The genus *Ficus* contains diverse growth forms, including free-standing trees, shrubs, epiphytes, and hemiepiphytes (Putz and Holbrook, 1989). The latter two habits are distinct in requiring that seeds germinate above ground level, using another tree for support. While epiphytes exploit a host tree for support throughout their life, hemiepiphytes eventually establish a connection with the soil, requiring host support only early in life history (Putz and Holbrook, 1986). The question arises as to what conditions provided by host trees are critical to early stages of hemiepiphytic life, but not to terrestrial adults.

Seeds of hemiepiphytic *Ficus* are deposited by frugivores in humus-filled cavities on potential host trees. Seedlings produce roots that adhere to the host’s trunk, growing into nutrient-filled crevices on the host tree (Putz and Holbrook, 1989), and down to the soil (Ramirez, 1977). As the sapling grows, its roots fuse into a cylindrical pseudo-trunk around the host stem, earning these hemiepiphytes the popular designation of “strangler” figs. They may grow so vigorously as to kill their host by girdling or shading it out (Ramirez, 1977).

Despite their aggressive growth habit, strangler figs occur only sporadically in the field. Putz and Holbrook (1989) noted that palm trees were the most common hosts for stranglers at their Venezuela field site. In Israel, Galil and Meiri (1981) found the most common host to be date palms. The trend is even more pronounced in the field. Putz and Holbrook (1989) noted that palm trees were the most common hosts for stranglers at their Venezuela field site. In Israel, Galil and Meiri (1981) also concluded that climatic rather than biotic factors were more important determinants of strangler fig distribution, and Titus, Holbrook, and Putz (1990) suggested that *Ficus* germination requires high humidity. In the present study we quantify the water relations required for seeds of the strangler *Ficus aurea* to germinate.

Minimum values of substrate water potentials required for germination of crops are well documented (Hillel, 1972; Fitter and Hay, 1987), but few studies have been extended to less commercial species (Choinski and Tuohey, 1991). Aside from orchids, bromeliads, and some mistletoes, epiphytic seed physiology has received little attention (Benzing, 1990). Germination and seedling establishment often determine species distribution (Stebbins, 1974), making it likely that palm crowns confer some benefit to strangler figs during early stages, which is not required by terrestrial adults.

In this study we subjected strangler fig seeds to solutions of various water potentials, testing the extent to which germination is sensitive to water availability. By quantifying the range of water potentials that permit germination, we compare *Ficus* germination requirements to field site in the Bahamas. Here, palms are the only host for stranglers despite the presence of *Lysiloma, Colubrina, Peltophorum*, and other large trees along with considerable open soil scattered with fig fruits and seeds. Given the aggressive growth habit and ample seed dispersal of stranglers, their targeting of few hosts has been difficult to explain (Corner, 1952). Putz and Holbrook (1989) found the humus that collects in palm leaf bases to be higher in nutrients and organic matter than was soil from their field site, but concluded that nutrients had less effect on fig distribution than did moisture availability. Galil and Meiri (1981) also concluded that climatic rather than biotic factors were more important determinants of strangler fig distribution, and Titus, Holbrook, and Putz (1990) suggested that *Ficus* germination requires high humidity. In the present study we quantify the water relations required for seeds of the strangler *Ficus aurea* to germinate.

Minimum values of substrate water potentials required for germination of crops are well documented (Hillel, 1972; Fitter and Hay, 1987), but few studies have been extended to less commercial species (Choinski and Tuohey, 1991). Aside from orchids, bromeliads, and some mistletoes, epiphytic seed physiology has received little attention (Benzing, 1990). Germination and seedling establishment often determine species distribution (Stebbins, 1974), making it likely that palm crowns confer some benefit to strangler figs during early stages, which is not required by terrestrial adults.

In this study we subjected strangler fig seeds to solutions of various water potentials, testing the extent to which germination is sensitive to water availability. By quantifying the range of water potentials that permit germination, we compare *Ficus* germination requirements to field site in the Bahamas. Here, palms are the only host for stranglers despite the presence of *Lysiloma, Colubrina, Peltophorum*, and other large trees along with considerable open soil scattered with fig fruits and seeds. Given the aggressive growth habit and ample seed dispersal of stranglers, their targeting of few hosts has been difficult to explain (Corner, 1952). Putz and Holbrook (1989) found the humus that collects in palm leaf bases to be higher in nutrients and organic matter than was soil from their field site, but concluded that nutrients had less effect on fig distribution than did moisture availability. Galil and Meiri (1981) also concluded that climatic rather than biotic factors were more important determinants of strangler fig distribution, and Titus, Holbrook, and Putz (1990) suggested that *Ficus* germination requires high humidity. In the present study we quantify the water relations required for seeds of the strangler *Ficus aurea* to germinate.

