Waterlogging Tolerance of 57 Plant Species Grown Hydroponically

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Additional index words. hydroponic experiment, ecological restoration, phenotype, provenance

Abstract. Plans for hydroponic experiments, as well as the flooding of watersheds for ecological restoration, require abundant evaluation information regarding plant species adapted to waterlogged environments. In this study, we observed the growth rate and phenotypes of 57 plant species, including nine provenances of four species grown hydroponically. The 57 species were from 22 families and 33 genera, and their waterlogging tolerance (WT) was classified into five categories according to the results of the evaluation: excellent, good, ordinary, poor, and very poor. We found that 60% of these plant species were able to survive in hydroculture for more than 10 weeks. They showed new shoot growth and had a survival rate of more than 60%. Species with excellent or good WT developed new leaves rapidly under waterlogging stress, whereas species with ordinary or poor WT exhibited old leaves dropping from the stem soon after waterlogging stress. In addition, phenotypic divergence occurred among provenances of the same species under waterlogging stress.

With the increasing frequency and intensity of extreme weather events because of climate change, more frequent rainstorms occur in many areas where existing drainage systems cannot handle the excess. Thus, the lower areas frequently encounter the potential risk of flooding during the rainy season. In forest management, information regarding WT of plant species is necessary to cope with flooding. In addition, ecological restoration in depression areas or flooded watersheds must involve waterlogging-tolerant plant species. To investigate these effects under controlled plant growth conditions, homogeneous components of growth nutrients in solution are necessary for plant physiology research, agricultural nutrition research, and even research under field conditions. A homogeneous nutrient solution is an ideal material for controlling experiments to explore the response of species to factors besides nutrition. Because of hypoxic stress, the growth of the same species differed in soil cultures and hydroculture, although the nutrition reagent was the same. Therefore, evaluation of plant species grown hydroponically can provide important reference information for flooding watershed ecological restoration, as well as for designing hydroponic experiments.

Received for publication 10 Jan. 2019. Accepted for publication 10 Jan. 2019.

This work was supported by the National Natural Science Foundation of China (grant no. 31600307), the Forestry Science and Technology Innovation Project from the Forestry Department of Guangdong Province (grant no. 2017KJCX03), and the Science and Technology Planning Project of Guangdong Province (grant nos. 2015A020209139 and 2015B020207002).

We thank Xiaomei Deng, Hao Huang, Boyong Liao, and Xiangbin Zhou for germinating seeds; Juncheng Li for technical assistance; Xinxing Hu for language improvement; and Rongjing Zhang and Huaming Lian for their valuable information about growth rate of tree seedlings under natural conditions.

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Materials and Methods

Plant materials. All 57 plant species shown in Supplemental Table 1 are indigenous evergreen trees from Guangzhou City and are adapted to tropical or subtropical environments. Seedlings, age 12 to 15 months, were classified into group I. Seedlings age 6 to 11 months were classified into group II. Group I and group II seedlings were collected locally in Feb. 2014. Group III included those seedlings germinated from seeds in Nov. 2013. All seedlings were grown outdoors in a nursing bag (diameter, 8 cm; depth, 12 cm) containing soil with moderate watering before the treatment. In Mar. 2014, after the roots were cleaned thoroughly, seedlings with healthy foliage and sprouts were transplanted individually into plastic pots (diameter, 9.5 cm; depth, 13.5 cm) containing modified Hoagland solution (pH = 6.0; Table 1), such that only the roots were submerged thoroughly in the solution. Provenances of the four species, including Melia azedarach, Toona sinensis, Anthocephalus chinensis, and Mytilaria laosensis were obtained based on the available germplasm resources of our research team. Geographic and environmental information for each provenance are shown in Table 2. Fifty seedlings of each species or provenance were collected initially. During collection, seedlings of the same species or provenance were chosen based on uniformity of size. The modified Hoagland solution in each pot was renewed every 4 d to maintain stable nutrient supplies.

