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LIGHT EFFECTS ON LEAF MORPHOLOGY IN WATER HYACINTH (EICHHORNIA CRASSIPES)

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ABSTRACT

Water hyacinth leaves in natural populations vary from being long and thin-petioled to being short with inflated petioles. A variety of factors has been used experimentally to alter water hyacinth leaf shape, but what controls the development of leaf morphology in the field has not been established. We measured photosynthetic photon flux density (PPFD) and spectral distribution of radiation in a natural water hyacinth population. PPFD in the center of the water hyacinth mat was reduced to 2.7% of full sunlight, and the red to far red (R:FR) ratio was reduced to 0.28. When shoot tips of plants were exposed to artificial light environments, only plants in the treatment with a R:FR ratio comparable to that in the natural population produced leaves with long, thin petioles. Shoot tips in full sun or covered with clear plastic bags or bags that reduced light quantity without greatly altering light quality produced shorter leaves with inflated petioles. We hypothesize that the altered light quality inside a mat is a major environmental control of water hyacinth leaf morphology.

THE WATER HYACINTH, *Eichhornia crassipes* Solms., displays marked foliar plasticity. A single plant can produce short leaves with swollen petioles or long leaves with narrow petioles. These different leaf types are found in different places in a water hyacinth population (Penfound and Earle, 1948; Musil and Breen, 1977; Richards, 1981; Watson, Carrier and Cook, 1982). Water hyacinths reproduce vegetatively by stolons, rapidly building up large, intertwined, free-floating mats. Plants at the edge of a mat produce small leaves with expanded petioles, while plants in the center of a mat produce long leaves with narrow petioles.

Various factors have been shown to affect water hyacinth leaf morphology. Boresch (1912) reported that rooting, warm temperatures, and shading promoted petiole elongation, whereas free-floating, cooler temperatures, and full sunlight induced petiole expansion. Nutrient concentration also affects leaf form. Plants grown in $\frac{1}{2}$ strength Hoagland's macronutrients, with or without micronutrients, produced long leaves with narrow petioles, while plants grown in distilled water produced small leaves with inflated petioles (Richards, 1982).

Gibberellic acid application also changes water hyacinth leaf morphology (Pieterse, Aris and Butter, 1976; Watson et al., 1982). When plants were grown in solutions with GA_3 con-

centrations ranging from 0 to 1 ppm, plants in higher concentrations produced leaves with longer, narrower petioles. Removal of plants from the GA_3 solutions resulted in rapid reversion to the small leaf form (Watson et al., 1982). Watson et al. (1982) suggested that gibberellins leaked from the plants could act as a pheromonal system regulating population density.

Although these factors can affect water hyacinth leaf morphology, to date no study has shown what normally induces the different leaf forms in the field. Experimental results have often been achieved with unrealistic levels of a given factor. For example, although gibberellin levels in *Eichhornia* habitats have not been measured, it is unlikely that concentrations affecting leaf morphology (≥ 0.03 ppm [Watson et al., 1982]) would be reached in water beneath natural populations or that a gradient between the mat center and edge would persist. Other examples of unrealistic levels or contradictory experimental results can be found when comparing nutrient and temperature levels measured within mats (Musil and Breen, 1977; Ultsch, 1973) to nutrient levels used or temperature differences measured in experiments (Richards, 1982; Boresch, 1912; Watson et al., 1982).