Minimum values of substrate water potentials required for germination of crops are well documented (Hillel, 1972; Fitter and Hay, 1987), but few studies have been extended to less commercial species (Choinski and Tuohey, 1991). Aside from orchids, bromeliads, and some mistletoes, epiphytic seed physiology has received little attention (Benzing, 1990). Germination and seedling establishment often determine species distribution (Stebbins, 1974), making it likely that palm crowns confer some benefit to strangler figs during early stages, which is not required by terrestrial adults.

In this study we subjected strangler fig seeds to solutions of various water potentials, testing the extent to which germination is sensitive to water availability. By quantifying the range of water potentials that permit germination, we compare *Ficus* germination requirements to field site in the Bahamas. Here, palms are the only host for stranglers despite the presence of *Lysiloma, Colubrina, Peltophorum*, and other large trees along with considerable open soil scattered with fig fruits and seeds. Given the aggressive growth habit and ample seed dispersal of stranglers, their targeting of few hosts has been difficult to explain (Corner, 1952). Putz and Holbrook (1989) found the humus that collects in palm leaf bases to be higher in nutrients and organic matter than was soil from their field site, but concluded that nutrients had less effect on fig distribution than did moisture availability. Galil and Meiri (1981) also concluded that climatic rather than biotic factors were more important determinants of strangler fig distribution, and Titus, Holbrook, and Putz (1990) suggested that *Ficus* germination requires high humidity. In the present study we quantify the water relations required for seeds of the strangler *Ficus aurea* to germinate.

Minimum values of substrate water potentials required for germination of crops are well documented (Hillel, 1972; Fitter and Hay, 1987), but few studies have been extended to less commercial species (Choinski and Tuohey, 1991). Aside from orchids, bromeliads, and some mistletoes, epiphytic seed physiology has received little attention (Benzing, 1990). Germination and seedling establishment often determine species distribution (Stebbins, 1974), making it likely that palm crowns confer some benefit to strangler figs during early stages, which is not required by terrestrial adults.
those reported for other species, and help define water relations conducive to Ficus establishment in nature.

**MATERIALS AND METHODS**

Dried fruits (syconia) from Ficus aurea were collected from two sources: a wild population in the dry tropical forest of Hummingbird Cay Tropical Field Station, 20 km west of Georgetown, Great Exuma, Bahamas, and syconia supplied by Dr. Robert Knight at the USDA-ARS Subtropical Horticulture Research Station in Miami, Florida.

**Germination**—Seeds (druplets) were removed from syconia, rinsed overnight in tap water, then placed in petri dishes on four pieces of filter paper moistened with 8 mL of D-mannitol (M 4125, Sigma Chemical Co., St. Louis, MO) solution. Osmotic agents such as polyethylene glycol (PEG) and sugar alcohols are metabolically inert in most seed plants (Salisbury and Ross, 1992). They are used to establish defined water potential gradients between plant material and the surrounding liquid medium. Laboratory-based estimates of germination in osmotic solutions closely agree with germination estimates derived under field conditions (Hadas, 1977). In preliminary work we discovered that low concentrations of PEG 400 and PEG 1000 are toxic to germinating Ficus seeds, despite the effectiveness of intermediate molecular-mass PEG as an osmotic agent in other systems (Zhang and Kirkham, 1995). As an alternative, using mannitol avoids PEG toxicity (Collier and Cummins, 1993), allowing developing and germinating seeds to be exposed to the osmotic agent for days or weeks (Georghiou, Thanos, and Passam, 1987; Egli, 1990; Wolswinkel, Ammerlaan, and Koerselman-Kooij, 1992). In our germination tests, we minimized the potential for mannitol-supported microbial growth by thoroughly rinsing pulp from seeds, and by imbibing seeds in solutions of mannitol alone, without hydroponic salts.

