

THE RELATIONSHIP BETWEEN ABOVEGROUND AND BELOWGROUND BIOMASS OF FRESHWATER TIDAL WETLAND MACROPHYTES

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(Received 13 February 1978)

ABSTRACT

Whigham, D.F. and Simpson, R.L., 1978. The relationship between aboveground and belowground biomass of freshwater tidal wetland macrophytes. *Aquat. Bot.*, 5: 355–364.

Aboveground and belowground biomass relationships of 15 annual and perennial freshwater tidal wetland macrophytes were examined. The data showed that regression equations may be used with confidence to estimate belowground biomass from aboveground biomass for most species. The linear regression model was suitable except for one species which had a large belowground component and for which the exponential model was more appropriate. Belowground:aboveground biomass ratios were significantly different for the 8 annual species examined. At peak biomass, all annuals allocated less than one third of the total net annual production into belowground structures. They exhibited distinct seasonal patterns of biomass allocation with more biomass incorporated into belowground components during the early part of the growing season. Perennial species exhibited 4 patterns of biomass allocation with *Peltandra virginica* (L.) Kunth having a significantly greater mean belowground:aboveground biomass ratio than other perennials. Factors that may control biomass allocation patterns include depth of rooting and life history strategies.

INTRODUCTION

Estimates of biomass and primary production of emergent herbaceous macrophytes in freshwater wetlands rarely include data on belowground materials (Bernard, 1974; Bernard and Bernard, 1973; Bernard and Gorham, 1978; Boyd, 1969, 1970, 1971) even though subterranean components may account for a large percentage of the total biomass and annual net primary production (Bernard and Gorham, 1978; Jervis, 1969; Likens, 1976). There have been even fewer studies of the partitioning of net primary production between aboveground and belowground components of freshwater tidal wetland macrophytes (Good and Good, 1975; McCormick, 1970; McCormick and Ashbaugh, 1972; Whigham and Simpson, 1977). In a recent review of biomass and primary pro-

duction of freshwater tidal wetlands (Whigham et al., 1978), it was shown that most investigators have underestimated biomass and net production because, in part, they did not estimate belowground production.

Freshwater tidal wetlands are highly diverse and include species that range from typical emergent herbaceous perennial macrophytes (*Pontederia cordata* L., *Peltandra virginica* (L.) Kunth, *Nuphar advena* (Ait.) Ait. f. *Thypha* sp., *Sparganium* sp. and *Scirpus* sp.) to a number of annuals of which *Zizania aquatica* var. *aquatica* L., *Bidens* sp. and several species of *Polygonum* are commonly dominant. Most of those species are taxonomically unrelated and, while much is known about convergence of leaf shape, heterophylly and types of belowground structures, primarily rhizomes and turions (Hutchinson, 1975), there is little information on how they allocate their resources.

Considering the unifying effect of natural selection, one might expect, however, that there would be convergence of biomass allocation patterns between species that occur in wetland environments where environmental selection pressures would appear to be similar. In this situation, environmental similarity might exist within the substrate where, at most, only the first few centimeters of substrate are aerobic. In this paper, we test that hypothesis by considering the relationships between belowground and aboveground components of 15 annual and perennial species that are widely distributed in freshwater tidal wetlands. Additionally, we consider the value of regression equations in estimating belowground biomass from aboveground biomass data. Nomenclature follows Gleason and Cronquist (1963) with the exception of *Acnida cannabinus* (L.) J.D. Sauer which follows Radford et al. (1968) and *Zizania aquatica* var. *aquatica* L. which follows Dore (1969).