Both light quantity and quality can influence leaf morphology (Smith, 1981; Vince-Prue and Tucker, 1983). The amount of light reaching the shoot apex is known to vary between the edge and center of a water hyacinth mat (Penfound and Earle, 1948; Knipling, West and Haller, 1970), but the mat light environment has not been examined in detail. Light trans-

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TABLE 1. Measurements of light under experimental conditions: sunlight = full sun; clear = inside clear plastic bags; black = inside plastic bags painted with black pigments; shade = inside plastic bags painted with pigments simulating natural shade

	Sunlight	Clear	Black	Shade
PPFD	2,127 ± 142	1,758 ± 224	21 ± 5	17 ± 9
% PPFD of full sunlight	100	82.7 ± 10.5	1.0 ± 0.2	0.8 ± 0.4
W m ⁻² , 400–700 nm	464 ± 30	382 ± 48	4.5 ± 1.0	3.6 ± 1.9
% W m ⁻² : 400–700/300–1,100	56.3 ± 1.4	55.0 ± 0.2	36.1 ± 1.5	5.8 ± 3.0
R:FR	1.24 ± 0.03	1.21 ± 0.00	1.00 ± 0.02	0.11 ± 0.05

mitted through leaves is spectrally altered (Smith, 1982). The ratio of quanta at 660 and 730 nm, which controls the phytochrome equilibrium and thus affects developmental processes in a variety of ways, is greatly reduced under vegetation (Smith, 1982). In order to understand the environmental controls on water hyacinth leaf morphology, it is crucial to study the effects of such spectrally altered radiation on leaf development.

In this paper we document the variations in light quantity (quantum flux density) and light quality (spectral distribution) between the edge and center of a water hyacinth mat; and we test experimentally whether levels of light quantity and quality comparable to those found in the mat environment can induce the appropriate leaf forms.

MATERIALS AND METHODS—Radiation measurements—A Li-Cor 1800 spectroradiometer (Li-Cor Instruments, Lincoln, NB 68504) with a wavelength range of 300–1,100 nm and half-peak bandwidth resolution of 6 nm was used for all measurements. Measurements in plant stands required a remote cosine-corrected sensor attached to a fibre-optic cable. The instrument was programmed to scan at 2 nm intervals, requiring approximately 50 s to complete a scan. The scans were integrated to reveal 1) PPFD—photosynthetic photon flux densities 400–700 nm in $\mu\text{mol s}^{-1} \text{m}^{-2}$ and 2) irradiances at 400–700 and 300–1,100 nm in W m^{-2} . It also calculated the quantum ratio of red (658–662 nm) to far-red (728–732 nm) wavelengths, the red to far-red (R:FR) ratio as defined by Smith (1982).

Radiation measurements were made in a natural water hyacinth (*Eichhornia crassipes* Solms.) population growing in a canal in Collier County on the north side of the U.S. Highway 41, 30 mi. west of Florida Highway 27. The canal was completely covered by water hyacinth plants. The spectroradiometer sensor was held horizontally both above and at the level of shoot apices inside the mat, and scans were made within 90 min of solar zenith. Mea-

surements were made on 18 May 1984, under skies with less than 30% cloud cover.

Percentages of PPFD of shade to those of direct sunlight were calculated by dividing each shade measurement by the mean of 5 direct sun measurements. The same procedures were used for measuring the experimental light environments described below.

Experimental conditions—The effects of altered light environments on the growth of water hyacinth plants were tested by exposing shoot tips of individual plants to four different light regimes. Different light environments were made by covering the apex and expanding leaves of each plant with a plastic bag approximately 15 × 30 cm. Each bag had a small hole punched in an upper corner to facilitate gas exchange, and the bags were open at the bottom. One set of plants was grown without bags. The experimental conditions were 1) full sunlight (no bags); 2) clear plastic bags; 3) plastic bags spray-painted with neutral black pigments; and 4) plastic bags sprayed with pigments to decrease PPFD and lower the R:FR ratio. The pigments and spraying conditions are described by Lee (1985).

Measurements of the distribution of spectral radiation inside the bags are presented in Table 1 and Fig. 1. The clear bags reduced PPFD to 82.7% of full sunlight but did not substantially alter the R:FR ratio. The neutral black and shade pigments reduced PPFD to app. 0.9% of full sunlight. The black pigments reduced the R:FR ratio to 1.00, comparable to the ratio measured in light gaps in forests (Lee, 1986). The shade pigments reduced the R:FR ratio to 0.11, which is comparable to the R:FR ratio of deep shade (Lee, 1986).

