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## Morphological adaptations and photosynthetic rates of amphibious *Veronica anagallis-aquatica* L. (Scrophulariaceae) under different flow regimes

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### Abstract

We investigated the influence of water velocity on the morphology of stem and leaves, and the photosynthetic rates of amphibious *Veronica anagallis-aquatica* L. (Scrophulariaceae), growing naturally in the Batise Springs, a shallow clear stream in the state of Idaho, USA. This amphibious species occurs with emerged and/or totally submerged leaves in low velocity areas and with totally submerged leaves at high velocity areas. Plants with emerged leaves have larger leaf area, thickness, density, dry mass, stem internode lengths, and internode diameters than plants with submerged leaves at high velocity. The stem internodes have similar anatomy, except for the pith region. In this region, a lumen is present in the apical and intermediate internodes from plants with emerged leaves. Emerged leaves presented the highest chlorophyll content and maximum photosynthetic oxygen evolution rates. Submerged leaves at low and high velocity had different chlorophyll content but similar photosynthetic rates under saturating CO<sub>2</sub>. The emerged leaves are similar in morphology to sun leaves while submerged leaves at low and high velocities are similar to shade leaves of terrestrial plants. The increase in stem diameter, length of internodes, and the presence of the lumen are apparently adaptations that allow the development of temporary aerial branches in the spring and summer, which develop flowers and fruits, allowing for sexual reproduction. The smaller internodes, leaf area, and thickness of submerged plants at high velocity apparently confer greater flexibility to the stem, allowing it to withstand the associated pulling forces of the water.

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*Keywords:* *Veronica anagallis-aquatica*; Stem morphology; Leaf morphology; Photosynthesis; Water velocity

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## 1. Introduction

Amphibious plants are a unique group that has the ability to grow in two distinct environments, air and water (Hutchinson, 1975). These plants present morphological and physiological variations because they have different requirements for light and gases in water and air. When they occur in rivers, amphibious plants show adaptations to fast waters. The emergent species may develop in waters with low flow because they have higher hydraulic resistance to water velocity. In faster flow, plants are often totally submerged and frequently overlap, protecting each other from velocity (Haslam, 1978).

Species of submerged macrophytes have different strategies that allow for growth and avoidance of mechanical damage at high water velocity. They may form monospecific patches that reduce the internal water velocity while individuals from the upstream areas of the patches remain under constant influence of the high velocity (Sand-Jensen and Mebus, 1996; Sand-Jensen and Pedersen, 1999). Another factor that apparently allows the development of aquatic plants in fast waters is the increased flexibility of the stem, which confers more mobility and reduces mechanical damage induced by high water velocity (Wainwright et al., 1976; Usherwood et al., 1997). Flexibility, according to Vogel (1994), is defined as the ability of the stem to deform with increasing velocity, reducing its rigidity and frontal area. Differences in rigidity are related to the stem diameter and the arrangement of structural elements of the stem. Some terrestrial species, with erect and, consequently, more rigid stems, when growing in water, may present increased quantity and altered placement of the mechanical tissues in certain cells which acts to reduce tension on the stem, allowing it to bend when submitted to high velocity (Usherwood et al., 1997).

Water velocity also influences photosynthetic characteristics of submerged macrophytes. Studies indicate that slow water velocity as opposed to stagnant water, improves photosynthetic rates (Westlake, 1975; Madsen and Søndergaard, 1983) due to the reduction in thickness of the boundary layer surrounding the macrophyte leaves and to the increase in aeration of the water with atmospheric carbon dioxide (Fox, 1996). At higher velocities, however, photosynthesis can be inhibited by current (Madsen et al., 1993). High velocity may also increase turbulence of the water, reducing light penetration and photosynthetic rates (Westlake, 1975).

*Veronica anagallis-aquatica* L. (Scrophulariaceae) is a homophyllous amphibious macrophyte (Sculthorpe, 1967) that is abundant in Batise Springs (Power County, ID, USA), an unshaded, shallow stream. This species has entire, lanceolate, and sessile leaves. In this stream, *V. anagallis-aquatica* occurs both as emerged and submerged forms at low water velocities where the substrate is a mixture of sand and silt. In areas of the stream where the water velocity is high, *V. anagallis-aquatica* occurs only as the submerged form growing on gravel substrate.

