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ORIGINAL RESEARCH

The Structural Adaptation of Aerial Parts of Invasive *Alternanthera philoxeroides* to Water Regime

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Abstract *Alternanthera philoxeroides* has successfully invaded diverse habitats with considerably various water availability, threatening biological diversity in many parts of the world. Because its genetic variation is very low, phenotypic plasticity is believed to be the primary strategy for adapting to the diverse habitats. In the present paper, we investigated the plastic changes of anatomical traits of the aerial parts of *A. philoxeroides* from flooding to wet then to drought habitat; the results are as follows: *A. philoxeroides* could change anatomical structures sensitively to adapt to water regime. As a whole, effects of water regime on structures in stem were greater than those in leaf. Except for principal vein diameter and stoma density on leaf surfaces, all other structural traits were significantly affected by water regime. Among which, cuticular wax layer, collenchyma cell wall, phloem fiber cell wall, and hair density on both leaf surfaces thickened significantly with decrease of water availability, whereas, pith cavity and vessel lumen in stem lessened significantly; wet habitat is vital for the spread of *A. philoxeroides* from flooding to drought habitat and vice versa, because in this habitat, it had the greatest structural variations; when switching from flooding to wet then to drought habitat, the variations of cuticular wax layer, collenchyma cell wall, phloem fiber cell wall, pith cavity area ratio, diameter of vessel lumen, and hair density on both leaf surfaces, played the most important role. These responsive variables contribute most to the adaptation of *A. philoxeroides* to diverse habitats with considerably various water availability.

Keywords *Alternanthera philoxeroides* · Water regime · Structural adaptation · Invasive weed

Introduction

Alternanthera philoxeroides (Martius) Grisebach (Amaranthaceae) (alligator weed) is a notorious invasive weed widespread in the world (Buckingham 1996). It occurs primarily in aquatic habitats, but can successfully invade diverse habitats with considerably varying water availability (from dry terrestrial to aquatic habitats), where it may be rooted into the bank or substrate beneath shallow water, or form independent free-floating mats. It does great harm to the crops when invading agricultural areas and blocking drainage and irrigation channels. It also causes water pollution from plant decomposition. The worst of all is that this species is currently spreading quickly and has become a serious threat to native plant diversity in many parts of the world (Julien et al. 1995). *A. philoxeroides* displays such a strong vegetative reproduction that even small plant fragments are readily established and spread in novel environments (Wang et al. 2005). Since it was introduced into China in the 1930s, it has occurred in most regions of southern China (Ye et al. 2003). At present, it has been listed to be one of the 12 most harmful alien invasive species in the country (Li and Xie 2002).

As an invasive species, it demonstrates resistance to salinity, heavy metals and herbicides (Balagtas-Burow et al. 1993; Eberbach and Bowmer 1995; Naqvi and Rizvi 2000). And the adaptation of vegetative propagation to nutrient enrichment and physical disturbances enables local *A. philoxeroides* populations to grow rapidly, and contributes greatly to the persistence of meta-populations at the watershed scale (Jia et al. 2008). However, despite broad

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ecological amplitudes and great ecological tolerance, the genetic diversity of *A. philoxeroides* as revealed by RAPD and ISSR markers is very low within or among distant populations (Xu et al. 2003, Ye et al. 2003, Wang et al. 2005). Genetic variation is the essential material that allows natural populations to adapt to changes in the environment (Hedrick and Miller 1992). Low genetic variation may weaken the power of natural selection and make local adaption less likely to occur (Conner and Hartl 2004). In such a case, development of phenotypic plasticity, the ability to adapt to varying environments, would highly compensate for the shortcomings of low genetic diversity (Parker et al. 2003; Xu et al. 2003).

The probability of successful invasion depends on the interactions between an exotic invasive species and its new habitat (Sans et al. 2004). In other words, biological invasions are essentially context-specific processes (Alpert et al. 2000; Daehler 2003). To date, the plastic responses of *A. philoxeroides* to abiotic factors, such as growth traits (Pan et al. 2006; Schooler et al. 2007), biomass allocation or morphological traits (Geng et al. 2006; Yu et al. 2007), have been documented, but its responses associated with anatomical structures are not well studied. Because *A. philoxeroides* can adapt to the habitats with very different water availability, it is highly probable that there is a response mechanism in the plant. In the present paper, we performed an experiment to explore its anatomical strategies to deal with water regime.

