Lacy R. Blanton, Jr. PRIMARY PRODUCTIVITY AND BIOMASS DISTRIBUTION OF AQUATIC MACROPHYTES IN THE LOWER CHOWAN RIVER. (Under the direction of Mark M. Brinson) Department of Biology, August 1976.

Primary productivity was determined for the two dominant rooted aquatic macrophytes, *Nuphar luteum* (L.) Sibthorp & Smith, and *Justicia americana* (L.) Vahl., in the lower Chowan River, North Carolina. The 1975 annual net production for *N. luteum* was 228.1 g dry wt/m^2 with a peak biomass range of 115-299 g dry wt/m^2. The average annual turnover rate for floating leaves and petioles was 5.7 times per year. Root productivity was calculated by assuming the same turnover rate as for rhizomes (0.14 per year) and by assuming a constant root-to-rhizome ratio. The average percent ash for *N. luteum* ranged from 9.1 (floating leaves) to 17.0 (roots). Generally, 77% of the *N. luteum* biomass was in the substrate, while 93% of the net primary productivity was contributed by aboveground structures. *Justicia americana* reached a peak biomass of 276.5 g dry wt/m^2 in August 1975 which probably approximated seasonal net primary productivity based on uniform growth and observed low mortality.

Biomass distribution for the aquatic macrophytes was estimated by aerial color photography at approximately 366 m (1,200 ft). Total macrophyte coverage was 277,306 m^2 (ca. 27.7 ha) of which 1% was *J. americana*. Biomass data from an extensive sampling survey for *N. luteum* (223.1 g dry wt/m^2) coupled with aerial coverage (ca. 272,267) gave an estimate of 60.7 MT of plant biomass for the study area.

PRIMARY PRODUCTIVITY AND BIOMASS DISTRIBUTION OF AQUATIC MACROPHYTES IN THE LOWER CHOWAN RIVER

A Thesis

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Lacy R. Blanton, Jr.

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OF AQUATIC MACROPHYTES

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I would like to dedicate this thesis to my wife and son whose understanding and patience made this work possible.

TABLE OF CONTENTS

TABLE OF CONTENTS - continued

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The purpose of this study is to measure the net primary productivity and biomass distribution of aquatic macrophytes in the lower Chowan River. The two dominant rooted macrophytes found growing in the littoral zone of the river are *Nuphar luteum* (L.) Sibthorpe & Smith (yellow water lily), and *Justicia americana* (L.) Vahl. (water willow). Both these species form essentially monospecific macrophyte stands in the littoral and mouths of tributary streams with *Nuphar* (floating-leaved species) being more widespread than *Justicia* (emergent species).

The importance of rooted aquatic macrophytes as primary producers in the littoral zone of lotic ecosystems too often has been assumed to be insignificant. However, as streams and rivers increase in size, and decrease in velocity of flow, the importance of primary productivity of lotic phytoplankton and aquatic macrophytes increases (Westlake 1973; Wetzel 1975, pp. 545-546). Direct contributions of aquatic vegetation may be an important energy source affecting various trophic levels, especially the energy source for decomposers (bacteria and fungi) as well as for detritus feeders (Westlake 1965).

Rooted aquatic macrophytes are often considered important to aquatic animals by providing support, shelter, food, and oxygen. When decomposition occurs, aquatic macrophytes contribute directly to the stock of organic detritus which in turn gives the system metabolic stability (Penfound 1956; Wetzel 1975, p. 546). When not present in extreme amounts, aquatic macrophytes increase species diversity by creating habitats for organisms not available in a system with flora entirely of phytoplankton. Thus, a high species diversity will tend to increase the stability of aquatic ecosystems by producing a more complex food web (Boyd 1971).

Net primary productivity, as defined by Westlake (1965), is the rate of accumulation of new organic matter, or stored energy; that is, the observed change in biomass plus all losses except respiration, divided by the time interval. However, if losses are continuous throughout growth, then methods using changes in biomass yield data that are difficult to interpret. These conditions require special investigations of such losses.

Early studies of aquatic macrophytes have often expressed peak aboveground biomass or seasonal maximum standing crop as annual net production. Several factors should be considered prior to such an interpretation. If there are few losses of the current year's production, or determination of the losses are possible, then peak biomass may be a useful parameter of production (Westlake 1969). Westlake (1965) reports that some species have been observed to have two maxima or peaks at different times of the year for different locations.

Perennials present additional problems due to their morphology and phenology of the plants and plant parts. In many cases involving perennials, below ground biomass (roots and rhizomes) are assumed to be negligible. This assumption is erroneous when underground organs can be more than half the total biomass of *Phragmites communis* and *Nuphar lutea* as well as other species (Westlake 1968, 1969; Wetzel 1975, p. 379). In addition, very little information exists concerning the age or turnover rate of underground organs. Without this necessary growth parameter, many years of biomass accumulation will tend to overestimate belowground production if the seasonal maximum standing crop is used as an evaluation of annual production (Westlake 1966).

The use of terminal biomass, which is normally sampled at the end of the growing season, is to be discouraged as a measure of average productivity due to biomass losses as a result of death, damage, and grazing. Depending upon environmental factors (storms, wave stress, erosion, etc.), death and damage may account for significant biomass losses. Wetzel (1975, p. 380) reports values of grazing losses ranging from 0.5 to 8 percent of the annual production.

In this study, monthly changes in biomass plus any losses of plant material are to be included in the estimation of net primary productivity of *Nuphar*. Floating leaves and petioles appear to have a high mortality throughout the growing season. Therefore, determination of their turnover rate is necessary. In addition, the age or turnover rate of belowground structures was determined since a large portion of the total biomass appears to be in the substrate. The determination of net primary productivity was estimated for *Justicia* by peak biomass.

DESCRIPTION OF STUDY AREA AND PLANTS

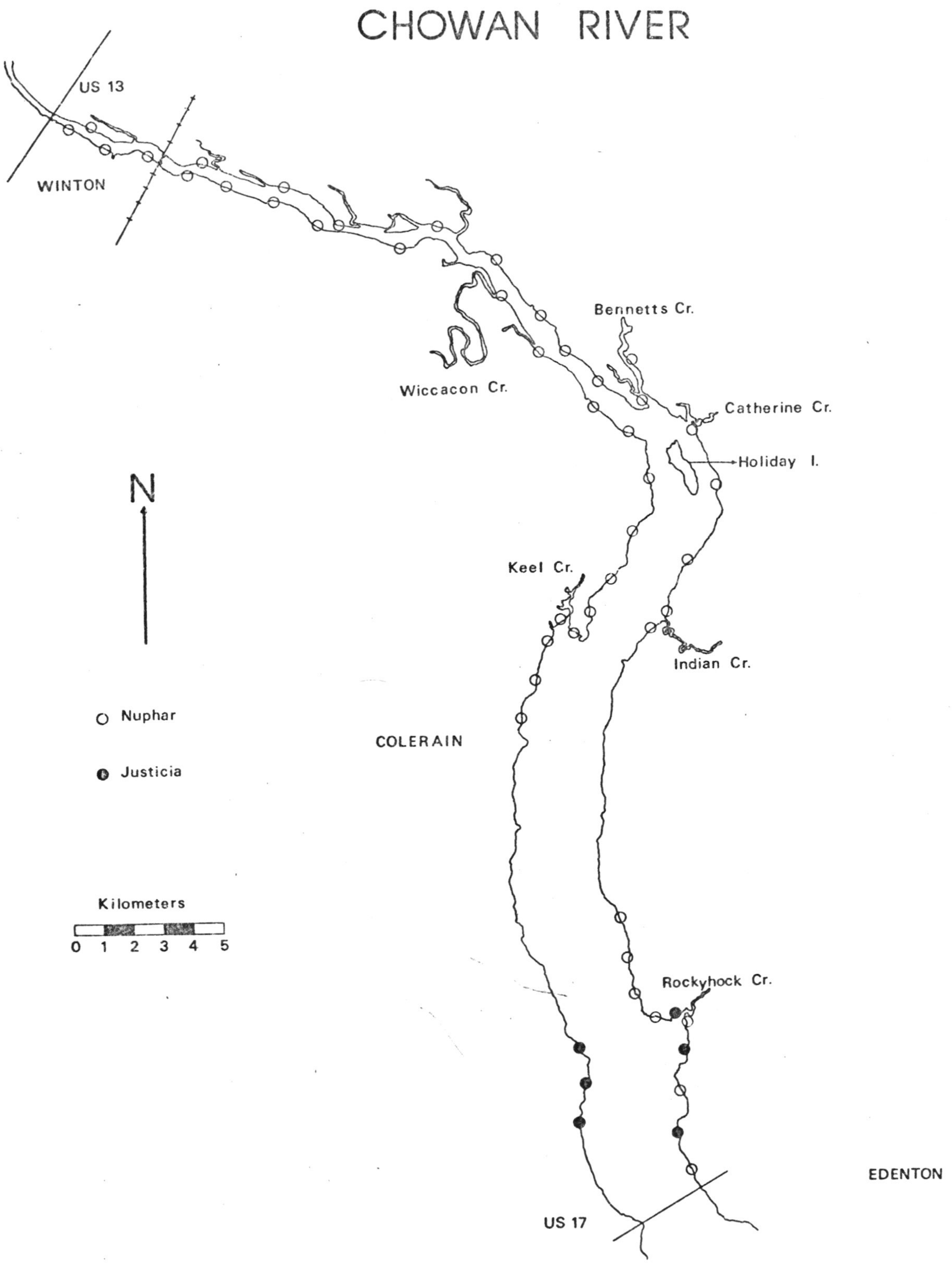
The Chowan River, located in the northeastern coastal plain of North Carolina, originates from the union of the Blackwater and Nottoway Rivers near the North Carolina - Virginia line and flows into the Albemarle Sound near Edenton, North Carolina ca. 81 km to the south. This length of the river has a surface area of approximately 116 km^2. The Meherrin River, in addition to the two tributaries mentioned above, arises in southeastern Virginia and forms a total drainage basin of 12,800 km^2 of which 3,269 km^2 lies within North Carolina (Smith 1963).

The sector of the Chowan River chosen for this study lies between Edenhouse Point near the U. S. highway 17 bridge at Edenton, North Carolina and extends ca. 52 km northward to the U. S. highway 13 bridge near Winton, North Carolina (36°03'N to 36°23'N and 76°43'E to 76°56'E) (Fig. 1).

The study area is largely rural, dominated by extensive swamps that border the river and most of its tributaries. These swamps are comprised mainly of *Taxodium distichum* (bald cypress) and *Nyssa aquatica* (tupelo gum), and are subject to frequent flooding by wind tides. Lunar tidal variation in the river is approximately 0.3 m, but wind tides vary by as much as 1.2 m at irregular intervals (Daniel, III 1975).

The littoral zone varies greatly within the study area proceeding northward from Edenhouse Point. The effect of waves and wind tides upon shore erosion is greatly pronounced in the lower 36 km of the river south of Holiday Island. Here the river width is at its maximum (2-4 km) allowing for greater wind fetch which results in larger waves compared with the upper portion of the river. The littoral substrate in this area

Figure 1. The Chowan River study area located in the northeastern coastal plain of North Carolina.


CHOWAN RIVER
US 13
WINTON
Bennetts Cr.
Wiccacon Cr.
Catherine Cr.
Holiday I.
N
Keel Cr.
Indian Cr.
Nuphar
Justicia
COLERAIN
Kilometers
0 1 2 3 4 5
Rockyhock Cr.
EDENTON
US 17

is composed mainly of sand with little organic matter except in sheltered coves or behind the cypress fringes.

Rockyhock Creek is located within this area and appears to have the characteristic littoral substrate for the lower river; that is, a mixture of silt and sand with a clay base. Here Nuphar and Justicia are found growing in association where their beds overlap in some instances. Justicia is restricted to the lower section of the Chowan River in areas generally subject to high erosion as a result of wind wave action. Vallisneria is found growing within the Justicia bed at Rockyhock Creek, but leaf blades seldom exceed a few centimeters in length. This dwarfed appearance may be a result of competition for nutrients and light.

Keel Creek lies within this lower region, but differs from less protected areas in having its littoral substrate of a highly organic ooze. A large swamp forest that borders the entire creek is apparently the source of the predominantly allochthonous organic material.