Hydroponic experiments were conducted in a well-ventilated glasshouse without shading from Mar. to May 2014. During the experiments, the indoor air temperature was 16 to 35 °C and the air relative humidity was 60% to 98%.
Seedling growth rate under natural conditions. Seedling growth rate (SGR) was recorded for all groups based on changes in seedling height. Three levels were specified to mark the SGR for each species: Rapid, indicating the SGR was greater than 20 cm/month; Common, for which the SGR was between 10 and 20 cm/month; and Slow, for which the SGR was less than 10 cm/month.

Survival rate calculation. The survival of seedlings was documented every 2 d. During the first week, the number of dead seedlings (D1) was recorded for each species. We attributed a D1 value less than three to root injury during cleaning. However, a D1 value greater than three indicated waterlogging stress.

After 10 weeks, the number of dead seedlings (D2) was recorded again. To exclude those with root injuries caused by cleaning, the survival rate after 10 weeks (SR2) was calculated as follows:

$$SR_2 = \frac{50 - D_1}{50} \times 100\%.$$  

Phenotype assessment. The growth performance of all 57 species was assessed based on leaf growth status every 2 d during the experiment. Growth performance was grouped as follows: A, new leaves had expanded; B, leaves had wilted and dropped from the stem; C, seedlings had grown very slowly or had ceased growing; D, all leaves had dropped rapidly whereas the terminal bud remained alive, which meant that the stem, branch, and terminal bud had not withered until the end of the experiment; and E, the entire plant had withered rapidly.

The regeneration time for leaves for each species was divided into four periods: old leaves, coexisting old and new leaves, no leaves, and new leaves (Fig. 1). Each period was defined as follows: old leaves indicates that all fully expanded leaves existed when the experiment started; new leaves indicates that all leaves expanded fully after the experiment start date; coexisting old and new leaves indicates that at least one old leaf and one new leaf coexisted; and no leaves indicates that no fully expanded leaves existed.

Results

Survival rate. In this study, the D1 values of 22 species were less than three. The SR2 values of nine species were greater than 95%. Of these, Dalbergia odorifera (no. 1), Ficus carica (no. 2), Canavalia ensiformis (no. 3), Jatropha curcas (no. 4), Acacia auriculiformis (no. 5), and Ficus altissima (no. 6) had SR2 values of 100%. Ten species (with different provenances) had SR2 values that ranged from 85% to 95%. Sixteen species had SR2 values between 60% and 85%, 24 species (with different provenances) had SR2 values less than 60%, and the last three species—Zenia insignis (no. 60), Castanopsis fissa (no. 61), and Magnoliaceae glance (no. 62)—had SR2 values of zero (Supplemental Table 1). In total, 60% of the plant species were able to survive in the hydroculture for more than 10 weeks, exhibiting new shoot growth and a survival rate greater than 60%.

Phenotypes. Phenotypes were assessed based on living individuals, except for those species that died rapidly, including Z. insignis (no. 60), C. fissa (no. 61), and M. glanca (no. 62). Overall, from high to low, 32% of the species exhibited phenotypes of A, B, and C combined; 31% were A; 16% were A and B combined; followed by 8%, 5%, 3%, 3%, 2%, and 0% for A and B combined, E alone, B alone, and C combined, D alone, A and C combined, and B alone, respectively (Fig. 3).

Table 1. Modified Hoagland nutrient solution contents (Liu, 2004).

| Component                | Conc (mg L–1) |
|--------------------------|---------------|
| Ca(NO3)2·4H2O           | 472           |
| KNO3                    | 202           |
| NH4NO3                  | 80            |
| KH2PO4                  | 100           |
| K2SO4                   | 174           |
| MgSO4·7H2O              | 246           |
| FeSO4·7H2O              | 27.8          |
| EDTA-2Na                | 37.2          |
| H3BO3                   | 2.86          |
| MnSO4·4H2O              | 2.13          |
| ZnSO4·7H2O              | 0.22          |
| CuSO4·5H2O              | 0.08          |
| (NH4)2MoO4·2H2O         | 0.02          |

Table 2. Geographic and environment information for provenances.