Materials and Methods

Experimental Site and Material Preparation

This study was conducted in an open marsh area on the campus of Nanchang University, Nanchang City, Jiangxi Province, China, in 2005–2006. The city has a subtropical climate. Its rainy season is from early April to July. So the high-water period of the marsh is in the rainy season and the low-water period is from August to the next March.

For simulation of water regime, an experiment with three “treatments” and three replications was conducted. Each replication consisted of a 3×0.8-m rectangular tank (with drainage holes at the bottom, height 25 cm). In early November 2005, all tanks were filled with the same kind of soil (red soil, pH=4.92). Ramets of *A. philoxeroides* from those growing above water line of the marsh were collected and cut into segments with uniform size of three nodes. Ten segments were cultivated randomly in each of the tanks.

Experimental Design

The study was designed mainly to compare anatomical structures of *A. philoxeroides* growing in field, which were under fairly homogeneous conditions, but subjected to different available water levels. For this purpose, we planted plants in tanks and allocated them in different sites of the marsh area with different water levels, as representative of different treatments (e.g., Gottardini et al. 2008; Mateos-Naranjo et al. 2008; Pan et al. 2006). We recognized that field studies are always subject to possible confounding factors which are difficult to control. To minimize their impact, several actions were undertaken. Firstly, the study domain was restricted to a small area, in or near the marsh (about 3,200 m^2; Gottardini et al., 2008). Secondly, we ensured replication and randomization within each “treatment” replicates (e.g., Gottardini et al. 2008; Mateos-Naranjo et al. 2008; see below), and thirdly, we unified the soil in all tanks.

When the experiment commenced in late April of 2006, the plants in the tanks were subjected to three levels of water “treatment”: (1) flooding (three tanks were allocated in scattered sites in the marsh, where soil in the tanks was always underwater 20–50 cm), (2) wet (three tanks were allocated in scattered sites above water line 1–3 m, where soil in the tanks was always kept saturated), (3) drought (three tanks were allocated in scattered pre-prepared mounds (1.5 m high) 30–35 m away from water line, where soil in the tanks was usually kept dry). The tanks representing replications were randomly allocated in order to allow randomization and interspersion for each treatment. During October 2006, five individuals in each tank were randomly sampled. Thus, a total of fifteen individuals under the same water treatment were collected.

Analytical Procedures

Mature leaves and stems from the sampled individuals were immediately cut into sections (stem section 1–1.5 cm long, leaf section 0.5 cm long) and preserved in formaldehyde acetic acid (FAA) for 48 h. The stem and leaf segments were made into 8-μm thick permanent slices of cross section for light microscopy, using the paraffin-sectioning procedure. In addition, the densities of stomata and hairs on both leaf surfaces were determined with temporary slices of cuticles. The steps to prepare temporary slices of upper cuticle were: (1) removing lower cuticle and mesophyll tissue with a blade, (2) fixing the intact upper cuticle in 95% ethanol for 5 min for optical microscopy. Preparation of slices of lower cuticle was similar. The measurements were performed under an Olympus BX40F-3 microscope. The considered variables were listed in Table 1.

Data Analysis

A two-way analysis of variance (ANOVA) was performed to compare the anatomical attributes of stem and leaf under

Table 1 Characteristics (variables) used in the study and their corresponding units

Stem
Thickness of cuticular wax layer (mm)
Pith cavity area to pith area ratio
Layer amount of collenchyma cells (layers (cross section)$^{-1}$)
Thickness of collenchyma cell wall (mm)
Amount of phloem fibers per vascular bundle (phloem fibers)
Thickness of phloem fiber cell wall (mm)
Amount of vessels per vascular bundle (vessels)
Diameter of vessel lumen (mm)
Leaf
Height of palisade tissue to height of mesophyll tissue ratio
Principal vein diameter (mm)
Amount of vascular bundles in principal vein (vascular bundles)
Density of leaf veins (leaf veins (visual field area)$^{-1}$)
Stoma density of upper epidermis (stomas (visual field area)$^{-1}$)
Epidermal hair density of upper epidermis (hairs (visual field area)$^{-1}$)
Stoma density of lower epidermis (stomas (visual field area)$^{-1}$)
Epidermal hair density of lower epidermis (hairs (visual field area)$^{-1}$)

