Weed Science Society of America

Differential Response of Palmleaf Morningglory (Ipomoea wrightii) and Pitted Morningglory (Ipomoea lacunosa) to Flooding

Author(s): David Gealy

Source: *Weed Science*, Vol. 46, No. 2 (Mar. - Apr., 1998), pp. 217-224
Published by: Weed Science Society of America and Allen Press
Stable URL: http://www.jstor.org/stable/4045940
Accessed: 26/06/2013 14:51

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Weed Science Society of America and *Allen Press* are collaborating with JSTOR to digitize, preserve and extend access to *Weed Science*.

http://www.jstor.org

This content downloaded from 199.133.134.8 on Wed, 26 Jun 2013 14:51:24 PM
All use subject to JSTOR Terms and Conditions

Weed Science, 46:217–224. 1998

Differential response of palmleaf morningglory (*Ipomoea wrightii*) and pitted morningglory (*Ipomoea lacunosa*) to flooding

David Gealy
Corresponding author. U.S. Department of Agriculture, Agricultural Research Service, National Rice Germplasm Evaluation and Enhancement Center, Stuttgart, AR 72160; dgealy@ag.gov

Palmleaf morningglory (IPOWR) and pitted morningglory (IPOLA) were compared in field and greenhouse tests under simulated rice field conditions to quantify flood tolerance characteristics of the two species. IPOWR survived a 13-cm flood in the field if the flood was applied 12 days after planting (DAP) or later. In contrast, IPOLA did not survive floods applied before 19 DAP. Only IPOWR survived a 5-cm flood applied 5 DAP in the field. In the greenhouse, both species were unable to emerge from under 1 cm of soil when flooded greater than 1 cm deep. Although both species emerged from water-saturated soil, IPOWR emerged earlier and produced more dry weight than did IPOLA. Emergence from the water surface of 2-cm-tall IPOWR was better than that of IPOLA when submerged in water up to 7 cm deep, and total dry weight (as a percent of a nonflooded control) was two to four times greater for IPOWR. Even a 5-cm flood reduced leaf area, height, dry weight, and photosynthesis of IPOLA more than that of IPOWR. At 20 C and low oxygen (1%), germination percentage of IPOWR was about four times higher than IPOLA. Germination, growth, and certain physiological processes of IPOWR are more tolerant than those of IPOLA to moderately deep floods (and low soil oxygen levels). Thus, IPOWR is potentially a greater weed problem than IPOLA in rice fields. The fact that neither species was capable of emerging from soil under even shallow flood depths helps explain why morningglories are prevalent only in shallow or water-saturated areas on rice field levees.

Nomenclature: Pitted morningglory, *Ipomoea lacunosa* L. IPOLA; palmleaf morningglory, *Ipomoea wrightii* Gray IPOWR.

Key words: Anoxia; germination; photosynthesis; emergence; rice, *Oryza sativa* L.; IPOLA; IPOWR.

Palmleaf morningglory (IPOWR) can be a troublesome weed in rice-growing areas in the southern U.S., and especially in heavy clay soils found in the delta regions adjacent to the Mississippi River in Arkansas, Mississippi, and Louisiana. IPOWR infested rice in the rice–fallow rotations in the 1950s, well before soybean [*Glycine max* (L.) Merr.] became widely grown in rotation with rice (R. J. Smith, personal communication). Control of IPOWR infestations in rice can be inconsistent because, unlike soybean for which numerous herbicides are available (Baldwin et al. 1996), few herbicide options are available to control morningglory species in rice. IPOWR can grow in rice in the flood or on levees, whereas pitted morningglory (IPOLA) and other morningglory species generally are found only on nonflooded tops of levees. IPOLA and other morningglory species are primarily weed problems in upland crops such as soybean and cotton (*Gossypium hirsutum* L.), which usually are grown on lighter soils with lower clay content. IPOLA germination has been shown to be substantially more tolerant than IPOWR to simulated drought stress (Crowley and Buchanan 1980).

Because rice tolerates low oxygen (hypoxia) conditions better than most weeds, flooding is an effective method of cultural control for many weed species (Helms 1994). Flood water in rice fields also can affect soil temperature, nitrogen fertility, and insect and disease interactions, and turbid flood water can inhibit growth of submerged weeds by shading. In combination, these factors give rice a competitive advantage over terrestrial weeds under flooded conditions.

Although published information on morningglory interference in rice appears to be lacking, well-established IPOWR on levees or in the flood would be expected to reduce rice growth. Interference between IPOLA and soybean is well documented. IPOLA densities of 3.3 plants m^{-2} reduced soybean yields 42% (Howe and Oliver 1987). However, yields were reduced more under dry than wet growing conditions.

Effects of flooding on leaf gas exchange (photosynthesis and transpiration) in IPOLA and IPOWR have not been reported previously. Flood-tolerant *Echinochloa* weed species exhibited higher photosynthetic activity than rice under a flood (Bouhache and Bayer 1993). However, flooding or waterlogging of even short duration can greatly reduce the leaf gas exchange of broadleaved crops of the South, including soybean (Oosterhuis et al. 1990) and cotton (Meyer et al. 1987). Flooding also has been shown to reduce growth and yield of the morningglory relative, sweetpotato (*Ipomoea batatas*) (Roberts and Russo 1991).

The ecological basis for the different habitat preferences of IPOWR and IPOLA in agronomic crops has not been published. The objective of this research was to determine the effects of the timing and depth of flooding and oxygen concentration on germination, growth, and photosynthetic productivity of IPOWR and IPOLA.