| Provenance               | Geographic location          | Latitude (N) | Longitude (E) | Elevation (m) | Mean annual temp (°C) | Mean annual precipitation (mm) |
|--------------------------|------------------------------|--------------|---------------|---------------|-----------------------|-------------------------------|
| Melia azedarach1         | Conghua, Guangdong, China    | 23°33’       | 113°35’       | 35            | 21.5                  | 1,670                         |
| Melia azedarach2         | Xingyi, Guizhou, China       | 25°04’       | 104°40’       | 1,217         | 16.8                  | 1,512                         |
| Toona sinensis           | Lechang, Guangdong, China    | 25°12’       | 113°33’       | 98            | 19.6                  | 1,522                         |
| Toona sinensis2          | Malipo, Yunnan, China        | 23°12’       | 104°70’       | 1,057         | 18                    | 1,054                         |
| Anthocephalus chinensis1 | Guangzhou, Guangdong, China  | 23°10’       | 113°21’       | 10            | 22.1                  | 1,697                         |
| Anthocephalus chinensis2 | Jinhong, Yunnan, China       | 21°03’       | 101°04’       | 553           | 21                    | 1,197                         |
| Anthocephalus chinensis3 | Nanping, Guangxi, China      | 22°33’       | 108°40’       | 80            | 21.7                  | 1,304                         |
| Mytilaria laosensis1     | Shangsi, Guangxi, China      | 21°53’       | 107°54’       | 412           | 21.5                  | 1,218                         |
| Mytilaria laosensis2     | Ruyuan, Guangdong, China     | 24°57’       | 113°26’       | 84            | 16                    | 2,800                         |

Superscript numbers (1, 2, and 3) after species names represent different provenances of same species.
Fresh biomass growth rate. Species such as *D. odorifera* (no. 1), with common SGR, exhibited an FBGR of 150%, demonstrating excellent adaptation to hydroculture. Younger seedlings, such as those of *C. ensiformis* (no. 3) and *J. curcas* (no. 4), which are classified as III in Supplemental Table 1, showed a greater FBGR, indicating they adapted well to hydroculture because of their rapid SGR and, to some extent, to a relatively low W. However, some species, such as *P. chypearia* (no. 53), *M. laosensis* (nos. 54 and 55), *A. mangium* (no. 56), *Elaeocarpus api- culatus* (no. 57), *Terminalia mantaly* (no. 58), and *A. falcata* (no. 59), exhibited a negative FBGR (Supplemental Table 1), which resulted from leaf loss that exceeded new shoot growth.

In addition, species from different provenances—such as *Melia azedarach* (no. 9) and *M. azedarach* (no. 12); *Toona sinensis* (no. 11) and *T. sinensis* (no. 14); *M. laosensis* (no. 54) and *M. laosensis* (no. 55); and *A. chinensis* (no. 30), *A. chinensis* (no. 38), and *A. chinensis* (no. 41)—displayed little variation in SR and FBGR, and phenotypes among provenances were similar (Fig. 2, Supplemental Table 1).

### WT Rating

In this study, six species with 100% SR were ranked Excellent, including *D. odorifera* (no. 1), *F. concinna* (no. 2), *C. ensiformis* (no. 3), *J. curcas* (no. 4), *C. ensiformis* (no. 3), *J. curcas* (no. 4), *A. auriculiformis* (no. 5), and *F. alitissima* (no. 6). Twelve species, including two with four provenances, were ranked Good. Nineteen species, including one with two provenances, were ranked Ordinary; and 18 species, two of which had three provenances, were ranked Poor. Three species were ranked Very Poor: *Z. insignis* (no. 60), *C. fissa* (no. 61), and *M. glanca* (no. 62) (Fig. 2).

### Discussion

After being grown hydroponically for 10 weeks, the survival rates of 27 species were greater than 60%. However, a number of species did not grow well under waterlogging conditions. This result is consistent with our first hypothesis, that the length of survival under waterlogging stress should be a criterion of primary importance for screening plant species for watershed ecosystem restoration.