In this study, we compare the leaf and stem morphology and the photosynthetic rates of two different phenotypes (emergent and submerged plants) of *V. anagallis-aquatica*. We also compare the leaf and stem morphology and photosynthetic rates on submerged plants at high and low water velocity. Our objective is to elucidate aspects of the intraspecific adaptation of *V. anagallis-aquatica* to air and water environments and to water velocity regimes.

## 2. Materials and methods

### 2.1. Plant material

Plants were collected at Batise Springs, Power County, ID, USA (42°55'N, 112°31'E), during June 2001. A detailed description of the stream is available in [Boeger \(1992\)](#). Stems and leaves were collected from 20 individuals for each situation: plants with emerged leaves at low velocity, plants with submerged leaves at low velocity, and plants with submerged leaves at high velocity. The water depth was measured using a ruler and water velocity was measured using a small OTT meter. Differences were tested using multivariate analysis of variance (MANOVA), followed by post-hoc comparisons of means.

### 2.2. Plant morphology

Total stem length and individual internode length and diameter were measured. Leaf sections and portions of apical, intermediate, and basal internodes were fixed in 70% ethanol (v/v). Leaves from the third and fourth node from the apex were used for all measurements. Leaf area (projected area) was calculated using Sigma Scan software (version 4.0, SPSS Inc., Chicago, IL, USA), from images created with a flatbed scanner (Hewlett-Packard, ScanJet 5100C, Greeley, CO, USA). Leaf thickness was measured from cross sections in the median area of the lamina using a light microscope (Leica DME, Wetzlar, Switzerland) with an ocular micrometer. Leaves were oven dried at 70 °C for 3 days to obtain leaf mass (mg). Specific leaf area (SLA) was calculated based on leaf dry mass and projected area ( $\text{mm}^2 \text{mg}^{-1}$ ); and leaf density ( $\text{mg mm}^{-3}$ ) was calculated by dividing specific leaf mass ( $\text{mg mm}^2$ ) by leaf thickness (mm) ([Witkowski and Lamont, 1991](#)).

Stem and leaf anatomy were analyzed from transverse sections cut with a razor blade. Leaf sections were taken from midway between the leaf edge and the mid-vein. All sections were stained with 0.05% toluidine blue. Drawings were made using a light microscope and camera lucida. For determination of chlorophyll concentration, 1  $\text{cm}^2$  of leaf tissue was homogenized in liquid nitrogen with a small Teflon pestle in a microcentrifuge tube. Chlorophyll was extracted with 80% acetone (v/v) and total chlorophyll content was determined spectrophotometrically (Shimadzu, UV-2401PC) using extinction coefficients determined by [Porra et al. \(1989\)](#).

### 2.3. Measurement of photosynthesis

The photosynthetic response of *V. anagallis-aquatica* leaves to irradiance at saturating  $\text{CO}_2$  was measured with a leaf-disk oxygen electrode (LD2, Hansatech Ltd., Kings Lynn, UK) as described by [Delieu and Walker \(1981\)](#). Intact plants were collected in the field and brought to the laboratory using plastic bags and immediately processed at arrival. Leaf tissue of 10  $\text{cm}^2$  (projected area) from a leaf at the third or fourth node of the stem apex was excised and placed in the chamber. Light was provided using a variable intensity, ultra-bright LED source (LH36, Hansatech). The light source was calibrated with a quantum sensor (LI-250 LI-Cor Inc.) in order to determine the amount of photosynthetically active radiation (PAR) that corresponded to the output reading for the light control box. Leaves were subjected

to an initial induction period consisting of four, 10–15 min repeated cycles of moderate irradiance (ca.  $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and darkness. The photosynthetic response to light was measured from lower to higher irradiances. The sample chamber was maintained at  $20^\circ\text{C}$  with a circulating water bath and was flushed with hydrated (>90% relative humidity) 10%  $\text{CO}_2$  (v/v) prior to measurement at each irradiance. Use of 15%  $\text{CO}_2$  (v/v) did not increase photosynthetic rates indicating that 10%  $\text{CO}_2$  was saturating for submerged and emerged leaves of this species. Light saturation curves were generated using light intensities ranging from 0 to  $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Dark respiration rate, light compensation point, initial rate of oxygen evolution and maximum photosynthetic rate were calculated for light saturation curves using Photosyn Assistant Software, ver. 1.1.2 (Dundee Scientific, Dundee, UK) which is based on the model function described by [Prioul and Chartier \(1977\)](#).