This content downloaded from 199.133.134.8 on Wed, 26 Jun 2013 14:51:24 PM
All use subject to JSTOR Terms and Conditions

Materials and Methods

Response of Morningglory Emergence and Growth to Flooding in Field Studies

Response to Plant Size/Flooding Date

A seedbed was prepared for field plots using standard agronomic practices for rice production in Arkansas (Helms 1994). IPOWR and IPOLA seeds were planted on May 27, 1994, and May 12, 1995, at the University of Arkansas Rice Research and Extension Center into moist Crowley silt loam (fine, montmorillonitic, thermic Typic Albaqualf). Soil pH was 6.8 and soil organic matter content was 0.9%. Nitrogen fertilizer was not applied to the plots. Morningglory seeds were planted about 2 cm deep with a six-row cone planter[1] in field plots 137 cm long. Two rows of each species were planted side by side, 18 cm apart, in the middle four rows of the planter. The two outer rows were not planted. One to 2 days after planting (DAP), a galvanized steel frame (30 cm deep by 76 by 76 cm) was pounded approximately 10 cm deep into the soil in the middle of each plot to create a watertight barrier (artificial levee) that encompassed two 76-cm-long rows of both morningglory species. In 1994, a 13-cm flood was established in separate frames 3, 11, 18, and 25 DAP, and was maintained throughout the growing season. In 1995, dry soil conditions delayed seedling emergence and early growth causing the initial flooding treatment to be delayed. Therefore, in 1995, the 13-cm flood treatments were established 7, 14, 21, and 28 DAP, which was 3 to 4 d later than in 1994. To simplify the presentation, the previously mentioned flooding dates in both 1994 and 1995 will be represented as 5, 12, 19, and 26 DAP, respectively. Plant sizes at the first flooding date (5 DAP) in both years were: IPOWR, 1 to 3 cm and cotyledon- to one-leaf stage; IPOLA, 2 to 4 cm and one- to two-leaf stage. Plant sizes at later flooding dates (1995 data only) were: 12 DAP, IPOWR 5.2 cm and 4.7 leaves, IPOLA 6.3 cm and 5.5 leaves; 19 DAP, both 11.8 cm and 7 leaves; 26 DAP, both 12.2 cm and 13.8 leaves.

To minimize soil disruption and turbidity in the plot, water was added slowly to plots. Proper flood levels within the steel frames were reestablished two to four times per week. Nonflooded control plots received water from natural rainfall and from irrigations as needed to maintain moist soil conditions. Drought conditions during the summer of 1995 reduced moisture levels and elevated temperatures within the metal frames and stunted control plants (data not shown).

Plants were harvested between flowering and seed set (beginning August 11, 1994, and July 28, 1995), and surviving plants and total dry weights were determined. Data were expressed as a percent of nonflooded control. The experimental design was a split plot, with flooding dates as main plots, species as subplots, and four replications. Year effects were considered as blocks. Therefore, data were combined over 2 yr and subjected to analysis of variance. Means were separated with a least squares means test at $P = 0.05$.

Response to Flooding Depth

Seedbed preparation and planting were conducted as above. At the 5-DAP flooding date, when IPOWR and IPOLA plants were approximately 1 to 3 and 2 to 4 cm tall, respectively, floods of 0, 5, and 13 cm were established in steel squares as described above. All other measurements and procedures were as above.

Response of Morningglory to Flood Depth in the Greenhouse

Germinating Seeds

Crowley silt loam was obtained from a field site at the University of Arkansas Rice Research and Extension Center at Stuttgart, AR, and placed in 20-cm-diam, 4-L watertight plastic pots. Fifty seeds of IPOWR or IPOLA were placed approximately equidistant from one another on the premoistened soil surface and covered with a 1-cm layer of dry soil. Soil was tamped lightly to simulate conditions in a drilled seedbed. The soil surface was 10 to 12 cm below the top of the pot. Immediately after planting, water depths of 0 (water-saturated), 1, 2, 5, and 10 cm were established in each pot and maintained until plants were harvested. A moist (soil at field capacity) 0-cm treatment was included as a control. Day and night temperatures were approximately 32 and 20 C, respectively. A 14-h photoperiod and maximum irradiance of approximately 900 $\mu mol\ m^{-2}\ s^{-1}$ were maintained with natural sunlight and supplemental 1,000-W metal halide lamps.

One, 2, and 3½ weeks after planting (WAP), the number of live seedlings that reached above the surface of the water (when present) was counted. For the remainder of the paper, this will be referred to as "emergence." At harvest (3½ WAP), average plant heights (from soil surface to tallest point on plant) were determined for each pot, and soil was washed from roots. Roots were separated from shoots, and the dry weights of roots, shoots, and the total plant were determined, as were root : shoot weight ratios. Data were expressed as a percentage of the moist-0-cm flood treatment. The experiment was a randomized complete block with four replications and was conducted three times. Experiment effects were considered as blocks. Therefore, data were combined over experiments and subjected to analysis of variance. Means were separated with a least squares means test at $P = 0.05$. Data from water depths greater than 1 cm were not included in the analysis because, at these depths, emergence from soil was usually zero, and where greater than zero, values were less than 1% of the nontreated control.

Emerged (2-cm-tall) Seedlings

Soil and pot preparation and planting were conducted as for the greenhouse flood depth experiment described above, except that pregerminated (experiment 1) or dry (experiment 2) seeds of IPOWR or IPOLA were planted in each pot. Pots were flooded when seedlings were approximately 2 cm tall. Generally, this was 1 d earlier for IPOLA than IPOWR. Because of differences in germination and/or emergence between the two species, final populations averaged 20 seedlings in IPOWR control pots and 14 seedlings in IPOLA control pots. These differences in plant population probably influenced interplant competition very little in these experiments because of the relatively small plant sizes and large soil volumes involved. Hourly averages of photosynthetic photon flux (PPF) and air temperature at pot level were recorded.[2] Day and night temperatures were 32 ± 3 (mean ± SD) C and 20 ± 2 C, respectively. A 14-h photoperiod and an average maximum PPF of 750 $\mu mol\ m^{-2}\ s^{-1}$ were main-

This content downloaded from 199.133.134.8 on Wed, 26 Jun 2013 14:51:24 PM
All use subject to JSTOR Terms and Conditions

tained with natural sunlight and supplemental 1,000-W metal halide lamps.

