

## Host-tree Selection by an Epiphytic Orchid, *Epidendrum magnoliae* Muhl. (Green Fly Orchid), in an Inland Hardwood Hammock in Georgia

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**Abstract** - We characterized the tree community of a mesic hardwood hammock in south-central Georgia as an oak-pine-hickory forest, with *Liquidambar styraciflua* (Sweetgum), *Magnolia grandiflora* (Southern Magnolia), and *Ilex opaca* Ait. (American Holly) as subdominants. We surveyed this forest for colonies of the most northerly distributed epiphytic orchid in the Western Hemisphere, *Epidendrum magnoliae* (Green Fly Orchid), and recorded the species and trunk diameter of 112 host trees (phorophytes) as well as the height and size of each orchid colony. We calculated a selectivity index (SI) to compare phorophyte frequency with availability, based on a point-transect survey. Green Fly Orchid occurred on 8 species of hardwood trees, but had a strong preference for Southern Magnolia as a host and a moderately strong preference for *Quercus virginiana* (Live Oak). Host trees were much larger (presumably older) than the average of available trees, and that effect was strongest for the most preferred host. Orchid colonies also occupied significantly greater areas on individual Southern Magnolia than on other phorophytes. It is likely that old-growth Southern Magnolia and Live Oak trees are critical to the viability of this population of Green Fly Orchid, which is rare in inland forests in Georgia. In addition to being the most persistent epiphyte substrates in this environment, their broadleaf evergreen canopies—which would be especially true of Southern Magnolia—may provide the most favorable microclimates in terms of shade, humidity, and frost protection.

### Introduction

It has been estimated that epiphytic vascular plants comprise 10% of all vascular plant species (Madison 1977) and 70% of all orchid species (Gentry and Dodson 1987). Further, 60% of all epiphyte species are members of the Orchidaceae (Kress 1986). Vascular epiphytes in general and epiphytic orchids in particular attain their peak species diversities in tropical forests, especially in the Neotropics (Gentry and Dodson 1987), but they also occur in subtropical forests, with many species found in southern Florida (Luer 1972). There are 7 species of *Epidendrum* found in the continental US, all of which are epiphytic; 6 of these are limited to subtropical hammocks of peninsular Florida (Hågsater 2002). *Epidendrum magnoliae* Muhl. (= *E. conopseum* W.T. Aiton) (Green Fly Orchid) is found in widely scattered patches of humid coastal plain forest in 7 southeastern states from North Carolina southward through central peninsular Florida and westward into southern Louisiana. Populations in eastern Mexico in the states of Nuevo León, San Luis Potosí, and Tamaulipas have been treated as *E. conopseum*

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var. *mexicana* L.O. Williams (Hágsater 2002, Luer 1972). Green Fly Orchid is the only species of epiphytic orchid found in the continental US outside of Florida and has the northernmost distribution of any epiphytic orchid in the Western Hemisphere (Correll 1950).

In some studies in Neotropical forests (e.g., Frei 1973), certain epiphyte species showed marked preferences for host tree (phorophyte) species, whereas in other studies little or no host specificity was seen (Trapnell and Hamrick 2006, Zimmerman and Olmstead 1992). Generally, epiphytes occur on a number of different phorophytes, but with variable frequency (Benzing 1990). Possible mechanisms for host-tree or phorophyte specificity in epiphytic orchids involve microclimate (see Callaway et al. 2002), propensity for exfoliation (bark sloughing), presence of certain bark chemicals (Frei and Dodson 1972), other bark characteristics (Benzing 1981), and distribution of mycorrhizal fungal symbionts. Epiphytic orchids have mycotrophic nutrition (carbon, other nutrients, and possibly water are supplied to the plant by mycorrhizal fungi) and have been shown to require a mycorrhizal symbiont for seed germination (McKendrick et al. 2000, Otero et al. 2005).

Green Fly Orchid shares its geographic range in the southeastern coastal plain with the “atmospheric” epiphyte *Tillandsia usneoides* (L.) L. (Spanish Moss) and the rooted, epiphytic fern *Pleopeltis polypodioides* (L.) E.G. Andrews and Windham (Resurrection Fern), although the latter two are far more common within that range. These species also commonly attach to branches, whereas Green Fly Orchid frequently grows on the main trunk of its host. Outside of Florida, Green Fly Orchid is limited to near climax hardwood forests and swamp forests within the most humid microclimates available, which means hammocks primarily found along the coastal strip and rarely found inland (Wharton 1989).

