

Leaf Size and Biomass Allocation in *Thelypteris dentata*, *Woodwardia virginica*, and *Osmunda regalis* in Central Florida

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ABSTRACT.—The sizes of leaves and division of biomass within leaves were examined for separate populations of *Thelypteris dentata*, *Woodwardia virginica*, and *Osmunda regalis* growing in similar habitats. All three species showed considerable variation in leaf characteristics. *Thelypteris dentata* had the densest population of leaves per m², the greatest within-species variation in leaf length and weight, the greatest specific leaf area (area:weight), and the highest ratios of leaf length: mass and leaflet:stalk. *Thelypteris dentata* exhibited leaf characteristics indicative of a stress-tolerant strategy, whereas *W. virginica* and *O. regalis* exhibited a number of the characteristics commonly associated with competitive plants.

Life-history characteristics of seed plants have been used to identify strategies that have evolved to fit environmental characteristics. In the three-strategy, C-S-R model proposed by Grime (1979), plants exist in particular places at particular times as a result of reaching an equilibrium between the intensities of stress, disturbance, and competition. Autecological studies of numerous plant species have allowed plant ecologists to generate a list of morphological, physiological, and life-history attributes associated with the three, main strategies; competitive, stress-tolerant, and ruderal (Grime et al., 1988). One characteristic used to distinguish between these strategies is growth, with the most rapid rates generally found in environments with abundant resources and relatively low disturbance, although plant species may differ widely in their relative rate of biomass production, even when grown as isolated individuals under productive conditions (Garnier, 1991). There are also differences in the growth of individual plants and of plant populations, which may be a mechanism whereby species with more competitive strategies rapidly monopolize resources and suppress the growth and regeneration of neighboring plants (Grime et al., 1988).

A second suite of characteristics used to distinguish plant strategies are those related to the size and composition of supporting and photosynthetic structures. Biomass allocation is typically defined in terms of leaf, stem, and root weight ratios and allocation to leaves and stems is of particular importance (Lambers and Poorter, 1992). Patterns, as well as shifts in allocation patterns, reflect selective pressures and may be a measure of the adaptive significance associated with specific plant structures (Harper, 1977). Some ratios are plastic, even in response to small differences in local conditions (Dong, 1995). Therefore, leaves

may represent a particularly sensitive barometer for assessing plant strategies used to adapt to, and succeed under, existing environmental conditions.

Plant strategies have been proposed for a number of herbs, trees and shrubs, bryophytes, and lichens (Grime et al., 1988) but this type of analysis has not been applied to ferns. The great variety in leaf sizes and textures among ferns has been used to qualify species as more primitive or recently evolved (Gifford and Foster, 1989) and also suggests that leaves may provide excellent models for determining life-history strategies appropriate for different environments. Certainly, the reproductive and physiological differences that distinguish ferns from other plants make such an analysis desirable.

We examined the sizes of leaves of three fern species that have contrasting leaf forms but grow in similar habitats. We determined how biomass was divided within the leaf, focusing on leaflets, which function as photosynthetic units, and leaf stalks, which have both photosynthetic and support functions. Underlying our investigation was the question of whether these species exhibit similar strategies under apparently similar environmental conditions in freshwater, forested habitats.

METHODS

A clearly defined, monospecific population of each of the three species was selected in the Ecological Research Area, a 220-ha tract of land located in Hillsborough County, west central Florida (28°05' N, 82°20' W) in July 1994. The populations of *Thelypteris dentata* (Forssk.) E. St. John and *Woodwardia virginica* (L.) Sm. were approximately 50 m from each other in a forested wetland dominated by elm (*Ulmus americana* L.) and oak (*Quercus laurifolia* Michx.). The population of *Osmunda regalis* L. was located approximately 1 km away, but in a similar habitat. Nomenclature follows that of Wunderlin (1982).

The density of leaves (number of leaves per square meter) for each species was calculated in three areas of each population. Twenty five leaves, over the size range represented, were collected to establish the relationship between length and weight during leaf growth. Their length was measured within 2 hours after collection and the weight of leaflets and leaf stalks measured after drying at 60°C for 2 days. A curve-fitting procedure (DeltaGraph 3.5) was used to determine the relationship between length and weight.

