BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 104, NO. 4, pp. 347–351 OCTOBER–DECEMBER 1977

Growth, mortality, and biomass partitioning in freshwater tidal wetland populations of wild rice (*Zizania aquatica* var. *aquatica*)[1]

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WHIGHAM, D., and R. SIMPSON. (Biol. Dept., Rider Coll., Lawrenceville, New Jersey 08648). Growth, mortality, and biomass partitioning in freshwater tidal wetland populations of wild rice (*Zizania aquatica* var. *aquatica*). Bull. Torrey Bot. Club 104: 347–351. 1977.—Wild rice is a common annual in Delaware River tidal wetlands. Net production was as high as 20.9 g m^{-2} day^{-1} and varied seasonally. The lowest production rates occurred during the seedling phenophase and the highest followed seedling establishment. On a percentage basis, more biomass was allocated into root production during the seedling phenophase. Population mortality was constant between May and early August.

Tidal wetlands, especially salt marshes, are dominated by perennials but recent studies have shown that herbaceous freshwater tidal wetlands contain several important annual species (McCormick 1970, McCormick and Ashbaugh 1972, Good and Good 1975, Whigham and Simpson 1975). In freshwater tidal wetlands the therophytes are found in almost all vegetation types and a few species are dominant or codominant in several community types (Whigham and Simpson 1975). Physiognomically, the annuals reach peak biomass during the second half of the growing season.

Wild rice (*Zizania aquatica* var. *aquatica*) has been shown to have a relatively long period of vegetation growth followed by a sudden transition to the flowering and fruiting phenophases (Rogosin 1958, Weir and Dale 1960). Germination begins during the last week of April in central New Jersey and vegetative growth continues throughout the growing season with flowering initiated during the second week of July and continuing until early September. Most seeds are shed by the third week in August with the majority dislodged by wind and rain storms in late July and early August. This concurs with reports by Dore (1969), McCormick and Ashbaugh (1972) and Weir and Dale (1960) that wild rice seeds are easily dislodged and that much physical damage is done to wild rice populations during summer wind and rain storms. Almost all individuals senesce by the third week in September and the remainder are killed by the first heavy frosts in October.

This investigation of wild rice (*Zizania aquatica* var. *aquatica*) was undertaken to determine rates of primary production, distribution of biomass as related to growth characteristics of the species, and how biomass accumulation in wild rice populations is related to seasonal changes in population density.

The research was performed in the Hamilton Marshes located on the New Jersey side of the Delaware River between Trenton and Bordentown. These are the northernmost freshwater tidal wetlands in the Delaware River drainage basin (Walton and Patrick 1973) and occupy approximately 500 ha of tidal and nontidal land (Whigham 1974). Tidal amplitude ranges from approximately 3 m in Crosswicks Creek to 30–50 cm on high marsh areas. Vegetation composition, primary production, and nutrient movement patterns within the wetlands have been studied by Whigham and Simpson (1975, 1976).

Methods. Eight wild rice populations were sampled from April into September

[1] This study was supported by grants from the National Geographic Society, the Hamilton Township Environmental Commission and a Rider College Faculty Research Grant-in-aid to the senior author.

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Received for publication April 25, 1977.

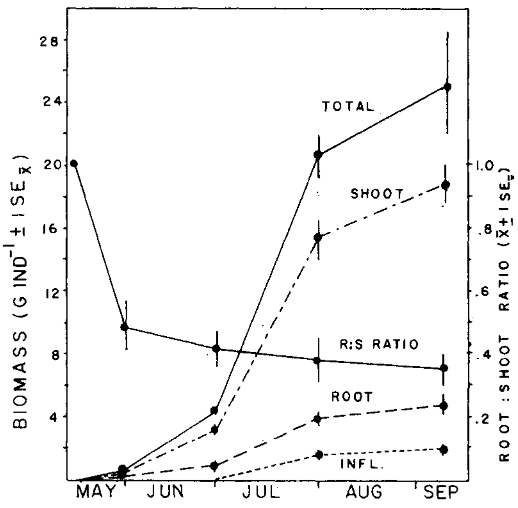

Fig. 1. Seasonal patterns of biomass changes of shoots, roots, inflorescences and root: shoot ratios.