Synthesizing the information from Fig. 1 and Supplemental Table 1, we see that species with excellent or good WT soon developed new leaves under waterlogging stress, and old leaves remained alive, whereas species with ordinary or poor WT soon dropped old leaves from the stem under waterlogging stress, although some of them developed new leaves. This indicates that plant species with poor tolerance dropped leaves almost immediately when suffering from waterlogging stress, whereas those species with good WT developed new leaves soon after encountering waterlogging conditions, and dropped fewer old leaves.

Variation in phenotype is related closely to physiological responses under waterlogging. When waterlogged roots become hypoxic, normal cell metabolism is restricted and the physiological activities of aboveground organs are affected accordingly (Kreuzwieser and Rennenberg, 2014). Changes in phenotype occur over time. For example, some plants exhibited leaves that wilted and dropped from the stem under waterlogging, which may be correlated with changes in endogenous abscisic acid, indole acetic acid, gibberellic acid, nitric oxide, and ethylene, among other compounds (Bailey-Serres et al., 2012; Herrera, 2013; Pagnussat et al., 2004) or their ratios (Kim et al., 2015). The effects of endogenous hormones on phenotype under waterlogging vary by genotype and ecotype (Gomathi et al.,...
In the current study, A. chinensis, C. bakeriana, P. clypearia, and M. laosensis were completely defoliated under waterlogging, after which A. chinensis gradually grew new leaves, but the other species remained leafless. Overall, the mechanisms of endogenous hormone regulation of defoliation and growth under waterlogging have not been fully revealed, and further exploration is needed.

Under waterlogging conditions, additional stress can arise because hypoxia or anoxia in the rhizosphere can induce the accumulation of large quantities of reactive oxygen species in roots and aboveground organs. This condition leads to saturation of the active oxygen scavenging system, resulting in increased peroxidation of membrane lipids, soluble sugars, and soluble proteins, as well as increased malondialdehyde production (Irfan et al., 2010). Chlorophyll breakdown also increases (Ye et al., 2003), and photosynthesis is restricted (Visser et al., 2003), inducing rapid death in some intolerant species, such as Z. insignis, M. glance, and C. fissa, according to our study.

Differences in abiotic stress tolerance among provenances of the same species from different climatic zones have been observed (Carsjens et al., 2014; Du et al., 2016; Yildiz et al., 2014), which is contrary to our second hypothesis that phenotypic divergence would not occur among provenances of the same species under waterlogging stress. This variability may be caused by differences among habitats and the duration of provenance separation. In our study, little variation in WT was found for M. azedarach, T. sinensis, M. laosensis, and A. chinensis provenances, although their WT did not exhibit the same trends as precipitation in their location of origin (Table 2). We presumed that WT is, to a large extent, determined by DNA, not the habitat for the species investigated in this study.

Adult trees have been found to be more tolerant to waterlogging than seedlings of the same species (Kreuzwieser and Rennenberg, 2014), and growth conditions of plants in hydroculture differ in certain aspects from those under waterlogging conditions in natural soil because of the vast differences in microelements and microbial communities. In addition, some plant species formed aerenchyma to cope with hypoxia under waterlogging, and thus maintained biomass production (Laan et al., 1991). In our study, Dalbergia odorifera, Ficus concinna, Canavalia ensiformis, Jatropha carcasas, and

Table 3. Metrics and weight values in the determination of waterlogging tolerance class.

| Parameter                        | Abbreviation | Weighting factor Wt value | Value or rank | Assigned value |
|----------------------------------|--------------|--------------------------|---------------|---------------|
| Survival rate after 10 weeks     | SR2          | a                        | 0.800         | Calculated    | N/A           |
| Phenotype                        | phy          | b                        | 0.133         | A             | 1.5           |
|                                  |              |                          |               | B             | 0.8           |
|                                  |              |                          |               | C             | 0.5           |
|                                  |              |                          |               | D             | 0.5           |
|                                  |              |                          |               | E             | 0             |
| Fresh biomass growth rate        | FBGR         | c                        | 0.067         | Calculated    | N/A           |
| Seeding growth rate              | SGR          | d                        | 0.033         | Rapid         | 3             |
|                                  |              |                          |               | Common        | 2             |
|                                  |              |                          |               | Slow          | 1             |