The bags caused air temperatures inside to increase up to 10 C above ambient air temperatures in full sunlight, but there were no significant differences in temperatures between the neutral black and shade bags.

Growth conditions—Plants used in the experiments were clones of a single plant col-

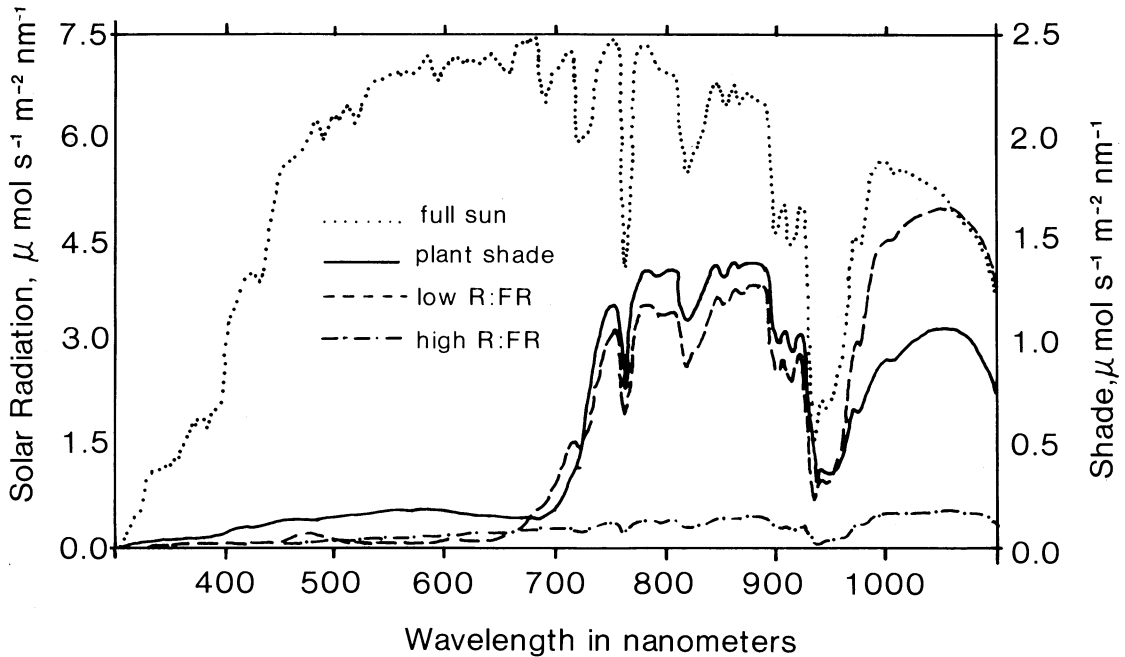


Fig. 1. Spectral distribution of radiation in the water hyacinth mat and experimental treatments. Different light environments are denoted by the legend. Note the different scales for solar radiation and shade.

lected at Fish Eating Creek Campground, Glades Co., FL. The plants were grown outdoors at Florida International University from February to April of 1984. Plants were contained in brown plastic tubs holding 10 liters of $\frac{1}{8}$ strength Hoagland's solution. The nutrient solutions were changed weekly. Each treatment had five plants grown together in one tub. Stolons which began to grow during the course of the experiment were removed before they could expand significantly. The experiments were performed twice, the first time for 5 wks and the second time for 7 wks.

Measurements—The oldest leaf covered by the bags at the beginning of the experiments was $\frac{1}{2}$ to $\frac{3}{4}$ expanded. This leaf was marked as the first treatment leaf, and subsequently expanding leaves were numbered from this one. A comparable leaf was marked on the plants growing in full sunlight. As leaves stopped expanding, they were removed from the bags, and the bags were repositioned on younger leaves. This arrangement insured that plants under all treatments had sufficient photosynthetic capacity to grow. In addition, the arrangement simulates the natural growth environment of dense water hyacinth populations, where the shoot apex is below the canopy, mature laminae are at the top of the canopy, and expanding leaves grow up through a changing

light environment. Bags were checked for positioning twice weekly.