Only plump cream-colored seeds were used since these had the highest germination percentage. Control seeds were germinated on filter paper moistened with deionized water and enclosed in petri dishes. Mannitol concentrations were varied (0.04, 0.1, 0.2, 0.4, 0.6, and 0.8 mol/L) to generate substrate water potentials of −0.1, −0.25, −0.50, −1.0, −1.5, and −2.0 MPa. The effect of solutes upon water potentials (Ψ) was calculated based on the expression:

\[ Ψ = -RTC \]

where \( R \) is the ideal gas constant, \( T \) the absolute temperature, and \( C_s \) the osmolarity of the solution (Taiz and Zeiger, 1991). For compounds with a dissociation coefficient of 1 such as mannitol, sucrose, and polyethylene glycol, a 1 mol/L solution generates a \( Ψ \) of −2.5 MPa under the conditions used in this study.

Each petri dish contained 50 seeds. Four dishes of seeds were tested at each of seven water potentials (six generated by mannitol concentrations, plus one deionized water control). Dishes were weighed, sealed with parafilm, and placed upside-down on a heating pad maintained at 27°C ± 2°C. Seeds were inspected daily for germination, indicated by emergence of the radicle. Every 3rd d, dishes were weighed, and any mass lost to evaporation was replaced by adding distilled water (0–0.6 mL). Observations ended after 6 wk, by which point no new germination had occurred within 10 d.

Viability of hydrated seeds was tested by tetrazolium assay (Moore, 1973). Hydrated seeds were cut in half. One-half of each seed was soaked in 0.1% aqueous solution of 2,3,5-triphenyltetrazolium chloride (T 8877, Sigma Chemical Co., St. Louis, MO) in darkness for 18 h, then inspected under a dissecting scope for deep pink color as a positive stain for metabolic activity (reduction through the respiratory chain) in the embryo. To control against false positives by nonmetabolic reducing agents, some seeds were killed by autoclaving prior to being hydrated, exposed to tetrazolium, and examined for color.

**Seedling growth**—Six days after germinating, sample seedlings from each treatment were measured for total length and for radicle length.

Samples were then cleared in lactic acid at 60°C for 1 wk, then stained with acid fuchsin and malachite green (Alexander, 1980) to measure cell lengths along the root-hypocotyl axis under the microscope using a calibrated ocular micrometer.

**Field conditions**—Temperature measurements were taken of ambient air, humus in palm leaf bases, and of open soil in the palm groves at our Bahamas field site, over a 10-d period in mid-March. To determine moisture content of available germination substrates, samples from the surface (<3 cm deep) of open soil and of humic material in palm leaf bases were collected and stored in plastic bags. Portions weighing 25 g were dried for 48 h at 80°C, then reweighed. Moisture content (in percentage water by dry mass) was calculated based on: %H₂O = [fresh mass - dry mass]/dry mass. Moisture loss over time was studied by saturating samples of each substrate, and allowing them to drain to field capacity, at which point samples were weighed. Samples at field capacity were then dried at 80°C and reweighed periodically over 2 d to monitor the progressive decrease in mass (due to water loss) with time.

Mineral nutrient content in leaf base humus was compared to that of open soil by digesting 2-g samples of dried material in 40% HNO₃, and testing for P, K, and Ca by dc plasma atomic emission spectrometry run by Applied Research Laboratories (Lowell, MA). Nitrogen was determined on dry undigested samples run through a Leco N analyzer that combusted each sample and determined N as NO₃ by gas chromatography.

**RESULTS**

Three kinds of flowers occur in each syconium (fig), only a fraction of which will set viable seed (Purseglove, 1968). Of 194 rinsed F. aurea seeds tested in tetrazolium solution, 87% (45%) stained positive for metabolic activity. Active seeds are plump and cream-colored instead of tan or brown. Upon rinsing figs overnight we selected plump cream-colored seeds for germination experiments.

**Germination**—Fifty seeds were in each petri plate supplied with deionized water or one of six mannitol solutions (from 0.0 to −2.0 MPa). Four replicates of each treatment were run, providing a total of 200 seeds exposed to each of seven water potentials (Fig. 1). Potential viability of plump cream-colored seeds remains near 100% for 6 mo after syconia are air dried and stored at room temperature. In prolonged room temperature storage, viability declines to virtually zero after 2 yr. Our experiments were performed on seeds <6 mo old. Pre-
liminary tests of temperature tolerance in the range of 15°–45°C showed germination percentage to be highest at 25°–30°C. At temperatures sustained above 35°C, no germination occurs in Ficus aurea.

