Measurement of Plant Architecture in Seven Aquatic Plants

by Eric D. Dibble, K. Jack Killgore, Gary O. Dick
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Measurement of Plant Architecture
in Seven Aquatic Plants

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The Principal Investigator for this study was Dr. K. Jack Killgore, Aquatic Ecology Branch, Ecosystem Research Division (ERD), EL, WES. The report was prepared by Dr. Eric D. Dibble, formerly at WES, now at Mississippi State University, Mississippi State, MS; Dr. Killgore; and Dr. Gary O. Dick, WES Aquatic Ecosystem Research Facility, Lewisville, TX. Results of this study were first published as an article in the Journal of Freshwater Ecology.

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Measurement of Plant Architecture in Seven Aquatic Plants

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ABSTRACT

We quantified architectural characteristics of seven aquatic macrophytes by measuring spatial complexity and shading properties. The plants were: Egeria densa, Hydrilla verticillata, Myriophyllum spicatum, Potamogeton nodosus, Potamogeton pectinatus, Vallisneria americana, and Zosterella dubia). Two replicates of each plant were cultured in aquaria in concrete raceways. Light transparency and vertical and horizontal interstices measurements were taken at three strata level in each plant species. Spatial complexity was calculated by adding the ratio between interstices frequency and size from both vertical and horizontal axes. Mean density and size of plant interstices differed significantly among plant species ($\chi^2=123$, df=6, $P < 0.01$) and were greatest along horizontal axes. Plant complexity was lowest in M. spicatum and highest in P. pectinatus. Shading properties were significantly different among plants ($\chi^2=40$, df=5, $P < 0.01$), and significant inter- and intra-plant strata differences were noted.

INTRODUCTION

Aquatic plants provide an important structural component to freshwater habitats, and architecture unique to aquatic plants is important to fishes (Lille and Budd 1992, Dionne and Folt 1991). Structural complexity (created by stems and leaves) in plant beds provides a habitat rich in macroinvertebrates (Pardue 1973, Gilinsky 1984, Keast 1984) and is important to growth and survival of fishes (Werner and Hall 1979, Crowder and Cooper 1982). Structural complexity interferes with foraging predators and decreases predator risk for young and small fishes (Mittelbach 1981, Savino and Stein 1982 and 1989), and shade created by plant structures improves visual acuity and increases foraging efficiency as well as predator avoidance by fishes (Diehl 1988, Helfman 1981, Lynch and Johnson 1989). Understanding architectural differences unique to aquatic plants and how structural differences influence quality of freshwater habitats is prerequisite to appropriate management of aquatic plants and fishes.

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Aquatic plant control and restoration programs and fish habitat management have been governed largely by plant abundance and density, and varied approaches have been used to estimate and characterize standing crops of submersed plants (Maceina et al. 1984, Chambers and Kalff 1985, Downing and Anderson 1985, Duarte 1987, Canfield et al. 1990). However, only a few have measured aquatic plants at an appropriate scale to determine structural characteristics important to fishes (Lillie and Budd 1992, Dionne and Folt 1991).

We investigated architectural differences among seven aquatic plants potentially important to the quality of freshwater habitats and growth and survival of fishes. A gap analysis was used to define structural complexity, and light measurements were conducted to quantify shading effect.

METHODS

Plant cultures

The experiment was conducted at the U.S. Army Corps Engineers, Aquatic Ecosystem Research Facility, Lewisville, Texas (May-July 1993). Seven species of aquatic plants were measured: four native species (Potamogeton nodosus, Potamogeton pectinatus, Vallisineria americana, Zosterella dubia) and three exotic species (Egeria densa, Hydrilla verticillata, Myriophyllum spicatum). Each plant was cultured in a 0.3 x 0.3 x 1.0 m (90 L) aquarium placed within a concrete raceway (Figure 1). Plant treatments were replicated twice. Except for V. americana, all plants matured and topped at the water surface. Water depth was maintained 1 m around plants in the aquaria during the growing period; water was drained from raceways to allow for easier access to plants for precise and accurate measurements, but water level within aquaria was maintained so as not to disturb the plant when measurements were made.

