WHY DO NONFOLIAR GREEN ORGANS OF LEAFY ORCHIDS FAIL TO EXHIBIT NET PHOTOSYNTHESIS?

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ABSTRACT

Nonfoliar organs of numerous epiphytic orchids, including fruit of Encyclia tampensis, are green. Regenerative rather than net photosynthesis is characteristic of these structures except when well-developed leaves are absent. The uneven distribution of photosynthetic capacity among the body parts of these plants can be explained by the relative cost-effectiveness of investing scarce resources (in particular, N) for autotrophy. Historical change in vegetative form and accompanying shifts in function during transitions become clearer when plant economics are considered.

ALLUSIONS to chlorophyll in plant organs that are primarily concerned with nontrophic functions abound in the orchid literature, but seldom do even those few studies that report photosynthesis at these sites (Avadhani et al., 1982) address its full implication. Crop scientists (e.g., Flinn, Atkins, and Pate, 1977; Pate, Sharkey, and Atkins, 1977) and others (e.g., Bazzaz, Carlson, and Harper, 1979) have demonstrated that carbon/energy inputs from what appear to be relatively trivial sources, together with associated influences on water economy, can be significant to plant performance. Emphasis was placed on the importance of nonfoliar supplements to yield—particularly seed production—but there are also potential consequences for historic change in plant form.

Because they so often grow in strong light and on impermeable substrata, orchids can utilize an exceptional variety of organs for energy harvest. Indeed, Encyclia tampensis, like thousands of its relatives, conducts photosynthesis in stems, roots, and fruit as well as in leaves, but not with equal intensity. Results of previous studies of this epiphyte (Benzing and Ott, 1981; Benzing et al., 1982; Benzing et al., 1983) and data provided below are used here to develop an economic perspective on why nonfoliar organs of so many leafy orchids are green yet possess insufficient photosynthetic capacity to exhibit net CO₂ consumption. This study also illustrates how a comprehensive cost/benefit analysis will help explain why such an extraordinary variety of body plans exists among the more advanced autotrophic orchids.

MATERIALS AND METHODS—Plants were collected in April, 1987 from a variety of photophyes in the mixed cypress/hardwood forest that occupies much of the Fakahatchee Slough in Collier County, Florida. Growth continued on lath strips in the Oberlin College greenhouse until flowering took place 3-5 months later. Following manual cross-pollination (2-6 flowers/inflorosity), plants were moved into a growth chamber where fruit developed under 14 hr of light (ca. 170 μmol m⁻² s⁻¹) and day/night temperatures of about 25 C and 20 C.

Subsets of a population of about 200 capsules produced by approximately 50 plants were examined at five stages during the 8-10 months required to reach dehiscence (Fig. 2). Stages 1 through 3 were defined by capsule width/length ratios of: less than 0.09; 0.15; 0.18; and 0.23; 0.26. Stages 4 and 5 were defined by time elapsed in the 6 to 15 weeks after the end of Stage 3.

Fruit and leaves were collected at 7 a.m. (at the end of the dark period) and at 7 p.m. They were weighed immediately, sectioned, and ground in 40 ml distilled H₂O. Acidity was measured by titrating the extract to pH 7.5 with 0.01 M NaOH. Chlorophyll content was determined spectrophotometrically according to Arnon (1949). A third set of oven-dried samples were wet-digested in H₂SO₄ using metallic selenium as a catalyst. Following neutralization with 30% NaOH, digests were steam-distilled and the distillate titrated with 0.01 HCl to determine total (Kjeldahl) nitrogen content. Seeds that initially represented little of the total mass could not be separated from Stage 1 and 2 fruit; thereafter, capsule values are for wall tissue only.

Gas exchange (CO₂ and H₂O) in detached fruit placed in a 250-ml cuvette was measured in a closed system using a LI-COR LI-6200 portable infrared gas analyzer fitted with a hygrometer. Data were collected between noon and 2 p.m. and between midnight and 2 a.m. Measurements were made in the growth chamber in order to avoid abrupt changes in conditions, particularly humidity, that might affect stomatal conductance. Several Stage
1 and 2 capsules were used for each determination; larger, older fruit was assayed singly. Occasionally, as few as three replicates were run, but usually n=8.