When presoaked and placed on filter paper moistened with deionized water, radicles emerge from control seeds after 6 d, and the plumule appears 2–3 d later. Timing of these events varied slightly in the 50-seed population of each petri dish, but 95.5% of all control seeds germinated within 3 wk (Fig. 2). Germination percentage declined with decreasing ambient water potential, and was almost completely suppressed at −1.5 MPa (Fig. 1). Compared to control seeds in deionized water, significant declines in germination percentage occur in seeds at −0.5 MPa (P ≤ 0.01), −1.0, −1.5, and −2.0 MPa (all P ≤ 0.001). Seeds of F. aurea are osmotically stressed at these lower water potentials. Germination occurs to a lesser extent germination occurs in Ficus aurea.

In control seeds, germination first appears after 6 d, then within two more days than half the seed germinates. In contrast, seeds in −1.0 MPa or lower take twice as long to begin germinating, and five times longer (11 more days) to reach 50% of the final germination percentage.

At the end of 6-wk germination trials, five seeds were removed from each of the inhibitory (−1.0 MPa and lower) treatments, and subsequently placed on filter paper soaked in deionized water, to test their capacity to germinate after having experienced water stress. Seeds that failed to germinate at low Ψ are able to subsequently sprout when transferred to deionized water. Eighty-five percent (17/20) of ungerminated seeds sampled from −1.0 MPa sprouted within 2 wk of being in deionized water, and 100% of seeds previously exposed to −1.5 or −2.0 MPa germinated, despite the failure of these same individuals to germinate at the lower (more negative) Ψ.

Seedling growth—Where available (down to −1.0 MPa) 6-d-old seedlings were measured along their axis to determine those sectors most sensitive to water stress. Measurements at the cell level were taken from at least three cleared and stained seedlings in each treatment, and at least 15 cells of the root-hypotyl axis were measured from each cleared seedling. Seedlings are significantly (P ≤ 0.01) shorter than controls when germinating in progressively more negative Ψ (Table 1). Significant differences from controls sprouting in water already appear in seedlings growing at −0.1 MPa. Differences increase in seedlings growing in progressively lower Ψ. Paralleling that, radicle length and cell length both decrease significantly from control levels, in seedlings growing in each negative Ψ tested. Length of the entire seedling axis is strongly correlated to both radicle length (0.964) and cell length (0.945).

Field conditions—Hummingbird Cay Tropical Field Station is located on a remote out-island in the Bahamas at 23° north latitude in the Exuma archipelago. The island covers 250 ha and is supplied by sporadic rainfall averaging 75 cm/yr. Tropical dry sclerophyllous forest dominates the vegetation. Palm (Sabal palmetto) groves occur in flat areas with dark soil composed of weathered oolitic marl and organic matter. Palm groves are the only areas on the island that support strangler figs. Field observations show that hundreds of syconia and seeds are spread throughout the open soil either by birds or by falling from Ficus branches above. Figs were collected from open soil are viable; they germinate within days of being soaked in water. Despite viable seeds being present in well-illuminated open soil, Ficus establishment is restricted to leaf bases of palm crowns where seeds are probably left by birds.

Both the palm leaf base and the open soil represent potential germination sites for Ficus, but their microenvironments differ substantially. Temperature in palm leaf bases is fairly constant throughout the day, ranging between 25° and 30°C (Fig. 3). In contrast, temperature of the open soil fluctuates dramatically, reaching well over 50°C by midafternoon as sunlight warms the dark surface. Humic substrate in each potential germination site also differs in moisture-holding properties. Material collected from palm leaf bases in mid-March contained 15.5% water by dry mass, while moisture content of open soil was only 6.7%. Differences are also apparent in field capacity. Leaf base material holds over four times (400%) its dry mass in water at field capacity, while material from open soil retains water equal (100%) to its dry mass (Fig. 4). Leaf base material is looser and less dense than is open soil, with the result that leaf base material loses water faster. Nevertheless leaf base material takes longer to dry from field capacity, since it holds four times more water than does open soil to begin with. After being soaked to field capacity and then held at 80°C, open soil.

Table 1. Length of seedling, radicle, and of epidermal cells in F. aurea germinated and grown for 6 wk at the Ψ indicated. Values represent the mean ± 2 SE.

