large distance from the ocean. A high rate of deposition is necessary for high levels of production in _Ammophila breviligulata_.

It has also been proposed by Seliskar and Huetre (1993) that the loss of vigor associated with _Ammophila breviligulata_ plants possessing older roots is linked to the decrease of exuded carbohydrates in those roots which limit _Azotobacter_ growth which limits nitrogen fixation and indirectly the growth of _Ammophila breviligulata_ (Seliskar and Huetre, 1993).

Another possible cause for the lower _Ammophila breviligulata_ biomass values on the primary dune could be a decline in _Ammophila breviligulata_ currently being observed on the east coast. Seliskar and Huettel (1993) have linked this dieout to pathogenic nematodes. Van der Putten (1993) has linked a similar dieout in Europe to pathogenic nematodes. Their current study suggests Ammophila breviligulata's productivity may be stimulated by newly deposited nematode free sand.

Rumex acetosella is an introduced species which was more prevalent on the older dune sites. Rumex is generally considered a major weed problem in permanent grassland and has been shown to cause a decreased yield in grasslands (Niggli et al., 1993). Rumex acetosella spreads vigorously by rhizomes. Fowler (1982) found Rumex acetosella exhibited dominance over herbaceous perennials in unfertilized environments in a competition experiment. Fowler (1982) suggested it is a quick colonizer of large patches of low soil fertility. Although a small contributor to aboveground biomass through the dune chronosequence, Rumex acetosella is well distributed throughout the chronosequence and is likely influential in the community dynamics of the dune system.

ABOVEGROUND NET PRIMARY PRODUCTION

Production calculated from the sum of species peaks was greater than community peaks because the life histories of the dune species on Hog Island vary in their seasonal growth peaks. This difference was greater on the older dunes because the higher species richness on the older sites leads to a greater chance of different seasonal peaks. Aboveground net primary production did not appear to vary greatly between sites. Production on the Hog Island dune chronosequence is limited by nitrogen. Day (1993) measured a clear growth response of dune plants to nitrogen additions on Hog Island. Beach and dune plants subjected to low nitrogen growth regimes have shown decreased biomass (Barbour et al., 1985).

Precipitation is the most important climatic variable controlling average annual aboveground net primary production in grasslands (Burke et al., 1991). Due to the very low water-holding capacity of the sand on Hog Island, patterns of precipitation may be as or more important than total precipitation (Barbour et al., 1985). Precipitation is also important in dune systems because of its role in leaching salts from the soil (Barbour et al., 1985). This study took place during a year of water stress. Differences in water table throughout the dunes appears to be an influential factor in controlling production along the Hog Island dune chronosequence. The difference of aboveground biomass and not aboveground net primary production along the chronosequence may be due to the extremely low water table during most of the study which may have put this resource out of the plants acquisition range. Thus, the biomass pattern found in 1993 may be due to a residual effect of the normal ground water levels on the distribution and density of vegetation along the chronosequence.

The aboveground net primary production (ANPP) from the sum of species peaks varied from 226 g m^{-2} yr^{-1} for the 24 year old dune to 274 g m^{-2} yr^{-1} for the 120 year old dune in 1993. These values are similar to other grassland LTER sites but there is a scarcity of dune sites with which to compare. The Central Plains Experimental Long Term Ecological Research Site had production ranges from 100 g m^{-2} yr^{-1} in the moisture stressed west to 500 g m^{-2} yr^{-1} in the east (Bark et al., 1991). The Niwot Ridge Long Term Ecological Research Site, Colorado, is an alpine tundra site which had production values of 136 g m^{-2} yr^{-1} for a dry meadow and 299 g m^{-2} yr^{-1} for a wet meadow (Bowman et al., 1993). These values from resource limited environments are much lower than tropical grassland values. Singh and Yadava (1974) recorded production values of 1974 g m^{-2} yr^{-1} in a tropical grassland near Kurukshetra, India.

SPECIES RICHNESS

The species composition of the community changed as the growing season advanced. The increase in species richness across the chronosequence explains the difference between the two methods of calculating production. The 120 year old dune had a greater number of species, leading to greater variation in seasonal growth peaks, while the six year old dune was dominated primarily by <u>Spartina patens</u>, resulting in a seasonal community peak more similar to the sum of species peaks by site. Average species richness was higher for the 24, 36, and 120 year old dune sites. This general pattern of increasing species richness is consistent with increasing system maturity and nutrient levels (Tilman, 1982). Bowman et al. (1993) observed an increase in species diversity with nutrient additions in a nutrient limited system.

FOLIAR N AND P

Foliar N values were low. Aboveground nitrogen increases only after the belowground storage pool increases (Chapin, 1980). These low foliar nitrogen values reflect a limited nitrogen pool and imply higher nitrogen use efficiency (Chapin, 1980). The N concentration in live aboveground vegetation is largely a function of nutrient availability (Vitousek, 1982; Chapin, 1988).

Foliar phosphorous values were lower for both species on the 120 year old site, but only significantly for Ammophila breviligulata. Chapin (1993) suggested nitrogen stress reduces the potential of roots to absorb phosphate; also, plants from infertile soil have a low capacity to absorb phosphate, but not nitrogen (Chapin, 1991). This could be related to the higher soil nitrogen at this site. A dune plant fertilization study on Hog Island (Day, 1993) found nitrogen fertilization to increase the amount of nitrogen and decrease the amount of phosphorus uptake into aboveground tissue. Chapin (1993) also suggested where a single nutrient is limiting growth, plants exhibit a high potential to absorb the specific limiting nutrient. Increased water stress on the 120 year old dune lowers the potential of roots to absorb nutrients (Chapin, 1991). This additional stress could contribute to the lower P values on the 120 year old site.

The significantly higher N concentrations for _Ammophila breviligulata_ than _Spartina patens_ on all sites could be attributed to differences in proportion of leaf N as rubisco and in the activity of rubisco that may account for some of the differences between leaf N in broad interspecific comparisons (Field and Mooney, 1986).

CONCLUSION

The barrier island dune chronosequence is useful for examining small or large scale differences in site development. However, Aplet and Vitousek (1994) found that even one environmental variable can have a dramatic influence on the rate and course of succession. Aboveground biomass patterns observed in this study appear to be driven by water table rather than successional development. While aboveground biomass varied greatly across dunes, aboveground net primary production did not. In natural systems the environment is rarely optimal for plant growth and the dune system on Hog Island represents an environment of nutrient and water stresses.

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