10. Capsules from Stages 3, 4, and 5 were first analyzed intact and then removed from the cuvette and bisected with a razor blade. The initial burst
Chlorophyll and total N concentrations in fruit walls decreased initially and leveled off after Stage 2 at about half to one-third that in leaves (Fig. 6).

The most conspicuous epidermal feature distinguishing fruit from foliage was stomatal location and density (Fig. 7, 8). Occurrence on leaves (abaxial side only; Fig. 8) averaged 46 mm⁻² while numbers on capsules were much lower — 2 mm⁻² near the three ribs (Fig. 1) and about 3 mm⁻² elsewhere. Stomata were recessed in fruit, one at the summit of each small papilla. Full-sized capsules were bounded by a thick-walled epidermis with a stout cuticle; sizable locular cavities had developed by Stage 3 (Fig. 1).

DISCUSSION—Perspectives on performance of, and broader implications of green tissue in capsules of Eucalyptus tannensis and many additional orchids (and also in their stems and roots) are improved through comparison with nonorchids. Developing pods of some Leguminosae and a variety of other green fruits exhibit substantial surface-to-volume ratios and fix modest amounts of atmospheric CO₂ as well as much respired carbon. Enough photosynthesis, including net CO₂ uptake during early development, occurs in Pisum sativum fruit to reduce appreciably the amount of imported photosynthate needed to produce seeds (Flinn et al., 1977). Specifically, capsules import 17% less dry matter because they are green, certainly a benefit for a plant destined to allocate one-third or more of its biomass to a single reproductive effort at the end of a short life. In contrast, capsules of perennial, slow-growing, xerophytic Eucalyptus tannensis continuously leak some CO₂ that foliage must replace. In effect, similarity in overall carbon balance between fruit and leaves of Pisum sativum and its kind exceed that of E. tannensis except when drought induces the orchid’s foliage to CAM-idle, as described below.

The fruit of C₃ P. sativum is not particularly watertight, although transpiration occurs at a lower rate than does that from leaves. If the water balances of the two species considered here are counted, pods of E. tannensis are the more resistant to desiccation relative to foliage — just how much more is impossible to determine without additional data. Nevertheless, at least quantitative differences in photosynthetic performance and water use (fruit versus leaf) exist, and they, along with the distinct environmental conditions prevailing in native habitats, prompt us to suggest that peculiarities of pea and E. tannensis capsules vis-à-vis water and carbon economy influence plant survival according to the following hypothesis.

Photosynthesis by fruit can yield several advantages that vary in relative importance, depending on the nature of that organ, the life style of the parent plant, and growing conditions. Green tissue
in fruit of slow-growing *Encylia tampensis* increases fitness through its positive effects on stress tolerance. In contrast, enhanced vigor is the principal advantage of capsule photosynthesis for *Psamnium sarvium* and for similar species in equable habitats where rapid maturation more than pronounced drought tolerance favors survival. Our argument that benefits from green fruit tissue reflect plant life history and conditions in home ranges, is inspired by successful interpretation of leaf form and function (Chabot and Hicks, 1982) using tools borrowed from economists (Bloom et al., 1985). Other green organs presumably operate under some of the same rules, hence are equally amenable to cost-benefit analysis using the same currencies (i.e., carbon, water, and nitrogen).

Plant economics dictate that photosynthetic performance is determined by constraints related to organ (or whole canopy, etc.) architecture, cost and longevity (Table 1), and by ambient aridity and nutrient availability. The efficacy of the *E. tampensis* capsule for net photosynthesis should be below that of *Psamnium sarvium*; benefit from fruit-enhanced conservation and efficient use of scarce resources (particularly water) should, on the other hand, be paramount for this and other similarly constructed xerophytes. In effect, the advantages of net versus strictly regenerative photosynthesis (a continuous process that is otherwise similar to the transitory, stress-induced, CAM-utilizing mechanism of CAM xerophytes) are determined by the way carbon and growth-limiting supplies of water, nitrogen, and possibly other mineral nutrients are deployed in fruit compared to the way they are used in leaves on the same plant.