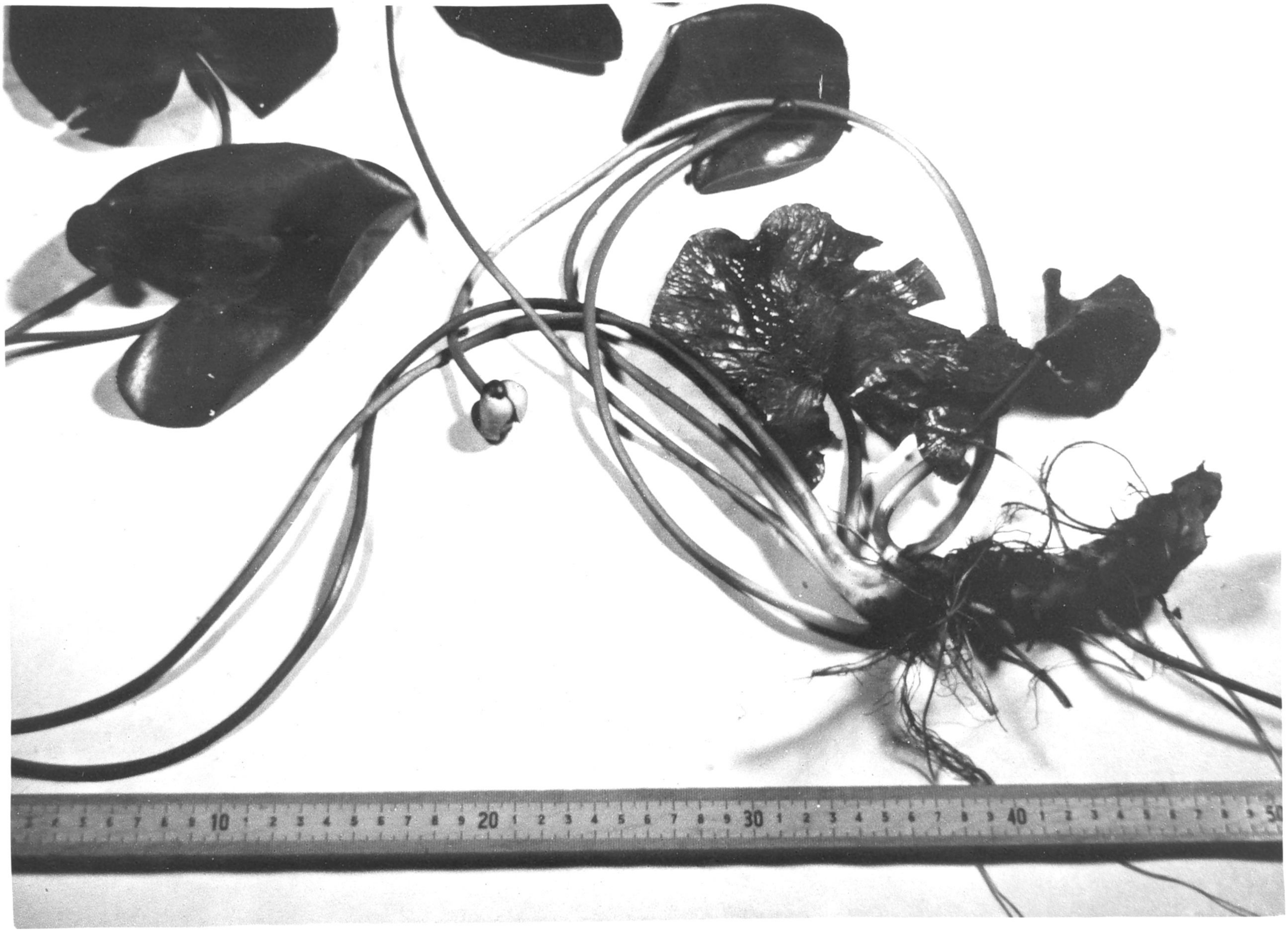
The littoral above Holiday Island is subjected to considerably less wind tidal stress due to the reduced width of the river (less than 1 km) and the shelter provided by surrounding swamp forest. Here the littoral substrate is silt, with many decomposing logs, and some sand deposition near home sites and piers.

Throughout the spring and summer months, afternoon thunderstorms occur frequently. These events create great wave stresses on the littoral zone during the growing season of aquatic macrophytes.

The habit of growth for mature Nuphar plants consists of fleshly, branching, submersed rhizomes with adventitious roots along their lower surfaces. Floating leaves and inflorescences, developing from rhizome apices, are borne on elongate petioles which extend longer than the water depth in which the plant is growing (Fig. 2). *Nuphar* is heterophyllous (i.e., the phenomenon of a single plant bearing two or more different kinds of leaf) with the development of flaccid and translucent submersed leaves. These submersed leaves persist throughout the winter. Reproduction may be sexual, but in well established colonies, is primarily lacking. Continued branching of the perennial rhizomes with subsequent death and decay of older portions, provides for indefinite perpetuation of individuals and often results in the formation of extensive clones (Beal 1956, DePoe and Beal 1969).

Justicia is also a perennial rhizomatous emergent aquatic macrophyte. Leaves are borne almost entirely on erect aerial stems with submersed stems providing a thick mat of adventitious roots below the water level (Boyd 1969, Fassett 1972).

Figure 2. Photograph of <u>Nuphar luteum</u> taken from the Chowan River, North Carolina.



MATERIALS AND METHODS

Primary Productivity

Harvest Method

Depending upon the type of vegetation to be sampled, several factors should be considered prior to choosing a harvest method for measuring net primary productivity. One important factor is sample size. Gathering, transporting and processing biomass samples is time consuming and costly due to large quantities of plant material encountered in rooted macrophyte communities. Therefore, many investigators studying rooted aquatic macrophytes have found it necessary to reduce the size of the sample quadrat to obtain a manageable amount of material for analysis (Waring 1970, Pearsall and Gorham 1956). However, by reducing the area of the sampling quadrat, increases in error due to the "edge" effect have been observed (Pearsall and Gorham 1956, Smith 1964).

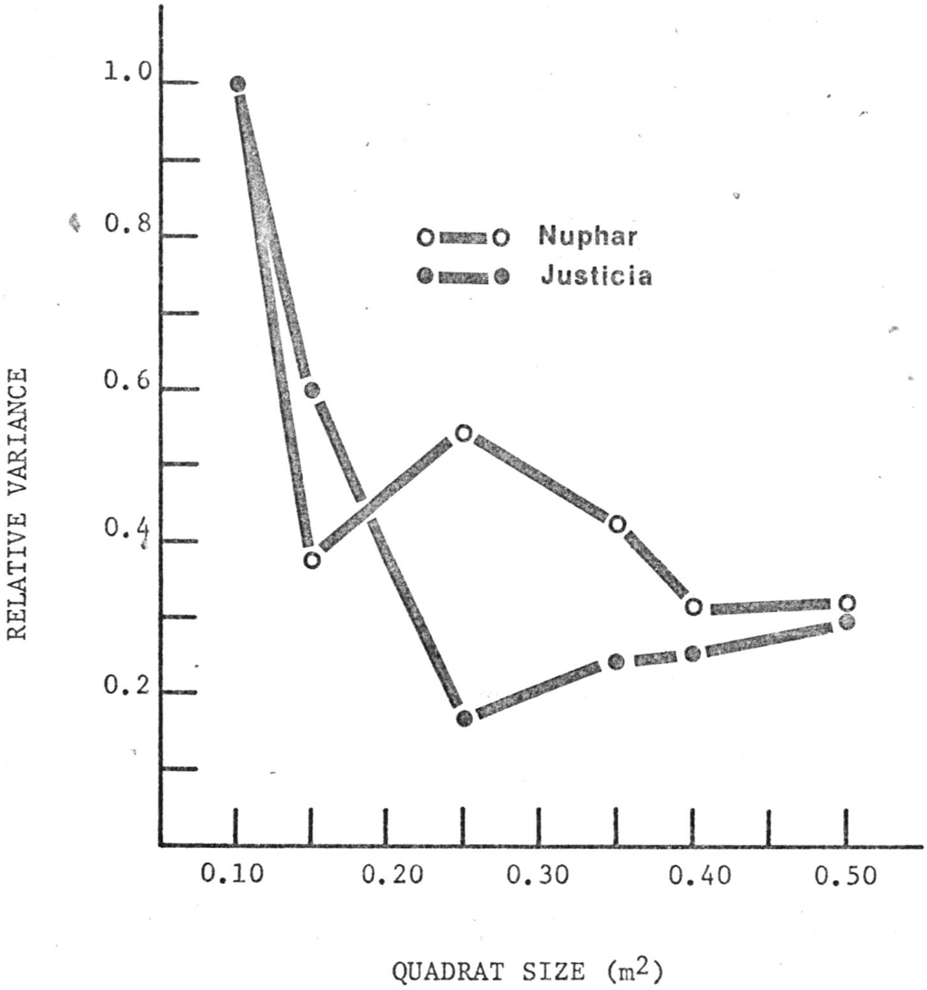
For this study, a suitable quadrat size was determined during June, 1974 with a method described by Wiegert (1962). Three sets of nested quadrats (0.10 m^2, 0.25 m^2, and 0.50 m^2) were placed randomly along a transect perpendicular to the shoreline across the width of the macrophyte bed. All plant biomass in each quadrat was removed to a substrate depth of approximately 30 cm; then all living plant material was dried and weighed. By addition, six possible quadrat sizes were obtained with the following relative areas: 0.10 m^2, 0.15 m^2, 0.25 m^2, 0.35 m^2, 0.40 m^2, and 0.50 m^2. A mean and variance was calculated for each quadrat size. By plotting the relative variance of the mean against quadrat size, the smallest quadrat size of 0.10 m^2 was excluded from consideration because of its comparatively high variance (Fig. 3). A quadrat size of 0.35 m^2 was chosen for routine sampling because it represented a compromise between the minimum variance and the maximum quadrat size. This method was applied to both *Nuphar* and *Justicia*.

The location of macrophyte beds for biomass sampling was determined from aerial photography taken in August, 1974. Four macrophyte beds (three beds of *Nuphar* and one bed of *Justicia*) were chosen for intensive sampling each month to represent a range of substrate types in the upper and lower portion of the Chowan River (Fig. 1).

Two sample sites were established at the mouth of Rockyhock Creek. Both *Nuphar* and *Justicia* were found growing in a sandy substrate which appeared to be influenced by shore erosion as a result of wave action. *Justicia* had colonized the more apparent stressful areas while *Nuphar* occupied a less exposed area. Some overlapping of the macrophyte stands was observed but this condition appeared to be restricted to Rockyhock Creek. Water depth within the macrophyte bed ranged from 0.3 m to 1.5 m.

The third sampling site for *Nuphar* was situated in the lower portion of the river at the mouth of Keel Creek. The substrate appeared to receive large quantities of organic matter from the surrounding swamp forest. Due to this high deposition of organic matter, harvesting of the total plant biomass was much easier in the soft substrate. Large quantities of filamentous algae (*Spirogyra* and *Oscillatoria*) were associated with the aboveground plant structures. Water depth ranged from 0.3 m to 2 m from the shore to the outer margin of the macrophyte bed.

Figure 3. Determination of optimum quadrat size based on relative variance. Quadrat size chosen was 0.35 m^2.


1.0
0.8
0.6
0.4
0.2
RELATIVE VARIANCE
Nuphar
Justicia
0.10
0.20
0.30
0.40
0.50
QUADRAT SIZE (m2)

The fourth sampling location was at the mouth of Wiccacon Creek in the upper portion of the river. The substrate was found to be relatively silty with large quantities of detrital material. The red algae Batrachospermum was found growing on many of the decomposing logs and stumps within the macrophyte bed. Water depth ranged from 0.5 m to 2 m.

In each bed, a 30 m transect parallel to shore was erected to serve as a reference point. At one meter intervals along this base line, points were chosen randomly by the use of a random numbers table and transects were run perpendicular to the shore across the width of the macrophyte bed. A 0.35 m^2 iron quadrat frame was placed at random points along this line, and all plant material removed to a substrate depth of 30 cm. A straight hoe was used for cutting around the edge of the quadrat and posthole diggers were used to remove the plant material. The plant material was placed on a wire screen, washed of dirt and detritus, placed in plastic bags, and transported to the laboratory on ice.

In the laboratory, the macrophytes were cleaned of periphyton with a nylon brush and separated into their components depending upon the species. Nuphar was separated into roots, rhizomes, emerged leaves, emerged petioles, submersed leaves, and submersed petioles. Justicia was partitioned into roots, rhizomes, stems, and leaves. The separated plant material was placed in paper bags, dried in the oven for 72 hours at approximately 85°C, and weighed. Ash free dry weight was determined for each component of each quadrat. The dried plant material was ground in a Wiley mill in order to assure sample homogeneity. A one gram dry sub-sample from each component was ignited at 480°C in a muffle furnace for three hours.

Total plant biomass (g dry wt/m^2) was statistically analyzed to determine macrophyte dispersion for each sample site. A method developed by Pielou (1960,1969) whereby the variance : mean ratio of plant biomass served as a criteria was used for the determination of regular, aggregated, or random macrophyte distribution.

Leaf area index (LAI) was determined for both macrophyte communities (one side only). All live leaves per 0.35 m^2 quadrat harvested were traced on paper and their surface area determined by the proportionality:

$$\frac{\text{Area of page}}{\text{Weight of page}} = \frac{\text{Area of leaf}}{\text{Weight of leaf trace}}$$

Biomass Losses

By harvesting biomass at monthly intervals, and accounting for any losses due to grazing or death of plant parts, net primary productivity can be determined (Westlake 1965, Wetzel 1975, pp. 376-378). Grazing was not measured in this study, but appeared to be low except for older *Nuphar* leaves at the Keel Creek study site. Biomass losses due to senescence or damage of floating leaves for *Nuphar* were monitored with tagging experiments. A 1 m x 12 m quadrat was established from the shore across the width of the macrophyte bed at Rockyhock Creek to study seasonal rhizome growth as well as emergent leaf turnover rates. Each rhizome meristem was located within the quadrat and its position marked with a metal stake pushed into the substrate. The stakes were carefully positioned at the end of the rhizome meristem in such a way that rhizome growth was not obstructed. Since these rhizome meristems would be harvested at the end of the growing season, the stakes provided an aid in locating lost rhizomes in the event that emergent leaf production was interrupted during the growing season.

Nuphar was found to have two different types of leaves present on the mature plant, (1) the emerged or floating leaf, and (2) the submersed leaf. Newly emerged leaves of Nuphar were tagged weekly beginning with the first emergent leaf of the growing season with a loosely tied plastic ribbon attached to labelled aluminum tags. A record was maintained of the number of new leaves emerged and of those lost for each individual rhizome meristem during the duration of the growing season. The number of annual leaf turnovers could be determined by dividing the number of days in the growing season by the average number of days that the tagged leaves were emerged. Using this estimate, annual net production for the emergent leaf blades and petioles could be calculated by multiplying the average standing crop for leaf blades and petioles for the growing season by the number of turnovers (Waring 1970).

Also, weekly leaf turnovers were calculated by dividing this number of new floating leaves produced weekly by the average number of floating leaves present for that week. This gave an estimate of leaf turnovers per week. The density of floating leaves times the average grams dry weight per leaf for each sampling site resulted in a value of grams dry weight per meter square for leaves. Therefore, multiplying the leaf weekly turnover rate times g dry wt/m^2 of leaf blades and petioles, productivity could be calculated in grams per meter square per week.

