

Biomass density and the relationship between submerged macrophyte biomass and plant growth form *

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Abstract

The utility of biomass density (biomass per unit volume) as a quantitative descriptor of the growth form of submerged macrophytes is evaluated and confirmed. Biomass density (BD) is a species specific characteristic which does not appear to be influenced by plant development. Secondly, BD reflects the growth form of the dominant species in the stand, because stands of species with a similar growth form also have similar BD's. Lastly, the BD of submerged macrophyte stands is closely related to the flowering pattern of the dominant species, and has important implications for light capture and light competition with neighbouring plants. Thus, BD should be a useful tool in the quantitative analysis of submerged macrophyte community structure.

Introduction

Plant growth form has an adaptive value in submerged macrophytes (e.g., Fassett, 1966; Hutchinson, 1975; Luther, 1983; Moeller, 1985) and therefore should have a major effect on the growth rate of different species (Hutchinson, 1975; Chambers & Kalff, 1987). Thus, it is reasonable to postulate a strong relationship between submerged macrophyte biomass and plant growth form. This relationship is, however, not expected to be a simple one, because species with different growth forms (e.g. *Littorella* spp. and *Myriophyllum* spp.) have overlapping biomass ranges.

We propose that the relationship between biomass and macrophyte growth form can be improved by considering the degree of packing of the biomass. We suggest that biomass density (BD), defined as the biomass per unit volume of macrophyte communities (units $M L^{-3}$), can be a suitable measure of the degree of biomass packing in macrophyte stands. Biomass density reflects the architecture of plant stands (White, 1981, 1985; Lonsdale & Watkinson, 1983; Duarte & Kalff, 1987), although not necessarily the particular form of the individual plant. To support our assertion we will demonstrate the usefulness of BD to summarize the relationship between the biomass and growth form of macrophyte commu-

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nities by examining (1) the relationship between BD and plant growth form, and (2) some ecological implications of BD.

Biomass density appears to be an important ecological characteristic of macrophyte communities because it is closely related to the influence of plants on the extinction of light within stands (Owens *et al.*, 1967). Biomass density is also related to the maximum weight that the individual plants can reach for a given density (White, 1981; Duarte & Kalff, 1987). Finally, BD also influences the abundance of benthic invertebrates in vegetated sediments (Rasmussen, 1988) and fish in weedbeds (Engel, 1985).

We will first assess whether BD is a species characteristic and whether it is subject to change during plant development. Next the association between the BD of stands of different species and important ecological and life history characteristics will be evaluated.

Materials and methods

Biomass density values were obtained during the summer of 1985 in 46 stands of submerged freshwater macrophytes in 6 southern Québec lakes and in Lake George, New York (Table 1). The stands sampled lacked gaps in their plant cover and were selected to maximize the ranges of plant biomass and height, as well as the number of species included. Thirteen of the 46 samples were from mixed stands, with the remainder from

'monospecific' stands, defined as those in which a single species contributed more than 90% of the total biomass.

At each site, SCUBA divers collected the aboveground biomass within 6 randomly placed quadrats. Small quadrats (0.01 m²) were used in dense stands (> 500 plants m⁻²) and 0.09 m² quadrats in sparser ones. The plants were refrigerated until processed, then carefully washed to remove animals and detritus, and spun in a lettuce dryer to remove excess water before being sorted to species. To compare our results with published values we converted the fresh weight to dry weight by using species specific biomass conversion factors developed in earlier sampling. The mean BD of stands was calculated as the average ratio of plant biomass (g dry wt. m⁻²) and average plant height (m) for the six quadrats (White, 1981; Lonsdale & Watkinson, 1983). Variability among replicated macrophyte biomass samples is typically large (Downing & Anderson, 1985), partially due to small scale patchiness and to sampling artifacts (e.g., edge effects). Because the error in estimating average height is much smaller than that in estimating biomass, the error associated with our BD estimates is largely attributable to biomass variability among replicates. Comparisons of the variability of BD estimates were based on the coefficient of variation (CV). We used Nested ANOVA (Sokal & Rohlf, 1969) to estimate the relative contributions of within and among stand variability to the variance in the BD of individual species.

Table 1. Limnological characteristics of the lakes studied. Latitude and longitude in degrees N and W, respectively; lake area (A) in km²; mean depth (Z) in m; electric conductivity (C) in $\mu\text{S cm}^{-1}$; chlorophyll *a* concentration (Chl *a*) in mg m⁻³; and Secchi disk transparency (Sd) in m.