Correll (1950) reported that *Epidendrum magnoliae* (as *E. conopseum*) grew primarily on *Magnolia grandiflora* L. (Southern Magnolia), and *Quercus virginiana* Mill. (Live Oak), but that it had also been collected on *Acer rubrum* L. (Red Maple), *Carpinus caroliniana* Walter (Hornbeam), *Fagus grandifolia* Ehrh. (American Beech), *Juniperus virginiana* L. (Eastern Red Cedar), *Liquidambar styraciflua* L. (Sweetgum), *Nyssa* spp. (Black Gum or Tupelo), and *Taxodium distichum* (L.) Rich (Baldcypress). We have also observed Green Fly Orchid on *Tilia americana* L. (Basswood) in a bluff forest community along the Withlacoochee River in western Lowndes County, GA, and epilithic on sandstone cliff faces (“Altamaha Grit” formation) at “Broxton Rocks” in Coffee County, GA (Patrick et al. 1995; R. Carter, unpubl. data).

In this study, we attempt to characterize the tree community of a rare inland hardwood hammock in Georgia (Wharton 1989), which hosts a sizable population of Green Fly Orchid, and examine the host-tree distribution and specificity of this epiphytic orchid within this community. We are not aware of any other similar studies of host-tree selection for this species.

### Field-site Description

Dudley's Hammock, owned by Moody Air Force Base, is a relatively undisturbed, elevated area, ca. 61 ha in size, within the Grand Bay wetland complex, which comprises ca. 7000 ha of shallow Carolina bays or pocosins and headwater streams in northeastern Lowndes and southwestern Lanier counties in extreme south-central Georgia. It is located 17.6 km NE of Valdosta at 30°57'02"N, 83°09'49"W (NAD27). The hammock rises 2–3 m above the surrounding cypress-gum swamps and pine flatwoods and is noted as a rare inland example in Georgia of undisturbed mesic hardwood hammock, which is also characterized as lowland broadleaf evergreen forest (Quarterman and Keever 1962, Wharton 1989). In the classification scheme of The Nature Conservancy, the vegetation of Dudley's Hammock appears to be most closely related to the Southern Coastal Plain Oak Dome and Hammock (CES203.494), with characteristics of the Southern Coastal Plain Hydric Hammock (CES203.501), but lacking *Sabal palmetto* (Walter) Lodd. ex Schult. & Schult. f. (Cabbage Palm; cf. NatureServe 2008).

Dudley's Hammock is roughly bisected by an east–west 2-track access road, and there has been some recent and historic disturbance (partial clearing, burning) resulting from military activities on the northern half (Bergstrom et al. 1994). Therefore, we limited our survey to the portion of the hammock south of the road, which is relatively undisturbed and where Green Fly Orchids had been observed.

Dominant trees in this less disturbed portion of the hammock include Southern Magnolia, Live Oak, *Q. nigra* L. (Water Oak), *Q. alba* L. (White Oak), *Q. michauxii* Nutt. (Swamp Chestnut Oak), *Ilex opaca* Ait. (American Holly), *Carya glabra* (Mill.) Sweet (Pignut Hickory), Sweetgum, *Nyssa sylvatica* Marshall (Black Gum), *Pinus glabra* Walter. (Spruce Pine) and *P. taeda* L. (Loblolly Pine). Owing either to the small size and isolation of Dudley's Hammock, or to soil properties, American Beech is not found at this site (Bergstrom et al. 1994), whereas it is a dominant tree of similar hammocks in northern Florida (Monk 1968).

Arboreal vascular epiphytes commonly found in Dudley's Hammock include Spanish Moss, Resurrection Fern, and Green Fly Orchid. Green Fly Orchid is protected in Georgia; its legal status is Unusual and its rank is S3 among Special Concern Plant Species (Georgia Department of Natural Resources 2007, Patrick et al. 1995).

