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IMPACT OF FLOODING ON *ANNONA* SPECIES

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Abstract. **Trees of 11 different seedling and grafted *Annona* spp. trees were screened for flood tolerance by subjecting them to 50 days of continuous flooding in a glasshouse. Scions of '49-11' ('Gefner' atemoya × *A. reticulata*), *A. reticulata* L. (bullock's heart), and 'Gefner' atemoya (*A. cherimola* ×× *A. squamosa*) tolerated flooding when grafted onto *A. glabra* (pond apple) rootstock. Seedlings and rootstocks of *A. reticulata* and *A. squamosa* (sugar apple) were intolerant to flooding (as evidenced by reduced leaf gas exchange and tree growth, and tree mortality), whereas *A. glabra* and *A. muricata* (soursop) seedlings were very tolerant. In a continuation of this trial, *A. glabra* and *A. muricata* seedlings, and '49-11' grafted onto *A. glabra* survived 12-months of continuous flooding. The results suggest that flood-tolerant rootstocks may enable *Annona* production in areas affected by periodic waterlogging, such as those adjacent to the Everglades National Park in south Florida.**

Episodic flooding is an increasing concern in agricultural areas of south Miami-Dade County, Florida, particularly since a major ecological restoration plan in the Everglades National Park has raised water tables in the area. Most fruit trees cultivated in South Florida are susceptible to flooding. Agricultural use of areas subjected to periodic water-logging will require identification of flood-tolerant species of economic potential (Schaffer, 1997).

The *Annonaceae* family includes several fruit trees of economic importance in tropical, subtropical, and temperate areas throughout the world (Morton, 1987; Popenoe, 1920). In subtropical South Florida, sugar apple (*Annona squamosa* L.) and atemoya (*A. squamosa* L. × *A. cherimola* Mill.) are grown commercially, while soursop (*A. muricata* L.), the most tropical of the annonas, is grown occasionally as a dooryard tree.

Pond apple (*A. glabra* L.) is a non-commercial species native to tropical and subtropical wetlands of the Americas, including swamps in south Florida. It has been suggested that *A. glabra* could be used as a rootstock for flood-sensitive *Annona* species (Popenoe, 1920; Kennard and Winters, 1960). To address the need for flood-tolerant fruit trees in South Florida, a research project has been underway at the Tropical Research and Education Center (TREC) in Homestead for the past 2 years to study physiological responses of different *Annona* species to flooding, and select scion/rootstock combinations that tolerate episodic waterlogging. This paper is an overview of our main findings to date on the responses of different container-grown *Annona* seedlings and rootstock/scion combinations to controlled flooding under glasshouse conditions.

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Plant material. The *Annona* material evaluated so far consisted of seedling, grafted, and interstock grafted trees (Table 1). Scions of 'Gefner' atemoya have shown compatibility problems when grafted directly onto pond apple. The incompatibility has been overcome by using the selection '49-11' ('Gefner' atemoya × *A. reticulata*) as an interstock between pond apple and atemoya. The selection '49-11' and '4-5' were developed by Gary Zill (Zill High Performance Plants, Boynton Beach, Florida) and are still under horticultural evaluation.

Glasshouse conditions, flooding method, and measurements. Flooding trials have been conducted during the past 2 years in a glasshouse at the TREC (Núñez-Elisea et al., 1997). Average glasshouse temperatures during the trials were 26 to 35°C (day), and 23 to 30°C (night). Relative humidity ranged from 65% to 85%.

Plants were grown in 20-liter plastic containers in calcareous soil (Krome very gravelly loam soil, loamy-skeletal, carbonatic, hyperthermic Lithic Rendoll), or in a peat: hardwood: sand (40:30:30 by volume) soil mix, depending on the experiment. Plants were flooded for a period of 50 days by placing the 20-liter containers inside larger, 35-liter plastic containers and adding tap water to 5 cm above the soil surface. Water was added as needed to the 35-liter containers to replace loss by evapotranspiration. Non-flooded, control plants were irrigated daily to maintain soil moisture near container capacity.