The submersed leaf annual production was determined in the same manner as the emergent leaves by the use of tagging randomly located rhizome meristems. The number of turnovers for submersed leaves multiplied by the average standing crop resulted in the determination of the annual production for submersed leaves.

To coincide with emergent leaf tagging, any flowers that emerged within the 1 m x 12 m quadrat were tagged and records maintained until their senescence. This was an estimate of the annual number of turnovers used in determining annual flower, peduncle, and fruit production per meter square for the growing season.

Early results showed that a large portion of the Nuphar biomass was in the substrate and could account for a considerable part of the total productivity. The necessity of observing the annual increment of underground growth to avoid an overestimation of annual productivity due to the accumulation of past years biomass has been emphasized (Westlake 1965, Szczepanski 1969). Therefore, the biomass and age of the underground plant material must be included in calculations of primary production (Westlake 1968).

To study belowground growth, a 15 m transect was constructed at Rockyhock Creek to determine monthly rhizome growth for Nuphar. A 0.50 m^2 metal quadrat frame was randomly placed along a transect perpendicular to the shoreline and each meristem was tagged using metal stakes positioned at the apical portion of each rhizomes. New rhizome growth was harvested at monthly intervals for five consecutive months (May through September). Results were expressed in units of grams dry weight per meter square per month.

At the end of the growing season, the tagged rhizome meristems used in analysis of emergent leaf turnovers were harvested. All growth past the metal stakes was designated as new growth. Prominent petiole and peduncle scars were counted on the new growth as well as the old portion of each rhizome. The total number of petiole and peduncle scars divided by the new petiole and peduncle scars gave an estimate of rhizome age. A general check was performed by comparing the number of newly tagged floating leaves and petioles plus peduncles with the total number of petiole and peduncle scars on the new rhizome growth. Also, the total rhizome length divided by the one year growth increment resulted in an estimation of average rhizome age. To calculate the annual production of rhizome meristems, the average rhizome biomass for the growing season per meter square was divided by the average rhizome age.

Root production for the growing season was determined by an indirect method since it was observed that considerable root growth occurs posterior to the growing apex. In June, 1975, an extensive biomass sampling of the study area was undertaken to determine between-bed variation in biomass. Seventeen *Nuphar* beds were chosen at random from aerial photographs for the entire study area. Two 0.35 m^2 quadrats of plant biomass were excavated with only one quadrat harvested for roots. These data were used in the determination of the average annual root production by the use of linear regression analysis based on annual rhizome growth.

Biomass Distribution

Aerial Photography

The distribution of *Nuphar* and *Justicia* was determined by aerial remote sensing. Three flights were taken; two in 1974 (August and September) and one flight in 1975 (June). The flight in June, 1975, was taken to coincide with an extensive sampling of the study area. All aerial photographs were taken in the morning (0800 - 1100 hours) at an altitude of 1,200 ft; (ca. 366 m) using handheld 35-mm single lens reflex cameras. The two types of cameras used were a Petri FT and a Nikkormat with a polarized filter. The use of the two cameras allowed uninterrupted overlapping photography of the littoral by loading one camera with new film while the other was in use.

Kodak Ektachrome-X color slide film was found to give the best results for this study. Several types of film, black and white (Plus-X), and color infrared, were tried with less than satisfactory results in 1974. Black and white film with the addition of the yellow filter reduced the contrast between the water and the macrophyte bed. Color infrared film increased contrast but, as in the case of black and white film, overemphasized the shading of trees upon the macrophyte beds. However, color film with its variety of hues and chromas offered superior interpretability. All film processing except black and white was done by Kodak.

The color slides were projected on paper and the margins of each macrophyte bed were traced. A planimeter along with a modified acreage grid was used to calculate macrophyte coverage for the study area. Calibration for scale was accomplished by "ground truth" of buildings, bridges, and other large stationary structures over the length of the study area.

Extensive Biomass Survey

During the month of June, 1975, an extensive biomass survey of the total study area was completed to determine variation between macrophyte beds in the upper and lower portion of the study area. Seventeen macrophyte beds were chosen randomly from a total of 42 beds based on flights taken in 1974. Two 0.35 m^2 samples were excavated from each *Nuphar* bed. Only one of the two 0.35 m^2 quadrats was harvested for roots. A correlation between roots and rhizomes was determined for the study area from these data.

RESULTS

Primary Productivity

Harvest Method

Net primary productivity of Nuphar could not be estimated from monthly changes in biomass due to losses of plant material between sampling dates and the high degree of variation between samples taken within the same plant bed (Appendix, Table A, B, & C). At the three sites, Nuphar was found to range in peak biomass between 115 g dry wt/m^2 (Keel Creek) and 300 g dry wt/m^2 (Wiccacon Creek) (Figs. 4, 5, & 6) Monthly biomass values (April through August, 1975) for the entire study area resulted in an average biomass of 154.9 g dry wt/m^2 (Table 1). The monthly total biomass samplings in Tables 1 and 2 were approximately within a month of each other with exact dates listed in Figures 4-6.

Figure 4 shows that a large initial biomass of Nuphar was present in January, 1975, with a large portion (99%) of the biomass in the substrate. Direct calculation of net primary productivity based on biomass changes could not be made because of the large variation in measurements between sampling dates. The Wiccacon Creek study site was higher in total biomass than the other sampling stations. A peak biomass of 300 g dry wt/m^2 occurred during August, 1975, of which 63 percent of the biomass was belowground (Fig.5). Nuphar peak biomass for Keel Creek (Fig. 6) for June, 1975, was approximately 115 g dry wt/m^2 with 71 percent of the total biomass in the substrate. Initial biomass in November, 1974, had an estimated 89 percent of the total biomass in the substrate.

Justicia (Fig. 7) reached a peak biomass of 276.5 g dry wt/m^2 during

Figure 4. Monthly mean biomass of Nuphar luteum at Rockyhock Creek for the 1975 growing season. Values above zero are aboveground biomass and those below zero are belowground biomass.

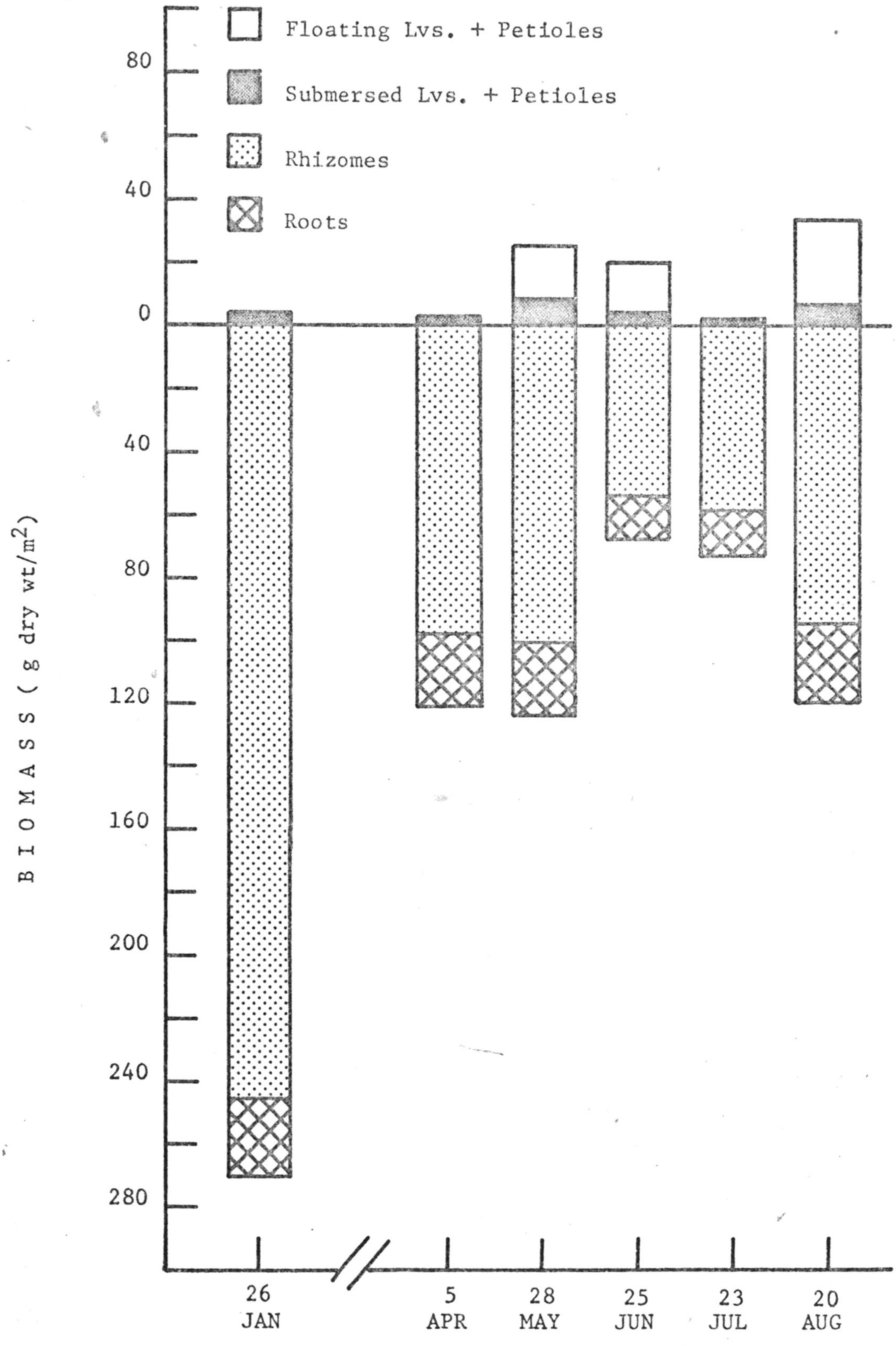

Floating Lvs. + Petioles
Submersed Lvs. + Petioles
Rhizomes
Roots
80
40
0
40
80
120
160
200
240
280
BIOMASS (g dry wt/m^2)
26
JAN
5
APR
28
MAY
25
JUN
23
JUL
20
AUG

Figure 5. Monthly mean biomass of *Nuphar luteum* at Wiccacon Creek for the 1975 growing season. Values above zero are aboveground biomass and those below zero are belowground biomass.