Architectural Measurements

Approximately 8 weeks after the macrophytes were planted we measured interstices (gaps among stems and leaves) along horizontal and vertical axes (modified after Dibble and Harrel 1995, Lillie and Budd 1992). A line intercept method for determining length and frequency of interstices was used (Bonham 1989). Interstices were defined as the area along a linear transect located between leaf or stem intercepts. Length and abundance of horizontal interstices (gaps between stems and leaves along a horizontal axis) were recorded with the rule placed within the plant and perpendicular to the vertical axis of the main stem. Length and abundance of vertical interstices (gaps between stems and leaves along a vertical axis) were taken with the rule positioned at center of the plant and parallel to the main stem. Measurements started where the first part (stem or leaf) of the plant intercepted the rule and ended at the last plant intercept. Three horizontal and vertical measurements for each plant were collected at the low, mid, and top strata of the macrophyte (Figure 1); thus, nine horizontal and nine vertical measurements were recorded for each replicate.

From these measurements, we calculated an index of spatial complexity as follows:

\[ I_{hv} = (f_h/l_h) + (f_v/l_v) \]
Where: $f_h =$ mean frequency or the number of interstices intercepted/m along a horizontal axis; $l_h =$ mean length (mm) of all interstices sampled along a horizontal transect; $f_v =$ mean frequency or the number of interstices intercepted/m along a vertical axis; $l_v =$ mean length (mm) of all interstices sampled along a vertical transect. The greater the $l_{iv}$ value, the higher the frequency and smaller the length of interstices (gaps) between plant structures.

**Shading Effects**

Light was measured at three levels with an underwater sensor (Li-Cor Quantum; Model LI-190SA). Fifteen readings were taken for each plant species, with five at each of the plant strata (low, mid, upper). The sensor measured light ($\text{umol s}^{-1} \text{ m}^{-2}$) in visible wavelengths of 380-770 nm. All light measurements were corrected for available surface light, and all were taken at 1200-1400 h under sunny conditions. Light data were treated as relative measurements among plants, and represented the percentage of light transmitted from the surface.

Variance in data comparison was determined by Bartlett's homogeneity statistic and because much of this variance was unequal and many parameters categorical, significant differences in light transmission and complexity measurements within and among plants were determined with the nonparametric Kruskal-Wallis statistic ($X^2$) (Statistix 1994). Pearson's correlative analysis and correlation coefficients ($r$) were used to examine relationship between spatial-complexity and light transmitted through plants.

![Diagram of interstice measurements](image)

**Figure 1.** Raceway containing replicates of cultured plants, and example of vertical and horizontal interstice measurements taken at three plant strata (Top, Mid, and Low).
RESULTS

Mean frequency and length of plant interstices significantly differed among plant species ($x^2=123$, df=6, $P<0.01$) and were greatest along horizontal axes (Table 1). *P. pectinatus* contained the greatest horizontal and vertical densities of interstices at 56.1/m and 25.1, respectively. The lowest number of interstices was recorded in *M. spicatum*. A mean of 8.9 interstices was recorded for horizontal axes; for vertical axes, the mean was 5.9 (Table 1).

Significant differences in spatial complexity among macrophytes ($x^2=156$, df=6, $P<0.01$) were noted and were due to innate differences in plant growth forms. Spatial complexity values ($I_{hv}$) ranged from 1.5 to 42.0. *M. spicatum* had the lowest complexity ($I_{hv}=1.5$), and *P. pectinatus* had the highest ($I_{hv}=42.0$). Spatial complexity was low for *P. nodosus*, and *V. americana* ($I_{hv}=3.5$ and $I_{hv}=3.6$, respectively). *E. densa* ($I_{hv}=12.4$), *Z. dubia* ($I_{hv}=8.2$), and *H. verticillata* ($I_{hv}=18.6$) demonstrated intermediate levels relative to the other plants measured.