METHODS

Plants were collected from five sites in the Hamilton Marshes, a Delaware River freshwater tidal wetland near Trenton, New Jersey, and previously described by Whigham and Simpson (1976). Perennials were harvested in 1975, 1976 and/or 1977 when aboveground and belowground biomass of each species was near peak standing crop. Entire plants of annuals and non-rhizome-forming perennials [*Peltandra virginica*, *Pontederia cordata*, *Sagittaria latifolia* Willd. and *Scirpus fluviatilis* (Torr.) Gray] were individually hand extracted while rhizome-forming perennials (*Acorus calamus* L., *Nuphar advena*, *Sparganium americanum* Nutt. and *Typha latifolia* L.) were extracted using 0.25 m² quadrats. The quadrats almost always enclosed entire clumps of the rhizome-forming species, but there were occasions when the samples underestimated belowground biomass because rhizomes extended beyond the quadrat boundary. Annuals were sampled on 4 dates in 1975 chosen to represent the following growth phases: (1) seedling, (2) shoot growth initiation following seedling establishment, (3) period of maximum net production and (4) mature plants. All samples were washed several times in the field and laboratory and then separated into aboveground (including stems, leaves and reproductive

structures) and belowground components. The samples were dried at 105° C and weighed. Data for each species were subjected to regression analysis using both linear ($Y = a + bX$) and exponential ($Y = ae^{bX}$) models (where Y was the belowground biomass and X was the aboveground biomass) for the purpose of developing a series of regression equations to estimate belowground standing stock from aboveground biomass.

RESULTS

Linear regressions provided the best fit for all species except *Peltandra virginica* where the exponential model produced a larger correlation coefficient. Regression equations for all perennials except *Sparganium americanum* were significant at the $\alpha = 0.01$ level and, except for *Polygonum sagittatum* L., were generally significant at the $\alpha = 0.05$ level or higher for the annuals (Figs.1 and 2).

The perennials exhibited 4 distinct biomass allocation patterns (Fig.1). The percentages of belowground biomass of *Acorus calamus* and *Typha latifolia* only varied slightly across the range of clone sizes sampled. Belowground biomass accounted for approximately 53% of the total biomass of *Acorus* and 36% for *Typha*. For *Pontederia cordata*, the percentages of belowground biomass increased as the aboveground biomass component increased. Small plants (aboveground biomass of 15 g) had 40% of the total biomass allocated into belowground structures while large individuals (aboveground biomass of approximately 50 g) allocated nearly 50% of their resources into belowground structures. The opposite allocation pattern was found for *Nuphar advena*, *Sagittaria latifolia*, *Scirpus fluviatilis* and *Sparganium americanum* where individuals with smaller shoots allocated larger percentages of their biomass into belowground components than did individuals with larger shoots. *Peltandra virginica* displayed a fourth allocation pattern. Both small and large individuals (aboveground biomass of 10 g and 100 g, respectively) allocated approximately 90% of their total biomass to underground structures while individuals with intermediate sized shoots (approximately 50 g) had less biomass (84%) in their belowground structures.

Belowground:aboveground biomass ratios (R:S) were calculated for each species (Table I). There were significant ($\alpha = 0.01$) differences between species and species comparisons made using Newman Keuls Tests (Sokal and Rohlf, 1969) showed that *Peltandra virginica* was the only species with an R:S significantly greater than all other species. The R:S of *Scirpus fluviatilis* was significantly less than that of *Peltandra virginica* but significantly greater than the values of the other species. The R:S of *Sparganium americanum* was significantly greater than that of *Typha latifolia* and *Sagittaria latifolia* but not significantly different from the values of *Nuphar advena*, *Acorus calamus* and *Pontederia cordata*.

Most of the net production of the annual species was allocated to shoot production and only during the seedling phenophase were relatively large per-

