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Allometric relationships of field populations of two clonal species with contrasting life histories, *Cladium jamaicense* and *Typha domingensis*

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Abstract

Allometric analysis was used to examine morphological relationships in field populations of two clonal plants, *Cladium jamaicense* and *Typha domingensis*, in a Florida Everglades wetland. We found that allometric relationships of individuals sampled from field populations could be adequately derived and applied to analyzing both leaf and ramet growth responses to site differences along a nutrient gradient. Overall, the allometric relationships showed a significant departure from isometry which indicates that the relationships were size-dependent. Leaf-level morphological relationships were significantly different between species and between sites along the nutrient gradient. These differences, however, were not expressed on the ramet-level. Neither species expressed a plastic allocation response to site differences along the nutrient gradient. Biomass allocation between above- and below-ground for both species indicated significant size-dependent relationships with decreasing relative allocation below-ground with increasing size. Models for predicting total plant biomass (above- and below-ground) for both *C. jamaicense* and *T. domingensis* were developed based on two non-destructive measurements that are easily obtainable in the field. The models followed the equation log (biomass) = $\alpha + \beta_1 \times$ log (height) + $\beta_2 \times$ log (basal area), where α was species specific while β_1 and β_2 were similar for both species but significantly different according to site along the nutrient gradient. Analysis of this model showed that plant height had a relatively greater influence on biomass than basal area at all sites. This difference was greatest at the un-enriched area where plants tend to be short and thick and the least at the moderately enriched site where the relative influence of both parameters was similar.

Keywords: Allometric analysis; Cattail; Sawgrass; Nutrient gradient; Biomass allocation

1. Introduction

Allometric analysis was first introduced by Huxley (1924) to correlate the relative growth of one part of an organism to another part, the whole organism, or a metabolic process. This analytic approach is useful for exploring changes in plant resource allocation resulting from disturbances that affect plant growth and size such as nutrient enrichment, elevated atmospheric CO_2 and altered hydrological regimes (Weiner and Thomas, 1992; McConnaughay and Coleman, 1999; Müller et al., 2000; Niinemets, 2005). Commonly, plant resource allocation strategies have been examined either by root-to-shoot biomass ratios, or by percentage allocation. Unfortunately, these relationships can be size related, vary with ontogeny and frequently do not reflect true plasticity of allocation patterns (Coleman et al., 1994; Gedroc et al., 1996). Comparing allocation changes using allometric analysis can distinguish true treatment effects and removes the confounding factors of plant size or ontogenetic variation.

Most empirical allometric studies evaluating resource allocation patterns were derived experimentally from individuals germinated from seeds, with the intention to compare even-aged plants and avoiding potential ontogenetic variation (McConnaughay and Coleman, 1999; Müller et al., 2000). It is not clear whether allometric relationships between various morphological traits and plant size can be applied universally for field populations of clonal plants, since these populations consist of a mix of seedlings and ramets (Krattinger, 1975) as well as a wide range of different aged individuals.

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Cladium jamaicense Crantz. (sawgrass) and *Typha domingensis* Pers. (cattail) are two wetland rhizomous macrophytes native to the Florida Everglades that occupy similar habitats and yet have contrasting life histories. *Cladium jamaicense* is well adapted to oligotrophic conditions and is the principle plant of the historical freshwater Everglades (Loveless, 1959); whereas *T. domingensis* was an ecologically minor species associated with local areas of site disturbance. In recent decades, however, *T. domingensis* has expanded its range and now dominates large areas of the Everglades that have been impacted by anthropogenic phosphorus inputs (Davis, 1994; DeBusk et al., 2001; Miao and DeBusk, 1999). *Cladium jamaicense* has life-history characteristics typical for plants adapted to low-nutrient environments such as low rates of photosynthesis, slow growth and long life cycles (Davis, 1994; Miao and DeBusk, 1999). *Typha domingensis*, on the other hand, has life-history characteristics indicative of opportunistic species such as high growth rates, high reproduction rates, shorter life cycles, high biomass turnover rates and a greater capacity for phosphorus uptake (Lorenzen et al., 2001; Newman et al., 1996; Miao, 2004; Miao and DeBusk, 1999). Based on biomass ratio analyses, resource partitioning in *T. domingensis* has been characterized as flexible, or plastic, under varying levels of phosphorus enrichment while *C. jamaicense* has been characterized as inflexible (Miao et al., 1997; Miao and Sklar, 1998; Miao et al., 2000; Lorenzen et al., 2001; Miao, 2004). However, does the flexibility in *T. domingensis* allocation result simply from changes in plant size or is it an expression of true allocation plasticity in response to its environment?