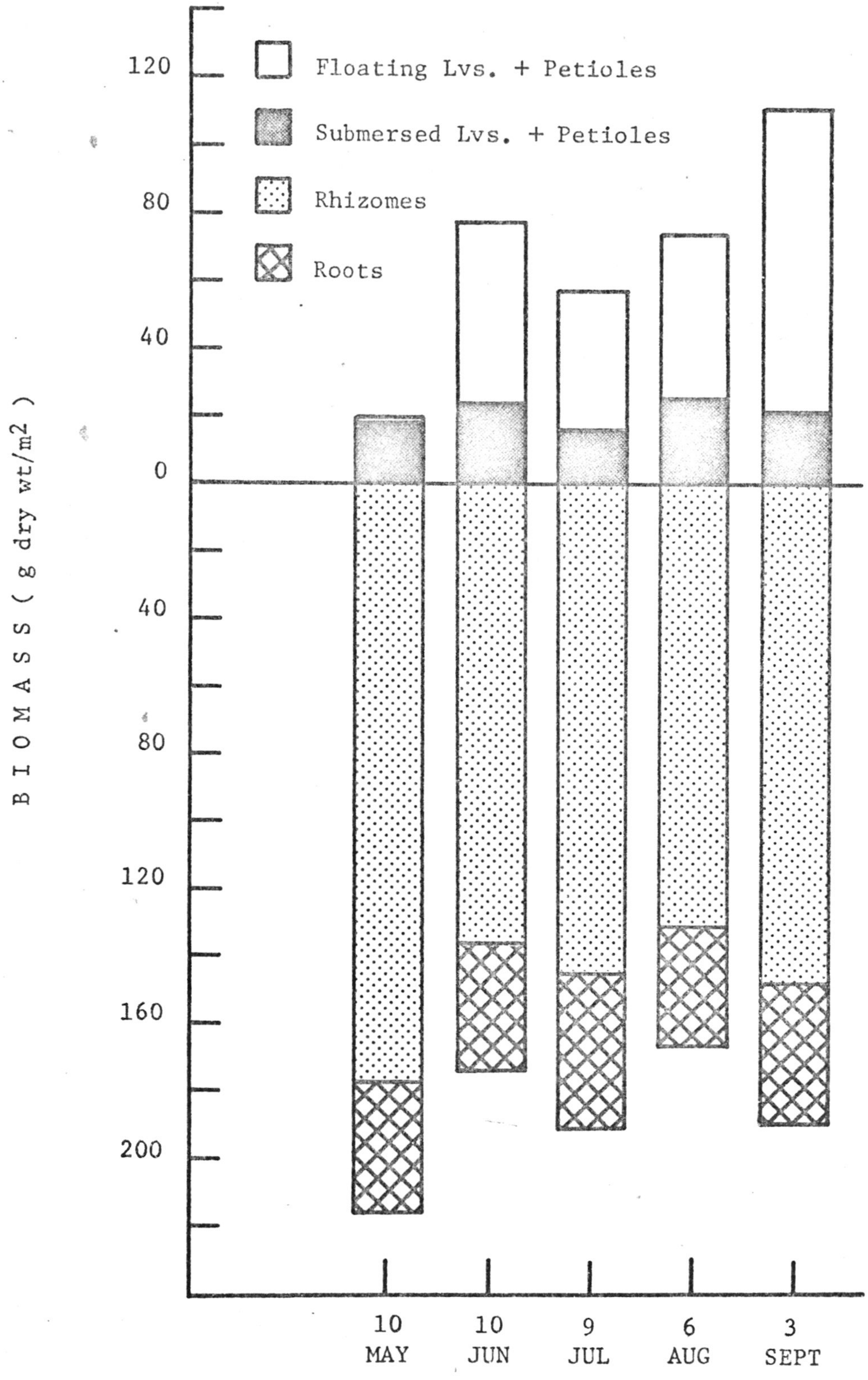
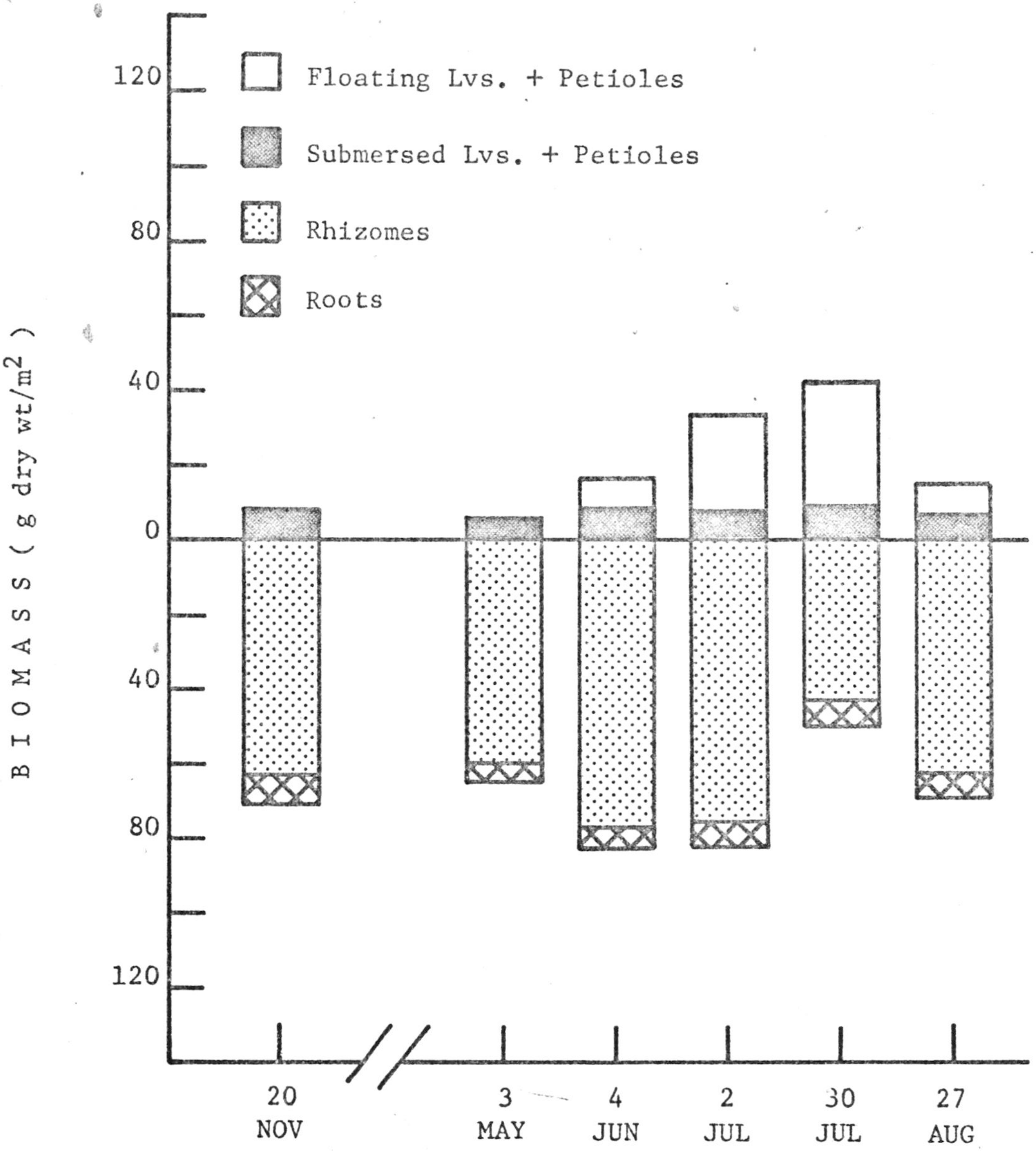

Floating Lvs. + Petioles
Submersed Lvs. + Petioles
Rhizomes
Roots
BIOMASS (g dry wt/m2)
120
80
40
0
40
80
120
160
200
10 MAY
10 JUN
9 JUL
6 AUG
3 SEPT

Figure 6. Monthly mean biomass of *Nuphar luteum* at Keel Creek during November, 1974, and the 1975 growing season. Values above zero are aboveground biomass and those below zero are belowground biomass.

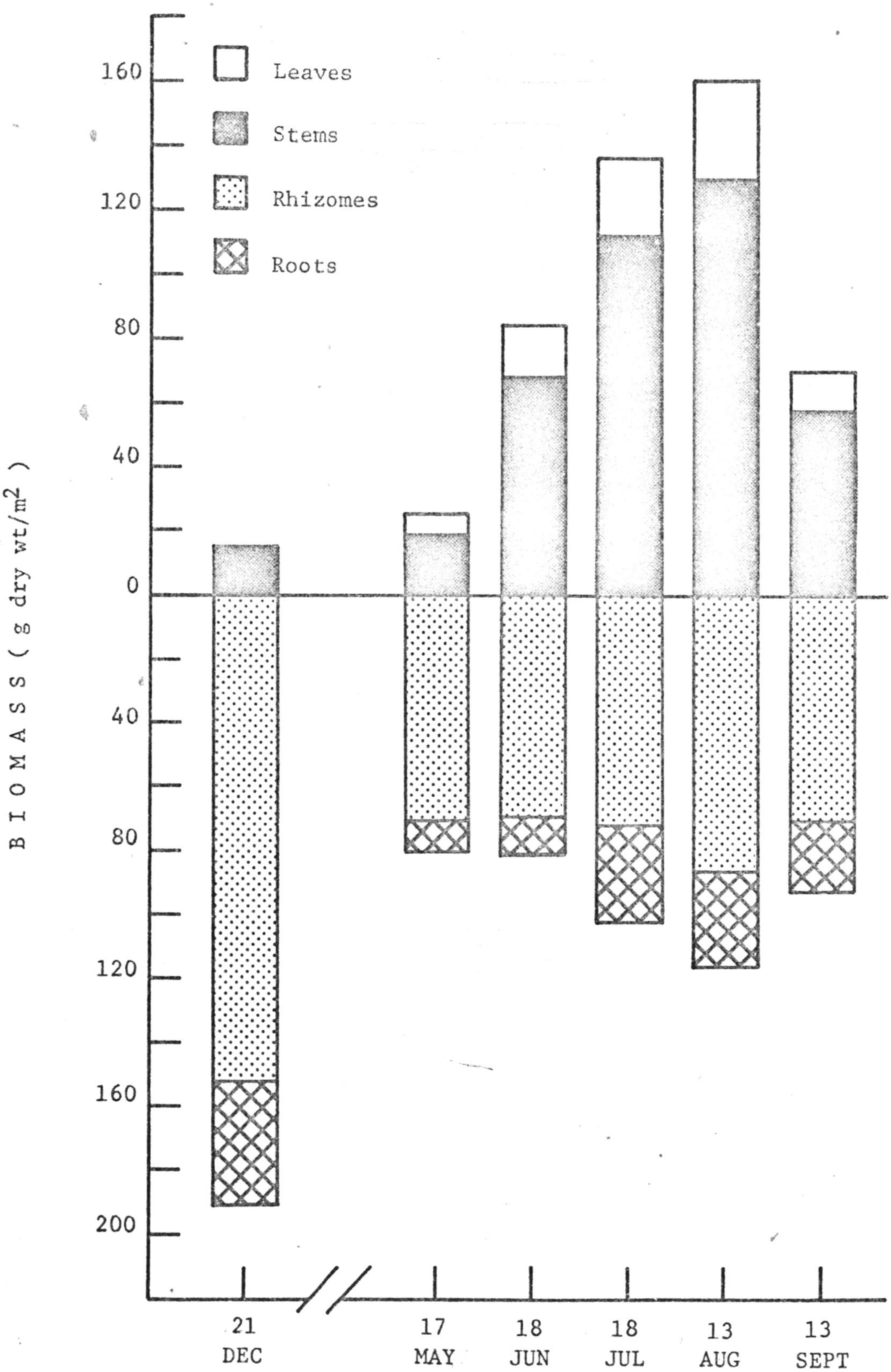


120
80
40
0
40
80
120
BIOMASS (g dry wt/m2)
Floating Lvs. + Petioles
Submersed Lvs. + Petioles
Rhizomes
Roots
20 NOV
3 MAY
4 JUN
2 JUL
30 JUL
27 AUG

Table 1. Summary of monthly biomass of *Nuphar luteum* for 1975. All values are monthly means for three sites and given in g dry wt/m^2.

Plant part	April	May	June	July	August	$\bar{X}$
Aboveground						
Floating leaves	0.2	14.9	12.7	11.6	17.8	11.4
Floating petioles	0.2	10.5	13.6	15.4	20.2	12.0
Submersed leaves	5.7	8.8	6.4	8.0	6.5	7.1
Submersed petioles	3.5	4.8	2.5	4.1	4.9	4.0
Flowers, peduncles, & fruits	0	0.4	1.6	0.3	3.5	1.2
Belowground						
Rhizomes	111.4	104.6	91.5	77.6	101.3	97.3
Roots	22.7	21.9	21.9	18.6	24.5	21.9
Total	143.7	165.9	150.2	135.6	178.7	154.9

Figure 7. Monthly mean biomass of _Justicia americana_ at Rockyhock Creek during December, 1974, and the 1975 growing season. Values above zero are aboveground biomass and those below zero are belowground biomass.


Leaves
Stems
Rhizomes
Roots
BIOMASS (g dry wt/m2)
160
120
80
40
0
40
80
120
160
200
21
DEC
17
MAY
18
JUN
18
JUL
13
AUG
13
SEPT

August, 1975, with an estimated 42 percent of the total biomass in the substrate. Uniform growth of aboveground structures (stems and leaves) was observed during the growing season. Substantial initial biomass of 205.7 g dry wt/m^2 was present in December, 1974 (Appendix, Table D). Average biomass for *Justicia* during the growing season (May through September) was 189.1 g dry wt/m^2 (Table 2).

Variance : mean ratios of total plant biomass indicated that both *Nuphar* and *Justicia* have aggregated distributions (Appendix, Tables E, F, G, & H). A ratio of one which is indicative of a random distribution (Pielou 1960) was exceeded in all cases. Values greater than one, which were found for all sampling dates and both species, suggest that the distribution is clumped.

Nuphar maximum leaf area index (0.82) was obtained during the month of August, 1975, at Wiccacon Creek (Table 3). The maximum leaf area index for *Justicia* was observed during June, 1975, with a value of 0.63 (Table 4).

Prior to harvesting macrophyte biomass, all floating leaves (*Nuphar*) and stems (*Justicia*) were counted per square meter for density analysis. The density of floating leaves was considerably higher at Wiccacon Creek reaching a peak of 31 leaves per square meter in August, 1975 (Table 3). Both Keel Creek and Rockyhock Creek had similar densities throughout the growing season. *Justicia* had a maximum stem density of 25 stems per square meter in July, 1975, at Rockyhock Creek (Table 4).

Biomass Losses

Annual net production of floating leaves was estimated by calculating

Table 2. Summary of monthly biomass of Justicia americana for 1975. All figures in g dry wt/m^2.

Plant part	May	June	July	August	September	$\overline{X}$
Aboveground						
Leaves	3.9	16.6	24.4	30.4	12.0	17.5
Stems	18.9	67.8	111.8	129.9	57.9	77.3
Flowers, peduncles, & fruits	0	0	0.1	0	0	0.02
Belowground						
Rhizomes	71.3	59.5	72.4	86.2	70.3	71.9
Roots	9.0	21.2	29.3	30.0	22.3	22.4
Total	103.1	165.1	238.0	276.5	162.5	189.1

Table 3. Leaf area index and density of floating leaves and petioles for *Nuphar luteum* in 1975.

Location	Month	No. of Samples ($0.35\ m^2$ quadrats)	Density Per m^2	LAI
Rockyhock Cr.	May	6	4	0.22
	June	6	4	0.17
	July	---	4	---
	August	6	8	0.30
Wiccacon Cr.	May	6	21	0.59
	June	6	15	0.39
	July	6	19	0.46
	August	6	31	0.82
Keel Cr.	May	6	4	0.08
	June	6	6	0.26
	July	6	4	0.24
	August	6	2	0.06

Table 4. Leaf area index and density of stems for *Justicia americana* in 1975.

Location	Month	No. of Samples ($0.35\ m^2$ quadrats)	Density Per m^2	LAI
Rockyhock Cr.	May	4	11	0.09
	June	6	17	0.63
	July	6	25	0.46
	August	6	20	0.51
	September	6	19	0.10

the number of leaf turnovers during the 1975 growing season (May 10 - November 2). The average life span of 579 floating leaves tagged from 35 separate rhizome apices was approximately 31 days (Table 5). The 176 days between initial growth (ca. May 10) and the first frost (ca. November 2) was divided by the 31 day average life span of floating leaves resulting in an average turnover rate of 5.7 times per growing season. This value times the mean biomass for the floating leaves (23.4 g dry wt/m^2) during the growing season gave an annual floating leaf production of 133.4 g dry wt/m^2 (Table 6).

Weekly floating leaf and petiole turnovers for *Nuphar* were highest during the month of May, but declined throughout the remainder of the growing season at Rockyhock Creek (Figs. 8, 9, 10). The lowest turnover rate for floating leaves was observed during the last week of July, 1975. By assuming the same turnover rate existed throughout the study area, productivity of floating leaves was calculated by multiplying the turnover rate by the density.

Rockyhock Creek (Fig. 8) had a total seasonal production of 41.9 g dry wt/m^2 for floating leaves. The almost constant biomass of floating leaves (ca. 6 g dry wt/m^2) times the weekly turnover rate generated a production curve similar to the one for weekly turnovers.

