

# Growth and Biomass Allocation Patterns During Waterhyacinth Mat Development<sup>1</sup>

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## ABSTRACT

Two experiments in ponds were conducted to determine growth rates and biomass allocation patterns of waterhyacinth during different life cycle and developmental stages and seasons. Experimental ponds were maintained below a pH of 8.5, and one pond was amended with 11.4 kg of nitrogen per week. Plants were separated into constituent parts after sampling, dried, and weighed to determine biomass. Early in development, plants allocated most production to root material, with little increase in average plant size. Once a critical

density was reached, plants increased in average weight and production of daughter plants, with reduced allocation to roots. At peak density, daughter plant production was reduced, but average plant size increased rapidly, resulting in plant mortality. Waterhyacinth exhibited a positive density dependent growth pattern early in development, and switched to the negative density dependent pattern after peak density was achieved.

*Key words:* mat formation, density-dependence, phenology, self-thinning, *Eichhornia crassipes* (Mart.) Solms.

## INTRODUCTION

Seasonal biomass allocation patterns of waterhyacinth (*Eichhornia crassipes* (Mart.) Solms) have been examined in small-scale (Luu and Getsinger 1990), pond (Madsen et al. in press), and field (Center and Spencer 1981) situations. The normal seasonal growth patterns determined from these

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studies are useful in examining critical stages for control of waterhyacinth, but the seasonal versus developmental stage (*e.g.*, stand age) components in allocation patterns have not been differentiated. For instance, early season allocation patterns may be largely due to the small size and low density of plants at that time versus the environmental effects on biomass allocation patterns. This study aims to distinguish the variations in biomass allocation patterns observed at different developmental stages of waterhyacinth populations.

## MATERIALS AND METHODS

Waterhyacinth populations were studied at the U.S. Army Engineer Waterways Experiment Station Lewisville Aquatic Ecosystem Research Facility near Lewisville, TX (Latitude 33°04'45"N, Longitude 96°57'33"W). Two experimental ponds (0.3 ha) were utilized. Both ponds were amended with hydrochloric acid and organic material (hay) to maintain appropriate pH (between 6.5 and 8.5), and Aquashade™ (1 mg l<sup>-1</sup>) to reduce algal growth. One pond was also amended with 11.4 kg of nitrogen fertilizer (as ammonium sulfate) per week (+N; nitrogen pond), while the other pond was not amended with fertilizer (REF; reference pond). Two studies ("run" and "ring") were performed using each pond.

**Run Study.** The run study was designed to examine the spatial development of waterhyacinth mats. Eighteen runs were used in each of the two ponds, each run being 1 m wide and 4 m long. Runs were constructed of a wooden frame with wire mesh sides, with a mean side height of 0.3 m. Water depths ranged from 10 cm at the base to 30 cm at the outer edge of the run. All 18 runs in both ponds were planted with 20 small rosettes (approximately 6 leaves, 2 g DW average) of waterhyacinth on 29 May 1991. Plant samples were taken at 5, 7, 9, 11, 13, and 15 weeks after planting; at each time three randomly selected runs were sampled. A given run was sampled only once. Samples were taken at the origin (or base), the front (*e.g.*, leading), and in the middle of the mat using a 0.1-m<sup>2</sup> quadrat, with plants counted, separated into shoots and roots, dried and weighed to determine biomass.

**Ring Study.** The ring study examined the temporal development of waterhyacinth at a given location across time. Rings utilized were 1 m<sup>2</sup>, made of wire mesh with floats to provide buoyancy, and attached to wire supports to maintain their position in the middle of the pond in approximately 0.5 to 1 m of depth. The rings were circular, with a height of 1 m total and a mean above-water height of 0.5 m. A total of 48 rings were used in each pond. This study was initiated by "planting" 5 small rosettes (approximately 6 leaves, 2 g DW) of waterhyacinth per ring. Three cohorts or time periods were used: cohort A was initiated 27 May 1991, cohort B was initiated 23 July 1991, and cohort C was initiated 24 Septem-

ber 1991. Three rings of plants were harvested for each sampling period for each cohort; cohorts were sampled at 0, 1, 2, 3, 5, 7, 9, 12, 15, 18, 22, and 26 weeks after the initiation of the cohort, or until the first week of December. The number of mature plants were counted, and these plants sorted to component parts, dried and weighed to determine biomass.