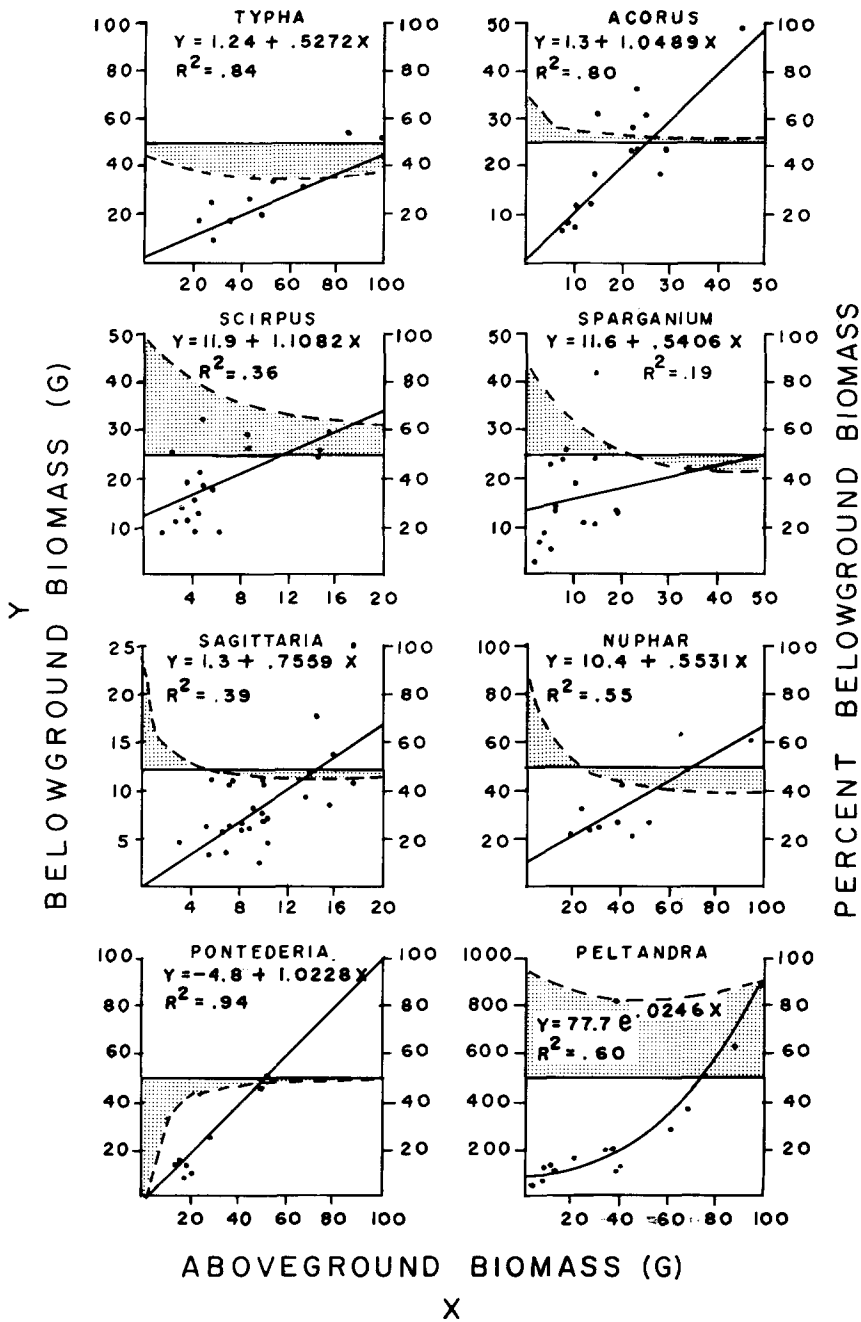


Fig. 1. Aboveground and belowground biomass relationships of 8 perennial freshwater tidal wetland macrophytes. With the exception of *Sparganium*, all regression equations are significant at the $\alpha = 0.01$ level. Shaded portions represent the difference between the observed allocation of belowground biomass and a 50% allocation pattern. Refer to Table I for a listing of species names.