Ten leaves of *T. dentata* and *W. virginica* and 10 clumps of *O. regalis* were randomly selected by throwing a marker into the population. The leaves were clipped at the surface and placed in a labeled plastic bag. The length and area of each leaf was measured within 2 hours of collection. Each leaf was then separated into leaflets and leaf stalks (petioles), placed in individual, labeled aluminum containers, dried at 60°C for 2 days, and weighed.

Two ratios were calculated, both reflecting relative contributions of energy invested in photosynthetic versus support tissue. Leaf length:mass ratios were calculated using the total leaf length and dry mass, and leaflet:stalk ratios were calculated using the dry mass of leaflets to the dry mass of stalks. The specific leaf area (leaf area/dry weight) was also determined.

TABLE 1. Leaf characteristics (mean and standard deviations with sample size in parentheses) of *Thelypteris dentata*, *Woodwardia virginica*, and *Osmunda regalis* in west central Florida.

Characteristic	<i>T. dentata</i>	<i>W. virginica</i>	<i>O. regalis</i>
Leaves per m ²	43 ± 16 (3)	18 ± 5 (3)	16 ± 3 (10)
Leaf length (cm)	16.4 ± 12.7 (10)	87.6 ± 27.2 (10)	65.9 ± 19.6 (10)
Dry weight of (g) leaves	0.06 ± 0.06 (10)	2.06 ± 1.21 (10)	2.22 ± 1.07 (10)
Specific leaf area (mm ² mg ⁻¹)	41.4 (10)	22.4 (10)	

RESULTS

All three species showed considerable variation in leaf characteristics (Table 1). *Thelypteris dentata* had the densest population of leaves, but the leaves were considerably smaller and lighter than those of the two other species. *Thelypteris dentata* also had the greatest within species variation in leaf length and weight. The specific leaf area (area:weight) of *T. dentata* was twice that of *W. virginica*. Leaf area was not measured in *O. regalis*, as the instrument used to measure the areas was unavailable.

The relationship between leaf length and mass for a range of leaf sizes was not linear (Fig. 1), but was most highly correlated with a parabolic curve. Thus, *T. dentata* and *W. virginica* devoted more energy to increasing leaf length (or height) early in their development while continuing to increase in biomass later in their development.

The ratio of leaf length:mass was significantly higher and more variable for *T. dentata* than for the other species (Fig. 2). Leaflet:stalk ratios were more consistent between populations than length:mass ratios and were generally highest for *T. dentata*, which also showed greater variation than the other two species (Fig. 3).

DISCUSSION

The populations of *Thelypteris dentata*, *Woodwardia virginica*, and *Osmunda regalis* showed inter- and intraspecific variation in leaf characteristics that could be the result of different adaptive strategies. *Thelypteris dentata* had the greatest variation in leaf characteristics, both in terms of being different from the other two species, as well as having high variability within the population. *Thelypteris dentata* is an introduced species in Florida, whereas *W. virginica* and *O. regalis* are native to this area. Some differences in characteristics may be due to this, although we cannot determine whether *T. dentata* is different from the native plants because it is introduced, as we have neither other populations nor other introduced species with which to compare our data.

Although variation in leaf size exists for all three species, our observation that plants invest more biomass in leaf height than leaf mass early in leaf expansion suggests that these ferns grow so as to equalize the height of the canopy within the population. The height of the canopy impacts new growth when shading