At the end of each experiment, plants were harvested and the following data taken: 1) number of leaves produced during treatment; 2) leaf position; 3) total leaf length; 4) lamina and petiole length; 5) lamina and petiole width at widest point; and 6) dry wt of roots, stems and leaves.

Morphological parameters were compared for two sets of leaves, leaves 4–6 and leaves 8–10. Dissections of plants comparable in size to those used in the experiment showed that leaves 4–6 were present in the unexpanded shoot tip when the experiment began. Leaves 8–10 were initiated after treatment began. Data on leaves 8–10 were obtained only in the second experiment. Differences among treatments were tested on an Apple IIe computer using the non-parametric statistical program in the Stats Plus statistics package (Human Dynamics Corporation, Northridge, CA).

RESULTS—Light environment in water hyacinth mats—Leaves in the natural population had very long, narrow petioles. The ratio of petiole width to total leaf length was 34.5 (Table 2). The ratio for small leaves with inflated petioles is less than 5 (Pieterse et al., 1976; Richards, 1981; Watson et al., 1982). The lamina was longer than wide in these long leaves

TABLE 2. Leaf measurements in cm for plants in water hyacinth mats in which light measurements were made

Total leaf length	756 ± 45
Lamina length	137 ± 13
Lamina width	112 ± 12
Petiole length	620 ± 39
Petiole width	22 ± 2
Ratio lamina length/width	1.2 ± 0.1
Ratio total leaf length/petiole width	34.5 ± 3.5
N	10

(Table 2), whereas small leaves have a lamina that is wider than long (Richards, 1981).

Measurements of quantum flux density and spectral distribution show that both light quantity and quality are altered as light passes through the water hyacinth leaves (Table 3; Fig. 1). In the natural population the amount of photosynthetically active radiation (PPFD) is reduced to 2.7% of full sunlight (Table 3). Radiation above 700 nm is reduced less than that below 700 nm and is not substantially altered in quality (Fig. 1).

Differential absorption of radiation by the water hyacinth canopy significantly alters the spectral distribution of light reaching the shoot apex and developing leaves. The R:FR ratio of full sunlight is greater than 1 (Table 3). Inside the mat the R:FR ratio is reduced to 0.28 (Table 3).

Effects of altered light environments on water hyacinth growth—Treatment did not produce significant differences in final dry wt or dry wt distribution in either experiment. The number of mature leaves expanded under treatment averaged 6.6 ± 0.6 in the first experiment and 11.6 ± 1.2 in the second. Differences among

TABLE 3. Light measurements above and at level of shoot apex in *Eichhornia crassipes* mat; PPFD = photosynthetic photon flux density; R:FR = ratio of quanta at 660 and 730 nm

	Sunlight	Shade
PPFD	1,894 ± 170	51 ± 19
% PPFD of full sunlight	100	2.7 ± 1.0
W m ⁻² , 400–700 nm	412 ± 37	11 ± 4
% W m ⁻² 400–700 nm/300–1,100 nm	54.5 ± 0.2	16.9 ± 3.3
R:FR	1.15 ± 0.02	0.28 ± 0.06

treatments in leaf number were not significant after 5 wks (expt. 1) but were after 7 wks (expt. 2) ($P = 0.008$). The significant difference was between the sun control ($x = 13 \pm 1$ leaves) and the shade treatment ($x = 10 \pm 1$ leaves).

Leaf length increased in all experimental treatments in both experiments (Table 4). The increase was greatest in simulated shade, both for leaves which were expanding at the beginning of the experiment (leaves 4–6) and for leaves which were initiated after the experiment began (leaves 8–10).