<table>
<thead>
<tr>
<th>Ψ (MPa)</th>
<th>Seedling length (mm)</th>
<th>Radicle length (mm)</th>
<th>Cell length (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0</td>
<td>22.6 ± 2.1</td>
<td>11.5 ± 1.9</td>
<td>115.7 ± 9.4</td>
</tr>
<tr>
<td>−0.1</td>
<td>17.1 ± 1.9</td>
<td>8.3 ± 0.9</td>
<td>99.8 ± 8.1</td>
</tr>
<tr>
<td>−0.25</td>
<td>16.5 ± 1.4</td>
<td>7.5 ± 0.9</td>
<td>96.0 ± 8.5</td>
</tr>
<tr>
<td>−0.5</td>
<td>9.5 ± 1.7</td>
<td>4.2 ± 0.6</td>
<td>80.3 ± 12.4</td>
</tr>
<tr>
<td>−1.0</td>
<td>3.7 ± 0.5</td>
<td>3.7 ± 0.5</td>
<td>22.3 ± 3.0</td>
</tr>
</tbody>
</table>

Fig. 2. Cumulative distributions of strangler fig germinations over time for seeds imbibed at the Ψ indicated.
May 1997] 719
SWAGEL ET AL.—GERMINATION IN Ficus

Fig. 3. Temperature fluctuations over the course of a sunlit day in mid-March at Hummingbird Cay, Bahamas. Readings were taken from the top centimetre of exposed soil, from palm leaf base humus, and from open air (in shade). Temperatures sustained above 35°C prevent germination.

Fig. 4. Rate of moisture loss from palm leaf base mulch and from open soil material as both substrates are dried at 80°C.

Table 2. Nutrient content of humic material collected from palm (Sabal palmetto) leaf bases, and from the top 3 cm of open palm grove soil at Hummingbird Cay, Bahamas. Values represent mean of three measurements. Standard deviations never exceeded 2% of the mean.

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>Leaf base</th>
<th>Open soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>% N</td>
<td>1.79</td>
<td>2.30</td>
</tr>
<tr>
<td>P</td>
<td>1.4</td>
<td>5.9</td>
</tr>
<tr>
<td>K</td>
<td>2.6</td>
<td>7.3</td>
</tr>
<tr>
<td>Ca</td>
<td>3.1</td>
<td>21</td>
</tr>
</tbody>
</table>

DISCUSSION

Our results support the hypothesis that strangler fig germination is highly sensitive to substrate water potential. In the tropical dry forest characterizing the vegetation at Hummingbird Cay and much of the Bahamas, water potentials that favor Ficus germination and seedling growth are found more consistently in palm leaf base humus than in open terrestrial soil. Substrate Ψ at germination and seedling establishment phases of Ficus life history plays a pivotal role in restricting the habitat of strangler figs to the palm groves of tropical dry forest.

At increased levels of water stress, fewer seeds germinate (Fig. 1), and those that do take more time to emerge (Fig. 2) compared to control seeds germinated in water. Dramatic delays in germination and declines in germination percentage appear at substrate Ψ of −1.0 MPa or lower, suggesting a threshold level of water stress beyond which Ficus germination is affected adversely. In substrate Ψ of −1.5 MPa, germination is impossible for >95% of strangler fig seeds. In nature, seeds falling on substrates with a Ψ < −1.2 MPa have little chance of establishing seedlings. If germination occurs at all, seedling growth would be very slow, placing individuals at high risk to attack by soil pathogens, predation by herbivores, and death during rapid drying of the substrate (Finch-Savage and Phelps, 1993). As in mesophytes such as onion, Ficus seeds appear least tolerant to dessication during radical emergence.

Growth of young Ficus seedlings is more sensitive to water shortage than is germination. Significant decreases in seedling growth are first seen when Ψ is as high as −0.1 MPa (Table 1), while germination requires −0.5 MPa to begin slowing (Fig. 2). In general, rapid growth of emergent seedlings depends on enlargement of cells already present, but unexpanded in the embryo. As cells of the radicle expand, the emergent seedling extends its first root away from the dry soil surface, into deeper layers that provide constant moisture. In F. aurea, elongation of the root-hypocotyl axis shows a 1.000 correlation to cell length (Table 2). The decline in seedling length found at water potentials from 0.0 to −0.5 MPa can be completely accounted for by inhibition of cell elongation. This would be predicted if substrate Ψ influences seedling growth by altering cell expansion. Under more severe water stress (Ψ ≤ −1.0 MPa), both cell expansion and proliferation apparently are affected, since decrease in cell size alone is insufficient to account for seedling stunting. As reported in other species, effects of severe water stress are reversible unlike toxic effects from external solutes (Greipsson and Davy, 1994). F. aurea seeds and seedlings recover when transferred from Ψ as low as −2.0 MPa to deionized water.