different water treatments. Standard statistical transformations (arcsine square root) were applied to two ratio variables (i.e., pith cavity area to pith area ratio and height of palisade tissue to height of mesophyll tissue ratio). Discriminant analysis (DA) was conducted to assess whether plant anatomical structure features of stem and leaf as shown in Table 1 could be used to discriminate alligator weed types with different water availabilities. The type sequence assigned for DA was, in turn, flooding, wet, and drought type, each containing 15 individuals. Three DA models were made: Model (1) stem anatomical structure (eight class variables), Model (2) leaf anatomical structure (eight class variables), and Model (3) stem and leaf anatomical structure combined (16 class variables). Principal component analysis (PCA) was employed to identify the importance of all anatomical structure features in switching from flooding to wet and then to drought habitat (16 class variables). ANOVA and DA were done with SPSS (version 11.5), PCA with PC-ORD software package (version 4).

Results

ANOVA of the Anatomical Structure

As a whole, effects of water regime on structures in stem were greater than those in leaf (see *P* and *F* values in Table 2). Except for principal vein diameter, stoma density on both leaf surfaces, all other structural traits were significantly affected by water regime (Figs. 1 and 2; Table 2). For example, thickness of cuticular wax layer, thickness of collenchyma cell wall, thickness of phloem fiber cell wall, and epidermal hair density on upper and lower epidermis increased significantly with water availability decrease, whereas pith cavity area to pith area ratio and diameter of vessel lumen decreased significantly. As for the amount of phloem fibers per vascular bundle, layer amount of collenchyma cells, and amount of vessels per vascular bundle, they showed no significant differences between flooding and wet, but exhibited significant increases between wet and drought. As far as height of palisade tissue to height of mesophyll tissue ratio being concerned, it was significantly lesser under wet than under drought or flood-

Table 2 Results of ANOVA for water condition effects on structural characters

Parameter	*df*	*F*	*P*
TCW	2	21.50	0.000
PC/P	2	18.83	0.000
LACC	2	4.46	0.018
TCCW	2	22.24	0.000
APF	2	8.35	0.001
TPFW	2	16.73	0.000
AV	2	4.25	0.021
DVL	2	27.17	0.000
PT/MT	2	4.06	0.024
DPV	2	0.01	0.988
AVB	2	3.39	0.043
DLV	2	2.59	0.049
SDU	2	0.57	0.572
HDU	2	53.12	0.000
SDL	2	1.93	0.158
HDL	2	29.06	0.000