In both experiments, petiole width decreased dramatically under shade conditions (Table 4). The decrease was rapid under treatment conditions, for it was present in leaves 4–6, as well as in leaves 8–10. Petiole width either remained the same or increased slightly for plants in the non-shade treatments (Table 4). Plants in full sunlight and those in the clear and black bags had petioles with more or less localized, swollen mid-regions, whereas plants in the

TABLE 4. Leaf measurements in mm before and after growth under experimental conditions. Values followed by the same superscript are not significantly different ($P \leq 0.05$)

	Control	Clear	Black	Shade	P
Leaf length ¹					
Before treatment	125 ± 16 ^a	133 ± 17 ^{ab}	144 ± 17 ^b	128 ± 15 ^a	0.003
Leaves 4–6	179 ± 22 ^a	175 ± 22 ^a	189 ± 19 ^{ab}	196 ± 15 ^b	0.001
Leaves 8–10	189 ± 13 ^a	207 ± 13 ^b	202 ± 14 ^{ab}	217 ± 22 ^b	<0.001
Petiole width					
Before treatment	25 ± 4	27 ± 6	28 ± 4	26 ± 4	NS
Leaves 4–6	29 ± 5 ^a	27 ± 5 ^a	29 ± 6 ^a	20 ± 5 ^b	<0.001
Leaves 8–10	31 ± 4 ^a	28 ± 4 ^{ab}	24 ± 6 ^{bc}	17 ± 5 ^c	<0.001
Ratio leaf length/petiole width					
Before treatment	5.1 ± 0.8	5.1 ± 1.1	5.3 ± 1.0	4.9 ± 0.7	NS
Leaves 4–6	6.3 ± 1.5 ^a	6.6 ± 0.9 ^a	6.9 ± 1.6 ^a	10.1 ± 1.9 ^b	<0.001
Leaves 8–10	6.1 ± 0.6 ^a	7.6 ± 1.3 ^{ac}	9.3 ± 2.9 ^{bc}	13.4 ± 3.1 ^c	<0.001

¹ Before treatment and leaves 4–6 data combined from two experiments (N = 20 and 27–30 per treatment, respectively); Leaves 8–10 data from 7 wk experiment only (N = 15 per treatment).