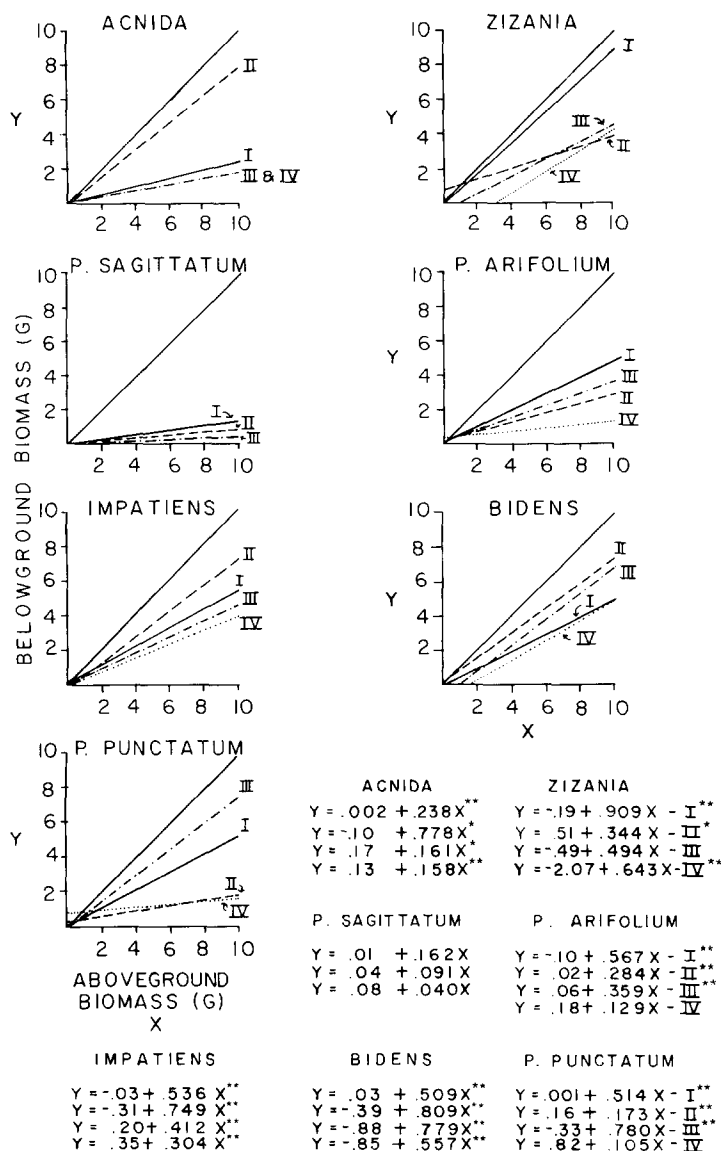


Fig. 2. Aboveground and belowground biomass relationships of 7 freshwater tidal wetland annuals. Regression equations are for the following 1975 sampling dates: I = June 7; II = June 21; III = July 3; IV = August 18. The unmarked line on each graph represents a 1:1 distribution of belowground to aboveground biomass. Significance levels are designated at $\alpha = 0.05$ (*) and $\alpha = 0.01$ (**), respectively. Refer to Table I for a listing of species names.

TABLE I

Belowground:aboveground biomass ratios at peak standing crop for annual and perennial species

Species	Mean \pm 1 S.E.	Maximum	Minimum	Sample size
Perennials				
<i>Acorus calamus</i>	1.11 \pm 0.36	2.13	0.63	17
<i>Nuphar advena</i>	0.86 \pm 0.28	1.39	0.48	10
<i>Peltandra virginica</i>	8.42 \pm 5.05	21.37	2.79	13
<i>Pontederia cordata</i>	1.30 \pm 1.14	3.86	0.54	7
<i>Sagittaria latifolia</i>	0.94 \pm 0.38	1.91	0.42	25
<i>Scirpus fluviatilis</i>	3.64 \pm 1.92	9.33	1.28	20
<i>Sparganium americanum</i>	1.92 \pm 1.01	4.23	0.64	16
<i>Typha latifolia</i>	0.55 \pm 0.17	0.91	0.42	10
Annuals				
<i>Acnida cannabinus</i>	0.24 \pm 0.07	0.39	0.18	10
<i>Bidens laevis</i>	0.41 \pm 0.17	0.78	0.17	15
<i>Impatiens capensis</i>	0.37 \pm 0.17	0.79	0.10	20
<i>Polygonum arifolium</i>	0.15 \pm 0.14	0.50	0.03	15
<i>Polygonum punctatum</i>	0.46 \pm 0.31	0.90	0.15	10
<i>Polygonum sagittatum</i> *	0.14 \pm 0.11	0.40	0.04	10
<i>Zizania aquatica</i> var. <i>aquatica</i>	0.41 \pm 0.19	0.66	0.20	10