Two and 4 WAP (harvest), emerged plants were counted as above. At harvest, average plant heights, dry weights of roots, shoots, and total plant, and root : shoot weight ratios were determined as described above. Data were expressed as a percentage of the moist-0-cm flood treatment. Experimental design and analysis were as described above, and the experiment was conducted twice. Means were separated with Fisher's LSD test at the P = 0.05 level of probability.

Effect of Flood Depth on Gas Exchange and Growth of Morningglory Seedlings

Seeds of IPOWR and IPOLA were planted and grown in pots in a greenhouse as described above such that a final population of 14 seedlings was achieved in each control pot. When seedlings were approximately 2 cm tall, flood levels of 5 or 0 cm (moist soil at field capacity) were established in each pot. The flood levels were reestablished approximately every other day. Hourly averages of PPF and air temperature at pot level were recorded.[2] A 14-h photoperiod was maintained with natural sunlight and supplemental 1,000-W metal halide lamps. Average daily maximum PPF was 940 μmol m^{-2} s^{-1}. Daily maximum and minimum air temperatures were 38 ± 4 (mean ± SD) C and 22 ± 1 C, respectively.

To characterize the soil environment under a 5-cm flood, pH, conductivity, and temperature were measured at the 1-cm depth in the soil with a combination probe[3] 4 and 28 d after planting (first experimental run only). A parallel study also was conducted during a 24-h flood at 30 C to determine reduction-oxidation (redox) potential, as an indicator of oxygen availability, in soil (unpublished data). The tips of platinum redox electrodes[4] were placed 1 cm deep in separate soil-filled pots similar to those described above. Floods of 0.1 (saturated), 2, or 7 cm were applied to soil, and redox potentials were monitored periodically for 24 h.

Twenty-eight days after planting, three young, fully expanded leaves of each species were subsampled for gas exchange measurements. The entire IPOLA leaf and the two largest IPOWR leaflets on each leaf were subsampled. Net photosynthesis, transpiration, and temperature of leaves were determined using a closed-system, portable infrared gas analyzer[5] and a 0.25-L acrylic assimilation chamber configured with a photosynthetically active radiation (PAR) sensor and an infrared leaf temperature sensor. During gas exchange measurements, leaves in the assimilation chamber were illuminated with a combination of natural sunlight and 1,000-W metal halide lamps to achieve a PPF of 900 to 1,200 μmol m^{-2} s^{-1}. Leaf net photosynthesis and transpiration were expressed in units of μmol CO_2 m^{-2} leaf area s^{-1} and mmol H_2O m^{-2} leaf area s^{-1}, respectively. To obtain a more realistic estimate of ambient leaf temperatures, the infrared temperature sensor was detached from the chamber following completion of gas exchange measurements and positioned approximately 1 cm below leaves in open air. The leaf area used to calculate gas exchange parameters of sampled leaves and the total leaf area per pot at harvest were measured with a leaf area meter–conveyor belt assembly.[6] The number of live emerged plants, plant heights, and aboveground plant dry weights were determined 30 d after planting.

To better understand the contributions of leaf gas exchange rates to overall plant and canopy productivity of these two species, "per plant" and "per pot" values were calculated for net photosynthesis and transpiration. Net photosynthesis "per plant" was estimated as the product of (leaf net photosynthesis; see above)(leaf area per pot in units per square meter) (1/number of plants per pot). Net photosynthesis "per pot" was estimated as the product of (leaf net photosynthesis; see above)(leaf area per pot in units per square meter). Transpiration "per plant" and "per pot" was calculated using the same correction factors as above. Values expressed "per pot" also can be expressed "per soil surface area covered" (data not presented) by dividing the "per pot" values by the soil surface area inside pots (0.0314 m^2). Experimental design and analysis were as above and the experiment was conducted twice. Means were separated with a least squares means test at P = 0.05.

Effect of Oxygen Concentration on Seed Germination

Bulk samples of IPOWR and IPOLA seeds were surface sterilized for 3 min with 1% aqueous sodium hypochlorite, rinsed thoroughly with tap water, and blotted dry. Thirty-three seeds of each species were placed on single layers of absorbent germination paper[7] in 60 separate petri dishes (10 cm diam) per species. Four milliliters of 10 mM PIPES (piperazine-*N*-*N*′-bis[2-ethane sulfonic acid]) buffer (pKa 6.8) was dispensed into each dish. Dishes without lids were placed into 18- by 20-cm (1,120-ml volume capacity) "leakproof" plastic[8] "zip-lock" style bags. To remove CO_2 inside the plastic bags, 1 g of calcium hydroxide/potassium hydroxide (soda lime) granules was placed in each bag prior to sealing. Ten bags of each species were then flushed for approximately 1 min each with approximately 4 L min^{-1} of oxygen : nitrogen mixtures of 0 : 100, 1 : 99, 5 : 95, 10 : 90, 20 : 80, or 40 : 60 and sealed. Bags were placed in growth chambers[9] in the dark at either a constant 20 or 30 C. The gas ratios were achieved by dispensing independently regulated[10] oxygen (99.5%) and nitrogen (99.99%) at approximately 10 kPa (1 atm) through flow meters[11] at rates proportional to the desired gas ratios. The independent airflows were channeled together in a common dispensing tube located downstream from the flow meters.

Bags were removed from the growth chambers, and germinated seeds were counted 7 DAP. Germination was defined as radicle protrusion of at least 2 mm. Radicles and coleoptiles were excised from the seeds and combined, and total dry weight was determined after drying plant material at 50 C for 2 d. The experiment was conducted with a factorial arrangement of treatments consisting of two species, two temperatures, and six oxygen : nitrogen ratios. The experiment was conducted once with five replications and a second time with four replications. The experimental design was a randomized complete block. Data were expressed as a percent of the 30 C and 20% oxygen treatment and were combined over experiments and subjected to analysis of variance as above. Means were separated with a least squares means test at P = 0.05.