Growth measurements recorded for flooded and non-flooded (control) trees included the percentage of budbreak, shoot growth, number of leaves and flowers, and basal trunk diameter. Leaf gas exchange measurements included net CO_2 assimilation (A), stomatal conductance (gs), and transpiration (E). One mature leaf per tree was selected for gas exchange determinations. A portable infrared gas analyzer (LCA-3, Analytical Development Co., Hoddeson, Herts., U. K.) was used as described by Larson and Schaffer (1991).

Changes in flooded soil redox potential (Eh) were recorded to detect the transition from aerobic (oxidized) to anaerobic (reduced) conditions in the plant rhizosphere. Anaerobic conditions occur at Eh ≤ 200 mV (Ponnamperuna, 1984). Soil Eh was monitored at a depth of 20 cm using platinum electrodes attached to a microvoltmeter.

Effects of continuous, long-term flooding. Sub-sets of seedlings and scion/rootstock combinations that survived the 50-day flooding period were kept flooded for up to 12 months to determine the effects of extreme waterlogging periods.

Effects of flooding on soil oxygen, plant growth, and leaf gas exchange. Flooding caused rapid anaerobiosis, with soil reaching Eh values ≤200 mV as early as 3 to 4 days after beginning the flooding treatment. Eh decreased to 79-110 mV by the 10^{th} day of flooding and stabilized at ca. -160 mV from day 20 to day 50. Thus, roots of flooded trees were deprived of oxygen for nearly the entire duration of the 50-day flooding treatment.

Plants most affected by flooding included seedlings of *A. squamosa* and *A. reticulata*, and all scion combinations using

Table 1. List of *Annona* germplasm tested for flood-tolerance under glass-house conditions in Homestead, Florida.

Seedlings	Grafted trees (scion/rootstock)	Intertock-grafted trees (scion/interstock/rootstock)
A. glabra (pond apple)	49-11[z]/*A. glabra*	*'Gefner' atemoya*[y]/*49-11*/ *A. glabra*
A. muricata (soursop)	49-11/*A. reticulata*	
A. squamosa (sugar apple)	4-5[x] /*A. squamosa*	
A. reticulata (bullock's heart)	4-5/*A. reticulata*	
	A. reticulata/*A. glabra*	
	'Gefner' atemoya/*A. squamosa*	

[z]'Gefner' atemoya × *A. reticulata*
[y]*A. cherimola* × *A. squamosa*
[x]'Priestley' atemoya × *A. reticulata*

Table 2. Chronology of flooding responses in the flood-sensitive species, *Annona reticulata* and *A. squamosa*.

Days of flooding	Symptom
<1	Net CO_2 assimilation ↓, stomatal conductance↓
2-3	Soil redox potential↓
5-8	Budbreak ↓, shoot growth ↓, leaf expansion↓
15-30	Leaf wilting and necrosis ↑, defoliation↑
30-50	Branch dieback ↑, tree death

these two species as rootstocks, particularly *A. reticulata*. As expected, *A. glabra* seedlings were highly tolerant of flooding. *A. muricata* has been reported to be adapted to areas with very high rainfall (up to 4,000 mm/yr), but not tolerant to poor drainage (Villachica, 1996). In our trials, however, container-grown *A. muricata* trees tolerated 50 days of flooding nearly as well as *A. glabra*.

A summarized chronology of flooding effects in susceptible plants is shown in Table 2. Significant reductions in leaf gas exchange (>50% of controls) were measured within 24 h of flooding. Reductions in shoot elongation, budbreak, and leaf expansion were evident after 5-8 days of flooding, probably as a result of the onset of soil anaerobiosis 3-4 days earlier. Severe damage consisting of leaf wilting and necrosis followed by defoliation, occurred by the fourth week of flooding. Irreversible damage consisting of branch dieback and tree death was observed for *A. reticulata* and *A. squamosa* 30-50 days after flooding was imposed. Branches displaying dieback did not recover upon release from flooding, while trees with necrotic and decaying main trunks died while still flooded.