*Data from 3 July were used for this species.

centages of the total biomass found in the root components. The percentages of root system biomass of *Polygonum sagittatum*, *Polygonum arifolium* L. and *Zizania aquatica* var. *aquatica* decreased continually throughout the sampling period. Whigham and Simpson (1977) have reported similar results from another study of *Zizania*. The percentages of root biomass of *Acnida cannabinus*, *Bidens laevis* (L.) BSP. and *Impatiens capensis* Meerb. increased after the seedling phenophase and then declined to minimum values in August. Initial decreases in the percentage of biomass of the root components of *Polygonum punctatum* Ell. were followed by increases in July and decreases in August. At peak aboveground standing crop, R:S ratios for the annuals averaged less than 0.5 (Table I) and there were significant differences ($\alpha = 0.01$) between species, Although *Polygonum arifolium* and *P. sagittatum* had smaller ratios than the other species, further testing failed to show which means were significantly different.

DISCUSSION

Our initial prediction was that species found in similar habitats should have similar patterns of biomass allocation because of the similarity in environmental selection pressures. While at peak biomass the annual species did have significantly different R:S ratios, a clear convergence is apparent because the

R:S ratios were always less than 0.5. The annuals exhibited seasonal patterns of biomass allocation (Fig.2) and the patterns may be related to several factors. Survival strategy may be an important factor for most species allocated more biomass to root structures during the seedling establishment phenophase when individuals were competing for rooting space. Following establishment, the plants entered a phase of rapid shoot growth and then began to allocate most of their net biomass into that component. This phenomenon has been verified by the work of McCormick (1970), McCormick and Ashbaugh (1972) and Good and Good (1975) who have shown that annuals have very high rates of shoot height growth following seedling establishment. Reproductive strategy is a second factor that contributes to the biomass allocation patterns of the annuals. Annuals are almost all *r* strategists which, according to Harper and White (1974), are species that allocate most of their net primary production into shoot growth that, in turn, supports high levels of seed production. Whigham and Simpson (1977), for example, concluded that wild rice had to be an *r* strategist because of very high seed mortality. Thirdly, substrate conditions may be an abiotic factor that is, in part, responsible for the allocation patterns exhibited by the annuals. Only the upper few centimeters of substrate are aerobic for extended periods (Simpson et al., 1978) and any species that roots below that zone must be able to withstand anaerobic conditions. Wild rice is the only annual species studied that tolerates anaerobic conditions and is also the only annual that has an extensive aerenchyma tissue which is usually associated with the ability to withstand anaerobic conditions (Hutchinson, 1975). The annuals which lack extensive aerenchyma are thus restricted to a very shallow rooting zone. In the Hamilton Marshes, almost all annual roots are concentrated very near to the surface (Whigham et al., 1978). Because the annuals have their roots in the aerobic zone, they are able to produce more stem and leaf biomass per unit of root biomass (Shaver and Billings, 1975).

The perennials also exhibited distinct biomass allocation patterns (Fig.1) but, with the exception of *Peltandra virginica* and *Scirpus fluviatilis*, they all had rather similar R:S ratios (Table I). R:S values for *Acorus calamus* were similar to those reported by Dykyjová et al. (1972). However, our *Typha* R:S values were lower than those reported by Boyd (1971), Jervis (1969) and McNaughton (1974). They found that *Typha* roots and rhizomes represented about 50% of the total biomass in non-tidal wetlands. Our estimate may be low because our sampling technique, based on an area sampling rather than extraction of entire clumps, did not always account for all of the belowground material.