### 3. Results

#### 3.1. Plant morphology

The mean water depth for areas of the Batise Spring that were sampled was  $58 (\pm 1.5)$  cm for the area with plants with emerged leaves,  $57 (\pm 0.8)$  cm for the area with plants with submerged leaves at low velocity, and  $66 (\pm 1.4)$  cm for plants in the high velocity area. Water velocity was  $<2 \text{ cm s}^{-1}$  for the areas defined as low velocity and  $19.0 (\pm 1.1) \text{ cm s}^{-1}$  for areas defined as high velocity.

The leaf area, SLA, dry mass, density, and thickness varied among the plants studied ([Table 1](#)). Leaf area for submerged leaves at low velocity was 28.7% greater and significantly different from submerged leaves at high velocity. Leaf areas were not significantly different between emerged leaves and submerged leaves at low velocity ([Table 1](#)).

Dry mass and density for emerged leaves was significantly higher than those observed for submerged leaves at low (75 and 83% for dry mass and density, respectively) and high (85 and 91% for dry mass and density, respectively) velocities ([Table 1](#)). Submerged leaves at high velocity have a greater dry mass and leaf density than submerged leaves at low velocity,

Table 1

Leaf and stem characteristics of *V. anagallis-aquatica* from three different growth habitats: emerged at low velocity, submerged at low velocity and submerged at high velocity

	Plants with emerged leaves at low velocity	Plants with submerged leaves at high velocity	Plants with submerged leaves at low velocity
Leaf area ( $\text{cm}^2$ )	29.9 (1.4) a	21.4 (1.5) b	30.0 (1.4) a
SLA ( $\text{mm}^2 \text{mg}^{-1} \text{DM}$ )	22.4 (3.9) a	79.9 (14.8) b	149.7 (10.2) c
Dry mass (mg)	123.0 (10.9) a	30.6 (2.8) b	21.3 (1.3) b
Density ( $\text{mg mm}^{-3}$ )	23.9 (1.6) a	3.7 (0.3) b	2.3 (0.2) b
Leaf thickness ( $\mu\text{m}$ )	520.2 (15.2) a	287.6 (10.4) b	324.4 (12.9) b
Total length of stem (cm)	86.9 (5.2) a	45.9 (3.3) b	50 (1.2) b
Total chlorophyll ( $\text{nmol cm}^{-2}$ )	36.9 (1.5) a	20.6 (1.3) b	12.8 (0.8) c

Values represent means  $\pm$  standard error. For leaf area and total length of the stem  $N = 20$ ; for leaf thickness, SLA, dry mass, density  $N = 10$ , and for chlorophyll content  $N = 5$ . Means followed by a different letter are significantly different at  $P < 0.05$  level.