Lake	Lat	Long	A	Z	C	Chl <i>a</i>	Sd
Bowker	45 25	72 13	2.3	26.0	47	1.0	7.8
D'Argent	45 18	72 18	0.9	4.6	87	3.5	2.7
George	43 30	73 40	110	18.0	90	0.9	8.5
Hertel	45 32	73 09	0.3	4.8	86	3.8	3.8
Lovering	45 10	72 09	4.6	10.3	57	2.1	2.8
Silver	45 38	72 48	0.7	27	110	3.5	5.8
Memphremagog	45 14	72 14	90	18	145	6.8	4.0

Results

The 46 stands sampled contained 18 species of submerged plants, and exhibited a wide range of growth form, biomass, height, and BD (Table 2).

Biomass density can be considered a species characteristic if the variability in maximum BD ratios within species is smaller than the variability between species. That this is the case is apparent because the BD values for those species sampled in sufficient stands to estimate among stand BD variability (i.e., *Elodea canadensis* Michx., *Myriophyllum spicatum* L., *Potamogeton praelongus* Wulf., and *Vallisneria americana* Michx.) range within very narrow limits (Fig. 1), whereas the overall BD range covered more than an order of magnitude (Table 2). Further, Nested ANOVA showed that most (>75%) of the BD variability of these species was attributable to (real or artificial) within stand variability (average CV of BD estimates for individual stands = 24.3%), compared to the smaller variability (<25%) attributable to differences among stands. *Elodea canadensis* was the species with the greatest within stand

Table 2. Mean and range of plant weight, height, density, and biomass density for the 46 macrophyte stands sampled.

	Mean	Range
Weight (g dry wt. plant ⁻¹)	0.20	0.06–1.05
Height (m)	0.46	0.05–2.72
Density (plants m ⁻²)	760	48–3250
Biomass density (g dry wt m ⁻³)	203	27–595

(average CV = 36.2%) and among stand variability (Fig. 1), probably reflecting its great phenotypic plasticity (Cook & Urmi-König, 1985).

The data also show a similar BD between species with related growth forms (Fig. 1). Species that often reach the water surface during their growth (e.g. *Myriophyllum spicatum*, *Potamogeton crispus* L., *Potamogeton amplifolius* Tuck., and *Potamogeton praelongus*) have the lowest BD (Fig. 1), whereas species that have elodeid (*sensu* Hutchinson, 1975) leaves (e.g. *Elodea canadensis*) or form thick understory vegetation (e.g. *Potamogeton robbinsii* Oakes, *Najas flexilis* (Willd.) Rostk. & Schmidt) have the highest BD values.

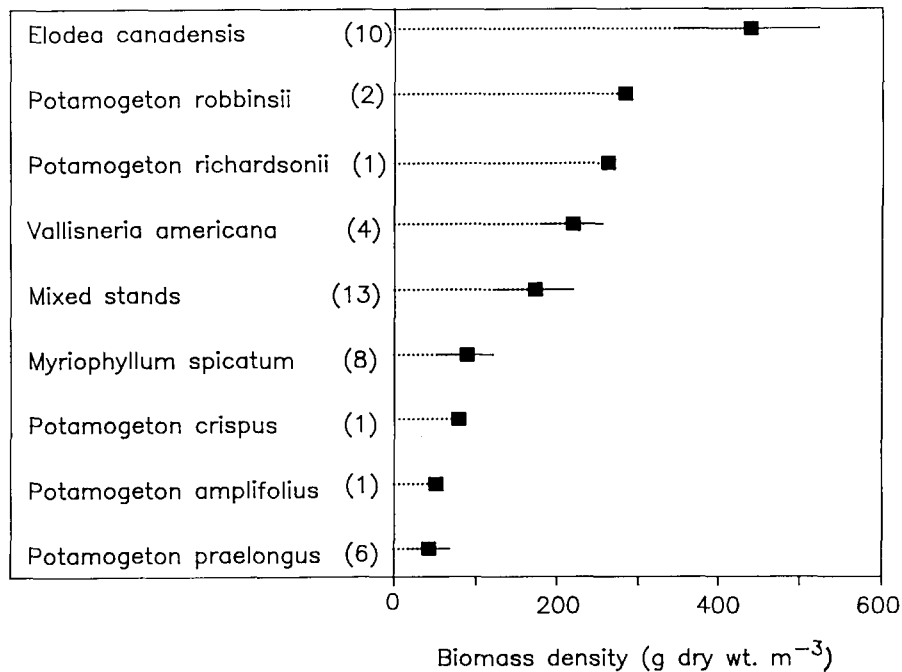


Fig. 1. Estimated biomass density (BD) for the species studied. The number in brackets is the number of stands sampled for each species, the bars are ± 1 standard deviation for those species with samples size sufficient for its computation.