The significant difference between the R:S of *Peltandra virginica* and the other perennials is obviously not related to division of the substrate into aerobic and anaerobic zones because all species possess extensive aerenchyma (Hutchinson, 1975). The differences may, however, be related to physiological adjustments associated with exploitation of different portions of the substrate. *Peltandra* is the only species that has a belowground system that may extend downward to between 1 and 3 m. The other perennials are all rooted in the

upper 50 cm of substrate and only have a few aerenchymatous roots that penetrate deeper strata. *Peltandra* exploits deeper sediments than the other species but it must also pay an energetic price for having roots that are in a continuously waterlogged and anaerobic substrate. Both of those conditions inhibit efficient uptake of nutrients and cause plants to produce larger amounts of root surface per unit of leaf surface (Shaver and Billings, 1975). The belowground:aboveground ratios of *Peltandra* may, therefore, be caused by a physiological response. We would expect that both the shallower rooted perennials and annuals would have smaller R:S ratios because they occur in that portion of the substrate where conditions are not always anaerobic and where there is some drainage during each tide cycle. *Scirpus fluviatilis* was the only species that did not follow this prediction. The perennials that root near the surface had R:S ratios that are rather similar even though they are taxonomically unrelated and represent a wide spectrum of morphological types. *Typha latifolia*, *Acorus calamus*, *Scirpus fluviatilis* and *Sparganium americanum* have linear leaves and either rhizomateous or creeping rootstocks for underground structures (Muenscher, 1944). *Nuphar advena*, *Sagittaria latifolia* and *Pontederia cordata* have arrowhead-shaped leaves, but dissimilar belowground structures. *Nuphar* is rhizomateous and *Pontederia* and *Sagittaria* have small non-rhizome-forming stems.

Sagittaria latifolia is interesting because it behaves like an annual for most of the growing season. The species overwinters with rootless turions that are usually found at a depth of between 10 and 30 cm in the substrate. In the spring, each turion produces a shoot that grows to the wetland surface where a plant begins to develop. Shortly after development begins, the turion and connecting shoot decay rapidly so that each individual plant consists of leaves, a stem and roots that are produced during the current growing season. New turions are not produced until very late in the growing season. If we eliminate turion biomass from the R:S calculations, the R:S of *Sagittaria* averaged 0.39 rather than 0.94 as shown in Table I. The former value is very similar to the ratio of the annuals (Table I). Physiological adaptations of species to rooting depths may, therefore, be important in regulating the allocation of biomass.

While this study has focused on the biomass allocation patterns of freshwater tidal wetland macrophytes, it has important implications for studies of primary productivity in freshwater wetlands dominated by macrophytes that are not grasses or sedges. Our data show clearly that regression equations can be used to estimate belowground biomass from aboveground biomass for perennials and most annuals using a relatively small (7–25) sample size. Generally, the linear regression model is most suitable but for species with an extremely large belowground component, such as *Peltandra*, an exponential model is more appropriate. With the use of regression equations, it is possible to accurately estimate belowground standing crop — indeed, net belowground production for annual species — thus greatly enhancing future wetland primary productivity studies. The need for inclusion of the belowground component in wetland productivity studies is urgent (de la Cruz, 1978) and as future studies

focus on this component, the specific factors that govern the patterns of biomass allocation reported here will be more fully elucidated.

ACKNOWLEDGEMENTS

We would like to thank our students and research assistants for their help and Ralph Good, John Falk and Steve Turitzen for their comments on the manuscript. This work was supported, in part, by grants from the Hamilton Township Environmental Commission, Hamilton Township Planning Department, Hamilton Township Department of Water Pollution Control and U.S. Department Interior Office of Water Research and Technology (Grant B-060-NJ).

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