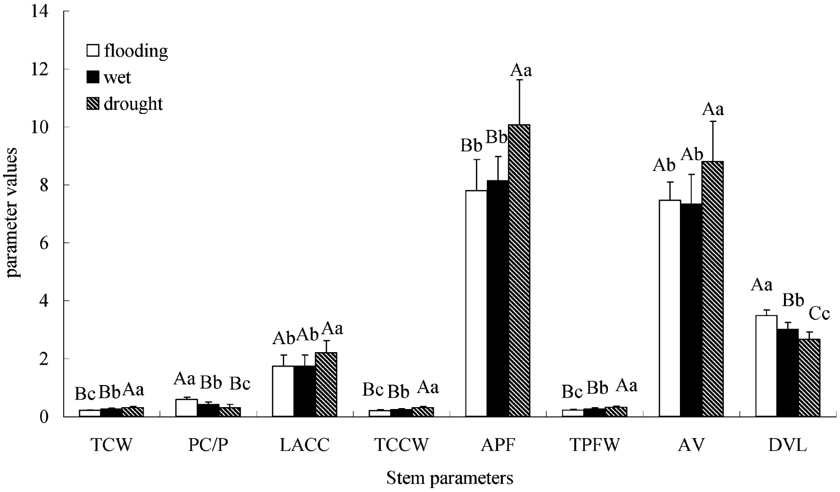

Fig. 1 Differences of stem parameters across a flooding to drought water regime. (1) *TCW* thickness of cuticular wax layer, *PC/P* pith cavity area to pith area ratio, *LACC* layer amount of collenchyma cells, *TCCW* thickness of collenchyma cell wall, *APF* amount of phloem fibers per vascular bundle, *TPFW* thickness of phloem fiber cell wall, *AV* amount of vessels per vascular bundle, *DVL* diameter of vessel lumen. (2) The data were obtained under microscope magnifying the object 100 times. (3) Capital letters mean $P<0.01$; Small letters mean $0.01<P<0.05$; Different capital letters mean significant difference at 1% fiducial interval, and different small letters mean significant difference at 5% fiducial interval; the letter order means the average order of parameters (from large to small)

ing, but no significant difference could be detected between flooding and drought. Density of leaf veins was significantly lesser under wet than under flooding, but not significantly lesser than under drought. At last, a significant variance only between flooding and drought could be discovered for amount of vascular bundles in principal vein.

Multivariate Analysis of the Anatomical Structure

Discriminant analysis, respectively for variables related to stem structure, leaf structure, and stem and leaf structures combined, all indicated complete separation of flooding type from drought type, but poor separation of wet type from the other two (Figs. 3, 4, and 5; Table 3). In Fig. 3, the plot of discriminant function based on stem structure resulted in scores for flooding type oriented in negative direction along the Function 1, while scores for drought type in the positive direction. Between them were scores for the wet type. However, location of wet type along the axis overlapped with those of other two types. DA using leaf features and combining both stem and leaf features indicated similar results of that based on stem features

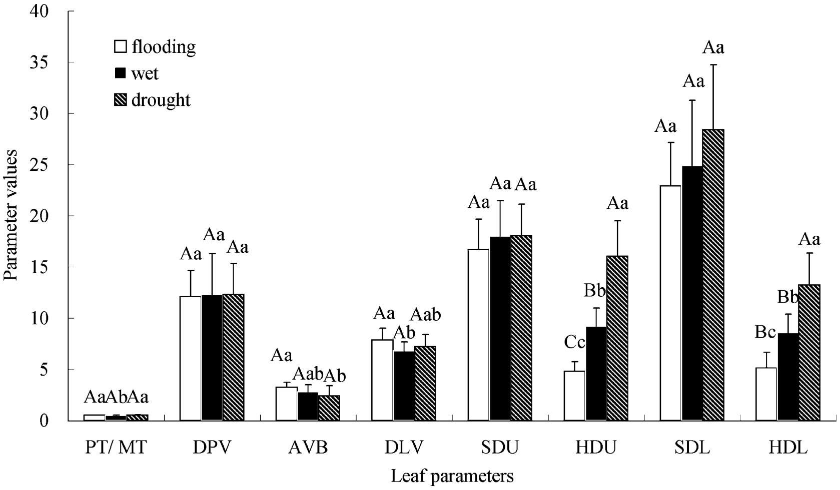

Fig. 2 Differences of leaf parameters across a flooding to drought water regime. (1) *PT/MT* height of palisade tissue to height of mesophyll tissue ratio, *DPV* principal vein diameter, *AVB* amount of vascular bundles in principal vein, *DLV* density of leaf veins, *SDU* stoma density of upper epidermis, *HDU* epidermal hair density of upper epidermis, *SDL* stoma density of lower epidermis, *HDL* epidermal hair density of lower epidermis. (2) Stoma density was obtained under microscope magnifying the object 400 times, while others 100 times