We investigated allometric relationships between morphological traits, biomass allocation and plant size for field populations of two clonal plants, *T. domingensis* and *C. jamaicense*, along a nutrient enrichment gradient in the Florida Everglades. Our objectives were to: (1) determine if leaf and plant-level allometric relationships could be accurately derived from individuals sampled from natural populations in the field; (2) examine whether changes in biomass allocation of either species from sites along the nutrient gradient were plastic or simply attributed to size or ontogenetic variations; and (3) develop an allometric model for determining whole plant biomass based on a few simple and easily measurable plant characteristics. In consideration of the life-history characteristics of these two species, we hypothesized that *T. domingensis* would express true plasticity in response to site differences along the nutrient gradient, while *C. jamaicense* would not.

2. Methods

2.1. Field sites

The study was conducted in the northern Florida Everglades in water conservation area 2A (WCA 2A), which is a 447 km^2 freshwater marsh impounded by levees. Apart from rainfall, most of the inflow to WCA 2A consists of agricultural runoff entering through four large spillways from the Hillsborough Canal on its northern boundary. This inflow of nutrient rich water has created a well-documented soil and water phosphorus (P) gradient extending approximately 8 km south of the spillways (Davis, 1994; DeBusk et al., 2001). King et al. (2004) classified three different landscape areas along this nutrient enrichment gradient within WCA 2A, which primarily differ in soil P levels: highly P-enriched (1434 mg P kg^{-1}), moderately P-enriched (1198 mg P kg^{-1}) and reference (578 mg P kg^{-1}). Overlapping the three P enrichment areas are three widely documented vegetation zones consisting of dense monotypic stands of *T. domingensis* in the highly P-enriched area, mixed *T. domingensis* and *C. jamaicense* stands in the moderately P-enriched area and the more typical Everglades *C. jamaicense* dominated ridge and slough communities in the reference areas (King et al., 2004; Rutchey and Vilchek, 1999).

2.2. Sampling design

Individual *C. jamaicense* and *T. domingensis* plants were selectively sampled to represent a large range of plant heights for each species in each of the three enrichment zones: highly P-enriched area, moderately P-enriched area, and reference or un-enriched area. The highly P-enriched area was heavily dominated by *T. domingensis* and therefore was difficult to find *C. jamaicense* plant samples over the entire size range. Between 18 and 33 plants of each species were sampled for a minimum of 50 plants from each enrichment area. Before removing the selected plants, the length of the longest leaf was measured from the soil surface to the leaf tip and is from here forward referred to as plant height, the number of live leaves for each plant was recorded, and two perpendicular basal diameters were measured at the soil surface. Stem basal area was calculated as the area of an eclipse based on the two measured basal diameters. To remove each plant from the soil, a long-bladed spade was used to cut around the leaf canopy perimeter for each plant to a soil depth of approximately 30 cm. When two plants were growing within the same canopy, the spade was used to separate the plants by cutting the soil substrate halfway between the two plants. Once the perimeter was cut, the spade was used to push the plants up and out of the soil. The plants were gently washed in the field and then placed in plastic bags for later processing.

At the lab, each plant was washed carefully to ensure that all living materials remained attached to the plant. Once the plants were free of soil particles, all dead materials (leaves, roots and rhizome) were removed and discarded. Each individual plant was then separated into leaves, roots, rhizomes and shoot bases. One live leaf was selected randomly from each plant to measure leaf length, leaf weight and leaf area with a LiCor 3100 leaf area meter. Specific leaf weight (SLW, g cm^{-2}) for individual leaves was calculated as dry weight divided by leaf area. All live components were dried at 60 °C until weights were constant. Total biomass for each plant was calculated by adding all of the individual dry weight components.

2.3. Data analysis

Allometric relationships between biomass and other plant morphological traits were derived for each species at each of