1974. Seedling densities were determined on May 15 in 3 quadrats (0.25 m^{-2}) within each population. On subsequent samplings, densities were determined and the biomass was harvested from 3 quadrats (0.25 m^{-2}) within the 8 populations. Entire plants were removed by hand and, based on preliminary sampling, we estimated that the samples contained approximately 90–95% of the root biomass. Rogosin (1958) and Bray et al. (1959) estimated similar success in sampling wild rice roots in northern nontidal wetlands. The plants were washed and dried at 105 C for 24 hours or until dry and then divided into root, shoot, and inflorescence components prior to biomass determination. Because wild rice produces adventitious roots, it became progressively more difficult to separate root and shoot components. To be consistent, we arbitrarily included into the root biomass component all portions of the stem that had developed adventitious roots. Inflorescences were randomly harvested from the eight populations near the end of the growing season and the potential numbers of seeds per inflorescence determined by counting the number of female flower bearing stalks in each panicle. Coincident with the biomass harvests, phenological observations were made according to the procedures described by Lieth (1970).

Results. Seedling densities were 188 ± 69 plants m^{-2} approximately 2 weeks after germination began and biomass averaged 15 g m^{-2} (Fig. 2) with less than 1 g per individual (Fig. 1). Root:shoot ratios were approximately 1.0 during seedling establishment, declined to approximately 0.45 by June 1, and remained relatively constant during the remainder of the growing season (Fig. 1). We have arbitrarily defined the seedling phenophase as the time between germination and the beginning of high net production rates which coincided with the drop in root:shoot ratios to approximately 0.5. Net primary production was 0.07 g per plant (10.2 g m^{-2}) during seedling establishment and increased to 0.44 g per plant (20.9 g m^{-2}) in July before decreasing again to 0.1 g per plant (10.8 g m^{-2}) in August and September (Fig. 1). The highest rates of net production coincided with the period of rapid height growth and the decline in production rates in late July corresponded with the onset of flowering and fruiting (Fig. 1). Almost all individuals (98.7%) produced one inflorescence and potential seed production averaged 655 ± 193 seeds per individual. Measurement of actual seed production in natural populations is very difficult because pistillate flowers and seeds are easily eaten or dislodged and seeds are not released at one time (Dore 1969, Weir and Dale 1960). Population density averaged 55 plants m^{-2} when biomass averaged 26.2 ± 3.4 g per plant and 1475 ± 225 g m^{-2} (Figs. 1 and 2) at the end of the growing season.

Discussion. The life cycle of *Zizania* has been described (Rogosin 1951 and 1958, Weir and Dale 1960, Dore 1969) and

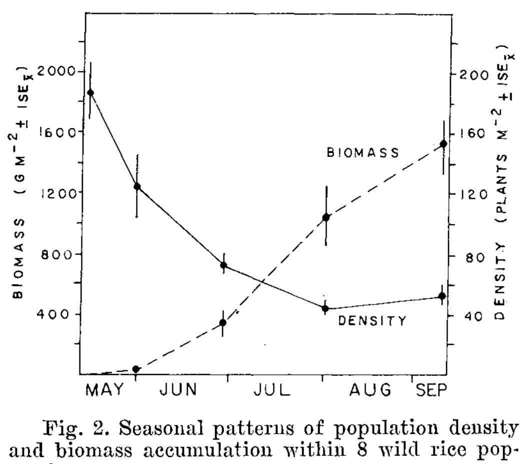

Fig. 2. Seasonal patterns of population density and biomass accumulation within 8 wild rice populations.

studied anatomically and morphologically (Weir and Dale 1960). *Zizania aquatica* var *aquatica,* southern wild rice, is widely distributed in eastern North America and is an important component of several vegetation types in Delaware River freshwater tidal wetlands (McCormick 1970, McCormick and Ashbaugh 1972, Good and Good 1975, Whigham and Simpson 1975). Wild rice is known to serve as a valuable food resource for birds, muskrats and other animals (Weir and Dale 1960, Sculthorpe 1967, Dore 1969, McCormick 1970), and decomposing leaves and stems are obviously important components of the detritus-based marsh ecosystem (Whigham and Simpson 1976). There have been a few studies of primary production of *Zizania* (Table 1) which show that net primary production of eastern populations of *Z. aquatica* var *aquatica* is much higher than Minnesota populations of *Z. aquatica* var *angustifolia* and *Z. aquatica* var *interior*. There appear to be no significant differences between nontidal and tidal populations in New Jersey wetlands although higher production values have been measured in tidal wetlands (Table 1). Production rates measured in this study (20.9 g m^{-2} day^{-1}) were as high as any previously reported for wetland species (Penfound 1956, Jervis 1969, Likens 1976).