### Methods

In August 1994, working in a three-person team, we intensively surveyed trees in the southern portion of the hammock for presence of the epiphyte along a series of north–south overlapping compass transects. One team member monitored the compass bearing, while the other two members scanned trees using Pentax® 7×50 6.2° binoculars. The presence of Green Fly Orchid was confirmed by two team members, and species and diameter at

breast height (DBH; cm) of phorophyte plus estimates of area of phorophyte surface colonized by *Epidendrum* and mean height above ground of epiphyte colony were recorded. At the time of the survey, fronds of Resurrection Fern were in a relatively dehydrated state, which increased the visibility of Green Fly Orchid plants.

In August 2006, we censused tree-species composition of the southern portion of the hammock by point-quarter sampling every 20 m along three 180-m transects, yielding 10 sampling stations per transect for a total of 120 quadrants (and point-quarter trees). The transects were placed by a stratified random method designed to traverse the area where Green Fly Orchid was most commonly found, and they were at oblique angles to each other (compass bearings 20°, 140°, and 240°). All observations were independent. The nearest tree (up to 15 m) to each point in each of 4 quadrants (NW, NE, SE, SW) that was at least 5 cm in DBH was chosen as the point-quarter tree, and its species and DBH were recorded.

Basal area for each tree was determined by the formula  $\pi r^2$  where  $r = \text{DBH}/2$ . Tree community profiles were constructed both by relative stem frequencies and by species importance values (ln basal area per species). A selectivity index (SI) modified from Ivlev (1961) was used to determine host-species selectivity of the orchid, based on that host-tree's availability in the habitat, as follows:

$$\text{SI} = (\text{Hs} - \text{As}) / (\text{Hs} + \text{As}),$$

where Hs was the relative frequency of the host species among the sample of actual host trees, and As was the relative frequency of that tree species among the 119 trees from the point-quarter survey. For the pool of available host-tree species for this index and to calculate As, we did not include pines (which are not known to be hosts of *Epidendrum*), and we included only species belonging to genera which actually were recorded as host trees in this study. We did a separate calculation of SI using relative basal areas of trees, by species, that were actual host trees (Hs) and relative basal areas, by species, of trees from the point-quarter transect (As), again including or not including species in the latter pool as per the above criteria. We present these two indices for each species as  $\text{SI}_s$  for stems and  $\text{SI}_b$  for basal area. This SI index can range from -1.0 for perfect avoidance to 1.0 for perfect selectivity, or total preference. An SI of 0.0 indicates the tree species serves as a host tree in the exact proportion that it is available in the habitat with neither preference nor avoidance.

## Results

In only one of the 120 point-transect quadrants did we fail to identify a point-quarter tree (because none of sufficient size occurred within 15 m of the point); therefore our random sample of trees to estimate host-tree availability and to characterize species composition of the hammock consisted of 119. Twelve species of trees were included among these, which accounts for

nearly all of the tree-sized woody species that occur on the hammock, except for Black Gum. Of these 119 trees, 19 were pines and 85 belonged to genera that were found to be host trees in this study. The latter formed the pool of available hosts and, by the criteria for inclusion, included 1 tree —of a species (*Q. hemisphaerica* Bartr. ex Willd. [Darlington Oak]) that did not serve as a host tree. Aside from the 2 pines, American Holly ( $n = 14$ ; mean DBH = 10.1 cm) was the only other species that had substantial representation in the point transects, but was not included in the pool of available hosts.

By stem count, Water Oak was the most abundant tree along the survey transects, followed by Pignut Hickory (Fig. 1a). Live Oak and Southern