To assess the generality of the measured BD values we compared them with BD values computed by us from the literature for temperate zone macrophyte stands from Europe, North America, Southern Africa, and Japan. (Fig. 2). The close similarity between the Québec-New York biomass densities (Fig. 1) and those from the literature for the same species (Fig. 2) is particularly striking considering the wide geographical origins of the data. This agreement supports our assertion that BD is a species characteristic. Species with closely related growth forms again showed some similarity in their BD values. The species of the genera *Elodea*, *Egeria*, and *Hydrilla* not only have very similar growth forms (Fasset, 1966) but also share similar biomass densities (Fig. 2). Furthermore, the very similar BD ratios

of *Myriophyllum spicatum*, and *Myriophyllum heterophyllum* Michx. parallels their similarity in growth form. Again, *Elodea canadensis* showed great variability among stands (Fig. 2), confirming its phenotypic plasticity (Cook & Urmi-König, 1985). However, the BD values observed (Figs. 1 and 2) apply only to the temperate zone because they increase with decreasing latitude (Duarte & Kalff, 1987).

Lastly we tested whether BD changes with changes in plant size (i.e., height), because changes during plant development would pose problems in the use of BD as a quantitative species characteristic. This was tested on *Myriophyllum spicatum* and *Elodea canadensis*, the only species for which a wide range of plant biomass and height were available. No significant

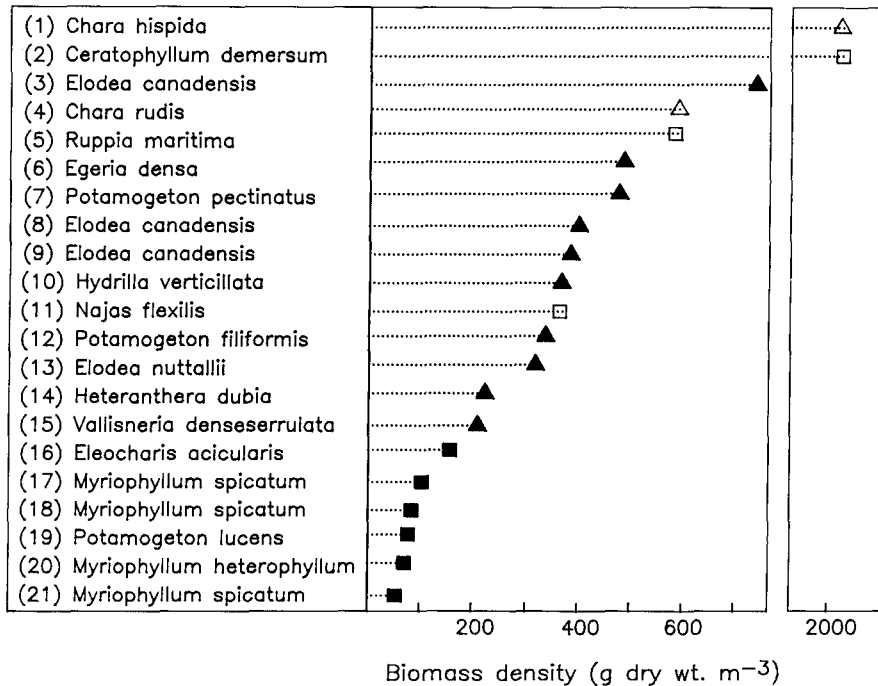


Fig. 2. Values of biomass density (BD) for stands of different species obtained from the literature. Average BD was used when several values were reported. The symbols indicate whether the plants lack flowers (Δ), have submerged flowers (\blacksquare), their flowers float on the surface (\square), or they have flowers raised above the surface on a short peduncle (\blacktriangle).

Data sources (1) Andrews *et al.* (1984); (2) Loeb (pers. comm.); (3) Pokorný *et al.* (1984); (4) Pereira-Ramos (1982); (5) Verhoeven (1980); (6) Getsinger & Dillon (1984); (7) Anderson (1978); (8) Rørslet *et al.* (1986); (9) Goldyn (1984); (10) Harland *et al.* (1985); (11) Petticrew (pers. comm.); (12) Jupp & Spence (1977); (13) Kunii (1984); (14) Petticrew (pers. comm.); (15) Ikusima (1966); (16) Grace & Tilly (1976); Keast (1985); (18) Geiger (1983); (19) Ozimek (1978); (20) Lind & Cottam (1969); (21) Grace & Tilly (1976).