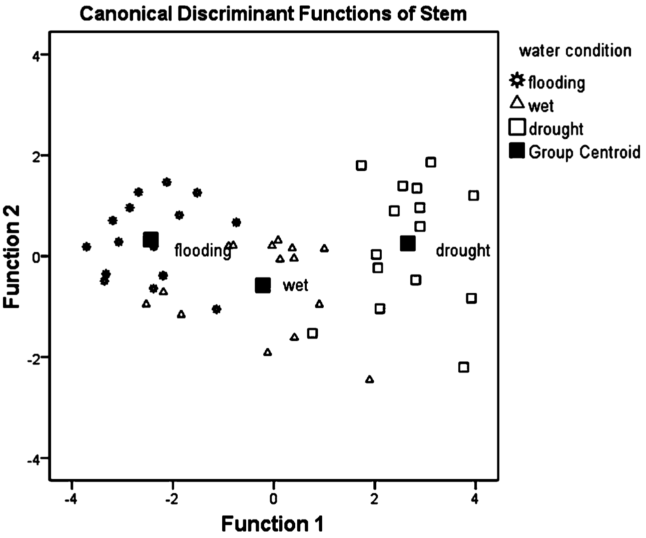

Fig. 3 Scatter plot of the scores of the first two canonical discriminant functions indicating the separation of the classes of water type of stems

(Figs. 4 and 5). Function 1 in Figs. 3, 4, and 5 explained 98.2%, 99.9%, 96.9% of the variance, respectively.

The highest degrees of classification accuracies in the three discriminant analysis were all in drought type (93.3% based on stem feature; 93.3% based on leaf feature; 100% based on stem and leaf features combined), whereas the lowest were all in wet types (66.7% based on stem feature; 80% based on leaf feature; 80% based on stem and leaf features combined; Table 3).

In PCA analysis, the first two axes comprised 46.6% of accumulated variance (Table 4). The responsible variables in the first axis were thickness of cuticular wax layer, thickness of collenchyma cell wall, thickness of phloem fiber cell wall, diameter of vessel lumen, pith cavity area to pith area ratio and epidermal hair density of upper epidermis, and stoma density of lower epidermis, while in the second were principal vein diameter, height of palisade tissue to height of mesophyll tissue ratio, density of leaf veins, and amount of vascular bundles in principal vein.

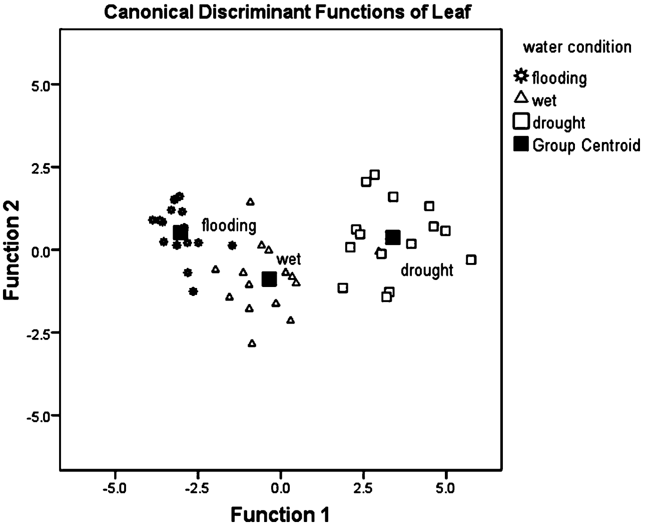

Fig. 4 Scatter plot of the scores of the first two canonical discriminant functions indicating the separation of the classes of water type of leaves

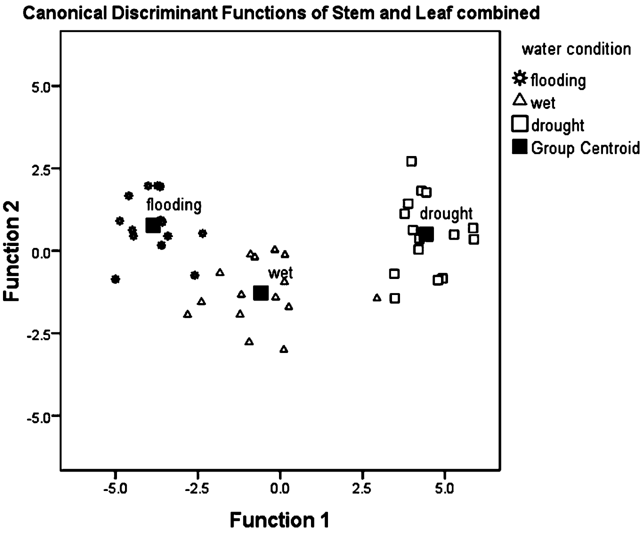

Fig. 5 Scatter plot of the scores of the first two canonical discriminant functions indicating the separation of the classes of water type of leaves and stems combined

