

Structure and Environmental Factors in Macrophyte Stands

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ABSTRACT

Aquatic macrophytes not only provide multistructured habitats for numerous autotrophic and heterotrophic aquatic organisms but also for spawn and juvenile stages of higher vertebrates. Two contrary growing types are distinguished: the pillar-type with a rather equal biomass distribution along the more or less parallel vertical axes of the individual plants in contrast to the canopy-type with a significant concentration of biomass in the top layers. These two types are differentiated from each other by data on the vertical distribution of biomass of *Myriophyllum spicatum* L., a pillar-type representative, and *Potamogeton pectinatus* L., a typical canopy type. The influence of vertical biomass distribution on the vertical light gradient is presented.

Key words: aquatic plants, biomass distribution.

INTRODUCTION

In aquatic ecosystems submerged macrophytes should not be considered as a biotic factor only, because their structure represents an abiotic factor as well. There are numerous interactions between structural features of weed beds and physical environmental factors, physiological functioning of the plant itself and organisms using this habitat.

The plants serve as a three-dimensional habitat for parasitic organisms (Sharma Subhasini Sharma and Mathur 1988). The surfaces of macrophytes are covered by sessile organisms like bacteria (Park-Lee 1986) or algae (Schwencke-Hofmann 1987) which are consumed by mobile grazers (Svenson and Stenson 1991, Horn 1989) that serve as a food source for predators (Hughes 1980). Temporary users are organisms which need macrophytes for attaching their spawn or those seeking refuge in the dense plant structures such as juvenile stages of fish (Hynes 1970). In this ecological context the description of structure and physical conditions within weed beds can also serve as an improved database for some limnological disciplines.

The term "structure" has been used in various ways when describing macrophytes. When using "structure" one should

keep in mind the chameleon-like semantics of this term. In the terrestrial environment, structure usually refers to the morphological, geometrical or spatial information of individual plants. Architecture, a higher order of the three-dimensional description of vegetation, has also no single meaning. It is used at the level of plant communities as a means of plant sociological interpretation, using the abundance of species as architectural elements. At the level of vegetational units or single plant stands the spatial interpretation uses the true geometrical and spatial arrangements, *i.e.* the structure of single species, as architectural elements. In this paper single species populations are evaluated and the term structure is used in its "transformed" meaning, keeping the term architecture for multispecies weed beds, but not necessarily for plant communities (Ross 1981, Myneni *et al.* 1989).

According to Myneni *et al.* (1989) the vertical leaf area density function, the leaf normal orientation distribution function and the distribution function of leaf spatial dispersion are paramount structural parameters. However, less sophisticated approaches are very common. Biomass per unit area, non-stratified leaf area index, number of individual plant organs, or even the number of species in a plant association found in sociological studies have been used as more or less valid ways to describe structure. In this study the vertical stratification of biomass and the number of individual plant organs (stems, leaves) have been used as a measure for spatial information.

Frequently the whole plant cover above ground is called the plant canopy (Myneni *et al.* 1989) in the context of structure and architecture. The term "canopy" will be used in a more restricted way here, confined to a single type of structure only and the use of different terms for other types of plant cover will be discussed.

MATERIAL AND METHODS

Collection and preparation of plant material. Samples of macrophytes were taken from central parts of beds in various water bodies, among them oxbows, cutoff sidearms and even littoral reaches of an impoundment at the River Danube. Whenever necessary, scuba-diving was used to work on stands in deeper water. Biomass was assayed by the stratified-clipping method (Monsi and Saeki 1953, Fujimori 1971, Myneni *et al.* 1989), dividing the stand into 10-cm

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horizontal strata. Four replicates were made of all samples. All plant parts were cleaned, counted and then used to determine fresh and dry matter per unit area.

Biometric assay. The counting of plant organs was done on a plastic sheet with a 5-cm-square grid. A minimum of 10 individual plants from different parts of a plant stand were placed on the sheet, photographed, and then the number of plant parts and branches was recorded. The average number of plants per square meter was determined and the mean area covered per individual plant was calculated. Considering the number of plant parts per plant, mean radial distances could be computed for different strata.