This content downloaded from 199.133.134.8 on Wed, 26 Jun 2013 14:51:24 PM
All use subject to JSTOR Terms and Conditions

TABLE 1. Effect of flooding date on survival and dry weight of palmleaf (IPOWR) and pitted (IPOLA) morningglory plants in a 13-cm flood in the field.[a,b,c]

	Surviving plants				Plant dry weight			
	Flooding date (days after planting)							
Species	5	12	19	26	5	12	19	26
	% of nonflooded control							
IPOWR	4 a	101 a	145 a	183 a	2 a	72 a	185 a	177 a
IPOLA	0 a	0 b	40 b	99 b	0 a	0 b	33 b	70 b

[a] Data presented are means of values from 1994 and 1995.
[b] Control values for surviving IPOWR and IPOLA plants were, respectively, 120 and 180 surviving plants m^{-2} in 1994 and 11 and 20 surviving plants m^{-2} in 1995. Control values for dry weights of IPOWR and IPOLA plants were, respectively, 210 and 270 g m^{-2} in 1994 and 35 and 62 g m^{-2} in 1995.
[c] Within columns, values followed by the same letter are not different at P = 0.05 according to a least squares means test.

Results and Discussion

Response of Morningglory Emergence and Growth to Flooding in Field Studies

Response to Plant Size/Flooding Date

IPOWR emerged about 1 d later than IPOLA and initially grew slower in the absence of a flood. For instance, 12 DAP in 1995, IPOWR control plants were 5.2 cm tall with 4.7 leaves per plant, and IPOLA plants were 6.3 cm tall with 5.5 leaves per plant (data not shown).

In a 13-cm flood, survival of IPOWR was greater than or equal to IPOLA at all flooding dates (Table 1). Survival of IPOWR in the 13-cm flood also was greater than IPOLA in the nonflooded control except at 5 and 12 DAP. Survival of both species increased at later flooding dates. IPOWR survived a 13-cm flood as early as 12 DAP, whereas IPOLA plants did not survive the flood until 19 DAP. IPOWR survival was greater than 100% of the control at flooding dates of 19 and 26 DAP, presumably because dry soil conditions inhibited growth of seedlings in the nonflooded control plots. This phenomenon was more pronounced in 1995 because rainfall was much less abundant than in 1994 (data not shown).

The responses of plant dry weight and plant survival to flooding date were similar (Table 1). Reduced plant survival appears to account for most of the reduction in dry weight at the earlier flooding dates. Flooding apparently inhibited flowering in IPOLA much more than in IPOWR. When flooding dates were averaged in 1995 (data not shown), IPOLA flowering at harvest was 0.5% of the moist control, compared to 93% for IPOWR.

Response to Flooding Depth

In a separate experiment (data not shown), IPOLA did not survive 5- or 13-cm floods applied 5 DAP in either year. Likewise, IPOWR did not survive a 13-cm flood either year, but did survive a 5-cm flood in 1995, where its final height and dry weight were reduced about 30 and 25%, respectively, compared to the nonflooded control. The reduced level of flood tolerance in IPOLA is further demonstrated by the fact that IPOLA plants did not emerge from the 5-cm water depth in either year even though they were slightly larger than IPOWR plants at the time of flooding.

Response of Morningglory to Flood Depth in the Greenhouse

Germinating Seeds

Neither species emerged from water depths greater than 1 cm (Table 2). Saturated soil (0 cm) reduced emergence compared to the control, except for IPOLA 3½ WAP, and was more inhibitory to IPOLA than to IPOWR, especially during the first 2 WAP (Table 2). At harvest, emergence of both species was similar. A 1-cm flood reduced plant heights of both species 3⅓ WAP by more than 85%. Plants in saturated soil were about the same height as the controls, although IPOLA plants were stunted nearly 35% (P = 0.13) compared to IPOWR plants. The ability of IPOWR to compensate in saturated soil for the initial delays in seedling emergence probably also contributes to its greater tolerance to flooded environments.

A 1-cm flood reduced total dry weight per pot of both species by 99% or more (Table 2). In saturated soil, shoot growth was inhibited 33% in IPOWR plants and twice that level in IPOLA, in comparison with the moist soil control. Root growth was not affected significantly by saturated soil, resulting in elevated root : shoot ratios, especially in IPOLA. Saturated soil did not affect dry weight per IPOWR plant but reduced dry weight per IPOLA plant more than 30%. The 1-cm flood reduced dry weight per plant relatively more than total dry weight per pot, presumably because the few surviving plants experienced less interspecific competition.

In pot experiments, seeds from the 2- to 5-cm water depths occasionally moved to the soil surface because soil was not adequately packed or had eroded away from seeds. This movement resulted in artificially elevated soil emergence levels, especially for IPOWR (data not shown). Therefore, the data were deleted. Such movement may occur in finely worked field soils as well, and could be beneficial to the flood survival of IPOWR, which has the ability to elongate under relatively deep water and extend above the water surface (data not shown).

Emerged (2-cm-tall) Seedlings

A 1-cm flood inhibited emergence of both species 50% or more (Table 3). This large apparent inhibition in a shallow flood probably occurred because some seeds in the moist control soil continued to germinate and emerge over an extended period, but seeds in flooded soil did not do this at depths of 1 cm or greater. This is consistent with the results shown in

This content downloaded from 199.133.134.8 on Wed, 26 Jun 2013 14:51:24 PM
All use subject to JSTOR Terms and Conditions

TABLE 2. Effect of flood depth on emergence, survival, and growth of palmleaf (IPOWR) and pitted (IPOLA) morningglory planted in soil in greenhouse pots.[a,b,c]

Species	Flood depth	Emergence 1 WAP	Emergence 2 WAP	Emergence 3½ WAP	Plant height 3½ WAP	Shoot dry weight 3½ WAP	Root dry weight 3½ WAP	Total dry weight 3½ WAP	Dry weight per plant 3½ WAP	Root : shoot ratio 3½ WAP
	cm	% of moist control								
IPOWR	0-moist	100 a	100 a	100 a	100 a	100 a	100 a	100 a	100 a	100 b
	0-sat.	60 b	70 b	65 b	110 a	67 b	76 a	69 a	95 a	115 b
	1	0.4 d	0.4 d	0.7 c	12 b	0.4 d	0.4 b	0.4 c	19 c	—
IPOLA	0-moist	100 a	100 a	100 a	100 a	100 a	100 a	100 a	100 a	100 b
	0-sat.	31 c	40 c	78 ab	73 a	35 c	107 a	48 b	69 b	305 a
	1	0.3 d	0.3 d	0.9 c	12 b	0.1 d	1.3 b	1.0 c	15 c	180 ab

[a] Values presented are means of three experiments. Data from depths greater than 1 cm were not included in the analysis and were omitted from the table because emergence at these depths was usually zero, and where greater than zero, values were less than 1% of the nontreated control. "Emergence" refers to the number of live seedlings that reached above the surface of the water (when present).