## RESULTS AND DISCUSSION

**Run Study.** Run study data provided information on both the development of waterhyacinth in one location (the origin) over time, and spatially across the developing mat. A plot of average shoot weight versus density of plants in the runs for all sample periods presents both spatial and temporal developmental trends (Figure 1A). Examining just origin samples (open and filled circles), developmental trends across time are indicated (Figure 1A, 1B). "Invading" origin plants began as

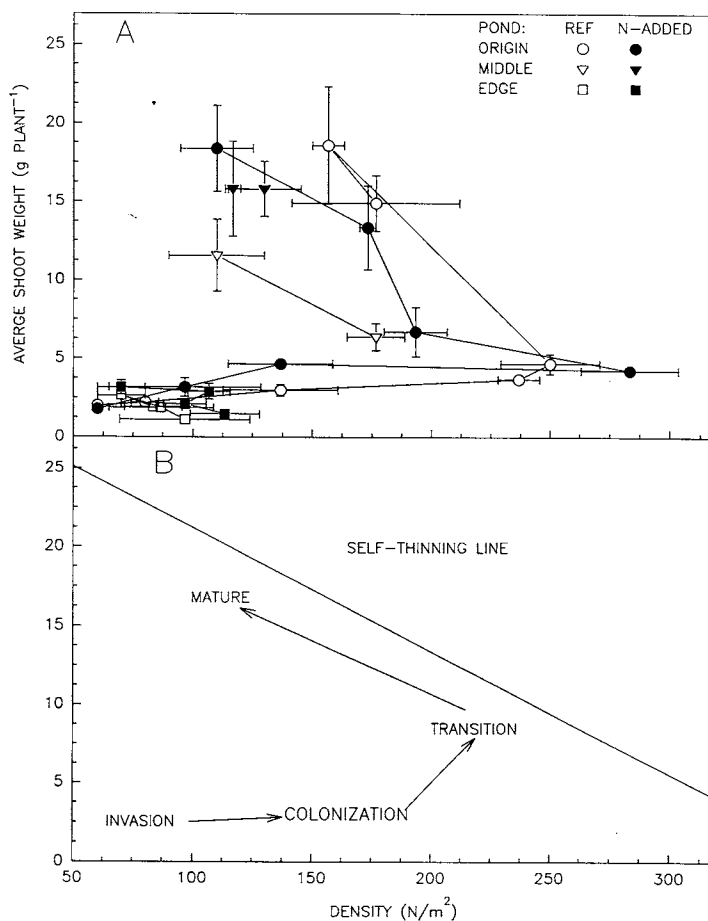


Figure 1. Developmental trends in the relationship between plant density (N m<sup>-2</sup>) and average shoot weight (g) for waterhyacinth in experimental runs. A) Mean ( $\pm$ 1 standard error) for plants from the mat edge, middle and origin of runs in the reference and nitrogen-added ponds; and B) a diagrammatic explanation of trends both temporally at one location and spatially across the mat from edge to origin.

relatively small, sparse rosettes (Figure 1B). Development occurred first through the increase in density or numbers, but all plants were small ("colonization," Figure 1B). As a critical density was reached at approximately 180 rosettes  $m^{-2}$ , plants began to increase in size (5 g DW) as well as density (colonization to transition, Figure 1B). These changes were a positive density-dependent increase: plants increased in size more rapidly as density increased. At a second critical density or inflection point of almost 250 rosettes  $m^{-2}$ , intraspecific competition began to take place, and density decreased as plants continued to increase in average size (up to 19 g DW). This change reflected a negative density-dependent relationship (transition to mature, Figure 1B). A maximum relationship of size and density followed the  $-3/2$  self-thinning relationship (Watkinson 1986). The second inflection point, from a positive to negative density-dependent developmental relationship, was important for other aspects of population development, as will be discussed in relation to ring study data.

The spatial relationship of growth forms within a waterhyacinth mat are also exhibited in the plot of average shoot weight to density (Figure 1A,B). Edge samples (that is, from the growing edge of the mat composed of the youngest rosettes represented by open and filled circles) were all of a similar size (2 to 4 g DW), but ranged in density from 50 to 150 individuals  $m^{-2}$ . At this point, shoot growth increased dramatically, and leaves were oriented vertically rather than horizontally. Transitional plants were intermediate in density and weight to mature plants. Mature basal samples paralleled the  $-3/2$  thinning line as adjacent plants competed for light and space.