Wiccacon Creek (Fig. 9) was found to have a much higher floating leaf density--thus a higher value of floating leaf biomass. Maximum biomass was reached in August with a value of approximately 50 g dry wt/m^2. Seasonal productivity for floating leaves was estimated to be 245.5 g dry wt/m^2.

The maximum floating leaf biomass occurred in June, 1975, at the

Table 5. Average life span of Nuphar luteum floating leaves and petioles in 1975.

Rhizome No.	No. of petioles on rhizome	Total days emerged
1	21	662
2	18	563
3	22	720
4	18	590
5	24	794
6	18	487
7	19	651
8	17	626
9	19	663
10	19	595
11	16	512
12	11	378
13	20	630
14	23	843
15	12	417
16	19	638
17	10	225
18	21	592
19	19	576
20	17	512
21	12	246
22	7	195
23	14	421
24	16	517
25	24	845
26	12	314
27	18	563
28	20	561
29	15	471
30	9	238
31	18	509
32	22	656
33	4	129
34	14	374
35	11	324
Total 35	579	18,037

Average days emerged = $\frac{18,037}{579} = 31$

Number of days in 1975 growing season (May 10 - November 2) = 176

Number of floating leaf and petiole turnovers = 5.7 turnovers

Table 6. Annual production of *Nuphar luteum* in 1975.

Plant part	Turnovers per year	Average biomass for the growing season g dry wt/m^2	Total production turnover x biomass g dry wt/m^2	% Ash (± 95% C.L.)	Organic g dry wt/m^2
Aboveground					
Floating leaves	5.7	11.4	65.0	9.1 ± 0.4	59.1
Floating petioles	5.7	12.0	68.4	15.9 ± 1.4	57.5
Submersed leaves	5.9	7.1	41.9	10.2 ± 0.5	37.6
Submersed petioles	5.9	4.0	23.6	15.9 ± 1.4	19.8
Flowers, peduncles, & fruits	10.4	1.2	12.5	15.9 ± 1.4	10.5
Belowground					
Rhizomes	0.14	97.3	13.6	10.4 ± 1.6	12.2
Roots	0.14	21.9	3.1	17.0 ± 1.2	2.6
Total		154.9	228.1	12.5 ± 0.7	199.3

Keel Creek sampling site (Fig. 10). Productivity was calculated to be 62.1 g dry wt/m^2 for the growing season (May through September).

Overall average seasonal productivity for <u>Nuphar</u> floating leaves using the values calculated from Figures 8, 9, and 10 was 116.5 g dry wt/m^2. This value was not used to determine net primary productivity of <u>Nuphar</u>. All floating leaf turnovers for each sample site was based on data collected at Rockyhock Creek.

The estimated net production of submersed leaves was calculated by tagging randomly selected rhizomes at Rockyhock Creek. The average life of 20 submersed leaves tagged on 11 rhizomes was approximately 30 days with an average turnover of 5.9 (Appendix, Table I). The average seasonal biomass (11.1 g dry wt/m^2) times the number of turnovers (5.9) gave an estimate for submersed leaf production of 65.5 g dry wt/m^2 (Table 6). Submersed leaves were observed to survive throughout the winter.

Annual production of flowers, peduncles, and fruits was calculated in the same manner as floating leaf production. Approximately 24 peduncles were produced with an average life span of 17 days. This value was obtained by dividing the total numbers of days survived by the total number of peduncles produced (Table 7). The 176 days in the growing season divided by the 17-day average survival for the peduncles suggested 10.4 turnovers per growing season. Thus, the annual flower, peduncles, and fruit production was obtained by multiplying the average standing crop of 1.2 g dry wt/m^2 by 10.4 turnovers. The estimated annual production by this method was 12.5 g dry wt/m^2 (Table 6). It was observed that waterfowl and insects grazed flower parts and fruits in some areas, particularly Keel Creek.

Figure 8. Turnover rate, biomass, and net primary productivity of floating leaves at Rockyhock Creek for 1975. Integration of the upper curve gave a net primary production of 41.9 g dry wt/m^2 for the growing season.

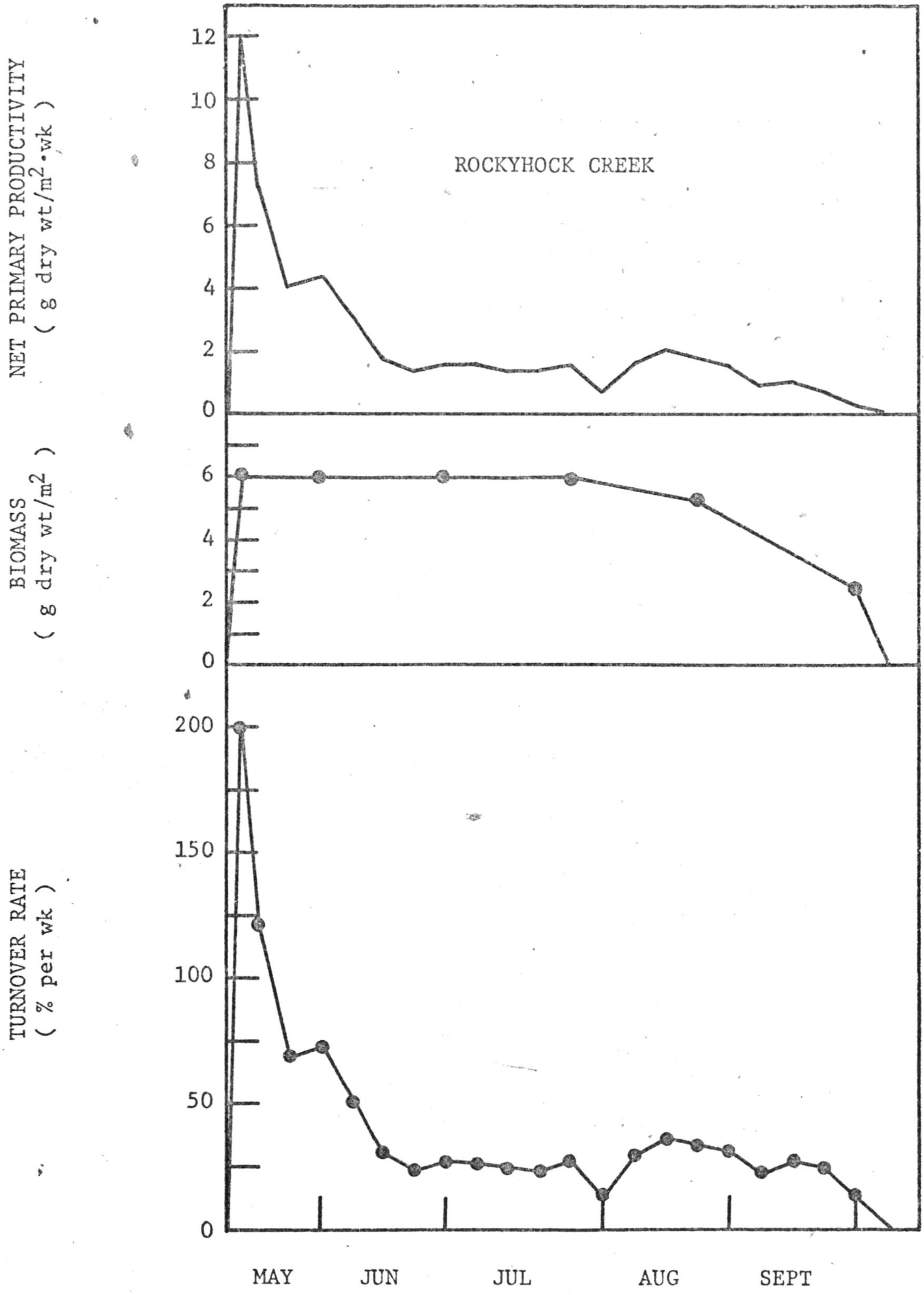

ROCKYHOCK CREEK
NET PRIMARY PRODUCTIVITY
(g dry wt/m2·wk)
12
10
8
6
4
2
0
BIOMASS
(g dry wt/m2)
6
4
2
0
TURNOVER RATE
(% per wk)
200
150
100
50
0
MAY
JUN
JUL
AUG
SEPT

Figure 9. Turnover rate, biomass, and net primary productivity of floating leaves at Wiccacon Creek for 1975. Integration of the upper curve gave a net primary production of 245.5 g dry wt/m^2 for the growing season.

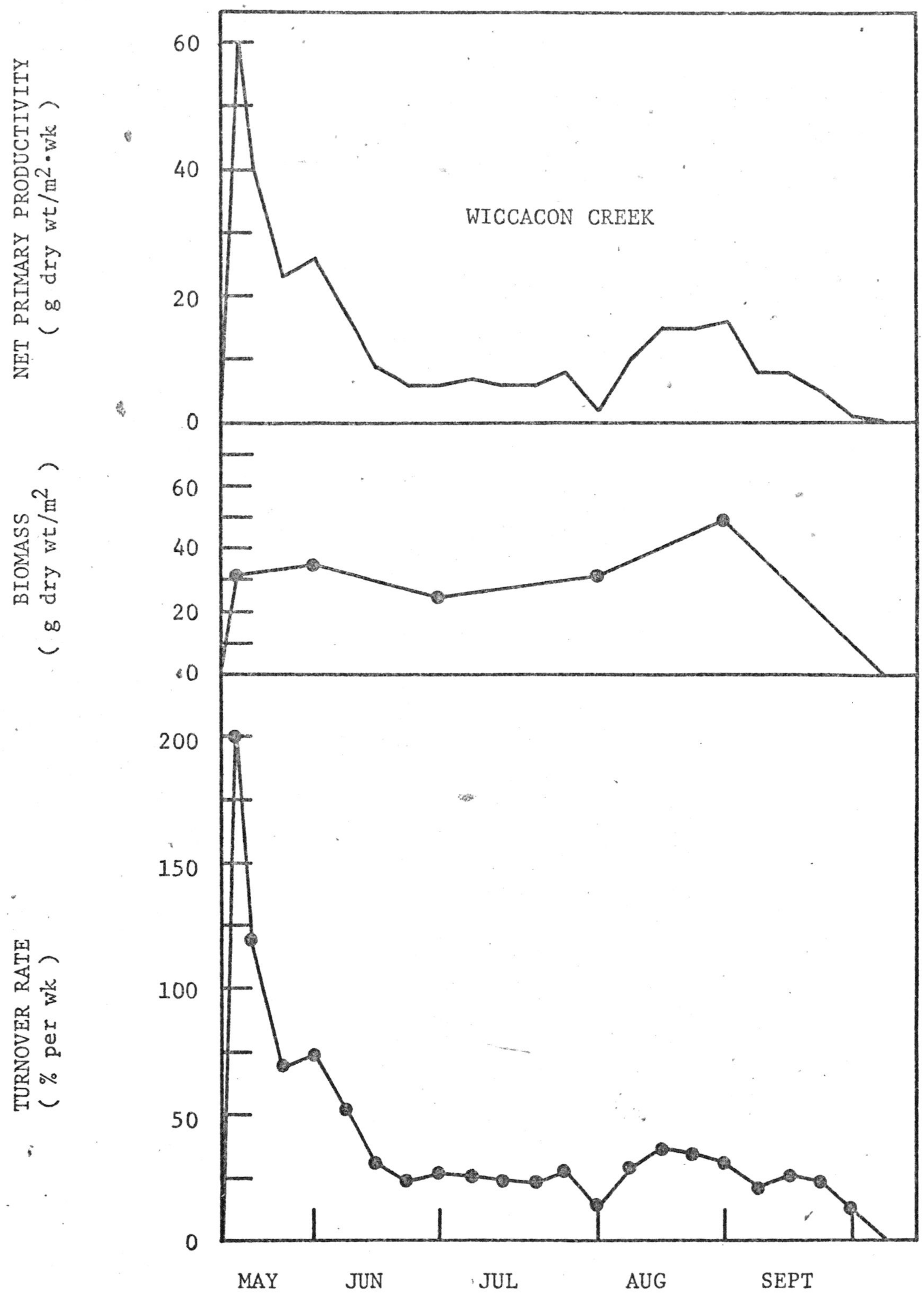

WICCACON CREEK
NET PRIMARY PRODUCTIVITY
(g dry wt/m2·wk)
60
40
20
0
BIOMASS
(g dry wt/m2)
60
40
20
0
TURNOVER RATE
(% per wk)
200
150
100
50
0
MAY
JUN
JUL
AUG
SEPT

Figure 10. Turnover rate, biomass, and net primary productivity of floating leaves at Keel Creek for 1975. Integration of the upper curve gave a net primary production of 62.1 g dry wt/m^2 for the growing season.