Table 4 Loading values of structural characteristics to the first two components in PCA analyses

The first two eigenvectors of stem and leaf combined

Parameters	Axis 1 (34.5%)	Axis 2 (46.6%)
TCW	*−0.35*	−0.22
PC/P	*0.3*	−0.08
LACC	−0.19	−0.11
TCCW	*−0.33*	−0.12
APF	−0.22	−0.17
TPFW	*−0.32*	−0.03
AV	−0.22	0.07
DVL	*0.32*	−0.15
PT/MT	−0.07	*0.52*
DPV	−0.01	*0.57*
AVB	0.22	*−0.32*
DLV	0.06	*−0.39*
SDU	−0.11	0.01
HDU	*−0.36*	*−0.1*
SDL	−0.22	−0.01
HDL	*−0.3*	0.01

The variables whose values are shown in italics were the ones responsible in the corresponding axes

Table 3 Classification accuracies of 15 individuals per water condition in discriminant analysis

Classification and correct classification rate

Original	Stem				Leaf				Stem and leaf combined			
	Flooding	Wet	Drought	%	Flooding	Wet	Drought	%	Flooding	Wet	Drought	%
Flooding	12	3	0	*80*	14	1	0	*93.3*	15	0	0	*100*
Wet	3	10	2	*66.7*	2	12	1	*80*	2	12	1	*80*
Drought	0	1	14	*93.3*	0	1	14	*93.3*	0	0	15	*100*

The percentage of correct classification of different water conditions are shown in italics

Discussion

The Structurally Adaptive Responses to Water Regime

That plant mechanical tissue increase with water availability decrease has been reported in many literatures (Fahn 1982; Schaffer et al. 1992; Nunez-Elisea et al. 1999). *A. philoxeroides* also has the same characteristic. For instance, as water availability decrease, the phloem fiber cell wall, collenchyma cell wall, significantly thickened. Meanwhile, layer amount of collenchyma cells and amount of phloem fibers per vascular bundle also changed similarly (Fig. 1). In addition, the significant increase of amount of vessels per vascular bundle and the significant decrease of diameter of vessel lumen under drought condition also enhanced mechanical function (Fahn 1982; Hacke and Sperry 2001). These changes might be highly helpful for the plant in drier habitat to withstand more rigorous physical twists (Fahn 1982).

Plants in drier habitats often have narrower vessels and higher vessel densities (Britta et al. 2006; Lens et al. 2004; Bañon et al. 2004; Vasellati et al. 2001). This was confirmed in our study. Biologically, cell size is mainly controlled by water availability at the time of cell enlargement (Gonzalez and Eckstein 2003). Hence, diameter of vessel lumen should decrease with decrease of water availability. Functionally, narrower vessel elements (smaller diameter of vessel lumen) could minimize the risk of cell embolism, thus promoting water conduction for *A. philoxeroides* in drier habitats (Hacke and Sperry 2001; Vasellati et al. 2001). However, narrow vessels always meant exponentially less flow than wide ones (Gartner et al. 2002). This shortcoming could be compensated for by more vessels (larger amount of vessels per vascular bundle) to transport sufficient water. As for diameter of vessel lumen and amount of vascular bundles in principal vein, their enlarging under flooding condition could increase water conductivity (Bañon et al. 2004) and thereby, be positive to dissipating redundant water in plant.

That the pith cavity area to pith area ratio became significantly larger was another obvious adaptive response of *A. philoxeroides* to water increase (Pezeshki 1994; Vasellati et al. 2001). A stem with larger pith cavity area could transport more oxygen from aerial parts to underground (or submerged) organs, and conduced to maintain their normal aerobic respiration and nutrient absorption. Moreover, larger pith lacuna could increase the floating ability of stems in flooding to uplift more branches and leaves in the sunlight and air. Therefore, the overall adaptation of this species to flooding habitat could obviously be related to the large areas of pith cavities in stems (Vasellati et al. 2001).