Lower case letters (a, b, c, and d) are weighting factors for SR2, phy, FBGR, and SGR, respectively. Their values are shown as Wt value. Upper case letters (A, B, C, D, and E) are rank marks for phenotype, while Rapid, Common, and Slow are rank marks for SGR. N/A = not applicable.
Acacia auriculiformis, and Ficus altissima exhibited new leaf growth and maintained high biomass production. We speculate that these species might form aerenchyma in hydroculture and should be suitable for use in ecological restoration of flooded watersheds in tropical or subtropical areas.

Taken together, our results indicate that some plant species cannot survive under hydroponic conditions. Evaluation of WT is essential before selecting species for use in hydroponic experiments or in flooding watershed restoration.

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Supplemental Table 1. Phenotypes and biomass growth rates for 57 plant species in hydroculture.

| No. | Name of species                  | SC  | SGR          | Survival rate (%) | Phenotypes† | FBGR (%) |
|-----|----------------------------------|-----|--------------|-------------------|-------------|----------|
| 1   | Dalbergia odorifera               | I   | Common       | 98                | A           | 95 ± 15  |
| 2   | Ficus concinna                    | I   | Common       | 100               | A           | 31 ± 5   |
| 3   | Canavalia ensiformis              | III | Rapid        | 100               | A           | 313 ± 54 |
| 4   | Jatropha curcas                   | III | Rapid        | 100               | A           | 109 ± 18 |
| 5   | Acacia auriculiformis             | I   | Common       | 100               | A           | 53 ± 8   |
| 6   | Ficus altissima                   | I   | Common       | 100               | A           | 28 ± 7   |
| 7   | Michelia chapensis                | I   | Common       | 98                | A           | 22 ± 4   |
| 8   | Michelia mucronei                 | I   | Common       | 96                | A           | 20 ± 2   |
| 9   | Melia azedarach                   | II  | Rapid        | 100               | A           | 50 ± 4   |
| 10  | Phoebe bournei                    | I   | Slow         | 98                | A           | 11 ± 3   |
| 11  | Toona sinensis                   | I   | Slow         | 98                | A           | 68 ± 7   |
| 12  | Toona sinensis                   | II  | Rapid        | 100               | A           | 63 ± 5   |
| 13  | Erythrophleum fordii             | I   | Slow         | 96                | A           | 20 ± 6   |
| 14  | Acacia decurrens                  | II  | Common       | 90                | A           | 65 ± 17  |
| 15  | Albizia lebbeck                   | I   | Common       | 90                | A           | 45 ± 25  |
| 16  | Leucaena leucocephala cv. Salvador | I   | Common       | 92                | A           | 50 ± 8   |
| 17  | Acacia sophorae                   | I   | Common       | 92                | A           | 32 ± 4   |
| 18  | Acacia salicina                   | I   | Common       | 90                | A           | 60 ± 16  |
| 19  | Bischofia javanica                | I   | Common       | 94                | A           | 11 ± 3   |
| 20  | Acacia longifolia                 | I   | Common       | 88                | A           | 12 ± 2   |
| 21  | Acacia spectabilis                | I   | Common       | 86                | A           | 21 ± 8   |
| 22  | Podocarpus nagi                   | I   | Slow         | 96                | A           | 11 ± 3   |
| 23  | Xanthostemon chrysanthus          | I   | Rapid        | 94                | ABC         | 16 ± 9   |
| 24  | Camellia oleifera                | I   | Slow         | 84                | ABC         | 10 ± 6   |
| 25  | Acacia mearnsii                   | I   | Common       | 86                | A           | 25 ± 3   |
| 26  | Acacia melanoxylon                | I   | Common       | 92                | A           | 39 ± 3   |
| 27  | Ilex rotunda                      | I   | Common       | 92                | AC          | 14 ± 1   |