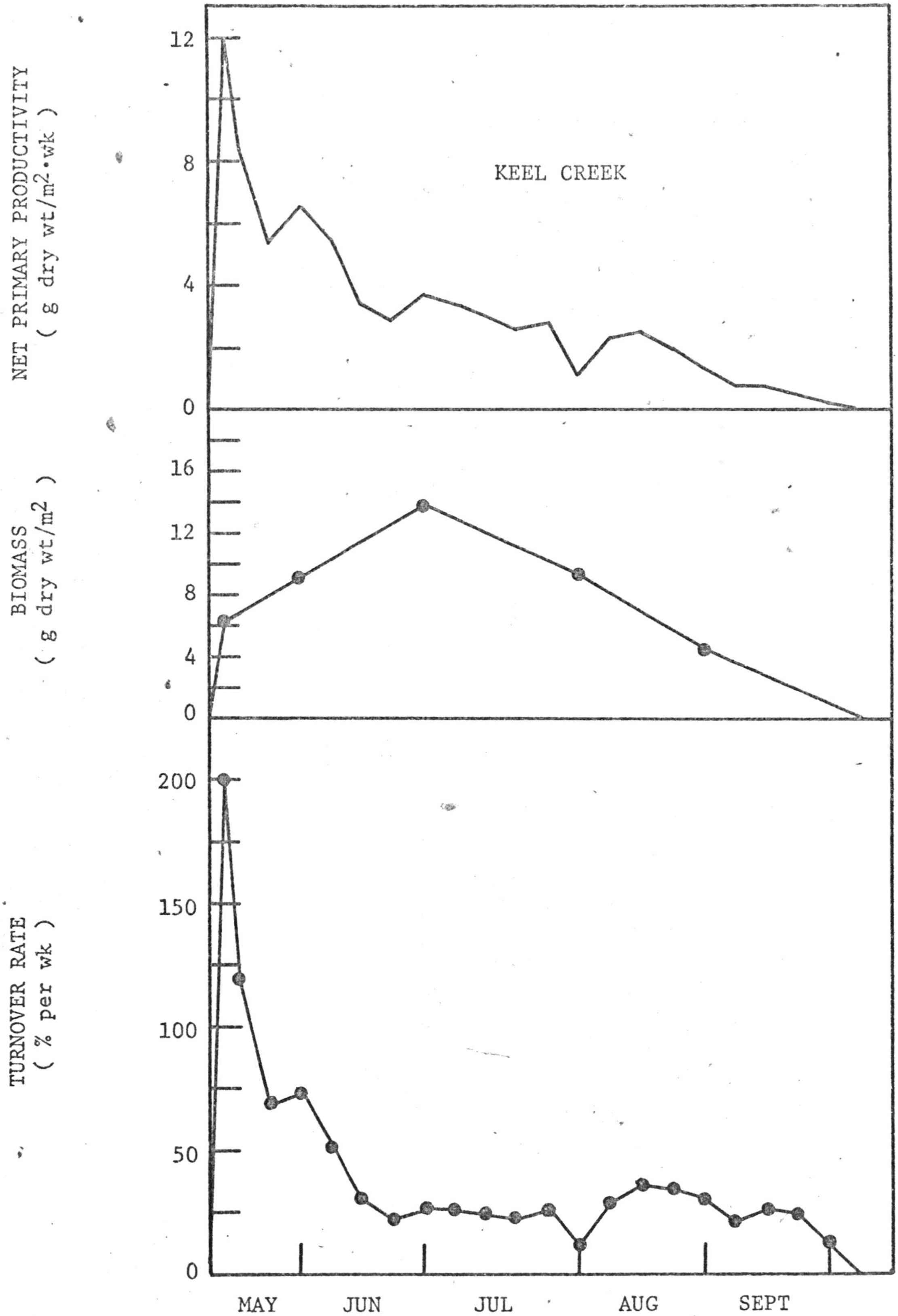

KEEL CREEK
NET PRIMARY PRODUCTIVITY
(g dry wt/m2·wk)
12
8
4
0
BIOMASS
(g dry wt/m2)
16
12
8
4
0
TURNOVER RATE
(% per wk)
200
150
100
50
0
MAY
JUN
JUL
AUG
SEPT

Table 7. Average life span of Nuphar luteum flowers, fruits, and peduncles in 1975.

	Rhizome Number	Number of flowers on rhizome	Total days emerged
	1	1	14
	2	1	14
	3	1	12
	4	1	14
	5	2	35
	6	3	39
	7	1	21
	8	1	35
	9	1	32
	10	1	28
	11	1	7
	12	2	35
	13	1	25
	14	1	14
	15	1	14
	16	1	17
	17	1	10
	18	1	17
	19	1	18
	20	1	7
Total	20	24	408

Average days emerged = $\frac{408}{24} = 17$

Number days in 1975 growing season (May 10 - November 2) = 176

Number of flower, fruit, and peduncle turnovers = 10.4 turnovers

Average rhizome biomass gave little information as to the annual rhizome production since some of the plant material surely represented a number of years growth. The average age of 25 rhizomes was approximately 7 years (Tables 8 and 9). Assuming that 97.3 g dry wt/m^2 was the accumulation of 7 years growth, the annual rhizome production was 13.6 g dry wt/m^2 (Table 6). The alternate method of calculating the rhizome production based on monthly rhizomes tagging was 1.1 g dry wt/m^2· mouth (Table 10).

By comparing the number of newly tagged floating petioles and peduncles with the total number of petiole and peduncle scars on the new rhizome growth, a check was available in the determination of rhizome age. In most cases, newly produced floating petioles scars were less than the total petiole and peduncle scars on the new rhizome growth. Thus, the remainder of the scars represented an estimate of the number of submersed leaves produced during the 1975 growing season. Approximately 520 scars were recorded on the new rhizome growth of 25 rhizomes with 392 floating petioles and peduncles accounting for 75 percent of the total scars.

Root productivity was calculated based on root-to-rhizome ratios from the June, 1975, extensive sampling survey and by assuming the same turnover rate as for the rhizomes (0.14 per year). A positive correlation was found to exist between root and rhizome biomass for the extensive sampling survey with a correlation coefficient value of 0.85 (Fig. 11). Root biomass was predicted by the equation $Y = 0.790 + 0.154X$, where Y = biomass of roots (g dry wt/0.35 m^2) and X = biomass of rhizomes (g dry wt/0.35 m^2). The average root biomass of 21.9 g dry wt/m^2 during

Table 8. Rhizome age estimates based on Nuphar luteum petiole scars for 1975.

Rhizome Number	Total petiole scars	Petiole scars in 1975	Age estimate from scars (years)
1	183	20	9.2
2	213	31	6.9
3	172	14	12.3
4	90	22	4.1
5	129	27	4.8
6	173	18	9.6
7	156	21	7.4
8	157	19	8.3
9	92	31	3.0
10	175	26	6.7
11	99	24	4.1
12	129	14	9.2
13	149	15	9.9
14	143	21	6.8
15	105	17	6.2
16	200	26	7.7
17	229	39	5.9
18	124	15	8.3
19	102	12	8.5
20	63	16	3.9
21	151	11	13.7
22	132	20	6.6
23	110	26	4.2
24	109	22	5.0
25	188	13	14.5
Mean ± s.d.			7.5 ± 3.0

Table 9. Rhizome age estimates based on *Nuphar luteum* rhizome length for 1975.

Rhizome number	Total rhizome length in cm	1975 growth length in cm	Age estimate from length (years)
1	76.1	8.2	9.3
2	156.1	15.9	9.8
3	39.0	6.7	5.8
4	77.2	9.2	8.4
5	69.2	13.9	5.0
6	39.2	3.7	10.6
7	57.8	9.4	6.1
8	79.3	11.3	7.0
9	33.6	7.1	4.7
10	70.6	9.1	7.8
11	33.9	7.9	4.3
12	58.8	9.0	6.5
13	52.1	7.3	7.1
14	92.1	10.0	9.2
15	23.8	5.3	4.5
16	41.9	7.8	5.4
17	78.4	8.2	9.6
18	39.1	6.1	6.4
19	27.6	2.8	9.9
20	18.2	8.2	2.2
21	56.1	4.7	11.9
22	80.3	10.1	8.0
23	34.9	9.7	3.6
24	102.8	11.9	8.6
25	122.8	11.6	10.6
Mean ± s.d.			7.3 ± 2.5

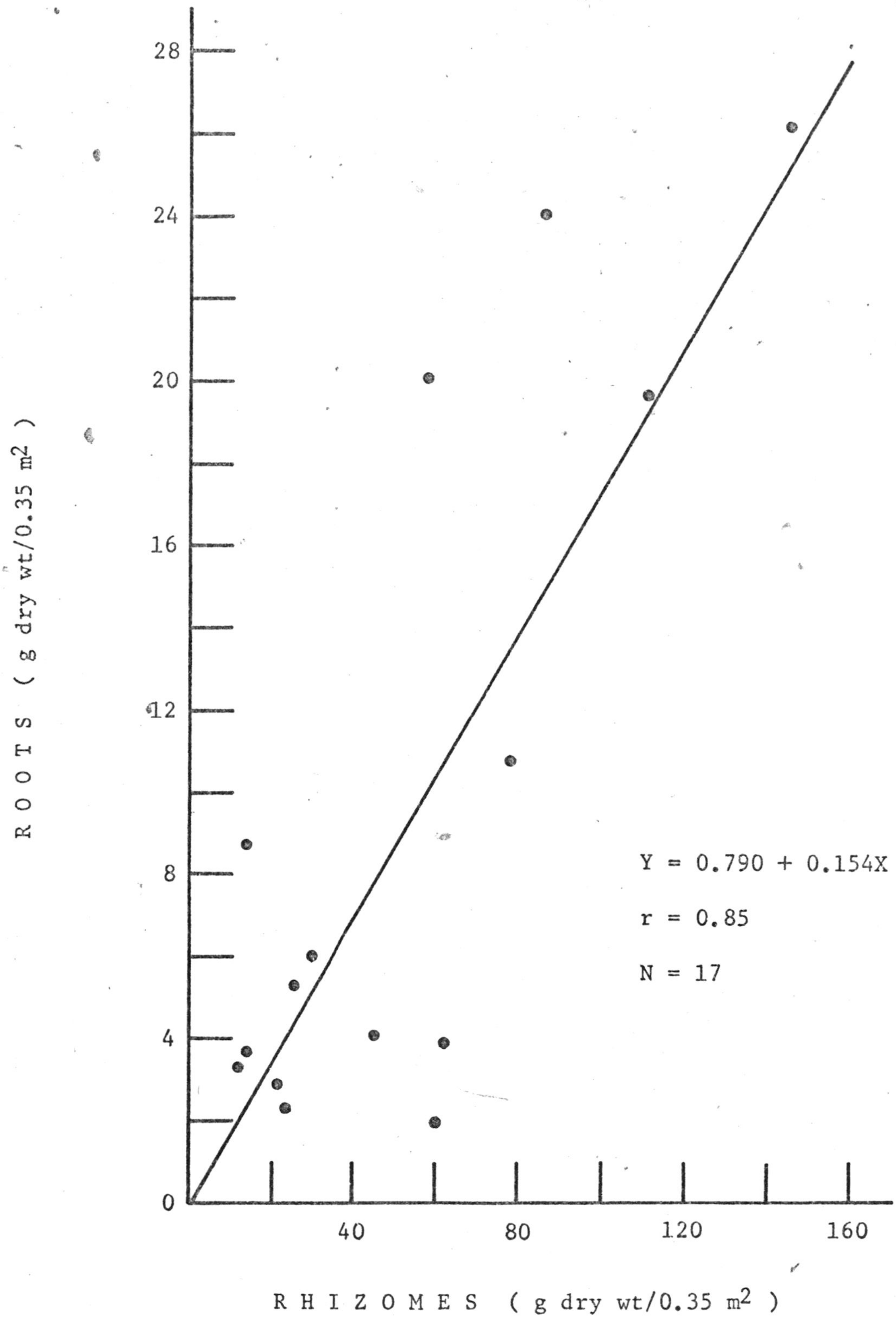
Table 10. Monthly rhizome productivity of *Nuphar luteum* based on tagging measurements for 1975.

Month	Rhizome g dry wt/m^2	Roots * g dry wt/m^2
May	0.4	0.1
June	1.7	0.3
July	1.2	0.2
August	1.2	0.2
September	0.9	0.2
Total	5.4	1.0
Mean	1.1	0.2

Extensive sampling root : rhizome ratio = 0.19

*Roots = rhizomes x 0.19

Figure 11. Correlation of root and rhizome biomass based on samples collected during June, 1975. Root biomass was predicted by the equation $Y = 0.790 + 0.154X$, where Y = biomass of roots (g dry wt/0.35 m^2) and X = biomass of rhizomes (g dry wt/0.35 m^2).


28
24
20
16
12
8
4
0
40
80
120
160
ROOTS (g dry wt/0.35 m2)
RHIZOMES (g dry wt/0.35 m2)
Y = 0.790 + 0.154X
r = 0.85
N = 17

the 1975 growing season times the turnover rate gave an estimate of 3.1 g dry wt/m^2 annual root production (Table 6). Root productivity calculated from monthly rhizome tagging would have been 0.2 g dry wt/m^2. month (Table 10).

The total annual production of Nuphar was 228.1 g dry wt/m^2 with a net organic (ash free) production of 199.3 g/m^2 (Table 6). Generally 77 percent of the Nuphar biomass was below the substrate while 93 percent of the net primary productivity was contributed by aboveground structures.

Unlike Nuphar, Justicia biomass accumulated rapidly during the growing season reaching a peak biomass in August, 1975, of 276.5 g dry wt/m^2 (Fig. 7). By subtracting the minimum biomass of 103.1 g dry wt/m^2 for May from the peak biomass, the observed net primary productivity of 173.4 g dry wt/m^2 was obtained. Some mortality was observed during the growing season; therefore, this value is considred an underestimation. Therefore, peak biomass probably approximated annual net primary productivity. Net annual organic (ash free) production based on peak biomass was 246.4 g/m^2 (Table 11). Grazing by herbivores was not measured for Justicia; however, losses appeared to be quite low during the sampling period.

Table 11. Annual production of *Justicia americana* in 1975 based on peak biomass.

Plant part	Biomass g dry wt/m^2	% Ash (± 95% C.L.)	Organic g dry wt/m^2
Aboveground			
Leaves	30.4	15.7 ± 0.7	25.6
Stems	129.9	11.4 ± 0.6	115.1
Belowground			
Rhizomes	86.2	8.5 ± 0.7	78.9
Roots	30.0	10.5 ± 0.5	26.8
Total	276.5		246.4

Biomass Distribution

Aerial Photography

Macrophyte coverage for the study area in 1974 (August through September) was estimated to be 262,335 m^2 or approximately 26.3 ha (Table 12). The values (m^2 coverage) for each of the northern strata (C, D, and E) were several times higher than those of the lower river (A and B). Coverage for *Nuphar* represented 99 percent of the total macrophyte communities in the study area. *Justicia* distribution was restricted to the extreme lower portions of the river (A and B) as small monospecific stands (Fig. 12).