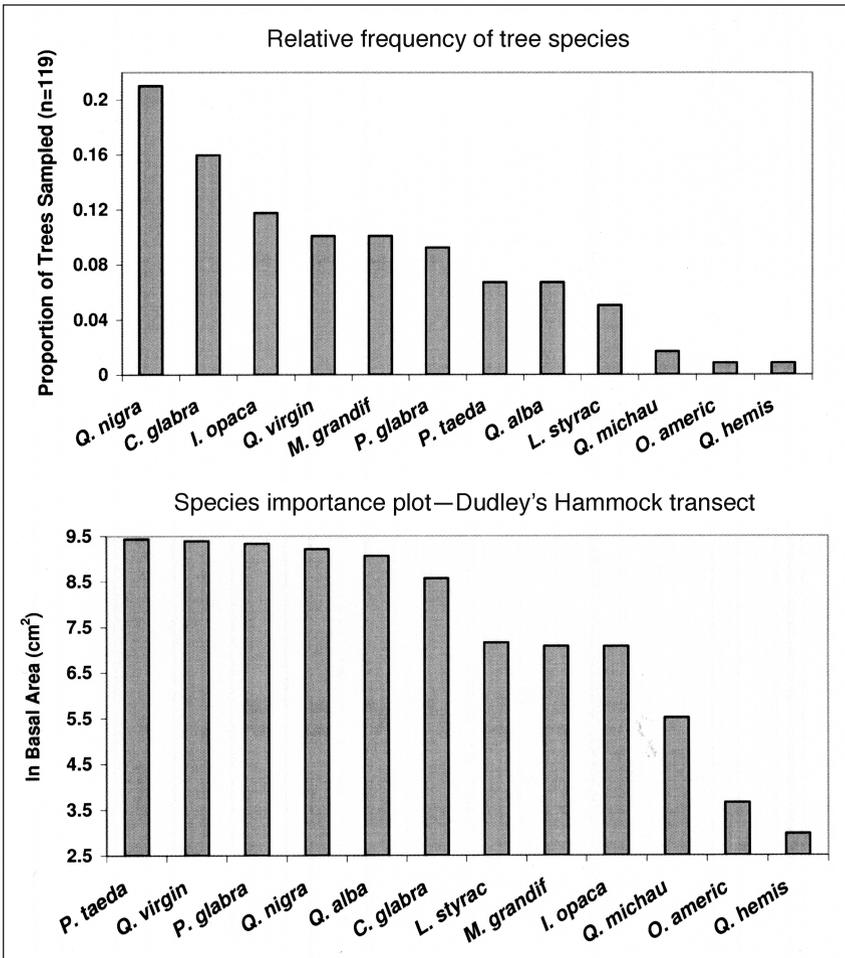


Figure 1. a (top): Most abundant tree species on Dudley’s Hammock by stem count, based on 119 point-transect trees. b (bottom): Species importance plot for Dudley’s Hammock trees based on ln basal area of 119 point-transect trees. See Methods for more details.

Magnolia were 4<sup>th</sup> and 5<sup>th</sup> most abundant, respectively. By ln basal area, a top tier of dominant species was apparent, including both pine species, three oaks (Live Oak, Water Oak, and White Oak), and Pignut Hickory (Fig. 1b). Sweetgum, Southern Magnolia, and American Holly formed a second tier of subdominant species (Fig. 1b).

The orchid survey identified 112 host trees of 8 species; 60 (54%) of these were Southern Magnolia, 35 (31%) were Live Oak, 7 (6.2%) were Sweetgum, 3 each (2.7%) were Pignut Hickory and White Oak, 2 (1.8%) were Swamp Chestnut Oak, and 1 each (0.9%) was Water Oak and Black Gum. Three of the host trees had recently died (2 Southern Magnolia, 1 Swamp Chestnut Oak).

Both SI indices indicated that Green Fly Orchid showed a strong preference for Southern Magnolia as a host and a moderately strong preference for Live Oak, but the difference between these two preferred hosts and the strength of selectivity for Southern Magnolia were greater for the SI<sub>B</sub> (Table 1). SI<sub>S</sub> indicated that Sweetgum and Swamp Chestnut Oak were nearly random with respect to selection by the epiphyte and that the remaining 4 species were strongly avoided (Black Gum is not included here, because 1 tree served as a host, but 0 trees were found on the point-quarter survey). A similar pattern was shown for these 4 less-preferred host trees by the SI<sub>B</sub>, except none was as close to random (all were avoided to some degree).