Substrates consumed for energy by developing
seed and associated heterotrophic tissue must be replaced at greater cost if, instead of being reflexed, the seed is lost through fruit walls. Carbon recycling, including CAM-photosynthesis, unlike net photosynthesis, is not transported nor energy inputs for phloem import, but these two advantages alone do not determine how green tissue in fruit can most effectively promote plant success. Neither does capsule shape (which is rather poor for efficient harvest and gas exchange in *E. tampensis*) fully explain why this epiphyte’s fruit never exhibits net CO₂ uptake. Other species possessing thicker organs (e.g., cactus cladodes) that are even less suitable for harvesting CO₂ and photons, occasionally provide most or all required photosynthetic carbon only for species that possess no other type of organ capable of delivering equal or greater return on plant investment.

Two constraints based on form and time, plus a third due to peculiarities of the growing capsule, militate against plant investments that would permit *E. tampensis* fruit to perform net photosynthesis. First, its foliage which, by its planar structure, is better suited for carbon gain than is any other part of the plant. Second, capsules live less than a year; foliage survives about three to four times longer, i.e., a year-old leaf has two to three more seasons to repay construction and maintenance costs and then turn an energetic profit. Finally, walls of ripening capsules tap an enriched internal CO₂ supply and fix it day and night with less protein (N) than leaves require to capture carbon at the same rate from the atmosphere—a more dilute and hence less accessible source in the sense of enzyme kinetics. Buildup and partial leakage of CO₂ indeed suggests that carboxylation capacity in *E. tampensis*
Table 1. Additional features that distinguish organs characterized by net or regenerative photosynthesis.

<table>
<thead>
<tr>
<th>Type of photosynthesis</th>
<th>Organ Structure</th>
<th>Function</th>
<th>Longevity</th>
<th>N investment</th>
<th>Water use efficiency</th>
<th>Diffusive conductance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Net</td>
<td>Superior for light harvest compared to other green organs of similar or greater life span produced by the same plant</td>
<td>Primarily trophic</td>
<td>Sufficient to produce more photosynthate than that required for construction and maintenance inversely related to photosynthetic rate</td>
<td>High</td>
<td>Relatively low</td>
<td>Relatively high</td>
</tr>
<tr>
<td>Regenerative</td>
<td>Various, but subordinated to non-photosynthetic functions</td>
<td>Secondary trophic</td>
<td>Various, but less than that sufficient to pay for construction and maintenance</td>
<td>Various, but often less concentrated than in foliage</td>
<td>Relatively high</td>
<td>Relatively low</td>
</tr>
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Although theoretically possible for *E. tampensis*, would probably also require unprofitable investments. Nitrogen inputs would have to be equivalent in capsule walls and in foliage, a condition that would reduce whole-plant nitrogen-use efficiency for autotrophy. Similar logic explains why most orchid roots and stems, including pseudobulbs, show no net photosynthesis (Avadhani et al., 1982). Although these organs may live as long as foliage, their stout structure, lack of a device to regulate gas exchange (roots lack stomata), and their predominant storage and absorptive functions render them less suitable than associated leaves for vigorous photosynthesis (Benzing and Ott, 1981; Benzing et al., 1983). A conservation system similar to that in *E. tampensis* capsules probably exists in many orchid roots and stems, although almost certainly carbon turnover there is slower than in fruit. Foliage temporarily falls into this same category when drought-imposed CAM-like stress eliminates access to atmospheric CO₂. This is also the period during which similarities in carbon and water balance (but not in budgets) between fruit and leaves of *E. tampensis* and those of *Fissidens latifolius* are greatest.

A few orchids lack developed foliage and instead photosynthesize via relatively N-rich roots (e.g., essentially shootless *Polyandra*: Benzing and Ott, 1981; Benzing et al., 1983) or stems (e.g., leafless *Vanilla*). These exceptional taxa raise important questions about plant resource economy and unusual tradeoffs during angiosperm evolution. They also remind us that some of the greatest challenges facing evolutionary botanists today concern the reasons why organs that appear to be much better designed for one particular service are occasionally

![Diagram](image-url)

Fig. 5. Mean rates of nocturnal water loss ± SD from intact fruit and leaves. Differences between columns with the same letter are not significant (K-W A, F=21.96; P<0.001; S-N-K, P<0.01).
co-opted for another wholly different function. Apparently, advantages powerful enough to override the biomechanical (Table 1) and environmental constraints that underlie the ancient division of labor that still describes tens of thousands of leafy relatives have affected several orchid lineages. The identity of these selective forces as well as important details of the shifts in form and function that represent responses to them remain largely unknown.

LITERATURE CITED