Figures 1 and 2 clearly show that there are seasonal variations in net production rates, allocation of biomass, and population density. Phenological data demonstrate that wild rice is characteristic of annuals which occur in environments of high predictability. Harper and White (1974) have suggested that those species have relatively long periods of vegetative growth followed by a sudden transition to flowering and fruiting phenophases. Mortality rates were constant for most of the growing season (Fig. 2) which would be another indication that environmental conditions are relatively stable in freshwater tidal wetlands. Annuals that are characteristic of stressed and unpredictable environments (Harper and White 1974, Sharitz and McCormick 1974) have the highest mortality rates during the seedling stage but wild rice does not have that typical type of convex survivorship curve.

Jervis (1969) measured seasonal variations in aboveground production of wild rice and also found that the seedling phenophase was characterized by low net production rates. It is also during that phenophase that densities are greatest, which would indicate that seedling competition for rooting space would be intensive and development of an adequate root system would be a necessary prerequisite for optimizing survival. We found that it was during that phenophase that the highest percentage of net biomass was allocated to root development (Fig. 1).

Net production rates were greatest and approximately 65% of the biomass was allocated to shoot system development during the phenophase when shoot weight and height were increasing most rapidly (Fig. 1). The rapid increase in shoot weight (13.6 g m^{-2} day^{-1}) occurred at the time when the plants were competing both interspecifically and intraspecifically for positions in the developing canopy of the marsh

Table 1.[5] Production data for *Zizania* in tidal and nontidal wetlands.

Species	Annual net production (g m^{-2})	Location	Type of wetland	Reference
Z. aquatica var *interior*	630[4]	Minn.	Nontidal	Bray *et al.* (1959)
Z. aquatica var *angustifolia*	90–200[3]	Minn.	Nontidal	Rogosin (1958)
Z. aquatica var *aquatica*	970[3]	N.J.	Nontidal	Jervis (1969)
Z. aquatica var *aquatica*	1,390[3]	N.J.	Tidal	McCormick and Ashbaugh (1972)
Z. aquatica var *aquatica*	1,436–1,600[3]	N.J.	Tidal	Good and Good (1975)
Z. aquatica var *aquatica*	1,117[3]	Pa.	Tidal	McCormick (1970)
Z. aquatica var *aquatica*	2,091[3]	Md.	Tidal	McCormick (1977)
Z. aquatica var *aquatica*	560	Va.	Tidal	Wass and Wright (1969)
Z. aquatica var *aquatica*	1,453 ± 225[4]	N.J.	Tidal	This study

[3] Aboveground production only. In two instances (Rogosin 1958 and Good and Good 1975) the values represent ranges. McCormick (1976) and McCormick (1970) are means of 2 and 4 data respectively.
[4] Aboveground and belowground production. Data for this study represent the mean ± 1 standard error of the mean.
[5] Nomenclature follows Dore (1969).

community. In another Delaware River freshwater tidal wetland Good and Good (1975) sampled wild rice during the same time period and measured shoot growth rates of approximately 6.5 cm $plant^{-1}$ day^{-1}.

The flowering phenophase began after the period of maximum shoot growth and was marked by a decline in net production rates during which time most of the net biomass was allocated to the development of the inflorescences (Fig. 1). Switching to the development of flowers and then seeds is obviously important for annuals because the populations must produce seeds to survive. This study has demonstrated that minimum energy is wasted in shoot and root growth once the plants enter the reproductive phenophases.

We estimated potential seed production (37,300 seeds m^{-2}) for the eight populations by multiplying the average number of seeds per plant by the mean number of seed producing individuals. Although comparisons of data from different years can be tenuous, the estimated potential seed production is so much greater than seedling density (188 ± 60 plants m^{-2}) that we conclude that seed mortality is very high and that perhaps as few as one percent of the seeds survive to germinate. Although Harper and White (1974) suggest that it is difficult to analyze data on seed production because of variability both within and between species, seed production in wild rice must be high because of high mortality levels, especially seed mortality. Others (Rogosin 1958, Dore 1969) have shown that wild rice seeds are consumed by birds and waterfowl in great numbers and they have also suggested that many seeds are lost prior to maturation. McCormick and Ashbaugh (1972) reported that large numbers of plants are destroyed during wind and rain storms before the seeds mature. We also noted large amounts of destruction caused by summer wind and rain storms and had one population which was almost completely destroyed during a July storm. Dore (1969) has shown that seeds which are shed prematurely are unlikely to germinate.