[b] The control values for IPOWR and IPOLA, respectively, were: emergence 1 WAP (19.2 and 13.9 plants pot^{-1}); emergence 2 WAP (21.5 and 14.7 plants pot^{-1}). The 3½ WAP (harvest) control values were: emergence (21.4 and 14.9 plants pot^{-1}); plant height (20.1 and 17.8 cm plant^{-1}); shoot dry weight (2.62 and 2.84 g pot^{-1}); root dry weight (0.95 and 0.72 g pot^{-1}); total dry weight (3.57 and 3.56 g pot^{-1}); dry weight per plant (0.163 and 0.224 g plant^{-1}); and root : shoot ratio (0.368 and 0.237 g g^{-1}).

[c] Within columns, values followed by the same letter are not different at $P = 0.05$ according to a least squares means test.

Table 2. At deeper depths, emergence of IPOWR tended to increase over time as plants slowly grew to the water surface (Table 3). Conversely, emergence of IPOLA from these depths remained constant or decreased over time. All flood depths less than 10 cm inhibited IPOLA more than IPOWR. Four weeks after planting, emergence of IPOWR from flood depths as great as 5 cm was similar to 1 cm, whereas emergence of IPOLA from flood depths of 5 cm or more was less than from 1 cm. IPOWR adapted to shallower water depths (1 and 2 cm) by growing taller than the moist controls even though total dry weight tended to be moderately reduced at these depths. As a percent of the moist control, both shoot dry weight and total dry weight of IPOWR ranged from approximately two to four times the IPOLA levels across all depths, indicating that IPOWR tolerates a broad range of water depths better than IPOLA. As in the previous greenhouse flood depth experiment (Table 2), shallow water tended to inhibit IPOLA roots less than shoots, especially at the shallower depths, resulting in a root : shoot ratio in the 1-cm treatment of more than four times that of the control (Table 3). In both species, 2-cm-tall seedlings (Table 3) tolerated a much deeper flood than did buried seeds (Table 2). Likewise, emerged rice seedlings tolerate flooding far better than rice seeds buried in shallow soil (Helms 1994).

Effect of Flood Depth on Gas Exchange and Growth of Morningglory Seedlings

A 5-cm flood generally reduced leaf photosynthesis and transpiration more in IPOLA than in IPOWR (Table 4). When expressed on a leaf area basis, the flood reduced net photosynthesis of IPOLA by 20%. However, in IPOWR, neither gas exchange parameter was affected, and transpiration of IPOLA increased by about 25%. Typically, both net photosynthesis and transpiration are reduced in both flood-tolerant and flood-susceptible crop cultivars exposed to flooding stress (Lakitan et al. 1992; Takele and McDavid 1994). It is unclear why IPOLA transpiration per leaf area increased (a trend observed with IPOWR) under the flood in the present studies. Soil moisture levels in the moist control pots during gas exchange measurements may have been less than optimum, which could have reduced transpiration of control plants below optimum levels. Such a condition could explain the apparent stimulation of transpiration in flooded plants relative to control plants.

The 5-cm flood reduced both photosynthesis and transpiration by at least 50% in both species when expressed on a "per plant" or "per pot" basis, and IPOLA usually was inhibited more than IPOWR (Table 4). The substantially reduced leaf area per plant and per pot in flooded treatments appears to account for the greater inhibition of gas exchange values when expressed on "per plant" or "per pot" bases, compared to the leaf area basis. In other words, the flood inhibited leaf area per plant and per pot and the number of emerged plants to such a great extent that the "per leaf area" values became a numerically minor component of these alternate expressions of gas exchange. It should be noted that the increased leaf areas present in nonflooded pots compared to flooded pots probably resulted in a significant amount of self-shading within nonflooded pots. Because leaves placed in the assimilation chamber experienced no self-shading during gas exchange measurements, the "per plant" and "per pot" gas ex-

This content downloaded from 199.133.134.8 on Wed, 26 Jun 2013 14:51:24 PM
All use subject to JSTOR Terms and Conditions

TABLE 3. Effect of flood depth on emergence and growth of 2-cm-tall palmleaf (IPOWR) and pitted (IPOLA) morningglory seedlings in greenhouse pots.[a,b,c]

Species	Flood depth	Emergence 2 WAP	Emergence 4 WAP	Plant height 4 WAP	Shoot dry weight 4 WAP	Root dry weight 4 WAP	Total dry weight 4 WAP	Root : shoot ratio 4 WAP
	cm	% of moist control						
IPOWR	0	100	100	100	100	100	100	100
	1	48	50	231	75	74	74	98
	2	48	51	179	85	77	82	94
	5	45	65	131	50	55	52	122
	7	20	33	94	15	15	15	241
	10	0	1	61	9	12	10	121
IPOLA	0	100	100	100	100	100	100	100
	1	40	33	99	31	80	42	424
	2	22	20	70	20	31	23	173
	5	21	13	57	13	15	14	212
	7	1	3	40	5	5	5	228
	10	0	2	43	4	4	4	123
	LSD (0.05)	NS	17	49	23	29	23	NS

[a] Values presented are means of two or three experiments. "Emergence" refers to the number of live seedlings that reached above the surface of the water (when present).