Table 1. Differences in mean frequencies and lengths of horizontal and vertical interstices among the seven aquatic plants.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>N</th>
<th>Mean Frequency (no./m)</th>
<th>Mean length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Horizontal</td>
<td></td>
</tr>
<tr>
<td>Egeria densa</td>
<td>149</td>
<td>27.3</td>
<td>3.1</td>
</tr>
<tr>
<td>Hydrilla verticillata</td>
<td>198</td>
<td>36.4</td>
<td>3.3</td>
</tr>
<tr>
<td>Myriophyllum spicatum</td>
<td>49</td>
<td>9.0</td>
<td>10.3</td>
</tr>
<tr>
<td>Potamogeton nodosus</td>
<td>83</td>
<td>15.3</td>
<td>6.1</td>
</tr>
<tr>
<td>Potamogeton pectinatus</td>
<td>306</td>
<td>56.1</td>
<td>1.7</td>
</tr>
<tr>
<td>Vallisineria americana</td>
<td>86</td>
<td>12.7</td>
<td>10.5</td>
</tr>
<tr>
<td>Zosterella dubia</td>
<td>109</td>
<td>22.6</td>
<td>4.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Vertical</td>
<td></td>
</tr>
<tr>
<td>Egeria densa</td>
<td>76</td>
<td>14.0</td>
<td>3.9</td>
</tr>
<tr>
<td>Hydrilla verticillata</td>
<td>120</td>
<td>22.0</td>
<td>2.9</td>
</tr>
<tr>
<td>Myriophyllum spicatum</td>
<td>33</td>
<td>6.1</td>
<td>9.8</td>
</tr>
<tr>
<td>Potamogeton nodosus</td>
<td>41</td>
<td>7.5</td>
<td>7.6</td>
</tr>
<tr>
<td>Potamogeton pectinatus</td>
<td>136</td>
<td>25.0</td>
<td>2.8</td>
</tr>
<tr>
<td>Vallisineria americana</td>
<td>33</td>
<td>4.6</td>
<td>14.8</td>
</tr>
<tr>
<td>Zosterella dubia</td>
<td>62</td>
<td>13.5</td>
<td>4.2</td>
</tr>
</tbody>
</table>
The percentage of available spatial-complexity varied among plant strata (Figure 2). *P. pectinatus, H. verticillata,* and *E. densa* contained most complexity in the upper portion of the plant, where the top strata complexity was >50% of the values in the mid and low plant stratum. Spatial-complexity in the lower plant strata of *Z. dubia,* however, was 60% greater than the top strata (Figure 2).

Overall shading properties were significantly different among plant species ($x^2 = 40, df = 5, P < 0.01$), and significant inter- and intra-plant strata differences were noted (Table 2). The percentage of available light in *M. spicatum, V. americana,* and *Z. dubia,* was relatively high (59.2%, 57.8%, and 58.4%, respectively). Available light in *E. densa, H. verticillata,* and *P. pectinatus* was intermediate (36.7%, 33.7%, 20.5%, respectively). The lowest available light was recorded in *P. nodosus* (6.8%).

The amount of light transmitted from the water surface through the plants to the bottom was affected by the levels of spatial-complexity measured among the plants. However, *P. nodosus* differed from the other plant species because it exhibited low spatial-complexity and low light levels. Transmitted light was moderately correlated with spatial complexity for all plant architectures ($r = -0.40; P < 0.01$), however, when *P. nodosus* was omitted from the analysis, a stronger correlation was noted ($r = -0.89; P < 0.01$).

### Table 2. Measurements of horizontal (h) and vertical (v) interstices ratios, spatial complexity ($I_{hv}$), and percent transmitted light in seven aquatic plants.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>N</th>
<th>Interstices ratio ($I_{hv}$)</th>
<th>Spatial complexity ($I_{hv}$)</th>
<th>Light transmitted (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Egeria densa</em></td>
<td>225</td>
<td>8.8</td>
<td>3.6</td>
<td>12.4</td>
</tr>
<tr>
<td><em>Hydrilla verticillata</em></td>
<td>318</td>
<td>11.0</td>
<td>7.6</td>
<td>18.6</td>
</tr>
<tr>
<td><em>Myriophyllum spicatum</em></td>
<td>82</td>
<td>0.9</td>
<td>0.6</td>
<td>1.5</td>
</tr>
<tr>
<td><em>Potamogeton nodosus</em></td>
<td>124</td>
<td>2.5</td>
<td>1.0</td>
<td>3.5</td>
</tr>
<tr>
<td><em>Potamogeton pectinatus</em></td>
<td>442</td>
<td>33.0</td>
<td>9.0</td>
<td>42.0</td>
</tr>
<tr>
<td><em>Vallisineria americana</em></td>
<td>119</td>
<td>3.3</td>
<td>0.3</td>
<td>3.6</td>
</tr>
<tr>
<td><em>Zosterella dubia</em></td>
<td>171</td>
<td>5.0</td>
<td>3.2</td>
<td>8.2</td>
</tr>
</tbody>
</table>