In the field, reduced growth of the root-hypocotyl axis in fig seedlings profoundly affects the ability of these trees to establish themselves. A short radicle reduces access to reliable moisture deep in the substrate, and reduced shoots burden seedlings with limited access to light. Our work suggests that a microenvironment with substrate Ψ of −1.0 MPa or greater is needed to provide...
Comparison of Substrate $\Psi$ Inhibitory to Seed Germination

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buffalo grass</td>
<td>0 MPa</td>
</tr>
<tr>
<td>Sugar beet</td>
<td>-0.5 MPa</td>
</tr>
<tr>
<td>Clover</td>
<td>1.0 MPa</td>
</tr>
<tr>
<td>Cabbage</td>
<td>1.5 MPa</td>
</tr>
<tr>
<td>Sugar beet</td>
<td>2.0 MPa</td>
</tr>
<tr>
<td>Rice (b)</td>
<td>2.5 MPa</td>
</tr>
<tr>
<td>Chickpea</td>
<td>3.0 MPa</td>
</tr>
<tr>
<td>Sorghum</td>
<td>-1.0 MPa</td>
</tr>
<tr>
<td>Winter wheat (d)</td>
<td>1.0 MPa</td>
</tr>
<tr>
<td>Alfalfa</td>
<td>0.5 MPa</td>
</tr>
<tr>
<td>Salsola kali (a)</td>
<td>-3.0 MPa</td>
</tr>
</tbody>
</table>

Fig. 5. Comparison of substrate $\Psi$ required for $F. aurea$ germination with germination requirements of other species reported in the literature.

for establishment of strangler figs, despite the ability of adult stranglers to tolerate drier conditions.

We were surprised to discover a native of dry sclerophyllous forest to be so sensitive to desiccation, predicting instead that seedlings of $F. aurea$ would tolerate strongly negative $\Psi$. The $\Psi$ needed for $F. aurea$ germination and seedling growth (-1.0 to -1.2 MPa), is similar to that required of many mesophytic crops, including tomato, sunflower, and corn (Fig. 5). These are irrigated to insure high germination (Hillel, 1972; Fitter and Hay, 1987). The threshold value (highest $\Psi$ that permits $\geq 50\%$ germination) for $F. aurea$ in nature may be lower than we report here. In our experiments, we soaked seeds in mannitol to arrive at a $\Psi$ value in the external medium that inhibited germination. In humus, soil, and other natural substrates there are ions that, unlike mannitol, cross cell membranes. This is especially true for seedlings actively absorbing nutrients. Salts taken up in this way could lower tissue $\Psi$ (by making osmotic potential more negative), ease the $\Psi$ gradient between tissue and substrate, and allow germination and early growth to proceed at lower substrate $\Psi$ than we determined from mannitol experiments. Our data are useful in allowing comparison of $F. aurea$ germination requirements to those of other species determined under defined laboratory conditions similar to ours (Fig. 5). While mannitol-based threshold values might shift for all species under field conditions, we expect the sensitivity of each species relative to the others to remain constant. Regardless of the numerical value for $\Psi$ that inhibits $F. aurea$ germination in the field, it will be very near the threshold value for cabbage, corn, alfalfa, and a host of other mesophytic crops (Fig. 5).

The seedling phase of $F. aurea$ appears to escape desiccation rather than tolerate it. Like seeds of perennial ryegrass (Allen, White, and Markhart, 1993), those of $F. aurea$ lack innate dormancy and do not form a persistent seed bank. Germinating at or near the soil surface puts seeds at high risk of desiccation as soil dries between the onset of seed hydration and the moisture-sensitive rate limiting step of radical emergence (Finch-Savage and Phelps, 1993). Given that $F. aurea$ seeds can germinate after being interrupted with several weeks at $-2.0$ MPa, it may be that germination in the field requires a total of 10 d at $\geq -1.0$ MPa, regardless of the number of interruptions by hydration-dehydration cycles. Seeds of Lolium perenne need a total of 2 d in water to germinate, but the process can be interrupted reversibly by $\Psi$ from -4 to -10 MPa (Allen, White, and Markhart, 1993).