[b] The control values of IPOWR and IPOLA, respectively, for emergence were: 2 WAP (18.9 and 11.8 plants pot^{-1}). The 4-WAP (harvest) control values were: emergence (19.3 and 14.6 plants pot^{-1}); plant height (14.0 and 13.6 cm plant^{-1}); shoot dry weight (2.43 and 1.94 g pot^{-1}); root dry weight (1.60 and 1.25 g pot^{-1}); total dry weight (4.03 and 3.20 g pot^{-1}); and root : shoot ratio (0.63 and 0.57 g g^{-1}).

[c] The LSD (0.05) can be used to compare all means within a column. The IPOLA root : shoot ratio of 424% at 1 cm is different from the control at P = 0.05 according to a least squares means test.

change rates in nonflooded pots probably were overestimated somewhat in these studies (Table 4).

Plant dry weights generally also were reduced in flooded pots compared to controls, and dry weight per pot of IPOLA was reduced to about half the level of IPOWR (Table 4). The flood reduced plant emergence equally in both species, but reduced the height of IPOLA only. The flood did not affect leaves per plant in either species. Consistently, throughout these studies, IPOWR elongated more than IPOLA when exposed to moderate flood depths (Tables 2–4). Stem elongation and maintenance of leaf gas exchange processes in a 5-cm flood appear to be important flood tolerance strategies for IPOWR.

Similar to the results with the two morningglory species in the present study (Table 4), flooding and waterlogging have been shown to affect gas exchange differently in flood-sensitive and flood-insensitive crop cultivars. For example, a 1-cm flood reduced leaf conductance, leaf photosynthesis, and leaf water potential more quickly in a flood-sensitive than in a flood-tolerant cultivar of snapbean (*Phaseolus vulgaris*) (Lakitan et al. 1992). Likewise, short-term waterlogging reduced stomatal conductance (an indicator of stomatal aperture) more in waterlogging-susceptible cultivars of cowpea [*Vigna unguiculata* (L.) Walp.] than in waterlogging-tolerant cultivars (Takele and McDavid 1994). However, waterlogging reduced leaf gas exchange rates, leaf water potential, and leaf area per plant to a similar extent in tolerant and susceptible cultivars. In general, flooding (low rhizosphere oxygen availability) appears to affect stomatal responses through interactions with factors such as root temperature, growth stage, mineral nutrition, duration of hypoxia, and soil factors (Sojka 1992).

One centimeter deep, soil pH was 6.8 and 6.7, conductivity was 359 and 437 μmhos, and temperature was 27.2 and 29.5 C for the 0- and 5-cm water depths, respectively, when averaged over the 4- and 28-d readings (data not shown). In the soil redox potential study, potentials 1 cm deep were similar (200 to 300 mV) under flood depths of 0.1 to 7 cm after 24 h, indicating similar low levels of oxygen availability in the flooded soils (data not shown). These redox levels are consistent with those reported in a waterlogging study where soil redox potential decreased from greater than 550 mV to less than 330 mV within several hours, indicating a near complete absence of oxygen (Blom et al. 1994).

Oxygen availability in flooded soils typically is reduced rapidly since respiring roots consume oxygen as do respiring microbes (Gambrell et al. 1991). Within hours to days, flooding usually leads to loss of most of the dissolved oxygen that is present more than a few millimeters below the soil surface (Gambrell et al. 1991). Oxygen levels in flooded rice fields appear to follow a somewhat different pattern. Illumination and the presence of rice plants have been shown to increase the oxygen levels in the upper 5 mm of flooded soil (Frenzel et al. 1992).

Effect of Oxygen Concentration on Seed Germination

Germination of both species was almost completely arrested (less than 10% of the control) at 0% oxygen. Germination tended to be greater for IPOWR than IPOLA at slightly higher oxygen concentrations (Table 5). For example, at 1% oxygen and 20 C, IPOWR germination was 46%, which was at least three times that at 30 C or for either of the IPOLA treatments (Table 5). Generally, germination was similar to the control at oxygen levels greater than 1%. The exception to this was germination of IPOLA at 20 C, which did not reach 50% of the control at any oxygen concentration. IPOLA germination was two to five times greater at 30 C than at 20 C at all oxygen levels above 1%.

The inhibition of germination and seedling dry weights at low oxygen levels followed similar trends (Table 5), but dry

This content downloaded from 199.133.134.8 on Wed, 26 Jun 2013 14:51:24 PM
All use subject to JSTOR Terms and Conditions

TABLE 4. Effect of a 5-cm flood on gas exchange and growth of palmleaf (IPOWR) and pitted (IPOLA) morningglory 4 WAP.[a,b,c]

Species	Flood depth	Leaf temp.	Leaf net photosynthesis (μmol CO_2/s)			Leaf transpiration (mmol H_2O/s)			Leaf area		Leaves	Emerged plants	Dry weight		Height
			Per m^2 leaf area	Per plant	Per pot	Per m^2 leaf area	Per plant	Per pot	cm^2 per plant	cm^2 per pot	No. per plant	No. per pot	g per plant	g per pot	cm per plant
	cm		% of moist control												
Controls	0	100 a	100 a	100 a	100 a	100 b	100 a	100 a	100 a	100 a	100 a	100 a	100 a	100 a	100 a
IPOWR	5	100 a	101 a	39 b	34 b	110 ab	45 b	39 b	49 b	42 b	93 a	67 b	70 a	49 b	106 a
IPOLA	5	101 a	81 b	27 c	15 c	124 a	34 b	19 c	37 c	21 c	86 a	50 b	68 a	24 c	76 b

[a] Values presented are means of two experiments, with the exception that data for leaf temperature, leaf net photosynthesis per plant and per pot, leaf transpiration per plant and per pot, and leaf area per plant and per pot were from one experiment only.