**Ring Study.** Invasive stage plants were typically small, low in biomass (2 g DW each, up to 100  $g m^{-2}$ ) and low in density (up to 50  $m^{-2}$ ), with a high allocation to root growth, prostrate buoyant leaves, and low allocation to flowering (Figure 2). Plants in the colonization phase of the mat edge were very similar in form to invasive plants, but root allocation was increased over invaders and daughter production was slightly higher. Typically, little flowering occurred in these plants. Once the colonizing plants filled in empty space, vertical leaf growth began. The mass of the mat itself became sufficient to float plants without bladders on the leaves, and leaves began a transition to the mature growth form. At this time, daughter plant production was at its peak and allocation to flowering increased. Also, shoot mass allocation increased more rapidly than root allocation. Plant densities reached their peak (up to 200  $m^{-2}$ ), with intense intraspecific competition following. Density then began to decline, as self-thinning occurred. Daughter plant production decreased dramatically, while average shoot size increased markedly. However, root allocation continued to decline. Biomass

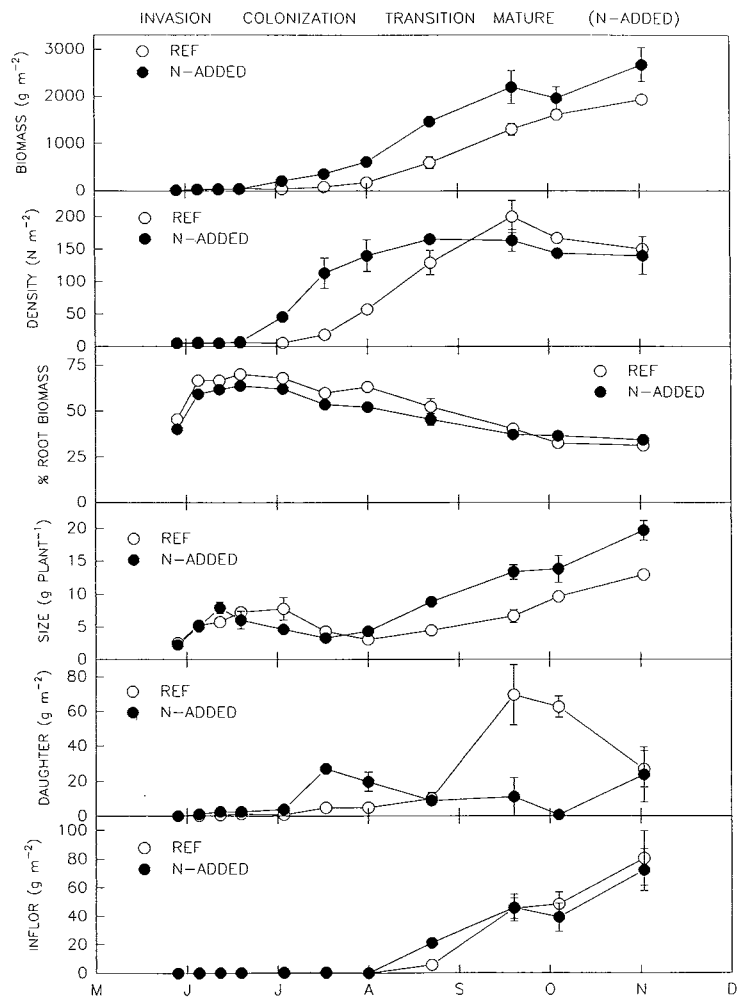


Figure 2. Developmental trends of waterhyacinth mats using data for the reference and nitrogen-added ponds, ring study (cohort A only) in the invasion, colonization, transition and mature phases for biomass, density, percent root allocation of total biomass, average plant size, daughter plant biomass, and inflorescence biomass (top to bottom). Bars indicate  $\pm$  standard error of the mean.

reached its peak (up to 3000  $g m^{-2}$ ) in mature stands of waterhyacinth. Since biomass and production are at their peak, but little vegetative propagation can occur, energy was diverted to extensive flowering and carbohydrate storage in stem bases. This may explain in part the observed increase in starch storage in stem bases in late summer and early fall reported in other studies (Luu and Getsinger 1990; Madsen *et al.* 1993). Trends were similar for both reference and nitrogen-added ponds, with a possible lag in developmental rate observed in the less fertile pond.

Many changes that are perceived as seasonal changes in plant allocation are actually related to a population achieving a given developmental stage at a given time. As plant populations develop in density and age, morphological changes occur due to density-dependent effects. In this study,

preliminary indications of some developmental effects of biomass allocation patterns were examined. Early in population development, individual waterhyacinth rosette size was small and density was low. Initial growth patterns resulted in increased rosette density, but little change in average rosette size. As densities reached 150 to 180 rosettes  $m^{-2}$ , rosettes increased in both density and size. Once a peak density of approximately 220 to 250 rosettes  $m^{-2}$  was reached, average rosette size increased more rapidly, but density began to decrease as a mature stand developed. With these mature stands, daughter production was greatly reduced, and biomass allocation was diverted to either flowering or stem base production from daughter production.

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