Host trees were much larger than available trees, being nearly twice the DBH for the entire sample, three times the DBH for Southern Magnolia, and 67% larger for Live Oak; there was no size difference between host and available trees for Sweetgum (Table 2). Among the 3 most common host trees, Green Fly Orchid covered a significantly larger area per host tree on Southern Magnolia (mean = 11.61 cm<sup>2</sup>,  $F_{2,99} = 8.71$ ,  $P < 0.0001$ ) than on the other two hosts. The range of mean heights above ground where orchid colonies grew was also significantly greater (mean = 5.52 m,  $F_{2,99} = 13.74$ ,  $P < 0.001$ ), and the minimum mean-height was significantly lower (mean = 4.37 m,  $F_{2,99} = 9.30$ ,  $P < 0.001$ ) for Southern Magnolia than for the other two hosts.

Table 1. Selectivity indices (SI) based on relative frequencies of occurrence (SI<sub>S</sub>) and relative basal areas (SI<sub>B</sub>) for the 8 Dudley's Hammock tree species that hosted *Epidendrum magnoliae* (Green Fly Orchid). SI ranges from -1.0 for perfect avoidance to 1.0 for perfect selection, with SI = 0.0 signifying neutral or random selection. Note: *N. sylvatica* was not encountered as a potentially available host tree on the point-transect survey. See Methods for more details.

| Host-tree species                               | <i>n</i> | SI <sub>S</sub> | SI <sub>B</sub> |
|---|----------|-----------------|-----------------|
| <i>Magnolia grandiflora</i> (Southern Magnolia) | 60       | 0.583           | 0.863           |
| <i>Quercus virginiana</i> (Live Oak)            | 35       | 0.378           | 0.275           |
| <i>Liquidambar styraciflua</i> (Sweetgum)       | 7        | -0.061          | -0.678          |
| <i>Carya glabra</i> (Pignut Hickory)            | 3        | -0.786          | -0.942          |
| <i>Quercus alba</i> (White Oak)                 | 3        | -0.557          | -0.961          |
| <i>Quercus michauxii</i> (Swamp Chesnut Oak)    | 2        | -0.136          | -0.232          |
| <i>Quercus nigra</i> (Water Oak)                | 1        | -0.941          | -0.883          |
| <i>Nyssa sylvatica</i> (Black Gum)              | 1        | n/a             | n/a             |

## Discussion

From our survey, Dudley's Hammock can be characterized as a pine-oak-hickory dominated forest, with Southern Magnolia, Sweetgum and American Holly as subdominants. Excepting American Beech, most of the elements of the climax forest overstory of the southern mixed hardwood forest (*sensu* Quarterman and Keever 1962) were present, but the co-dominance of Loblolly Pine and Water Oak may indicate some recent disturbance, which means the hammock is in a subclimax state at present. Nevertheless, it is a densely shaded and humid microclimate with abundant growth of epiphytes and as such provides one of the few habitats in the region for Green Fly Orchid.

Although occurring on 8 different hardwood tree species in Dudley's Hammock, Green Fly Orchid had a very strong preference for Southern Magnolia as a host and a moderately strong preference for Live Oak. The strong host preferences yet lack of strict phorophyte specificity of Green Fly Orchid observed at Dudley's Hammock is not surprising given earlier reports of this species (Correll 1950) and other epiphytic orchids (Zimmerman and Olmsted 1992) occurring on a range of host species. Laube and Zotz (2006) showed the distribution of 103 vascular epiphyte species in a lowland tropical forest to be neither host-specific nor random.

At Dudley's Hammock, both Loblolly Pine and Spruce Pine have high importance values (Fig. 2) and bark with markedly different physical characteristics. The bark of Spruce Pine is distinctively ridged and furrowed and perhaps structurally more similar to Live Oak than to its congener

Table 2. Comparison of mean tree sizes (DBH in cm) of tree species hosting *Epidendrum magnoliae* (Green Fly Orchid) ( $n \geq 3$ ) and the pool of "available" trees from the point transect. See Methods for more details.