[b] The control values for IPOWR and IPOLA, respectively, were: leaf temperature (34.9 and 36.0 C); net leaf photosynthesis per m^2 leaf area (10.5 and 8.7 μmol CO_2 s^{-1}); net leaf photosynthesis per plant (0.075 and 0.053 μmol CO_2 s^{-1}); net leaf photosynthesis per pot (0.76 and 0.67 μmol CO_2 s^{-1}); leaf transpiration per m^2 leaf area (2.8 and 6.6 mmol H_2O s^{-1}); leaf transpiration per plant (0.020 and 0.013 mmol H_2O s^{-1}); leaf transpiration per pot (0.21 and 0.17 mmol H_2O s^{-1}); leaf area per pot (601 and 740 cm^2); leaf area per plant (58.3 and 58.0 cm^2); leaves per plant (5.0 and 5.5); emerged plants per pot (12.9 and 14.8); dry weight per pot (4.0 and 4.4 g); dry weight per plant (0.31 and 0.31 g); and plant height (12.4 and 16.9 cm).

[c] Within columns, values followed by the same letter are not different at P = 0.05 according to a least squares means test (note: g = per plant of both IPOWR and IPOLA was different from nonflooded controls at P = 0.08).

weights generally were inhibited more and at higher oxygen levels than was germination. Dry weight of all treatments was inhibited at least 15% at 10% oxygen, whereas germination of all treatments except IPOLA at 20 C was inhibited less than 15% at 5% oxygen.

Germination and seedling size of IPOLA generally were greater at 30 C than at 20 C (Table 5). By contrast, the IPOWR values for the two variables tended to be similar at these temperatures.

Dry weights of IPOWR and IPOLA at 20% oxygen were 20 and 70% less, respectively, at 20 C than at 30 C, and the difference in dry weight between the two temperatures became greater at 40% oxygen (Table 5). Presumably, the higher oxygen concentrations and higher temperature enhanced cell division and elongation to produce a greater mass of plant tissue.

The greater ability of IPOWR to germinate and grow at low oxygen levels may be partly responsible for its advantage over IPOLA in flooded conditions. Clearly, IPOWR seeds germinated and grew better than IPOLA at low oxygen levels (1 to 5%), especially at 20 C, suggesting that IPOWR may have an even greater advantage over IPOLA at low temperatures. Thus, the competitive advantage of IPOWR over IPOLA in rice may be enhanced further because temperatures in flooded rice generally are lower than in nonflooded soil.

It should be noted that the bag system used in the present studies may underestimate the true inhibition experienced by germinating seeds in flooded field soils. Gas diffusion rates are substantially slower in water than in air (Armstrong 1979), and accumulation of inhibitory exudates near the seed surface from seeds placed in liquids also apparently reduces seed germination in anoxic conditions (Setter and Ella 1994).

Although the underlying physiological and anatomical factors responsible for superior germination, survivability, and growth of IPOWR under flooded conditions generally were not addressed in the present studies, much information exists for other species. In rice, enhanced ethanol synthesis in germinating seeds correlates with tolerance to submergence and anoxia (Setter et al. 1994). Flooding-tolerant *Rumex* species have adapted to flooded environments by producing longer leaves and petioles and producing more adventitious roots, which may be mediated by ethylene (Blom et al. 1994; Voesenek et al. 1992). Similarly, the hydrophyte *Typha domingensis* L. apparently is better adapted than *Cladium jamaicense* L. to thrive in wetlands at anaerobic (250 mV and below) soil redox levels, because under these conditions, it produces more adventitious roots and greater air space (aerenchyma tissue), enabling it to transport more O_2 to roots (Kludze and DeLaune 1996).

Collectively, these results indicate that germination, growth, and certain physiological processes of IPOWR are significantly more tolerant than IPOLA to moderately deep floods (and low soil oxygen levels). These differences appear to explain in large part the observations that IPOWR is potentially a much greater weed problem than IPOLA in rice fields. The fact that neither species was capable of emerging from soil under even shallow flood depths helps explain why morningglories typically are prevalent only in shallowly flooded fields or water-saturated areas on rice field levees.

These results suggest that cultural practices, such as deep flooding in dry-seeded systems or water seeding, may reduce morningglory infestations, whereas conservation tillage sys-

This content downloaded from 199.133.134.8 on Wed, 26 Jun 2013 14:51:24 PM
All use subject to JSTOR Terms and Conditions

TABLE 5. Effect of oxygen concentration and temperature on seed germination and seedling dry weight of palmleaf (IPOWR) and pitted (IPOLA) morningglory.[a,b,c]

Species	Temperature	Germination						Seedling dry weight					
		Oxygen concentration (%)											
		0	1	5	10	20	40	0	1	5	10	20	40
	C	% of 30 C, 20% oxygen control											
IPOWR	20	8 a	46 a	98 a	87 a	101 a	93 a	2 a	11 a	58 a	77 a	80 b	75 b
	30	5 a	15 b	83 a	93 a	100 a	105 a	1 a	7 a	53 a	74 a	100 a	115 a
IPOLA	20	9 a	10 b	29 b	19 b	32 b	43 b	2 a	4 b	22 b	12 b	30 c	32 c
	30	7 a	12 b	90 a	93 a	100 a	100 a	1 a	1 b	69 a	85 a	100 a	124 a

[a] Values presented are means of two experiments.
[b] The germination control values (at 30 C, 20% oxygen) for IPOWR and IPOLA were, respectively, 15.4 and 6.6%. The seedling (radicle plus coleoptile) dry weight control values for IPOWR and IPOLA were, respectively, 100 and 41 mg per plate.
[c] Within columns, values followed by the same letter are not different at P = 0.05 according to a least squares means test.

tems, which leave weed seeds on or near the soil surface, may increase infestations of IPOWR in rice.

Sources of Materials

[1] Self-propelled cone planter, Hege Equipment Co., Route 1 Box 34A, Colwich, KS 67030. All trade names and company names are included for the benefit of the reader and do not imply endorsement or preferential treatment of the product by the U.S. Department of Agriculture.

[2] Model LI-1000 weather station, LI-COR Inc., 4421 Superior Street, P.O. Box 4425, Lincoln, NE 68504.

[3] Model 5566-22, water quality analyzer, Cole-Parmer, Chicago, IL 60648.