In summary, this study has shown that wild rice can be characterized as having very high production rates and producing large numbers of seeds. Since this study we have been able to gather preliminary data on biomass allocation of other annuals in the Hamilton Marshes and it appears that *Zizania* is typical of most species. Most of the net primary production is used in shoot growth with the exception that a larger percentage of biomass is allocated to root development during the seedling phenophase. Net production rates are also generally low during the seedling phenophase and then increase to a maximum during a period of rapid shoot growth which is followed by lower growth rates during the flowering and fruiting phenophases.

Literature Cited

BRAY, J. R., D. B. LAWRENCE, and L. C. PEARSON. 1959. Primary production in some Minnesota terrestrial communities for 1957. Oikos 10: 38–49.

DORE, W. G. 1969. Wild rice. Publ. No. 1393. Canada Dept. Agric. Ottawa, Canada. 84 p.

GOOD, R. E., and N. F. GOOD. 1975. Vegetation and production of the Woodbury Creek–Hessian Run freshwater tidal marshes. Bartonia 43: 38–45.

HARPER, J. L., and J. WHITE. 1974. The demography of plants. Ann. Rev. Ecol. and Syst. 5: 419–463.

JERVIS, R. A. 1969. Primary production in the freshwater marsh ecosystem of Troy Meadows, New Jersey. Bull. Torrey Bot. Club 96: 209–231.

LIETH, H. 1970. Phenology in productivity studies. *In:* D. E. Reichle, ed. Analysis of Temperate Forest Ecosystems. Springer-Verlag, N.Y. pp. 29–46.

LIKENS, G. E. 1976. Primary productivity of inland aquatic ecosystems. *In:* H. Lieth and R. H. Whittaker, eds. Primary Productivity of the biosphere. Springer-Verlag, N.Y. pp. 185–202.

MCCORMICK, J. 1970. The natural features of Tinicum Marsh, with particular emphasis on the vegetation. *In:* McCormick, J., R. R. Grant, Jr., and R. Patrick. Two studies of Tinicum Marsh, Delaware and Philadelphia Counties, Pa. The Conservation Found. Washington, D.C. 104 p.

————. 1977. Productivity of freshwater tidal marsh vegetation. Bull. N.J. Acad. Sci. 22. (in press)

———— and T. ASHBAUGH. 1972. Vegetation of a section of Oldmans Creek tidal marsh and related areas in Salem and Gloucester Counties, New Jersey. Bull. N.J. Acad. Sci. 17: 31–37.

PENFOUND, W. T. 1956. Primary production of vascular aquatic plants. Limnol. Oceanogr. 1: 92–101.

ROGOSIN, A. 1951. An ecological life-history of wild rice. Cont. Minn. Comm. on Wild Rice. St. Paul. 29 p.

———————. 1958. Experimental growth of wild rice in relation to water levels, seedling densities, and fertilizer application. Proc. Minn. Acad. Sci. 25–26: 95–97.

SCULTHORPE, C. D. 1967. The Biology of Aquatic Vascular Plants. St. Martin's Press, N.Y. 610 p.

SHARITZ, R. R. and J. F. MCCORMICK. 1973. Population dynamics of two competing annual plant species. Ecology 54: 723–740.

WALTON, T. E., and R. PATRICK (eds.). 1973. Delaware River estuarine marsh survey, a report to the National Science Foundation RANN program. 172 p.

WASS, M., and T. WRIGHT. 1969. Coastal wetlands of Virginia. Interim report to the Governor and General Assembly. Virginia *Inst.* of *Marine Sci., Spec. Rept.* in *Appl. Mar. Sci.* and *Ocean Eng.* 10. 154 p.

WEIR, C. E., and H. M. DALE. 1960. A developmental study of wild rice, *Zizania aquatica* L. Can. Jour. Bot. 38: 719–739.

WHIGHAM, D. 1974. Preliminary ecological studies of the Hamilton Marshes. Progress report for the period ending January 1974. Rider College, Lawrenceville, N.J. 66 p.

———————, and R. L. SIMPSON. 1975. Ecological studies of the Hamilton Marshes. Progress report for the period June, 1974–January, 1975. Rider College, Lawrenceville, N.J. 185 p.

———————, and ———————. 1976. The potential use of freshwater tidal marshes in the management of water quality in the Delaware River. *In:* J. Tourbier and R. W. Pierson, Jr., eds. Biological Control of Water Pollution. Univ. Penn. Press, Phil. pp. 173–186.