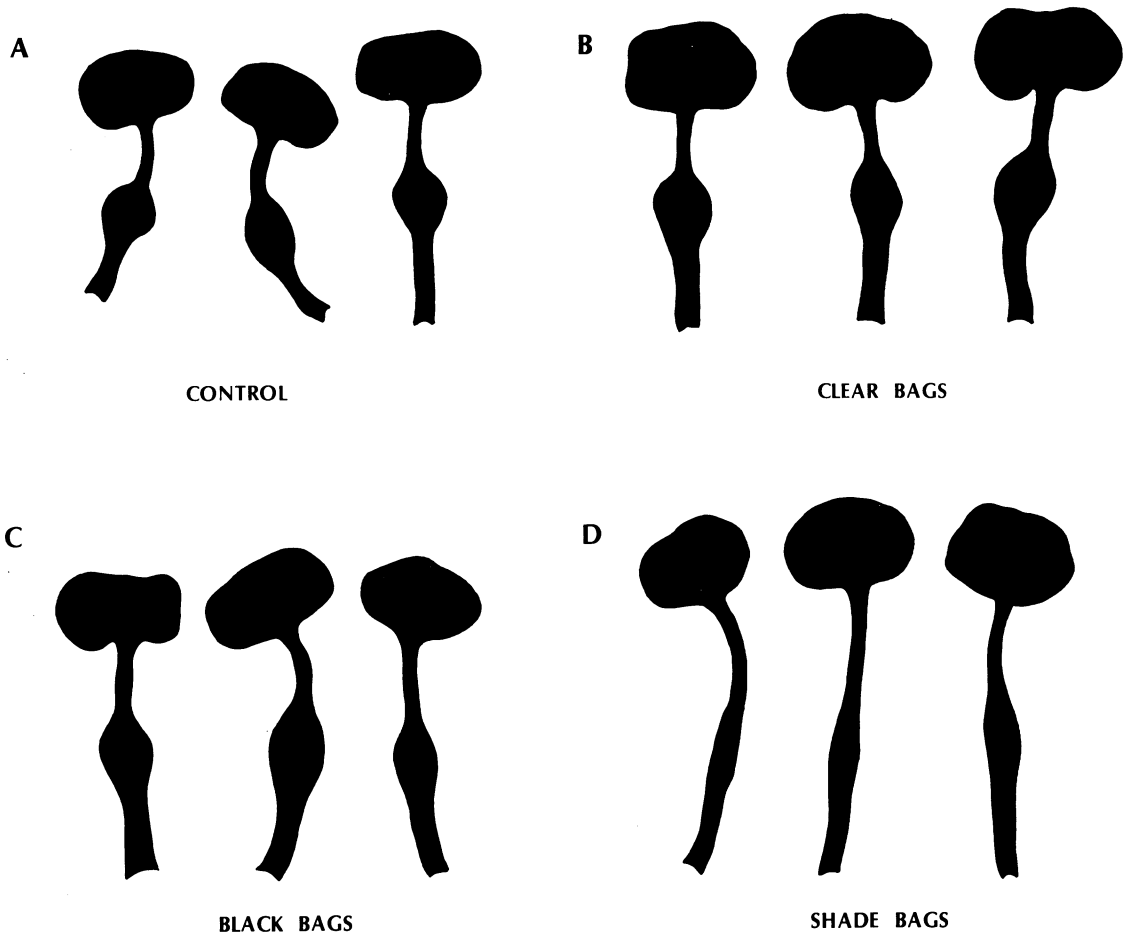


Fig. 2. Silhouettes of leaves 8–10 from plants in experimental light environments. Leaves in shade bags are longer than and lack the localized petiole swelling present in leaves from other treatments.

shade-simulating bags lacked or had only slight swellings (Fig. 2).

The ratio of total leaf length to petiole width increased significantly in shade-simulating conditions (Table 4). This ratio was largest in the shade treatment for both leaves 4–6 and leaves 8–10. In the other treatments the two sets of leaves showed differences in this ratio. The control, clear bags, and black bags did not differ significantly in leaves 4–6, while the shade bags were significantly different from the other three treatments (Table 4). For leaves 8–10, however, the control differed significantly from the black bags, as well as the shade bags (Table 4).

Lamina length and width did not vary significantly among treatments, but the ratio of lamina length to lamina width was significantly different ($P = 0.002$). In both experiments the largest ratio was found under shade-simulating conditions.

DISCUSSION—*Light environments in water hyacinth mats*—The R:FR ratio is approximately 0.3 in temperate forests and wet tropical forests (Smith, 1982; Lee, 1986). In dense parts of a water hyacinth population the R:FR ratio is comparable to these forest values. The % PPFD in wet tropical forest shade ranges from 1.17% to 1.49% (Lee, 1986), while % PPFD in a water hyacinth mat is 2.7%. Thus, although shifts in spectral quality in forests are similar to those in water hyacinth mats, the amount of light available for photosynthesis is greater in the mat. Light inside the mat, however, has a greater alteration in spectral quality per given amount of photosynthetic radiation.

Radiation beneath any canopy is the sum of light filtered through foliage and light passing unobstructed through small gaps in the canopy. Leaves typically reduce R:FR ratio to 0.04, compared to 1.10 for radiation striking the leaf surface (Lee et al., 1986). A water hyacinth

stand develops a low, dense canopy. Penumbra radiation is not important in these low canopies, and very little direct solar radiation penetrates. The discrepancy in R:FR ratio per amount of PPF noted above could be accounted for by this difference in the contribution of skylight.