| Species   | <i>n</i> | Mean DBH | S.D. | <i>t</i> | <i>P</i> |
|---|----------|----------|------|----------|----------|
| All Hosts                                       | 112      | 39.8     | 13.0 |          |          |
| All Available                                   | 85       | 20.3     | 18.8 | 8.59     | <0.0001  |
| <i>Magnolia grandiflora</i> (Southern Magnolia) |          |          |      |          |          |
| Host  | 60       | 37.7     | 9.8  |          |          |
| Available                                       | 12       | 10.6     | 4.0  | 15.84    | <0.0001  |
| <i>Quercus virginiana</i> (Live Oak)            |          |          |      |          |          |
| Host  | 35       | 53.9     | 22.1 |          |          |
| Available                                       | 12       | 32.2     | 16.0 | 3.65     | 0.0012   |
| <i>Liquidambar styraciflua</i> (Sweetgum)       |          |          |      |          |          |
| Host  | 7        | 13.6     | 3.8  |          |          |
| Available                                       | 6        | 14.5     | 6.7  | -0.32    | 0.82     |
| <i>Carya glabra</i> (Pignut Hickory)            |          |          |      |          |          |
| Host  | 3        | 17.2     | 0.72 |          |          |
| Available                                       | 19       | 16.8     | 8.82 | 0.23     | 0.82     |
| <i>Quercus alba</i> (White Oak)                 |          |          |      |          |          |
| Host  | 3        | 17.0     | 6.7  |          |          |
| Available                                       | 8        | 33.7     | 16.4 | -2.39    | 0.044    |

Loblolly Pine. However, Green Fly Orchid is absent from both species. Presumably, chemical incompatibility between epiphyte and phorophyte accounts for the complete absence of Green Fly Orchid from Loblolly Pine and Spruce Pine. Laboratory studies have shown chemical attributes of bark may affect germination and early development by epiphytic orchids (Frei and Dodson 1972).

Southern Magnolia and Live Oak have very different bark characteristics, growth habits, and patterns of branching and leaf abscission. The low, broad crown of Live Oak with its massive spreading branches presents a greater horizontal (or near-horizontal) surface for colonization by epiphytes than Southern Magnolia with its more upright habit, more cylindrical form, and absence of massive spreading branches. The bark of Live Oak is thick and rough with prominent ridges and furrows, whereas that of Southern Magnolia is smooth and relatively thin. It is presumed that bark development in Southern Magnolia is slower than in Live Oak and that diminished exfoliation would result in reduced shedding and thus greater persistence of epiphytes. The predominance of Green Fly Orchid on phorophytes with such markedly different physical bark characteristics suggests other factors more strongly influence host selection. Unlike the other, less-preferred phorophyte species observed, both Southern Magnolia and Live Oak have a dense evergreen canopy that would provide deep shade and decrease evaporative water loss year-round, including winter when ambient humidity is lower.

Southern Magnolia and Live Oak differ in their patterns of leaf abscission. Southern Magnolia is distinctly evergreen, and Live Oak is barely evergreen with its leaves gradually falling during late winter, especially just prior to the initiation of new growth in early spring. The absence of full-canopy protection in Live Oak could make Green Fly Orchid more vulnerable to desiccation and frost effects during late winter and early spring. This lack of canopy protection may be partly compensated, as we observed, by orchid colonies often growing under the horizontal limbs of large live oaks. Inland populations of Green Fly Orchid near the northern limit of its range are presumably all the more vulnerable to freezing temperatures, most likely making frost protection an even more critical factor at Dudley's Hammock.

Other studies have shown a positive correlation between the occurrence of vascular epiphyte species and large host-tree size, presumably resulting from greater available surface area and longer time for colonization provided by larger, older phorophytes (Catling and Lefkovitch 1989, Clement et al. 2001, Dunn 2000, Migenis and Ackerman 1993, Muñoz et al. 2003). Given that no host trees were encountered among the 119 randomly chosen point-quarter trees and that host trees were much larger than the average for those randomly encountered, it was also apparent that Green Fly Orchid generally selected (and/or persisted on) only the largest host trees. Thus, the largest and oldest Southern Magnolia and Live Oak trees are vital to this population of Green Fly Orchid. A study of diversity and host-tree preference in a

temperate rainforest in southern Chile suggests combinations of particular tree species and sizes promote epiphyte diversity (Muñoz et al. 2003). While the vascular epiphyte diversity, actual and potential, for Dudley's Hammock is much lower than reported by Muñoz et al. (2003), the results of our study nevertheless suggest habitat with a mixture of mature trees of Southern Magnolia and Live Oak is essential for the conservation of large, viable populations of Green Fly Orchid.

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