Flights taken in June, 1975, revealed total macrophyte coverage to be 277,306 m^2 (ca. 27.7 ha). Several macrophyte beds of both *Nuphar* and *Justicia* observed in stratum B were overlooked during the 1974 flights, but were included in the 1975 estimation (Table 13). Stratum B had the least macrophyte coverage for the study area, and the most obvious signs of shore erosion.

Extensive Biomass Survey

To estimate the total biomass in the lower Chowan River area, and determine the amount of variability between macrophyte beds, an extensive sampling survey was completed in June, 1975. Seventeen *Nuphar* beds were randomly selected for sampling based on 42 beds that could be delineated from the 1974 aerial photographs (Fig. 12). The river was divided into an upper portion (N of Holiday Island) where eight beds were sampled, and a lower portion (S of Holiday Island) where nine beds were sampled. Two 0.35 m^2 quadrats were harvested from each bed with only one

Table 12. Coverage (m^2) of Nuphar and Justicia communities on the lower Chowan River for August - September, 1974.

	WEST		EAST		
STRATA	NUPHAR	JUSTICIA	NUPHAR	JUSTICIA	TOTAL
A	----	610	11,261	2,120	13,991
B	18,571	----	----	----	18,571
C	74,457	----	11,869	----	86,326
D	60,831	----	19,595	----	80,426
E	32,425	----	30,597	----	63,022
TOTAL COVERAGE					262,335

Figure 12. Approximate locations of *Nuphar* and *Justicia* beds. The five strata (A-E) between the U. S. 17 bridge and the U. S. 13 bridge correspond to those in Tables 12 & 13.

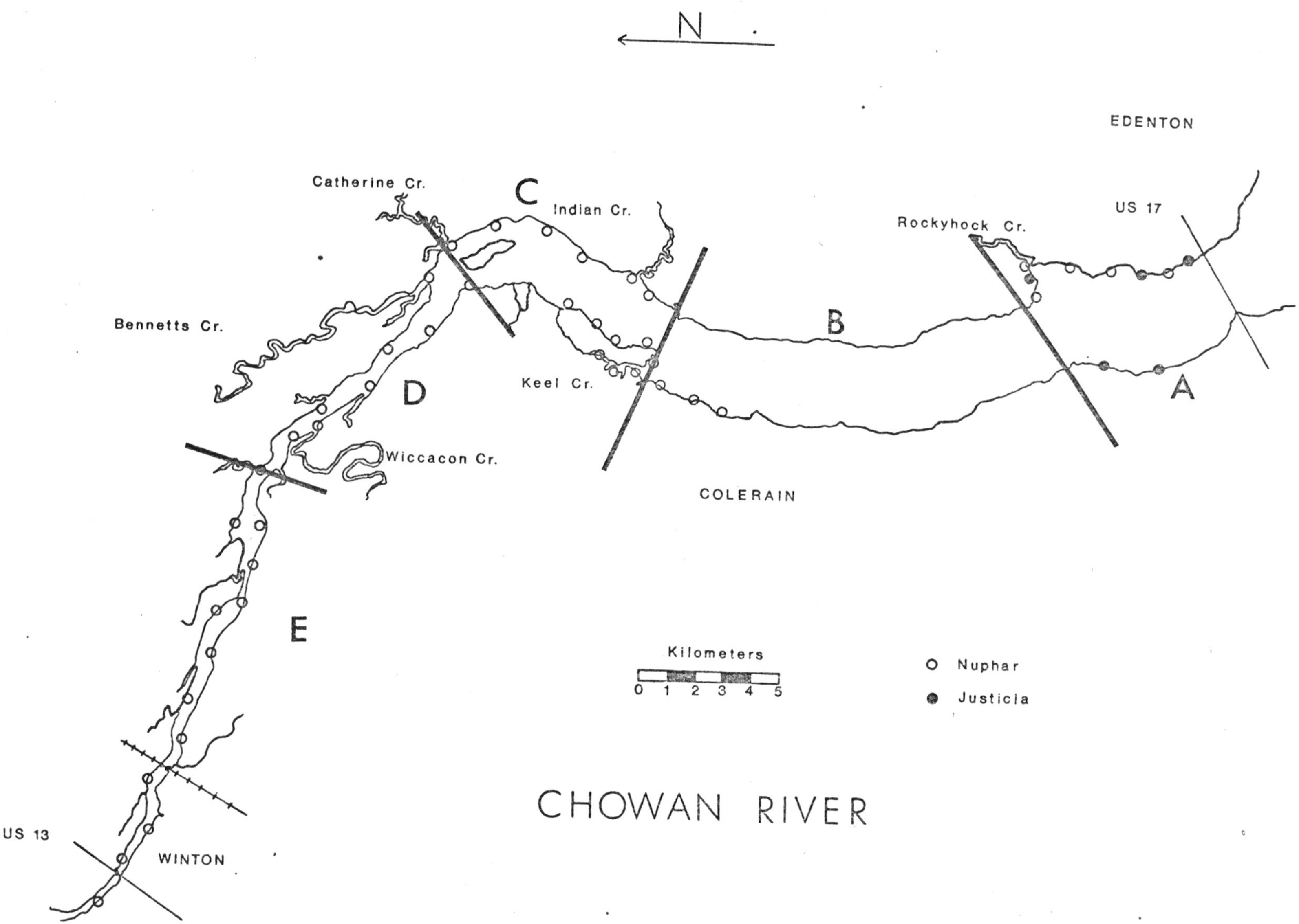

N
EDENTON
US 17
Rockyhock Cr.
Catherine Cr.
C
Indian Cr.
Bennetts Cr.
B
A
D
Keel Cr.
Wiccacon Cr.
COLERAIN
E
Kilometers
0 1 2 3 4 5
Nuphar
Justicia
CHOWAN RIVER
US 13
WINTON

Table 13. Coverage (m^2) of *Nuphar* and *Justicia* communities on the lower Chowan River for 16 June 1975.

	WEST		EAST		
STRATA	NUPHAR	JUSTICIA	NUPHAR	JUSTICIA	TOTAL
A	----	2,760	26,255	2,064	31,079
B	9,319	----	11,942	215	21,476
C	74,589	----	9,008	----	83,597
D	31,049	----	42,470	----	73,519
E	44,400	----	23,235	----	67,635
TOTAL COVERAGE					277,306

quadrat excavated for roots. The roots were calculated as before by linear regression analysis. The biomass in each macrophyte bed was calculated from the average of the two 0.35 m^2 quadrats.

The average biomass for the upper river was 247.8 ± 84.7 g dry wt/m^2 ($\bar{x}$ ± 95% C.L.) with a lower river biomass of 201.3 ± 100.1 g dry wt/m^2 (Table 14). Average biomass for the entire study area was 223.1 ± 65.3 g dry wt/m^2 ($\bar{x}$ ± 95% C.L.). Analysis of variance showed no significant difference at the 5 percent level between the upper river and the lower river (Table 15).

Multiplying the average biomass data from the extensive sampling survey for the total river (Table 14) by the aerial coverage (Table 13) in June, 1975, gave an estimate of 60.7 MT for Nuphar. The total peak biomass for Justicia was approximately 1.4 MT or 2 percent of the total macrophyte biomass.

Table 14. Extensive biomass survey in the lower Chowan River of *Nuphar luteum* for June, 1975.

Area	Bed No.	Biomass g dry wt/m^2	Area	Bed No.	Biomass g dry wt/m^2
Upper River	12	177.0	Lower River	1	71.6
(N = 8)	17	158.7	(N = 9)	3	81.4
	19	389.3		6	16.7
	20	188.0		7	289.1
	21	143.5		11	193.7
	22	154.3		36	492.2
	24	457.9		37	141.0
	29	313.5		39	165.7
				41	359.9
Total		1,982.2			1,811.3
Mean		247.8			201.3
S.E.		43.2			51.1

Summary of Table 14.

Area	No. of beds	Biomass g dry wt/m^2 ($\pm$ 95% C.L.)
Upper River	8	247.8 $\pm$ 84.7
Lower River	9	201.3 $\pm$ 100.1
Total River	17	223.1 $\pm$ 65.3

Table 15. Analysis of variance comparing *Nuphar luteum* biomass between the upper and lower Chowan River. F-value is not significant at the 0.05 level.

Source	df	ssq	msq	F
Between	1	1,123.5	1,123.5	0.47
Within	15	35,808.7	2,387.2	P = 0.05
Total	16	36,932.2		

DISCUSSION

Primary Productivity

Nuphar Productivity

Evaluation of annual net primary productivity based upon changes in biomass at monthly intervals during the growing season could not be applied to the *Nuphar* community. This was due to a high floating leaf mortality during the growing season, and the past years of underground biomass accumulation. The calculation of net primary productivity for *Nuphar* thus necessitated the determination of leaf turnovers, and the annual increment of underground organs.

The approach of estimating net primary productivity by equating it to the observed aboveground peak biomass has been criticized by some authors (Westlake 1969, Waring 1970, Wetzel 1975, pp. 376-377). This reasoning ignores losses of plant material due to death and damage which could account for two to ten percent of the maximum biomass with grazing losses in the range of 0.5 to 8 percent of the total biomass (Wetzel 1975, pp. 379-380). This procedure has assumed that few biomass losses have occurred between samplings and that the productivity of belowground organs could be considered negligible. The latter assumption in the case of some emergent and floating-leaved aquatic vegetation is questionable where underground organs often comprise a large portion of the total biomass (Westlake 1968, Waring 1970, Fiala 1973).

Nuphar peak biomass had a wide range (115-300 g dry wt/m^2) depending upon the location of the macrophyte bed within the study area. The maximum biomass occurred in the northern portion of the river at Wiccacon

Creek, while the minimum biomass was observed at Keel Creek (Fig. 1). Results of other macrophyte studies utilizing peak biomass as a criteria for net primary productivity were compared with the peak biomass of Nuphar (Table 16). The peak biomass measurements reported by Bernatowicz and Pieczynska (1965) of 53-358 g dry wt/m^2 for N. luteum approximated the range found in this study. Waring (1970) observed a peak biomass in July, 1968, for N. advena of 1,329 g dry wt/m^2 with 81 percent of the biomass in the substrate. Such different values are probable due to the variation of species in response to a variety of physical and chemical characteristics of both the water and the sediment (Boyd 1967). This has produced spatial and temporal extremes in heterogeneity in both distribution and productivity (Wetzel 1964; Westlake 1965, 1969; Wetzel and Hough 1973).

The number of floating leaf and petiole turnovers was calculated to be 5.7 times for the 1975 growing season. This rate was determined by dividing 31, the average life span of all floating leaves and petioles tagged, into 176, the number of days between initial growth (ca. May 10) and the first frost (ca. November 2). Waring (1970) determined the number of turnovers for leaves and petioles to be approximately 4.4 times per growing season in 1968. The average life span of leaves and petioles were similar for both Nuphar luteum (31 days) and Nuphar advena (34 days).

Differences in the calculated production of floating leaves and petioles based on weekly turnover rates appeared to be a function of their density. Rockyhock Creek and Keel Creek had a much less floating leaf density than Wiccacon Creek (Table 3). Therefore, this difference was responsible for the higher floating leaf production of 245.5 g dry wt/m^2

Table 16. Estimations of peak biomass for some aquatic macrophytes.

Location	Species	g dry wt/m^2	Source
Submergents:			
Lawrence L., Mich.	Scirpus	338	Rich et al. 1971
Borax L., Calif.	Ruppia maritima	60	Wetzel 1964
Kitty Hawk Bay, N.C.	Ruppia maritima Myriophyllum spicatum	8 274	Hall et al. 1976
River Yare, England	Potamogeton	380	Owens and Edwards 1962
River Test, England	Ranunculus	100 - 400	Owens and Edwards 1961
Floating-leaved:			
Pennsylvania		1,329	Waring 1970
Poland	Nuphar luteum Nymphaea alba	53 - 358 60 - 610	Bernatowicz and Pieczynska 1965
Wisconsin	Nymphaea advena	205	Rickett 1924
Chowan River, N. C.	Nuphar luteum	115 - 299	This study
Emergents:			
New York	Typha angustifolia	1,730	Harper 1918
England	Phragmites communis	1,300	Pearsall and Gorham 1956
England	Glyceria maxima	656	Westlake 1966
Minnesota	Zizania aquatica	500	Bray et al. 1956
L. Ogletree, Ala.	Justicia americana	2,458	Boyd 1969
Chowan River, N. C.	Justicia americana	276	This study

at Wiccacon Creek. This assumed that the same turnover rates for Rockyhock Creek was constant throughout the river.

Submersed leaves and petioles were present throughout the year. Hutchinson (1975, p. 159) and Arber (1920, p. 29) have reported that so-called water leaves can persist throughout the winter in localities which do not freeze. However, on several occasions (winter and spring of 1975) when a strong northeast wind was blowing, submersed leaves were exposed above the normal water level in shallow areas of the macrophyte bed. Severe damage resulted because of the high intensity of sunlight upon these structures.

The 1975 annual production for submersed leaves of 65.5 g dry wt/m^2 was considered an underestimate since they were present all year and data was not collected during the winter.

The annual production of flowers, peduncles, and fruits was 12.5 g dry wt/m^2. Waring (1970) calculated the total production for flowers, peduncles, and seed pods to be 16 g dry wt/m^2 by summing their monthly biomass estimates. He reported that the first flowers appeared in May and that seed pods persisted into the month of September. In this study, flowering was first observed in early June and proceeded until the latter part of August. Aquatic insects and waterfowl grazed heavily upon the fruits and flower parts during the growing season, especially at Keel Creek. Martin and Uhler (1939) have indicated that the parts most consumed of Nymphaeaceae (spatterdocks, yellow pondliles) were the seed pods and seeds. This grazing reduced the seasonal average biomass and thus resulted in an underestimation of net primary productivity for these structures.