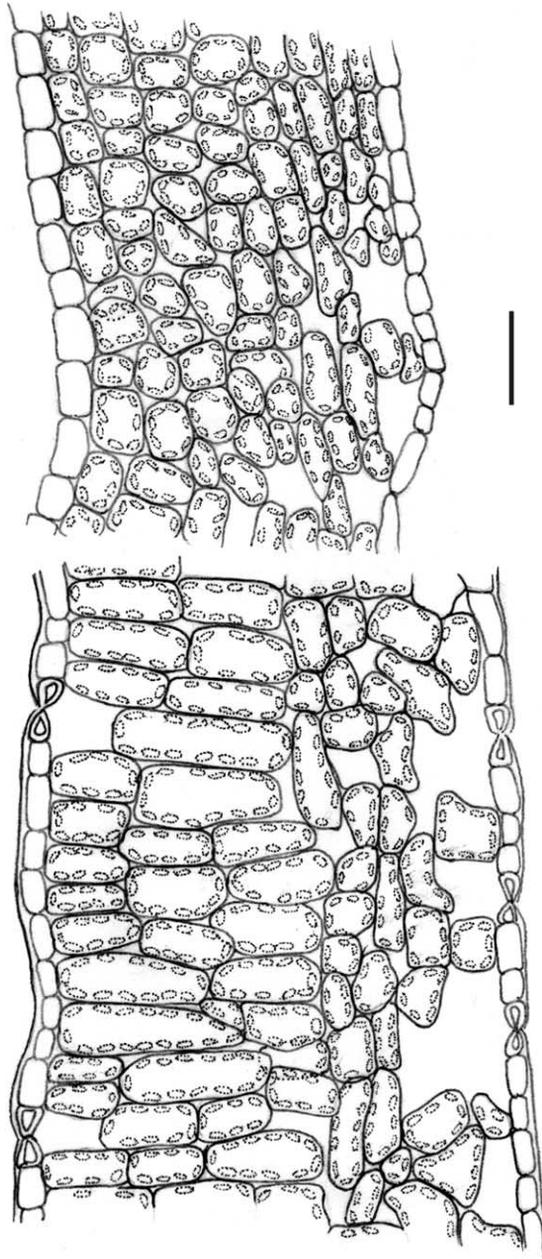


Fig. 1. Transverse section of leaves from the amphibious plant, *V. anagallis-aquatica*. The emerged: (a) submerged at high water velocity (similar to submerged at low water velocity); (b) growth habitats are shown. Scale bar = 0.1 mm.

but values were not significantly different. SLA was statistically different among the three groups of plants (Table 1). Submerged leaves at low velocity had the highest SLA while emerged leaves had the lowest SLA. Emerged leaves were 38% thicker than submerged leaves at low velocity and 45% thicker than submerged leaves at high velocity (Table 1). Plants with emerged leaves presented a typical palisade parenchyma, composed of long and narrow cells (Fig. 1a). Leaves from submerged plants at low and high velocity have similar structure, which lack distinctive palisade cells and have mesophyll formed by isodiametric cells and small intercellular spaces (Fig. 1b).

The first five apical internodes of all plants presented similar diameters. Plants with emerged leaves had the largest internode diameter (between 6 and 16° internodes from the apex), while plants with submerged leaves at low velocity had the smallest internode diameter (Fig. 2a). Plants with emerged leaves had the longest total stem length of all plants examined. Plants with submerged leaves at high and low velocity had similar total stem lengths that were 48 and 43% lower than for emerged leaves (Table 1). The total length of

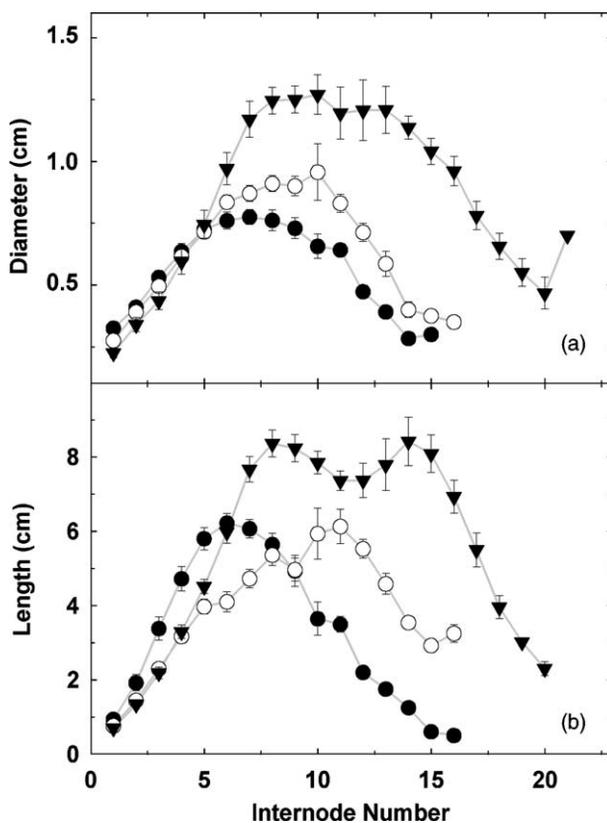


Fig. 2. Internode diameter: (a) and internode length; (b) for stems of *V. anagallis-aquatica* taken from three different growth habitats. Measurements were made from plants with leaves emerged from the water ( $\blacktriangledown$ ), and from those submerged and growing either at high ( $\circ$ ) or low ( $\bullet$ ) water velocity. Symbols represent means from at least 20 measurements  $\pm$  S.E. Internodes were numbered from the most apical to the most basal.

submerged plants at high and low velocities is not statistically different. However, the basal internodes of plants at high velocity are longer than those of plants at low velocity (Fig. 2b). As a consequence of stem length, plants with emerged leaves had a higher total number of internodes and plants with submerged leaves at high and low velocity presented a smaller number of internodes (Fig. 2b).