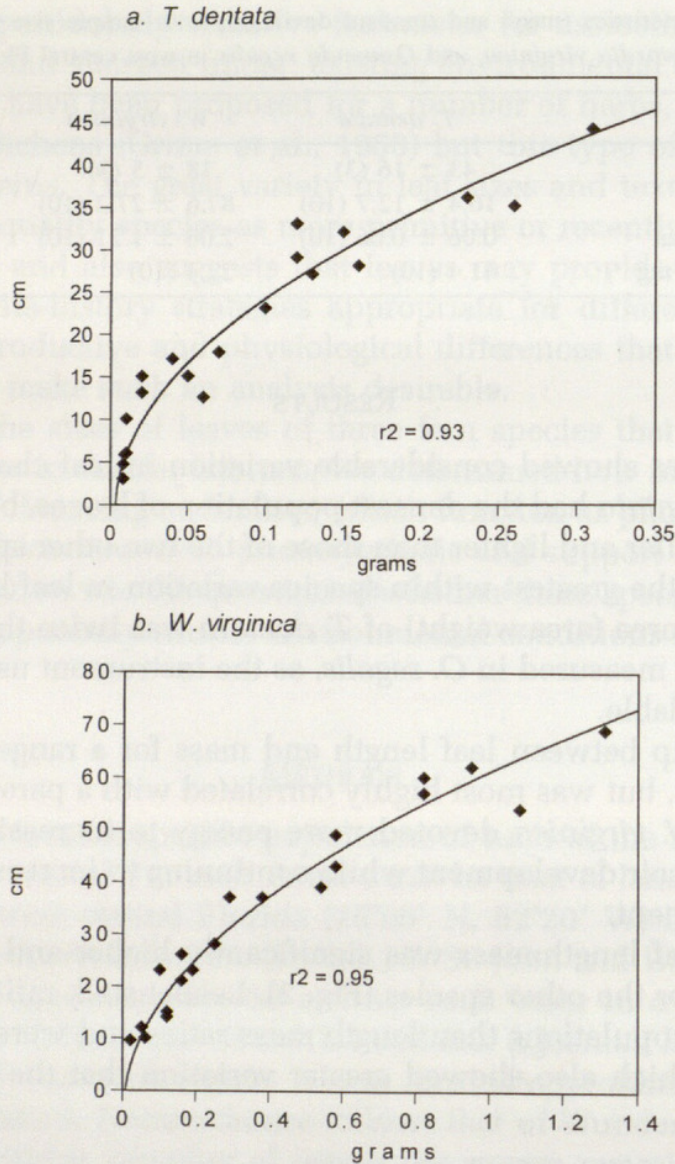


FIG. 1. Relationship between leaf length and leaf mass for (a) *Thelypteris dentata* and (b) *Woodwardia virginica*.

from standing litter (dead leaves) influences the density, size, and growth rate of emerging shoots (Ekstam, 1995). *Thelypteris dentata* does not produce much biomass, and leaves decompose quickly once they become brown and dry. Similarly, *O. regalis* grows in clumps that are slightly more elevated and where drier conditions and increased oxidation promote higher rates of decomposition. However, *W. virginica* has high biomass production, creating dense litter that does not decompose as rapidly and which may affect the size of emerging leaves.

Thelypteris dentata allocates more energy to producing photosynthetic leaf material than supporting leaf material. This is evident not only from the data on ratios of length:weight and leaflets:leaf stalks but also from the qualitatively fragile nature of these leaves. *Thelypteris dentata* also has a higher specific leaf area and may capture more light by displaying leaves horizontally. These leaf adaptations are indicative of a stress-tolerant strategy (Grime et al., 1988). Fur-

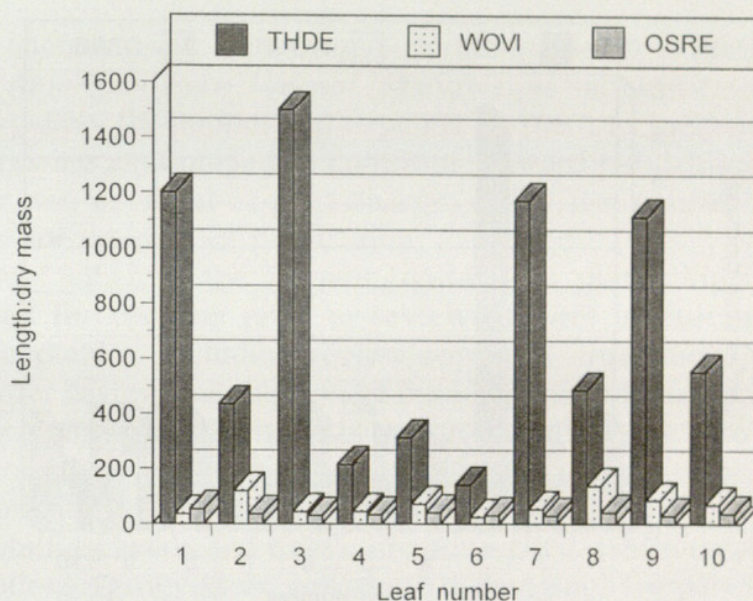


FIG. 2. Ratios of leaf length to leaf biomass for individual leaves of *Thelypteris dentata* (THDE), *Woodwardia virginica* (WOVI), and *Osmunda regalis* (OSRE).