Light measurements. Light attenuation was measured with a LI-COR and a SKP-200 light-meter, respectively, using submersible quantum sensors (400 to 700 nm). The sensors were attached to a 70-cm horizontal metal bar fixed to a vertical bar graded at 5-cm distance at a right angle. Misalignments from the vertical axis less than 15 deg had no influence on readings (Machata-Wenninger and Janauer 1991). By means of the horizontal bar it was possible to place the sensor correctly entering the plant stands carefully from a sideways position. If any disturbances of the spatial arrangements of the stand occurred, the sensor was removed and cautiously entered again. If any fluctuation at a single sensor position was observed, up to 10 individual readings were made. The mean value was taken as representative for this stratum of a profile. Incident light intensity was taken just above the water surface in full sunlight, and relative light intensities were calculated from readings taken in 0.2-cm depth and at each full 10-cm depth. At least four individual vertical profiles were assessed.

RESULTS AND DISCUSSION

Original data are presented from *Myriophyllum spicatum* L. and *Potamogeton pectinatus* L. In addition, data of *Berula erecta* (Hudson) Coville, *Myriophyllum verticillatum* L., *Potamogeton lucens* L. and *Potamogeton perfoliatus* L. are discussed.

Vertical distribution of biomass. The effects on light and temperature gradients in plant stands are caused by the structure of the individual plants of the plant population.

The structure of a species may be different from that of single plants, especially due to seasonal changes. Thus architecture is well-fitted to describe the structure of woody plant stands, but much less so with herbs.

In the aquatic environment synonymous use of structure, architecture and even pattern occurs because single species stands often predominate. In the case of multispecies macrophyte stands, often interpreted as plant communities in the sociological sense (which may be wrong in many cases),

the horizontal extension and hardly visible vertical strata, as compared to a multistoried forest, explain why describing three-dimensional attributes fail to be well determined at present.

The vertical distribution of biomass is an uncomplicated but still meaningful way of describing structure when relations with some physical factors of the environment of the plants are desired. In Figure 1, biomass data (grams dry matter per unit area) are compared for 10-cm strata of *P. pectinatus* and *M. verticillatum*. Two structural types can be distinguished in Figure 1. The canopy-type has a significant concentration of biomass in the top layers, e.g. *P. pectinatus*, *P. lucens* and *B. erecta*. The same situation is reported for *Hydrilla verticillata* Royle (Haller and Sutton 1975). Other canopy-forming species are *Utricularia purpurea* Walt. and *Potamogeton natans* L. (Chambers 1987, Chambers and Kalff 1987). In contrast the pillar-type exhibits a rather equal biomass distribution along the more or less parallel vertical axes