The average length of the first five internodes for plants with emerged leaves was similar to those observed for plants with submerged leaves at low and high velocities. However, the remaining internodes of emerged plants were longer (Fig. 2b).

Stem anatomy was similar among the three groups of plants studied, except for the pith region. In transverse section, the epidermis was uniseriate and the walls of the cortical parenchyma cells adjacent to the epidermis were thick. The cortex is formed by parenchyma cells with large intercellular spaces that occupied all cortical regions. The cambium was continuous and present in all internodes. Xylem and phloem were poorly developed and did not vary in position among the studied groups.

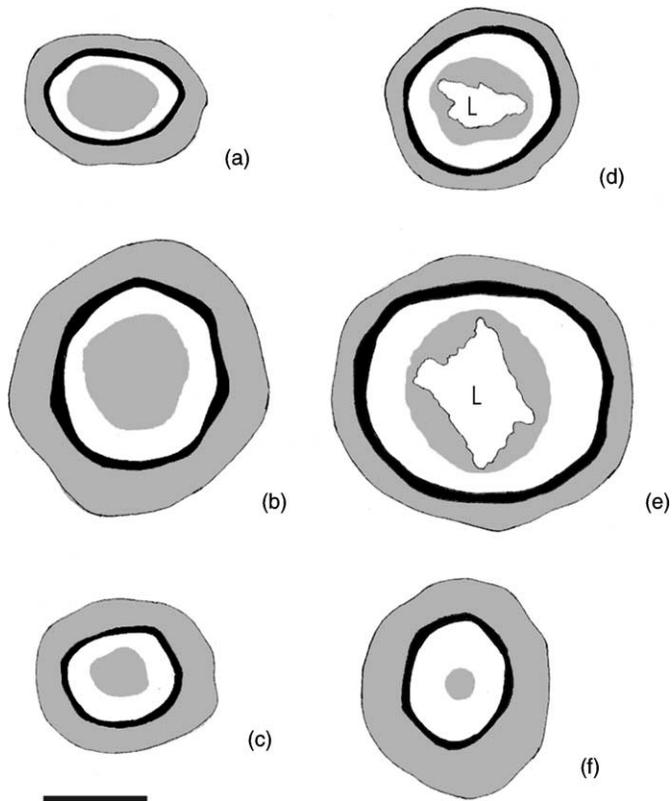


Fig. 3. Schematic drawings of transverse sections of *V. anagallis-aquatica* stems growing submerged at high and low water velocity (a–c) or emerged from the water (d–f). Apical (a and d), intermediate (b and e) and basal (c and f), internodes are shown. Gray regions represent aerenchyma, black regions represent vascular tissue and white regions represent parenchyma. L: lumen. Scale bar = 0.4 cm.

The pith of all internodes of plants with submerged leaves at low and high water velocities was formed by aerenchyma (Fig. 3a–c). Plants with emerged leaves had a central lumen, in both apical and intermediate internodes (Fig. 3d and e). The cavity that forms the lumen is continuous within each internode, being interrupted by the nodal region. At the basal internodes, the pith is formed by aerenchyma (Fig. 3f). The aerenchyma occupies the entire length of each internode, being interrupted at the nodal regions where it is less developed.

Table 1 shows the mean values for total chlorophyll for *V. anagallis-aquatica* plants. When total chlorophyll content is presented on an area basis, emerged plants have 1.7 and 2.9 times more chlorophyll than do submerged plants at high and low velocities, respectively. However, since submerged plants have higher SLA than do emerged plants, there is less difference among plant types when chlorophyll data are presented on a weight basis, although values are still statistically significant.