thermore, we have not observed spore production in *T. dentata* in nearly three years of monitoring this population, and lack of investment to reproduction is another measure of a stress-tolerant strategy (Grime et al., 1988).

Woodwardia virginica and *O. regalis* exhibit a number of the characteristics associated with competitive plants including robust and mesophytic leaves, a rapidly ascending monolayer canopy, and high investment in support tissue to provide height growth which increases competitive effectiveness for radiation (Grime et al., 1988). It is not possible to quantify competitive interactions in the absence of shared environmental effects (Mitchell-Olds, 1987) but it is likely that intraspecific competition for light resources occurs in both populations due to the high density of leaves in *W. virginica* and the clumped growth of *O. regalis*.

Competitive plants also tend to have high turn-over rates for leaves since, in a competitive situation, the ability to redistribute resources from old leaves to new and better placed ones may be crucial (Grime 1979). Some of the leaves measured in this study may have been produced at different times during the season, serving different functions as environmental conditions changed over time. The value of a leaf varies with its developmental age (Harper, 1989), and we cannot assume that larger leaves were necessarily older leaves in the case of these ferns.

Although there is a growing body of research related to fern populations (Werth and Cousens, 1990) there continues to be a need for fundamental studies such as these to build our understanding about basic characteristics within this group of plants. In addition to identifying strategies for exotic versus native ferns, future research related to plant strategies should strive to include allocation to reproductive as well as vegetative structures since plant strategies reflect a trade-off between efficiencies in maintaining local populations (growth)

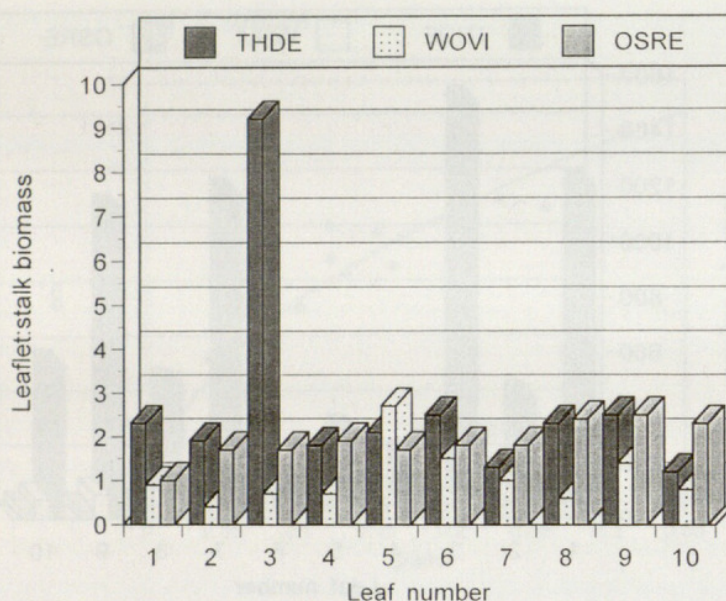


FIG. 3. Ratios of the biomass invested in leaflets (photosynthetic) to that invested in stalk (support) for individual leaves of *Thelypteris dentata* (THDE), *Woodwardia virginica* (WOVI), and *Osmunda regalis* (OSRE).

and expanding populations (reproduction). Our study does not include reproductive allocation, because only *W. virginica* produced sori, although both *T. dentata* and *O. regalis* are capable of producing sori and viable spores. This raises interesting questions about the absolute and relative allocation to reproduction among and between ferns, particularly between species that produce similar fertile and vegetative leaves (where sori are borne on “normal” leaves) versus those that produce modified fertile leaves resembling stalks bearing sori.

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