Morphological adaptations of flood-tolerant material. Flooded plants often develop adaptations to survive under deprived oxygen-depleted conditions (Kozlowski, 1997; Schaffer et al., 1992). Flood-tolerant *Annona* plants included *A. glabra* and *A. muricata* seedlings, as well as the scion/rootstock combinations where *A. glabra* was used as the rootstock (scions 49-11, *A. reticulata*, and atemoya). Tolerant plants survived the 50-day flooding period without visual damage, although morphological modifications occurred during exposure to flooding (Table 3). Adaptations of *A. glabra* to flooding, either as seedlings or rootstock, included development of adventitious roots which extruded into the flood water, development of hypertrophied (swollen) lenticels on both trunk and adventitious roots and, most noticeably, a swelling of the trunk base (Fig. 1) which was attributed to the development of stem aerenchyma (Kozlowski, 1997).

Flood adaptation in *A. muricata* seedlings appears to be different than in *A. glabra*. Profuse emission of new vegetative shoots occurred at the base of the trunk (Fig. 2), but no trunk swelling or abundant hypertrophied lenticels were observed.

Table 3. Morphological adaptations to flooding in *A. glabra* and *A. muricata*. Plus signs (+) indicate relative intensity of occurrence for each species.

Morphological adaptation[z]	*A. glabra*	*A. muricata*
Hypertrophied lenticels	+ + +	+
Root extrusion into flood water	+ + +	+
Thickening of trunk base	+ + +	+
Shoot formation at trunk base	+	+ + +
Enhanced root development[zy]	+ + +	+ + +

[z]Adaptations observed in container-grown plants during a 50-day flooding period.
[y]Root growth increased after 6 months of continuous flooding

The different morphological adaptations to flooding between *A. muricata* and *A. glabra* may indicate different physiological strategies and alternate metabolic pathways for increasing oxygen uptake and eliminating anaerobic by-products.

Long-term flood tolerance. Seedlings of *A. glabra* and *A. muricata*, and grafted trees of 49-11/*A. glabra* survived 12 months of continuous flooding under glasshouse conditions. Growth rates of all trees decreased after 6 months of flooding, as evidenced by shorter internodes, reduced flushing frequency and diminished leaf size. These reductions were greater for *A. muricata* than for *A. glabra* seedlings or grafted trees. After 6 months of flooding, flooded plants had much larger root systems than non-flooded trees. We speculate that enhanced

Figure 1. Basal trunk swelling and hypertrophied lenticels on trunk of *A. glabra* (pond apple) caused by exposure to flooding, and non-flooded (control) tree (right). Photograph was taken 48 days after flooding treatment commenced.

Figure 2. Vegetative sprouting at the base of trunk in a seedling tree of *A. muricata* (soursop) as a result of exposure to 50 days of continuous flooding. Non-flooded trees produced no vegetative shoots along the base of the trunk.

root development in response to long-term flooding was an additional adaptation for increasing oxygen uptake in flooded trees.

Summary. We have shown that an *A. glabra* rootstock could allow different flood-intolerant *Annona* scions to be grown under flooded conditions. We will continue to test the graft-compatibility and flood tolerance of commercially important species and cultivars grafted onto *A. glabra.* Little is known about the graft-compatibility of *A. muricata* with other important *Annona* species, and it is unclear how trees grafted onto this species would perform in south Florida. Although cold temperatures cause defoliation of *A. muricata* and trees have been killed by freezes, roots of trees killed by freezes in south Florida have survived and sprouted to form new trees. Thus, cold-tolerant scions grafted onto *A. muricata* may tolerate both flooding and severe cold, but it is clear that more research is needed to test these assumptions.

A. glabra and *A. muricata* need to be tested as rootstocks in areas with natural flooding patterns and environmental changes. One possibility with *A. glabra* is to top-work native trees growing in swamps using scions of different *Annona* species and cultivars. It would also be advantageous to find *A. glabra* clones which are directly compatible with commercial atemoya cultivars, thus eliminating the need for an interstock and reducing plant production costs (G. Zill, personal communication, 1998).

Much work is still needed to achieve a commercial flood-tolerant *Annona* for south Florida. Our findings that *A. glabra* is compatible with and allows survival of flood-intolerant annonas in flooded conditions, and that *A. muricata* also tolerates long-term flooding, offer new and exciting possibilities that may ultimately lead to a flood-tolerant or flood-adapted perennial fruit tree for flood-prone or poorly drained areas in south Florida.

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