All higher plants carry a partial or continuous coverage of amorphous epicuticular wax. It is extremely important for plant vigor and survival, especially under the changing growth environment (Jenks and Ashworth 1999). Much thicker cuticular wax layer, in drier habitat, filmed on *A. philoxeroides* stem could reduce epidermal conductance of water vapor and protect the plant from excessive water loss (Lakusic et al. 2006). Documents repeatedly reported that stoma density significantly increases with water decrease (Bañon et al. 2004; Kofidis et al. 2007; Lakusic et al. 2006). This seemed to conflict with the water-retaining demand of plants in drier condition, because stomata number plays a positive role in water transpiration. In contrast, for *A. philoxeroides*, stoma density on both leaf surfaces did not increase significantly along water reducing. It is also seemed to imply that in the process of adaptation to water decrease, *A. philoxeroides* had more reasonable adjustment of stoma density than the reported plants. Furthermore, a higher hair density on the upper epidermis of leaf could increase leaf reflectance, thus reducing solar inception and heat load; while the lower epidermis could provide a non-turbulent dead air layer. Both of them reduced evaporation and ultimate water loss (Syros et al., 2006; Kofidis et al. 2007; Lakusic et al. 2006). Leuschner (2002) investigated the long-term impact of water vapor saturation deficit of the air on leaf anatomy of eight woodland herbaceous species, indicating that for all species, a substantially smaller fractional palisade layer always appeared at higher air humidity levels rather than at lower. In our study, the change of height of palisade tissue to the height of mesophyll tissue ratio only between wet and drought condition was consistent with Leuschner's result. It maybe because the leaf response to water vapor saturation deficit in flooding environment differed with that in terrestrial environment. The remarkable smaller palisade tissue ratio under wet condition might serve to improve CO_2 and H_2O exchange inside the leaf mesophyll because of a larger cross-sectional area of the diffusion pathway. Whereas the higher ratio under drought condition might contribute to provide a higher photosynthetic capacity, and turn out to reduce water loss (Wright et al. 2003).

The Characteristics of the Adaptive Responses

The adaptive responses as discussed above have the following characteristics which mainly contribute to the interpretation as to why *A. philoxeroides* can easily invade new environment with different water availability. The structural changes in the four aspects are as follows, relate to the water-retaining capacity of *A. philoxeroides* when water availability decreases: (1) significant thickened leaf hair density, (2) significant increase of cuticular wax layer, (3) significant increase of palisade tissue ratio and (4) more reasonable adjustment of stoma density. Among which, the former two aspects were prior (Table 4). Because leaf hair density and thickness of cuticular wax layer are sensitive to changes in plant physical environments (i.e., temperature, relative humidity, soil moisture; Kim et al. 2007; Baker 1982; Percy et al. 1994), the former two aspects are very easily realized.

The mechanical function directly relates to the cell number and cell size of mechanical tissue (Vasellati et al. 2001; Chen et al. 2006). As for *A. philoxeroides*, mechanical function was enhanced by two ways: (1) strong thickening of the phloem fiber cell wall and collenchyma cell wall and strong narrowing of diameter of vessel lumen (Hacke and Sperry 2001; the three variables belonging to cell size), (2) strong increase of layer amount of collenchyma cells, amount of phloem fibers per vascular bundle and amount of vessels per vascular bundle (the three variables belonging to cell number; Fig. 1, Table 4). Nevertheless, (2) was of minor importance than (1) (Table 4). This suggested that mechanical function was strengthened more by adjusting cell size than by increasing cell number. Because the former could be achieved only by fewer cells, it might be easy and efficient.

The flooding type and drought type formed two distinct groups with overlap of individuals of wet type among them (Figs. 3, 4, and 5). This fact strongly suggested that flooding type was distinct from drought type in anatomical structure, and wet type was transitional between them. Classification accuracies in wet type were always the lowest (Table 3), implying that *A. philoxeroides*, under wet conditions, has the strongest variation capacity in structure. A similar result was obtained by Geng et al. (2006) in morphology and biomass allocation. Therefore, we conjecture that wet habitat might be vital for the spread of alligator weed from flooding to drought habitat (or from drought to flooding habitat) because in wet habitat, it could develop into anatomical structures belonging to those in both flooding and drought habitat. This might be the partial reason why alligator weed is widespread in areas with more rain.

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