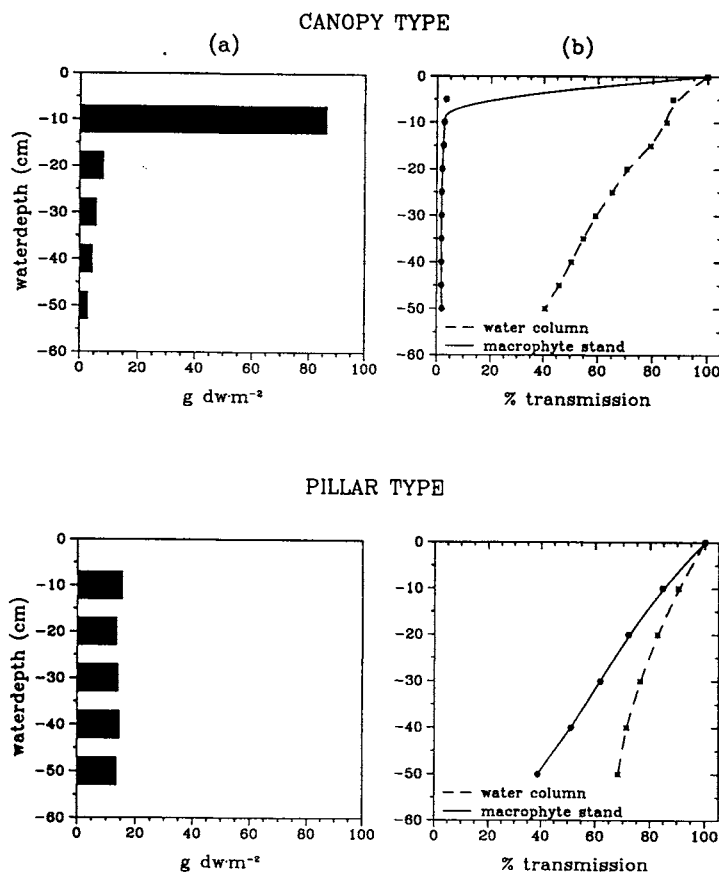


Figure 1. a. Average amount of biomass (in grams dry matter) per unit area in each stratum (in cm) of *P. pectinatus* representing the canopy-type and *M. verticillatum* the pillar-type, and b. Attenuation of light intensity in a stand representing the canopy-type (*P. pectinatus*) and a stand representing the pillar-type (*M. spicatum*), both in comparison to percent transmission in a water column without macrophytes.

of the individual plants. *M. spicatum*, *M. verticillatum* and *P. perfoliatus* are typical representatives of this structural type (Janauer 1991). *Potamogeton crispus* L. and *Elodea canadensis* Michx. are also included in this growth form by some authors (Chambers 1987).

According to our experiences, however, *Ceratophyllum demersum* L. and *M. spicatum* are not forming canopies in still waters observed in the floodplain system of the River Danube (Janauer *et al.* 1990, Janauer 1991). These divergent observations demonstrate the pronounced structural variation the growth form of some species may show under different habitat conditions.

Furthermore, this classification seems to be correct for mature macrophyte stands only. During the course of a single growth period, the development of biomass of *P. pectinatus* clearly shows that the canopy-type is reached only in late summer (Wyche 1989). Earlier in the year biomass is more evenly distributed among the strata and the structural appearance of the plant stand is more like the pillar-type.

Considering the plant organ spatial dispersion within a stratum (Figure 2), the number of leaves and stems can be counted and the mean radial distances can be calculated. It is apparent that the spatial dispersion of leaves and stems of *P. pectinatus* shows a distinct vertical variation depending on the time of the growing season.

The calculation of mean radial distances does not take into account that the leaves, leaf sheath and side branches of *P. pectinatus* are not evenly distributed in space, but will rather keep a plagiotrope position, at a certain angle, close to the main axis under natural conditions. The appearance of the plants in Figure 2 was produced by preparation of the sample for the counting, spreading the secondary axes sideways. However, the mean radial distances can be a generalized measure for the density of plant parts within a specific stratum. This is an important habitat variable for pelagic animals, *e.g.* juvenile stages of fish (Lillie and Budd 1992).

Other methods of describing the spatial dispersion (Myneni *et al.* 1989) or the total impediment to horizontal visibility (Lillie and Budd 1992) have been reported, but calculating and especially assaying the exact nature of the dispersion of plant parts, be it truly regular, providing equal distances for optimal perception of incident radiation in some species, or rather clumped around the vertical axes, is still a task for future work. New sampling techniques like video techniques or freeze coring in the plant stands might provide additional information.

Effects of structure on the incident radiation. Light measurements have been carried out in macrophyte stands mainly for nondestructive biomass estimation (Westlake 1974). But vertical attenuation can also serve as a means for estimating the extent and type of stratification of biomass. This is of