### 3.2. Photosynthesis

Maximum rates of photosynthetic oxygen evolution for *V. anagallis-aquatica* presented on a leaf area basis were eight times higher for emerged leaves, as compared to submerged leaves at low velocity and nearly five times higher as compared to submerged plants at high velocity (Fig. 4). Maximum rates for submerged plants at high velocity were up to 1.7 times higher than rates for submerged plants at low velocity and differences were statistically significant at light intensities greater than  $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ . When photosynthesis data were presented on a chlorophyll, rather than a leaf area basis, light-saturated rates of photosynthesis were statistically different for emerged, as compared to submerged leaves, but were similar for submerged leaves at high or low velocity. Dark respiration rates, light compensation points and initial rates of oxygen evolution were not statistically different among leaf types.

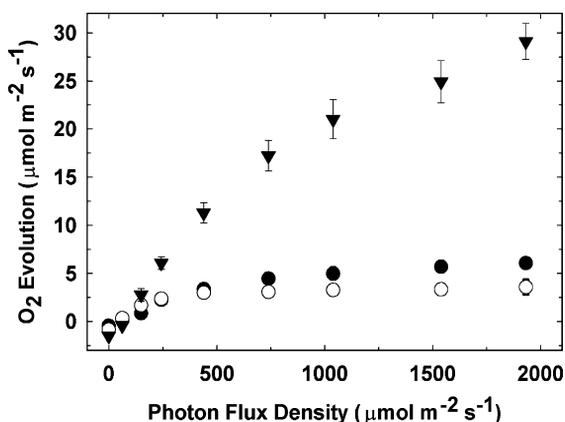


Fig. 4.  $\text{CO}_2$ -saturated response of photosynthetic oxygen evolution to light for emerged leaves of *V. anagallis-aquatica* (▼), submerged leaves at high water velocity (○) and submerged leaves at low water velocity (●). Symbols represent means for at least five measurements  $\pm$  S.E.

#### 4. Discussion

The variation in leaf structure observed for *V. anagallis-aquatica* is similar to that observed for other species in comparative studies of emerged versus submerged leaves for amphibious plants and shows the phenotypic plasticity of this species (Sculthorpe, 1967; Sand-Jensen and Frost-Christensen, 1999). The structure of emerged leaves is similar to that of typical sun-adapted leaves, which are exposed to high light intensity (Givnish, 1987; Chazdon and Kaufmann, 1993). Leaves exposed to high light tend to produce several layers of palisade parenchyma that facilitate the distribution of collimated light into the leaf and also distribute light energy evenly to cells throughout the leaf thus allowing for a more uniform rate of photosynthesis throughout the leaf (Donahue, 1991; Vogelmann, 1994).

Structurally, submerged leaves at high and low velocity are similar to shade leaves of terrestrial plants. The cell shape and the smaller thickness of the leaves are related to lower photosynthetic rates, since a sustained low photon irradiance can be utilized more effectively by thinner organs (Thompson et al., 1992). Studies on shade leaves of *Thermopsis montana* suggest that the spongy mesophyll functions as both a diffuser and reflector. The relative proportion of spongy mesophyll in shade leaves enhances leaf absorbance because of increased internal light scattering (Donahue, 1991; Vogelmann, 1994).

In terrestrial leaves under high light intensity, leaf area tends to be smaller, which is recognized as a mechanism of water conservation (Taiz and Zeiger, 1998). However, in *V. anagallis-aquatica*, emerged leaves are similar in size to submerged leaves at low velocity. Differences between the response of terrestrial and aquatic leaf area to light intensity is likely associated with high water availability for aquatic leaves. Leaves of land plants are exposed to intense light and are often under water deficit, which does not occur with the emerged leaves of amphibious plants (Maberly and Spence, 1989). The presence of stomata on both sides of the leaves for *V. anagallis-aquatica* supports this hypothesis (Fig. 1a). When there is no water deficiency and the light intensity is high, the leaves of land plants are usually thick and amphistomatic. Stomata on both faces of the leaves occur in plants with higher photosynthetic capacities and reduce the diffusion distance for gases within the leaf, thus facilitating CO<sub>2</sub> uptake (Parkhurst, 1978; Mott and Michaelson, 1991). The efficiency of this gas exchange depends on the stomatal frequency on both sides of the leaf.