($P > 0.05$) correlation was found between BD and the average plant height in these stands, indicating that the variability in BD among stands, of these two species does not bear any systematic relationship to plant size.

Discussion

The results support the contention that the biomass density of submerged macrophyte stands is related to their growth form (Duarte & Kalff, 1987), and that biomass density, although variable within species, can be considered as a species characteristic. Our findings also suggest that the variability of biomass density among different stands of the same species is independent of plant size. Further support for this is provided by the strong linear relationship between the biomass and height of non-canopy forming stands of *Elodea canadensis* Michx. in a Norwegian lake (Lake Steinsfjord; Rørslett *et al.*, 1986), because a linear biomass-height relationship implies that BD (i.e., the slope of the regression equation) is independent of stand height.

The ranking of submerged plants according to BD (Fig. 2) indicates a close correspondence between their flowering pattern and BD. Species that have to reach the surface for flowering and subsequent pollination (e.g. *Myriophyllum spicatum*, *Potamogeton praelongus*, *Potamogeton amplifolius*) have the lowest BD, whereas the highest values belong to species that do not reach the surface during their life cycle (Fig. 2). The later include species without flowers (e.g., *Chara* spp., *Isoetes* spp.) and species with underwater flowers and pollination (e.g. *Najas flexilis*, *Ceratophyllum demersum* L., and *Ruppia maritima* L.). Species whose flowers float on the surface attached to a peduncle (e.g., *Vallisneria americana*) have intermediate BD values. The only exceptions to this pattern are those species with a growth form similar to *Elodea canadensis* (e.g., genera *Elodea* and *Egeria*), which have flowers that float on the surface and yet have a very high BD (Fig. 2). However, they also rarely flower, and as a result depend largely on vegetative reproduction (Cook

& Urmi-König, 1985; Sculthorpe, 1967), which does not require a reaching of the surface.

Thus, it appears that the flowering mode is well correlated with the architecture of submerged macrophytes stands, as measured by the BD. The relatively low BD of species that reach beyond the surface to flower allows them to do so with little investment in biomass. Similarly, the long peduncles developed by species with floating flowers (Hutchinson, 1975) makes it possible to flower while most of the biomass is well below the surface, developing denser stands (i.e., greater BD) than competing species which need to reach the surface for flowering.

The relationship between the flowering pattern and BD suggests that the pattern of sexual reproduction can constrain the growth form of submerged plants. The problems associated with underwater pollination (Cox, 1983; Ackerman, 1986) are such as to render this pollination path highly inefficient compared to pollination driven by wind, insects or other animals, at or above the water surface (Sculthorpe, 1967). However, Sculthorpe (1967) does suggest that underwater pollination is a requirement for the colonization of high-energy aquatic environment. Surface pollination is impossible for plants growing at sites subject to intense wave action or growing at considerable depths (Sculthorpe, 1967) in an unstable underwater environment (cf., Rørslett, 1985, 1987).

Differences in the BD values of macrophyte stands have important implications for the outcome of light competition. Species with a large BD are also subject to a high light extinction within the stand (Owens *et al.*, 1978). Consequently, they are more readily self-shaded than species with a lower BD, who experience a greater light penetration into the stand. Furthermore, species with a low BD grow taller for each unit of biomass increase than those with higher values, thereby reducing intra-specific light competition. Since the extinction coefficients attributable to the plants themselves and to other substances in the water column are approximately additive (Kirk, 1982) the effect of a high BD on self-shading will be greatest in deep and turbid waters. Stands of

species with low BD's are, because of their greater proximity to the water surface, more exposed to physical damage by waves than stands of similar biomass and greater BD (i.e., shorter plants). Consequently, the BD of a species should influence the balance between a greater reproductive efficiency and avoidance of light competition on the one hand, and sheltering from wave damage on the other.

In conclusion, our results show the utility of biomass density to summarize the link between plant growth form and stand biomass, as well as highlight the ecological implications of the way in which plants occupy their environment (White, 1981; Lonsdale & Watkinson, 1983; Duarte & Kalff, 1987). The results indicate that the study of pattern in the community structure of submerged macrophytes will benefit from attention to the biomass density of species in order to be able to quantify the relationships between plant growth form and community structure.

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