| 28  | Ancephalus chinensis              | II  | Rapid        | 90                | AD          | 5 ± 3    |
| 29  | Castanopsis hystrix               | I   | Slow         | 96                | ABC         | 3 ± 1    |
| 30  | Ficus virens var. sublanceolata   | I   | Common       | 100               | ABC         | 9 ± 4    |
| 31  | Cinnamomum camphora               | I   | Slow         | 98                | ABC         | 5 ± 1    |
| 32  | Acacia maidenii                   | I   | Common       | 98                | ABC         | 12 ± 2   |
| 33  | Syzygium cumini                   | I   | Common       | 98                | ABC         | 13 ± 7   |
| 34  | Cassia surattensis                | I   | Common       | 90                | ABC         | 22 ± 6   |
| 35  | Pinus massoniana                  | I   | Common       | 98                | ABC         | 5 ± 2    |
| 36  | Ancephalus chinensis              | II  | Common       | 92                | AD          | 3 ± 4    |
| 37  | Ormosia pinnata                   | I   | Common       | 94                | ABC         | 16 ± 4   |
| 38  | Acacia crosseirope                | I   | Common       | 80                | ABC         | 5 ± 4    |
| 39  | Ancephalus chinensis              | II  | Common       | 92                | AD          | 1 ± 3    |
| 40  | Grevillea banksii var. forsteri   | I   | Common       | 86                | ABC         | 7 ± 9    |
| 41  | Acacia podalyrifolia              | I   | Common       | 90                | ABC         | 4 ± 2    |
| 42  | Acacia junifolia                  | I   | Common       | 86                | ABC         | 5 ± 3    |
| 43  | Acacia adunca                     | I   | Common       | 86                | AD          | 16 ± 20  |
| 44  | Bauhinia purpurea                 | I   | Common       | 80                | ABC         | 5 ± 4    |
| 45  | Cassia bakeriana                  | I   | Common       | 90                | AD          | 89 ± 20  |
| 46  | Rhodoliae championii              | I   | Common       | 88                | ABC         | 7 ± 13   |
| 47  | Radermacheria hainanensis         | I   | Rapid        | 80                | ABC         | 9 ± 13   |
| 48  | Acacia decurrens                  | I   | Common       | 76                | ABC         | 4 ± 7    |
| 49  | Syygium rehderianum               | I   | Common       | 78                | ABC         | 8 ± 8    |
| 50  | Phoebe shearer                    | I   | Slow         | 80                | BC          | 3 ± 6    |
| 51  | Pithecellobium elyptoearia        | I   | Common       | 80                | AD          | 40 ± 4   |
| 52  | Mytilaria laosensis               | II  | Rapid        | 82                | D           | 200 ± 13 |
| 53  | Mytilaria laosensis               | II  | Rapid        | 78                | D           | 210 ± 15 |
| 54  | Acacia mangium                    | II  | Common       | 82                | ABC         | -11 ± 7  |
| 55  | Elaeocarpus apicatus              | I   | Rapid        | 78                | ABC         | -7 ± 4   |
| 56  | Terminalia mantaly                | I   | Rapid        | 76                | ABC         | -15 ± 3  |
| 57  | Acacia falcata                    | I   | Common       | 50                | BC          | -32 ± 5  |
| 58  | Zenia insignis                    | II  | Rapid        | 72                | E           | —        |
| 59  | Castanopsis fissa                 | I   | Common       | 50                | E           | —        |
| 60  | Magnoliasceae glanca              | I   | Rapid        | 60                | E           | —        |

†SC = seedling age class at time of test. I = ≈15 mo. old; II = ≈8 mo. old; III = ≈3 mo. old.

Phenotypes: A = new shoots grew; B = leaves wilted and dropped from the stem; C = growth slowed or ceased; D = all leaves withered or dropped rapidly with the terminal bud remaining alive; E = the entire plant withered rapidly.

Superscript numbers (1, 2, and 3) after species name represent different provenances of same species.

SGR = seedling growth rate under natural conditions; FBGR = fresh biomass growth rate.