Effects of light quantity and quality on leaf morphology—The major effects on water hyacinth leaf form are produced by a reduced R:FR ratio. The decrease in R:FR ratio has two results: 1) petiole swelling is reduced; and 2) leaf length increases. Petiole swelling is a unique response of water hyacinth leaves to environments with high R:FR ratio. Previous studies have related the presence of leaves with inflated petioles to high irradiances (Boresch, 1912; Penfound and Earle, 1948). The results of this study indicate that it is spectral quality, not light quantity, that is the major factor controlling petiole inflation.

The second effect, an increase in leaf length, results primarily from a change in petiole length, since lamina length did not differ significantly among treatments. The percent increase in length in leaves 4–6 for the control, clear, and neutral black treatments was 43.2%, 31.6% and 31.3%, respectively, while the increase in length for the shade treatment was 53.1%. The low R:FR ratio thus stimulates petiole elongation.

The effect of lowered R:FR ratio in increasing internode length is well documented for many herbaceous heliophiles (Kasperbauer, 1971; Vince-Prue, 1977; Frankland and Letendre, 1978; Child, Morgan and Smith, 1981; Young, 1981; LeCharney and Jacques, 1982; Whitlam and Johnson, 1982; Corre, 1983). Petioles of the strawberry (*Fragaria X Ananassa* Duch.), a rosette plant morphologically similar to water hyacinth, lengthen in response to end-of-day far-red (Vince-Prue, Guttridge and Buck, 1976). Petioles of white clover, *Trifolium repens* L., a prostrate, stoloniferous plant, also respond dramatically to increased far-red (Dennis and Woledge, 1983; Boller and Nosberger, 1985). Thus, in rosette and prostrate plants ability to respond to reduced R:FR ratios resides in petioles rather than internodes.

The ratio of lamina length to width was greatest under decreased R:FR, so that the shade treatment resembled laminas from the mat center more than the other treatments. Laminas, however, were much less responsive than petioles to R:FR ratios, reflecting basic differences in their physiology.

The response of leaf length to treatment occurs as the leaf is expanding, and, therefore, the change in leaf form is quite rapid. Straw-

berry and white clover leaves also show very rapid responses to reduced R:FR ratio (Vince-Prue et al., 1976; Dennis and Woledge, 1983; Boller and Nosberger, 1985). Since leaves which are already initiated are able to respond to the change in light quality, the particular leaf morphology is determined late in development of individual leaves. In addition, as the experimental bags covered just the shoot apex and expanding leaves, perception of the change in light environment must reside in these parts, rather than in mature leaves.

Environmental controls on water hyacinth leaf morphology—The agreement between our measurements in a natural population and our experimental results indicates that the light environment, especially spectral quality, is a major factor controlling water hyacinth leaf morphology. Temperature, rooting, and nutrients, which have been shown experimentally to affect water hyacinth leaf form (Boresch, 1912; Penfound and Earle, 1948; Weber, 1950; Richards, 1982), may be significant in specific cases but are probably not major regulators of water hyacinth form in natural environments. Since gibberellic acid application produces leaves similar to those found in a dense mat (Pieterse et al., 1976; Watson et al., 1982), light may act by regulating the concentration or form of endogenous gibberellins.

Center and Spencer (1981) found that a seasonal increase in water hyacinth density was followed by an increase in leaf length in a population in north-central Florida. This correlation is consistent with the hypothesis that light is a major morphogenetic factor in water hyacinth populations. When water hyacinth plants are sparsely distributed and have short, inflated petioles, mature leaves do not shade the shoot apex and expanding leaves. As crowding increases, shading changes the light environment. This change stimulates the production of leaves with long narrow petioles that elevate laminas above the existing canopy. The change in light environment, brought on by increased plant density, functions as an environmental cue to alter leaf morphogenesis, which in turn increases canopy ht.

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