Higher leaf area for submerged plants at low velocity, as compared to submerged leaves at high velocity, may be associated with the need for a larger surface area for gas exchange. Diffusion of dissolved gases is slower in water than in the air (10<sup>4</sup> times). Submerged leaf surfaces tend to have a well-developed diffusive boundary layers and CO<sub>2</sub> is rapidly depleted around the leaf during photosynthesis (Madsen and Breinholt, 1995). Thin and entire leaves may be a response to the low flux of CO<sub>2</sub> into the leaf, which requires relatively small amounts of photosynthetic machinery for processing (Black et al., 1981).

High water velocity appears to be a stress factor that induces developmental, morphological and anatomical changes for submerged plants. *V. anagallis-aquatica* is not heterophyllous and the entire blade of its leaves can be easily damaged by fast-flowing water. Smaller and thinner leaves as observed in the submerged plants at high velocity (Table 1) have decreased hydraulic resistance, thereby reducing mechanical damage to the leaf by fast-flowing water (Fox, 1996; Schutten and Davy, 2000). Although submerged leaves of plants at high water velocity have higher dry mass than submerged leaves at low velocity, the

difference is not statistically different. This was not expected, because submerged leaves of plants at high velocity also have the smallest leaf area and thickness (Table 1). One possible explanation for a larger leaf mass is the smaller size of cells associated with the pulling forces of high velocity water. Leaves of terrestrial plants under mechanical stresses such as wind generally have smaller and more densely packed leaf cells, which can influence the total leaf mass (Lecoeur et al., 1995; Lu and Neumann, 1998).

Differences in SLA also tend to be related to anatomical responses of leaves to their environment. Submerged plants at low velocity have the greatest SLA, due to their thinner and larger leaves. These leaf characteristics allow for greater surface area for absorption of light and CO<sub>2</sub>. The same pattern is observed in the shade leaves of terrestrial plants (Chazdon and Kaufmann, 1993). In the emerged leaves, increased leaf thickness leads to greater values of dry mass, which reduces the SLA. This is also observed for sun leaves of terrestrial plants (Lichtenthaler et al., 1981). For leaves of plants at high velocity, SLA is statistically different than that for submerged leaves of plants at low velocity apparently because of the larger dry mass and lower leaf area. These variables, separately, are not significantly different between the two groups but are inversely related (Table 1) which alters the SLA.

Differences in leaf density are also related to changes in leaf anatomical characteristics. Greater thickness and dry weight of emerged leaves increases leaf density (Table 1) (Niinemets, 1999). Although not statistically significant, the density of leaves for submerged plants in high velocity is larger than that observed for low velocity because of smaller thickness and area for low velocity leaves (Table 1). Leaf density tends to be greater for leaves of greater thickness and smaller area, as observed for sun leaves of land plants (Marques et al., 2000).

Morphological variation of the stem was also observed among the plants studied. The increase in length and diameter of the internodes in emerged plants is likely associated with flotation of the emerged branches. This increase is related to the presence of cortical and medullar aerenchyma and to the development of a medullar lumen in the intermediate and apical internodes. This anatomical characteristic has also been documented for other species (Boeger, 1994; Usherwood et al., 1997). The absence of a central lumen in the basal internodes is explained by the anchoring function of this portion of the stem, allowing the plant to oscillate according to the water flow (Usherwood et al., 1997). For *V. anagallis-aquatica* at high velocity, the velocity of the water also may represent a mechanical stress factor for the stem structure that leads to comparatively shorter length and smaller diameter of the internodes. Smaller plant size appears to reflect the need for greater flexibility in plants at high water velocity. When exposed to fast currents, aquatic plants tend increase the flexibility of the stem by reducing its length. This reduces the resistance of the stem to high velocity water and minimizes mechanical damage (Schutten and Davy, 2000). However, the internode length of plants at high velocity can also be influenced by changes in local environmental conditions. The greater density of plants increases the shading of the lower internodes, which could result on the increment of the length for basal internodes at high water velocity.

Submerged *V. anagallis-aquatica* in low water velocity depicts a stem structure that is similar to that of submerged leaves in high velocity. The medullar stem in these plants is composed of aerenchyma, which provides a flotation means for the stem and the branches.