**DISCUSSION**

Lillie and Budd (1992) described characteristics on one plant species (*Myriophyllum spicatum*), but no previous study to our knowledge has attempted to quantify species specific morphology by measuring differences in architecture among more than one plant type. Structural differences (i.e., gap length-frequencies and shading properties) among the plants measured in this experiment suggest aquatic plants are unique in structure and supply specific criteria that may
influence the quality of habitat for fishes and other animals. This is in agreement with previous studies suggesting habitat value of aquatic plants may be due to specific placement and arrangement of leaf and stem surfaces and that this architecture may control both the spatial and temporal distribution of macroinvertebrates and fish (Lillie and Budd 1992, Dionne and Folt 1991).

A pattern in spatial complexity and light measurements was observed among the macrophytes measured in our experiment. Plants with low complexity typically exhibited higher light readings and offered less shading, whereas plants with higher spatial complexity, especially in lower strata, exhibited additional shading effect. However, light transmission was not always dependent on spatial complexity as defined herein (i.e., interstices measurements), but also was dependent on differences in plant architecture (i.e., leaf size, arrangement and position). For example, *P. pectinatus* exhibited relatively high complexity at each stratum, and light intensities decreased from top to low strata. The combination of these measurements from this plant accurately described a morphology that contains no canopy with many horizontal leaves at each plant stratum, whereas the relatively low light levels and low complexity values in *P. nodosus* suggested a canopy and relatively low numbers of stems and leaves in the strata.

Aquatic plants exhibiting a morphology that provides more shade than spatial complexity may be important to young fishes. Johnson (1993) showed that shaded habitats with low complexity were selected by bluegills sunfish over habitats with high complexity and no shade. The shade that is created by the canopy of *P. nodosus* may improve visual acuity and improve forage and predator avoidance (Diehl 1988, Helfman 1981, Lynch and Johnson 1989). However, lack of spatial complexity allow fishes more mobility, especially larger ones, to pursue prey and/or escape predators.

![Figure 2. Differences in the spatial-complexity values (*I_m*) calculated at different strata among the seven aquatic plants. *Vallisneria americana* was measured only at mid and low strata.](image-url)
ACKNOWLEDGMENTS

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**ABSTRACT:**
Architectural characteristics of seven aquatic macrophytes were quantified by measuring spatial complexity and shading properties. The plants were *Egeria densa*, *Hydrilla verticillata*, *Myriophyllum spicatum*, *Potamogeton nodosus*, *Potamogeton pectinatus*, *Vallisneria americana*, and *Zosterella dubia*. Two replicates of each plant were cultured in aquaria in concrete raceways. Light transparency and vertical and horizontal interstices measurements were taken at three strata in each plant species. Spatial complexity was calculated by adding the ratio between interstices frequency and size from both vertical and horizontal axes. Mean density and size of plant interstices differed significantly among plant species ($\chi^2 = 123$, df = 6, $P < 0.01$) and were greatest along horizontal axes. Plant complexity was lowest in *M. spicatum* and highest in *P. pectinatus*. Shading properties were significantly different among plants ($\chi^2 = 40$, df = 5, $P < 0.01$), and significant interplant and intraplant strata differences were noted.

**SUBJECT TERMS:**
- Eelgrass
- Eurasian watermilfoil
- Fish habitat
- Hydrilla
- Pondweed
- Spatial complexity

**LIMITATION OF ABSTRACT:**
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