How does the desiccation sensitivity of $F. aurea$ seedlings relate to conditions faced by fig seeds in the field? At Hummingbird Cay Tropical Field Station, fig seeds occur throughout the palm groves, but more than a decade of observation has failed to find $F. aurea$ seedlings or saplings on the ground. Seeds on the ground are viable; collected from the dried fruit, they germinate readily in the laboratory. Passing through an animal’s digestive system is not a requirement for germination. Nevertheless, in the dry sclerophyllous forest seeds on the ground do not grow. Instead, $F. aurea$ saplings are restricted to leaf bases in palm crowns.

Temperature- and moisture-related factors promote germination and establishment in the humic material of palm leaf bases over that on open soil. Temperature of the germination substrate in leaf bases holds constant, in the $25\text{°}-30\text{°}$C range (Fig. 3), optimum for $F. aurea$ germination. Temperature is probably moderated by shading and evaporative cooling through transpiration from large palm fronds. Humic substrate is constantly moist. We have collected it in both the wet and dry seasons. Moisture content is consistently 15–16% by mass, translating to a $\Psi$ of $\geq -1.0$ to $-1.1$ MPa, following Hunter and Erickson’s (1952) relationship between substrate moisture percentage and its $\Psi$. In the field, moisture collects in leaf base humus from rain runoff (Raich, 1983). During long intervals between rains, water vapor may leak into deep recesses of leaf bases from the parenchymatous palm stem. The thick stem, composed mostly of turgid parenchyma, represents a substantial water reservoir collected by palms during the wet season (Holbrook and Sinclair, 1992) and used conservatively during dry months. Field observations show strongly developed root masses of $F. aurea$ firmly embedded around old leaf bases and wedged in fissures of palm bark. Despite careful and repeated efforts to remove individual Ficus roots from palm bark and old leaf bases, we were unable to dislodge root tips without breakage. The intimate connection between Ficus root and palm stem may be hydraulic rather than simply mechanical. Evidence for water leakage from palm stem to Ficus root awaits work with isotopes or tracer dyes delivered to palm stems and sub-
sequently sought in roots of epiphytic stranglers. Alternatively, magnetic resonance imaging (MRI) might resolve connections between *Ficus* roots and ground or vascular tissue in palm stems.

Regardless of the source, moisture reaching the humic substrate in leaf bases is retained. Palm leaf base humus potentially holds four times as much water as does open soil, and it retains moisture longer (Fig. 4). In the field, leaf base humus is never exposed to dry out. Instead, trapped humus provides a favorable microhabitat with only slight fluctuations in temperature and moisture. In contrast, open soil presents strong impediments to germination including high surface temperatures that completely inhibit germination (Fig. 3), and a substrate quick to dry down to <7% moisture content (Fig. 4), translating to Ψ below −2.0 MPa (Hunter and Erickson, 1952).

Of the two substrates we studied for *F. aurea* germination at our field site, only humus in palm leaf bases maintains a high enough Ψ to allow seedling establishment under field conditions. The occurrence of strangler fig in the dry forest at all is due to availability of moist microhabitat, rather than xerophytic adaptations in seed germination physiology.

Nutrient levels have been implicated as a feature determining host preference by strangling figs in the seasonal savanna of Venezuela (Putz and Holbrook, 1989). At Hummingbird Cay, nutrient levels in leaf base humus and in open soil (Table 2) are similar to those of other depauperate substrates in the tropics, including those reported by Putz and Holbrook (1989). However at our site, nutrient concentration in leaf base humus was one-third or less of that in open soil (Table 2). Enhanced availability of nutrients and of light provided by the open soil is not enough to support *F. aurea* germination and establishment in that substrate. Instead, our results show *F. aurea* to require uniquely sheltered areas with substrate protected from evaporation and high temperatures. Perhaps because rainfall is roughly half that of in the llanos, there are fewer microhabitats that provide moist substrates for enough time to allow seedling establishment. In the sclerophyllous forest of the Bahamas, the condition of sustained moisture (substrate Ψ of ≥−1.2 MPa) is met in humus of palm leaf bases, making palm crowns a “micro-oasis” for establishment of strangler figs. Given the importance of sustained substrate moisture to early growth of strangler figs, it is not surprising that the variety of germination sites increases in progressively wetter climates (Lodge, 1994), resulting in more widespread occurrence of strangers there.


**ANNOUNCEMENT**

The *American Journal of Botany* encourages authors of Invited Special Papers to submit one color plate per article, which will be paid for by the journal. Final selection, based on merit and suitability, of a color plate will be made by the Editor-in-Chief.