The smaller size of these plants appears to be related to the lower relative gas content of the water and the well-developed diffusive boundary layer around submerged plants that influences photosynthetic rates (Fig. 4).

Lower total chlorophyll content per unit leaf area for submerged, as compared to emerged leaves, has been observed previously and is often correlated with the higher SLA for the submerged leaves (Nielsen and Sand-Jensen, 1989; Nielsen, 1993). In addition, submerged leaves also have smaller leaf thickness (Nielsen and Sand-Jensen, 1989), at high and low velocities (Table 1). For *V. anagallis-aquatica*, differences in total chlorophyll content among leaf types was partially, but not entirely accounted for by differences in SLA. Differences in chlorophyll content on a leaf weight basis may be due to leaf acclimation to the light environment while emerged leaves are in sun conditions. Shade–light conditions may be induced for submerged leaves at high velocity and, to a less extent, at low velocity by increased water turbulence. High turbulence of water leads to greater turbidity and, thus, to shade conditions through decreased penetration of light into the water and may also induce changes in the quality or wavelength composition of the water.

Higher maximum photosynthetic rates have been observed for emerged versus submerged amphibious plants previously and attributed to higher chlorophyll content (Nielsen and Sand-Jensen, 1989; Nielsen, 1993), higher Rubisco content and activity (Beer et al., 1991) and higher CO<sub>2</sub> availability (Madsen and Breinholt, 1995; Sand-Jensen and Frost-Christensen, 1999). Light and CO<sub>2</sub>-saturated rates of photosynthesis for emerged versus submerged leaves of *V. anagallis-aquatica* are significantly different when data are presented on both an area (Fig. 4) and chlorophyll basis indicating that differences in photosynthetic responses are not due entirely to differences in chlorophyll concentration. Differences in photosynthetic rates for submerged leaves at high, as compared to low velocity, however, are reduced and are not statistically significant when based on chlorophyll content rather than leaf area, indicating that these differences are due to different total chlorophyll concentrations for these leaf types.

Since photosynthetic measurements were made under saturating CO<sub>2</sub>, observed differences among leaf types were also not likely due to differences in CO<sub>2</sub> availability for leaves during measurements. When photosynthesis for amphibious plants is measured under field conditions or in laboratory settings under ambient concentrations of CO<sub>2</sub>, high velocity plants have been shown to have lower rates of photosynthesis (Madsen et al., 1993). However, our study indicates that when differences in total chlorophyll concentration are accounted for, submerged leaves at high and low water velocity, have similar rates of photosynthesis under saturating CO<sub>2</sub>. Thus, differences reported under field conditions may be associated with direct inhibition of photosynthesis under fast water flow (Madsen and Søndergaard, 1983; Madsen et al., 1993; Carr et al., 1997) or by mechanical stress in the form of agitation or stretching of leaves (MacFarlane and Raven, 1985). In field conditions, turbulence in fast flow may also increase self-shading of leaves and loss of organic metabolites (Fox, 1996). Reductions in photosynthesis that are caused by mechanical stress could be counteracted or partially reversed by increased CO<sub>2</sub> supply to plants at higher velocities due to reduction of the boundary layer effect (Madsen et al., 1993; Sand-Jensen and Frost-Christensen, 1999). Under our conditions of saturating CO<sub>2</sub>, the most likely explanation for observed differences in maximum photosynthetic rates between emerged and submerged leaves is that emerged leaves are more sun-adapted and may have higher content

and activities of Rubisco and other photosynthetic enzymes (Salvucci and Bowes, 1982; Maberly and Spence, 1989; Beer et al., 1991).

The results of this investigation suggest that the interaction of environmental factors such as concentration of CO<sub>2</sub>, hydraulic stress and light availability (among others) greatly influences the morphological, anatomical, and physiological traits of *V. anagallis-aquatica*. The observed phenotypic plasticity apparently favors the success of *V. anagallis-aquatica* in the colonization of distinct areas of the stream. Sexual reproduction is limited to emergent individuals since these are the only forms that develop flowers. In the spring and summer, aerial branches produce flowers and seeds that will originate new individuals. Some propagules are transported to areas of higher water velocity and, due to the plasticity of the species, will develop into new individuals. The success of these individuals is dependent on the morphological adjustment of the plants and in the efficiency of their vegetative reproduction.

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