[4] Redox combination platinum electrode, Corning, New York, NY 14831.

[5] Model CI-301PS infrared gas analyzer, CID, Inc., 4018 Northeast 112th Avenue, Suite D-8, Vancouver, WA 98682.

[6] Model LI-3050A 4TBA 1364 leaf area meter–conveyor belt assembly, LI-COR Inc., 4421 Superior Street, P.O. Box 4425, Lincoln, NE 68504.

[7] 312M 76# heavy weight germination paper, Anchor Paper Co., 480 Broadway, P.O. Box 65648, St. Paul, MN 55165-0648.

[8] Saranex bags, 3 mil, National Bag Co. Inc., 2233 Old Mill Road, Hudson, OH 44236.

[9] Model PGR15 growth chambers, Controlled Environments Inc., 601 Stutsman Street, P.O. Box 347, Pembina, ND 58271.

[10] Model 250-125-540/208-39148 compressed nitrogen regulator, Victor Equipment Co., Denton, TX 76205.

[11] Model GF-4550 flow meters, Gilmont Instruments, Inc., Barrington, IL 60010, or Model PO4/1-NO92-04ST, Cole-Parmer, Chicago, IL 60648.

Acknowledgments

I thank Howard Black, Dawn Novak, and Robert Dilday for their technical support, and Delvar Peterson for assistance with statistical design and analysis. I also thank Dick Oliver for supplying the palmleaf morningglory seed, and Eric Webster and Dick Oliver for their helpful suggestions and peer review of this paper. This research was supported in part by funding from the Arkansas Rice Research and Promotion Board. Contribution from Agricultural Research Service, U.S. Department of Agriculture Science Paper.

Literature Cited

Armstrong, W. 1979. Aeration in higher plants. Adv. Bot. Res. 7:225–332.

Baldwin, F. L., J. W. Boyd, and G. B. Guy. 1996. Recommended Chemicals for Weed and Brush Control. University of Arkansas Cooperative Extension Service, MP 44. Little Rock, AR: University of Arkansas. 134 p.

Blom, C.W.P.M., L.A.C.J. Voesenek, M. Banga, W.M.H.G. Engelaar, J.H.G.M. Rijnders, H. M. Van De Steeg, and E.J.W. Visser. 1994. Physiological ecology of riverside species: adaptive responses of plants to submergence. Ann. Bot. 74:253–263.

Bouhache, M. and D. E. Bayer. 1993. Photosynthetic response of flooded rice (*Oryza sativa*) and three *Echinochloa* species to changes in environmental factors. Weed Sci. 41:611–614.

Crowley, R. H. and G. A. Buchanan. 1980. Responses of *Ipomoea* spp. and smallflower morningglory (*Jacquemontia tamnifolia*) to temperature and osmotic stresses. Weed Sci. 28:76–82.

Frenzel, P., F. Rothfuss, and R. Conrad. 1992. Oxygen profiles and methane turnover in a flooded rice microcosm. Biol. Fertil. Soils 14:84–89.

Gambrell, R. P., R. D. Delaune, and W. H. Patrick, Jr. 1991. Redox processes in soils following oxygen depletion. Pages 101–117 *in* M. B. Jackson, D. D. Davies, and H. Lambers, eds. Plant Life Under Oxygen Deprivation. The Hague, The Netherlands: SPB Academic Publishing.

Helms, R. S., ed. 1994. Rice Production Handbook. University of Arkansas Cooperative Extension Service, MP 192. Little Rock, AR: University of Arkansas. 90 p.

Howe, O. W., Jr. and L. R. Oliver. 1987. Influence of soybean (*Glycine max*) row spacing on pitted morningglory (*Ipomoea lacunosa*) interference. Weed Sci. 35:185–193.

Kludze, H. K. and R. D. DeLaune. 1996. Soil redox intensity effects on oxygen exchange and growth of cattail and sawgrass. Soil Sci. Soc. Am. J. 60:616–621.

Lakitan, B., D. W. Wolfe, and R. W. Zobel. 1992. Flooding affects snapbean yield and genotypic variation in leaf gas exchange and root growth response. J. Am. Soc. Hortic. Sci. 117:711–716.

Meyer, W. S., D. C. Reicosky, H. D. Barrs, and R.C.G. Smith. 1987. Physiological responses of cotton to a single waterlogging at high and low N-levels. Plant Soil 102:161–170.

Oosterhuis, D. M., H. D. Scott, R. E. Hampton, and S. D. Wullschleger. 1990. Physiological responses of two soybean (*Glycine max* L.) cultivars to short-term flooding. Environ. Exp. Bot. 30:85–92.

Roberts, W. and V. Russo. 1991. Time of flooding and cultivar affect sweet potato yield. HortScience 26:1473–1474.

Setter, T. L. and E. S. Ella. 1994. Relationship between coleoptile elongation and alcoholic fermentation in rice exposed to anoxia. I. Importance of treatment conditions and different tissues. Ann. Bot. 74:265–271.

Setter, T. L., E. S. Ella, and A. P. Valdez. 1994. Relationship between coleoptile elongation and alcoholic fermentation in rice exposed to anoxia. II. Cultivar differences. Ann. Bot. 74:273–279.

Sojka, R. E. 1992. Stomatal closure in oxygen-stressed plants. Soil Sci. 154: 269–280.

Takele, A. and C. R. McDavid. 1994. Effects of short-term waterlogging on cultivars of cowpea [*Vigna unguiculata* (L.) Walp.]. Trop. Agric. 71:275–280.

Voesenek, L.A.C.J., A.J.M. VanderSman, F.J.M. Harren, and C.W.P.M. Blom. 1992. An amalgamation between hormone physiology and plant ecology: a review on flooding resistance and ethylene. J. Plant Growth Regul. 11:171–188.

Received June 17, 1997, and approved November 18, 1997.

This content downloaded from 199.133.134.8 on Wed, 26 Jun 2013 14:51:24 PM
All use subject to JSTOR Terms and Conditions