The annual rhizome productivity of Nuphar was 13.6 g dry wt/m^2. This estimate was obtained by dividing the average seasonal biomass per square meter by the average rhizome age. This method assumed that rhizomes of different ages had similar growth characteristics and that each year the rhizome meristem grew the same length and produced the same number of petioles as in 1975 (Tables 8 and 9). However, with these questionable assumptions, these two techniques allowed a method of determining rhizome age for a single growing season. Westlake's (1965, 1968) tagging methods used to determine the annual production of aquatic macrophytes with extensive rhizomes would have required many growing seasons. This procedure was thus applied to Nuphar during the 1975 growing season.

Grainger (1947), in studying N. lutea, observed yearly scars left by peduncles and deduced that the weight of the rhizome between successive groups of peduncle scars represented a year's production. This method could not be applied in this study since many of the rhizomes flowered several times during the growing season.

The average monthly rhizome growth was 1.1 g dry wt/m^2 which was considered an underestimation since increases in rhizome biomass occurred in circumference as well as length. The tagging of selected rhizomes allowed for both of these growth parameters to be measured on a seasonal basis in the 1 m x 12 m quadrat at Rockyhock Creek.

Records of individual plants of Nuphar have suggested a life span of more than a century (Heslop-Harrison 1955). The age of Nuphar advena in Waring's study was approximately 4 years which was somewhat lower than observed for this study (7 years). Other studies in the age of underground rhizomes have been reported by Westlake (1965) as follows: Glyceria maxima - 2 years; Phragmites communis - 2 to 3 years; Sparganium erectum - 2 years; and Scirpus lacustris - 3 years. The ecological role of the rhizomes in supplying energy reserves and asexual vegetative propagation has been reviewed by Sculthorpe (1967) and Hutchinson (1975). Rhizomes apparently furnish the energy necessary for the emergent organs in the spring.

The calculated root production of Nuphar was 3.1 g dry wt/m^2. This estimate may have been an underestimation since it was not possible to excavate the roots which penetrated deeper than 30 cm into the substrate. Another problem encountered during sampling of roots was the fragmentation of the roots during harvesting. This fragmentation of roots were lost during the washing of the sample material.

Total root and rhizome production for Nuphar was 26.7 g dry wt/m^2 or 22 percent of the average belowground biomass for the growing season (Table 6). Waring (1970) found that the combined root and rhizome production for N. advena was approximately 27 percent of the standing belowground biomass. Both of these values were lower than were reported by Westlake (1965) for Typha which had 50 percent of the belowground biomass replaced yearly.

Nuphar had an annual net primary productivity of 228.1 g dry wt/m^2 for the 1975 growing season. By multiplying the Nuphar coverage (Table 13) in June, 1975, times the productivity, an estimated production of 63.3 MT of plant biomass was determined for Nuphar in the study area. If extrapolated to the entire river surface area within the study (100 m^2), annual productivity would be approximately 0.6 g dry wt/m^2 or 0.3 g C/m^2 (assumes C = 0.45 x ODW and ash content of 12.5% of the g dry wt). Phytoplankton annual productivity in the Chowan River was estimated at 100 g C/m^2 (Don Stanley, personal communication). Therefore, since Nuphar coverage was determined to be less than 1 percent of the study area in contrast to approximately 100 percent coverage by phytoplankton, Nuphar productivity appears to be insiginificant to the river carbon budget. This same condition was observed in the Pamlico River estuary by Vicars (1976) with submersed macrophytes. Annual productivity of phytoplankton was approximately 40 - 80 g C/m^2 with macrophyte production estimated at 83 g C/m^2. However, macrophyte coverage was only 1 - 2 percent of the total estuary.

The importance of aquatic macrophytes in the lotic ecosystem has been emphasized from the standpoint of their contribution to the detrital structure of the system (Wetzel and Rich 1973, Wetzel 1975, p. 546, Whitton 1975, pp. 235-236). Microbial degradation of detrital macrophyte material has appeared to contribute significantly to the lotic food web where detrital heterotrophic metabolism dominates in most cases.

Approximately 77 percent of the *Nuphar* biomass was in the substrate, while 93 percent of the net primary productivity was contributed by aboveground structures. The probable function between biomass distribution and productivity of *Nuphar* was viewed in its habit of growth. Since *Nuphar* was found to be a perennial, a necessary large supply of stored food must be required to produce new floating leaves and petioles for photosynthesis each spring. This requirement was furnished by the starch material stored in belowground rhizomes which was produced during the past growing seasons. Continued growth of the rhizomes and subsequent decay of their older portions has furnished *Nuphar* an effective and rapid asexual mechanism for colonization of the Chowan littoral. The organs also reduce the probability of uprooting of macrophyte beds by furnishing a strong holdfast to the muddy substrate.

Laing (1940a,b) found that the rhizome of *Nuphar advena* was capable of anaerobic metabolism when the plant was in darkness and could live anaerobically for long periods of time. Also, the production of shoots in N. advena and Peltandra virginica was greatest when the rhizome was almost entirely deprived of oxygen (Laing 1941). This adaptation would allow for the survival of Nuphar in the Chowan River especially in such areas as Keel Creek.

Justicia Productivity

The estimated net primary productivity based upon peak biomass measurements for Justicia was 276.5 g dry wt/m^2 (Table 11). However, Justicia peak biomass was considerably lower than the value reported by Boyd (1969) of 2,458 g dry wt/m^2 in Lake Ogletree, Alabama. Rootstock standing crop was not measured prior to the beginning of the growing season in Boyd's study and was assumed negligible. In this study, a large initial biomass was present in May, 1975, of 103.1 g dry wt/m^2 (Table 2). Normally, the determination of net primary productivity has been estimated by substracting the initial biomass from the seasonal peak biomass. Although mortality of plants and plant parts were not measured for Justicia, peak biomass probably gave an estimate of annual net primary productivity.

Community Structure

The density for floating leaves of Nuphar was highest at Wiccacon Creek with a maximum of 31 floating leaves per square meter (Table 3). Density for Rockyhock Creek and Keel Creek were probably lower due to the increased width of the littoral and increased stress from wind wave action.

Both Nuphar and Justicia formed a clumped distribution which was indicated by the variance : mean ratios of greater than one. Westlake (1969) has indicated that spatial variation in the macrophyte community was often non-random, being both aggregated and related to gradients such as increasing depth. Moore (1965) has also indicated the non-random distribution of vascular aquatic communities to be the result of vegetative forms of reproduction.

Nuphar had a maximum leaf area index (LAI) of 0.82 at Wiccacon Creek (Table 3). Odum (1971, p. 48) in referring to terrestrial communities, has stated that a LAI of 4 was optimal for net production. The LAI value for this study appears to be somewhat low as compared with the value given by Nicholson and Best (1974) of 4.7 for Nuphar variegatum and Nymphaea odorata. However, Nicholson and Best (1974) found LAI and community production were not well correlated in many cases. One probable reason for such a low LAI for Nuphar was the high number of turnovers for floating leaves during the growing season that may have been induced by wave action damage.

Biomass Distribution

Aerial photography has been suggested as a means for determining the distribution and abundance of aquatic macrophytes (Lukens 1968, Kelly 1969). Terrestrial ecologists have used remote photography for mapping plant distributions, identifying geological features, and studying the interrelationship between biological communities and the environment (Kelly and Conrod 1969).

The determination of biomass distribution for aquatic macrophytes within the study area would have been virtually impossible if attempted by boat. Low altitude flights combined with limited harvest sampling has proven a suitable alternative to conventional methods. Therefore, the main advantage of the use of aerial photographic methods has been their efficiency in ecological interpretations (Gustafson and Adams 1973).

Vertical photographs are necessary for mapping because the scale is nearly constant over the entire photograph. Lukens (1968) and Fritz (1970) have emphasized the problems encountered in oblique photography such as decreasing scale across the photograph, skylight reflections from the water surface, and haze. In this study, all aerial photographs were taken vertically at an altitude of 1,200 feet (366 m).

Species differentiation was found to be superior with color photography and color infrared photography as compared to black and white photography. Since little information appeared to be gained from the color infrared imagery about bed size and macrophyte distribution, color photography was used for mapping in this study. Interference resulting from shading by surrounding trees was minimized in the color photographs.

The macrophyte coverage for 1974 (August through September) was 262,335 m^2 with the 1975 (June) coverage of 277,306 m^2. This difference (ca. 5 percent) is probably not statiscally significant.

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APPENDIX

Table A. Monthly biomass of *Nuphar luteum* at Rockyhock Creek for 1975. All figures in g dry wt/m^2.

Plant part	JAN 26	APR 5	MAY 28	JUN 25	JUL 23	AUG 20
Aboveground						
Floating leaves	0	0	8.9	7.9	0	11.9
Floating petioles	0	0	7.3	8.2	0	14.1
Submersed leaves	2.9	1.6	5.9	1.9	1.4	4.4
Submersed petioles	0.9	1.4	2.4	0.8	0.5	1.8
Flowers, peduncles, & fruits	0	0	0	0.9	0	1.4
Belowground						
Rhizomes	246.3	98.1	100.4	53.8	58.6	94.4
Roots	24.1	23.1	23.3	13.8	14.8	25.7
Total	274.2	124.2	148.2	87.3	75.3	153.7
N	4	5	6	6	6	6
S.E.	18.3	13.0	21.3	23.6	23.9	41.1

Table B. Monthly biomass of Nuphar luteum at Wiccacon Creek for 1975. All figures in g dry wt/m^2.

Plant part	MAY 10	JUN 10	JUL 9	AUG 6	SEPT 3
Aboveground					
Floating leaves	0.7	31.5	19.3	23.0	39.1
Floating petioles	0.6	20.6	18.7	25.1	42.2
Submersed leaves	11.5	14.9	11.7	17.3	11.2
Submersed petioles	7.1	9.2	3.9	7.9	9.9
Flowers, peduncles, & fruits	0	1.2	3.4	0.8	9.1
Belowground					
Rhizomes	176.7	135.9	145.0	131.4	147.5
Roots	39.5	37.2	45.7	34.6	41.0
Total	236.1	250.5	247.7	240.1	300.0
N	4	6	6	6	6
S.E.	62.2	70.7	50.4	54.5	43.1

Table C. Monthly biomass of Nuphar luteum at Keel Creek for 1975 and November, 1974. All figures in g dry wt/m^2.

Plant part	NOV 20	MAY 3	JUN 4	JUL 2	JUL 30	AUG 27
Aboveground						
Floating leaves	0	0	4.4	11.0	11.9	2.5
Floating petioles	0	0	3.5	14.0	21.1	4.3
Submersed leaves	5.3	4.1	5.5	5.5	5.4	3.9
Submersed petioles	2.9	2.1	2.9	2.8	3.8	3.0
Flowers, peduncles, & fruits	0	0	0	0.4	0	0
Belowground						
Rhizomes	63.1	59.5	77.4	75.7	42.9	62.1
Roots	6.5	5.5	5.1	6.3	6.5	6.7
Total	77.8	71.2	98.8	115.7	91.6	82.5
N	3	5	6	6	6	6
S.E.	26.6	22.9	26.6	65.3	16.1	19.1

Table D. Monthly biomass of *Justicia americana* at Rockyhock Creek for 1975 and December, 1974.

Plant part	DEC 21	MAY 17	JUN 18	JUL 18	AUG 13	SEPT 13
Aboveground						
Leaves	0	3.9	16.6	24.4	30.4	12.0
Stems	15.1	18.9	67.8	111.8	129.9	57.9
Flowers, peduncles, & fruits	0	0	0	0.1	0	0
Belowground						
Rhizomes	151.7	71.3	59.5	72.4	86.2	70.3
Roots	38.9	9.0	21.2	29.3	30.0	22.3
Total	205.7	103.1	165.1	238.0	276.5	162.5
N	4	4	6	6	6	6
S.E.	19.3	15.6	31.7	65.0	92.4	55.4

Table E. Variance-to-mean of total *Nuphar luteum* biomass at Rockyhock Creek for 1975.

Date	N	Mean	V/M
01/26/75	4	274.2	4.9
04/05/75	5	124.2	6.8
05/28/75	6	148.2	18.4
06/25/75	6	87.3	38.3
07/23/75	6	75.3	45.5
08/20/75	6	153.7	65.8

Table F. Variance-to-mean ratios of total Nuphar luteum biomass at Wiccacon Creek for 1975.

Date	N	Mean	V/M
05/10/75	4	236.1	65.5
06/10/75	6	250.5	119.8
07/09/75	6	247.7	61.5
08/06/75	6	240.1	74.1
09/03/75	6	300.0	37.1

Table G. Variance-to-mean ratios of total Nuphar luteum biomass at Keel Creek for November, 1974 and the 1975 growing season.

Date	N	Mean	V/M
11/20/74	3	77.8	27.4
05/03/75	5	71.2	36.9
06/04/75	6	98.8	43.0
07/02/75	6	115.7	221.3
07/30/75	6	91.6	17.1
08/27/75	6	82.5	26.5

Table H. Variance-to-mean ratios of total *Justicia americana* biomass at Rockyhock Creek for December, 1974 and the 1975 growing season.

Date	N	Mean	V/M
12/21/74	4	205.7	7.3
05/17/75	4	103.1	9.5
06/18/75	6	165.1	36.4
07/18/75	6	238.0	106.5
08/13/75	6	276.5	185.2
09/13/75	6	162.5	113.4

Table I. Average life span of Nuphar luteum submersed leaves and petioles in 1975.

	Rhizome No.	No. of petioles on rhizome	Total days present
	1	2	65
	2	2	51
	3	1	36
	4	2	78
	5	1	35
	6	1	53
	7	3	75
	8	1	43
	9	1	25
	10	2	63
	11	4	81
Total	11	20	605

Average days present = $\frac{605}{20} = 30$

Number of days in the growing season = 176

Number of submersed leaf and petiole turnovers = 5.9 turnovers