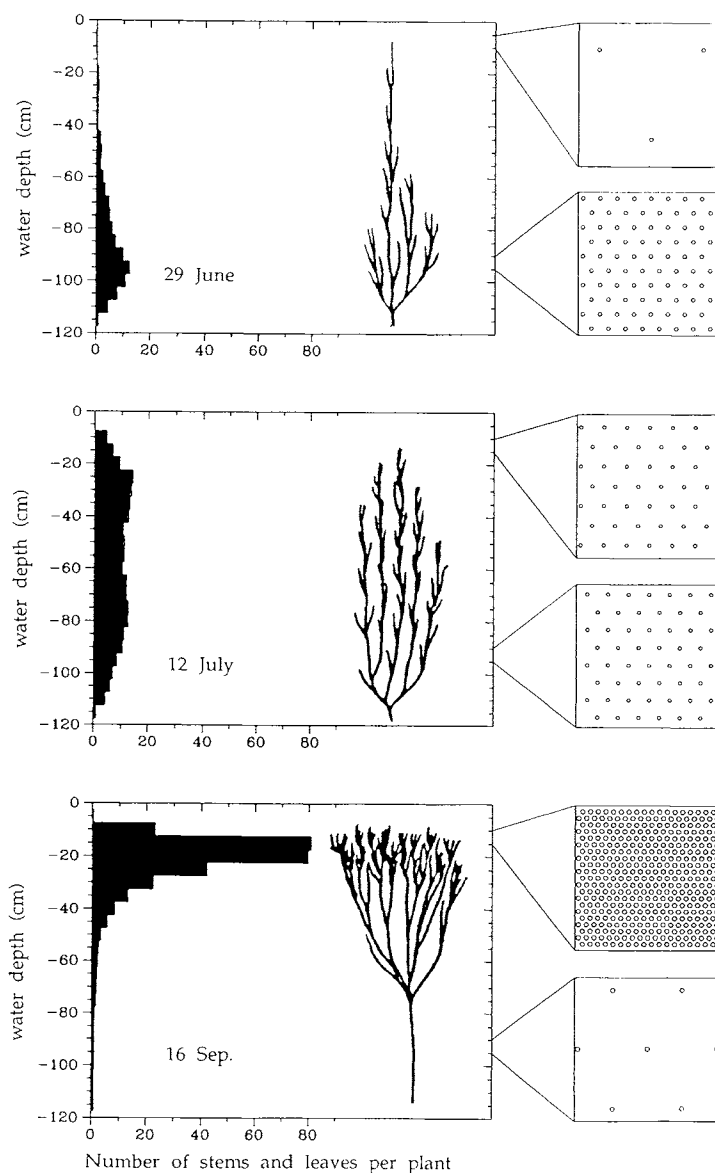


Figure 2. Changes in the plant organ (leaves and stems) number in each stratum (in cm) of *P. pectinatus* during the course of the season, right side: Mean radial distances of plant organs of *P. pectinatus* in a stratum between 10 and 15 cm, and 90 and 95 cm, respectively, during the course of the season.

importance not only for the analysis of structure, but also for discriminating euphotic from dysphotic strata within the plant stands. Effects on the composition of photosynthetic pigments influenced by the light conditions within a weed bed can be expected in strata with moderate or almost no light (Van *et al.* 1977). Figure 1 shows the light attenuation, expressed as percent transmission, in a mature canopy-type plant stand of *P. pectinatus*. The pronounced decrease in light intensity correlates well with the 70% of the total biomass which is found in the top 10-cm stratum (Wyche 1989). Only 5 cm below the surface in a canopy stand, 3.4% of incident light

could be recorded, implying that photosynthesis may be impossible in the lower layers of the leaf canopy. Rather similar information is reported by Westlake (1975), although the data were derived from plant stands in a river.

Although slight, an increase in light intensity in the strata close to the bottom was detected where the biomass consists mainly of defoliated stems. It has been reported that some diffused lateral light (Janauer 1991, see also Titus and Adams 1979) may reach the stand. However, the intensity is low (2% transmission) and no photosynthetically active plant parts are present. So far, no data have been collected by the authors on the effect of lateral diffused light on the photosynthetic efficiency of single plants or the whole stand.

Contrasting results are found in pillar-type plant stands (Figure 1b). *M. verticillatum* that had reached the water surface had 22.5% light transmission in a depth of 50 cm, and *M. spicatum* in the same depth had 38.8%, respectively (Wegleiter 1990). The absence of a dense cover of biomass at the surface, which is the characteristic attribute of the pillar-type, permits light to penetrate the plant stand much deeper and apparent photosynthesis may occur to the base of the plants.

Plant populations in flowing waters which are bent in the direction of flow show intermediate light attenuation attributes. *Ranunculus penicillatus* (Dumortier) Barbington var. *calcareus* (R.W. Butcher) C.D.K. Cook (Westlake 1975) and *Ranunculus trichophyllus* Chaix in Villars (Janauer, unpublished data) reached the 1% transmission level in approximately 40 to 60 cm of depth (counted from the top level of the stand). Other flowing water species like *Ranunculus fluitans* Lamarck, however, represent a true canopy-type (Janauer, unpublished data), which is valid also for *Groenlandia densa* (L.) Fourreau (Machata-Wenninger and Janauer 1991) as far as the characteristics of the light attenuation are concerned.

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