EXAMINING THE SHADE/FLOOD TOLERANCE TRADEOFF HYPOTHESIS IN BOTTOMLAND HERBS THROUGH FIELD STUDY AND EXPERIMENTATION

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While there is growing evidence that shade/flood tolerance tradeoffs may be important in distributions of bottomland hardwood trees and indications that they should apply to herbs, no studies have definitively explored this possibility. Four years of field data following historic flooding were supplemented with a greenhouse experiment designed to identify interactions congruent with tradeoffs. Fifteen bottomland species were grown in two levels of water availability and three levels of shade over 10 weeks.

Results indicate responses of *Fimbristylis vahlii* and *Ammannia robusta* are consistent with tradeoffs. Modification of classical allometric responses to shade by substrate saturation indicates a potential mechanism for the tradeoff in *A. robusta*. Responses indicating potential for increased susceptibility to physical flooding disturbance are also discussed.
ACKNOWLEDGEMENTS

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# TABLE OF CONTENTS

**ACKNOWLEDGEMENTS** ........................................................................................................................... iii

**LIST OF TABLES** ........................................................................................................................................ vi

**LIST OF ILLUSTRATIONS** .................................................................................................................... x

**INTRODUCTION** ........................................................................................................................................ 1

- Bottomland Hardwood Forests .................................................................................................................. 1
- History and Development of the Shade/Flood Tolerance Tradeoff Hypothesis ........................................ 2
- Objective .................................................................................................................................................. 10

**MATERIALS AND METHODS** .................................................................................................................. 12

- Field Study .............................................................................................................................................. 12
- Greenhouse Study .................................................................................................................................. 16

**RESULTS** ................................................................................................................................................ 22

- Field Study Community Dynamics ...................................................................................................... 22
- Greenhouse Study .................................................................................................................................. 30

- *Carex hyalinolepis* ................................................................................................................................. 30

- *Bromus pubescens* ................................................................................................................................. 33

- *Elymus virginicus* ................................................................................................................................. 37

- *Eupatorium coelestinum* ........................................................................................................................ 41

- *Rumex crispus* ....................................................................................................................................... 44

- *Eclipta prostrata* ................................................................................................................................... 48

- *Dicliptera brachiata* ............................................................................................................................... 51

- *Cyperus erythrorhizos* ........................................................................................................................... 55
LIST OF TABLES

Table 1  Comparison of tradeoff patterns reported for species in published literature ..... 7
Table 2  Greenhouse study species and their tolerances .............................................. 16
Table 3  List of transformations performed on response data for each species.............. 21
Table 4  CA scores for species associated with the fall 2007 sampling....................... 29
Table 5  Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of Carex hyalinolepis. ........ 30
Table 6  Effects of shade on the performance of Carex hyalinolepis. ......................... 33
Table 7  Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of Bromus pubescens ...... 34
Table 8  Effects of shade on the performance of Bromus pubescens ......................... 34
Table 9  Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of Elymus virginicus ....... 37
Table 10 Effects of shade on the performance of Elymus virginicus .......................... 40
Table 11 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of Eupatorium coelestinum 41
Table 12 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of Rumex crispus .......... 45
Table 13 Effects of shade on the performance of Rumex crispus .............................. 48
Table 14 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of Eclipta prostrata .......... 48
Table 15 Effects of shade on the performance of Eclipta prostrata .............................. 51
Table 16 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of *Dicliptera brachiata* ........... 52

Table 17 Effects of shade on the performance of *Dicliptera brachiata* ......................... 52

Table 18 Effects of water availability on the performance of *Dicliptera brachiata* .......... 55

Table 19 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of *Cyperus erythrorhizos*... 55

Table 20 Effects of water availability on the performance of *Cyperus erythrorhizos*..... 58

Table 21 Effects of shade on the performance of *Cyperus erythrorhizos*. ................. 58

Table 22 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of *Ammannia robusta* ........... 59

Table 23 Effects of water availability on the performance of *Ammannia robusta*........... 59

Table 24 Effects of shade on the performance of *Ammannia robusta* ......................... 62

Table 25 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of *Bidens frondosa*......... 63

Table 26 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of *Sorghum halepense*.... 66

Table 27 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of *Solidago* sp................. 71

Table 28 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of *Carex crus-corvi*......... 76

Table 29 Effects of shade on the performance of *Carex crus-corvi*. ......................... 76
Table 30 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of Cardiospermum halicacabum. .............................................................. 77

Table 31 Summary table of two-way ANOVA assessing the effects of shade, water availability and their interaction on the performance of Fimbristylis vahlii .............. 81

Table 32 Effects of shade on the performance of Fimbristylis vahlii ........................................ 81

Table 33 All possible seedling tolerance combinations to shaded (S), lighted (L), saturated (SA) and drained (DR) conditions......................................................... 84

Table 34 Results summary of Spearman rank correlation of field distribution for select greenhouse study species with regard to percent canopy cover and elevation .. 96

Table A.1 List of all species represented over four years of sampling in the Lake Lewisville/Ray Roberts Greenbelt Corridor with WIS and native status .......... 113

Table A.2 Fall 2007 sampling summary with species, WIS and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor ...................... 116

Table A.3 Spring 2008 sampling summary with species, WIS and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor ...................... 117

Table A.4 Fall 2008 sampling summary with species, WIS and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor ...................... 119

Table A.5 Spring 2009 sampling summary with species, WIS and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor ...................... 121

Table A.6 Fall 2009 sampling summary with species, WIS and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor ...................... 122
**Table A.7** Spring 2010 sampling summary with species, WIS and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor ......................... 124

**Table A.8** Fall 2010 sampling summary with species, WIS and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor .......................... 126

**Table A.9** Spring 2011 sampling summary with species, WIS and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor ......................... 128
LIST OF ILLUSTRATIONS

Fig. 1 Hypothetical response for a species exhibiting a shade/flood tolerance tradeoff. 11
Fig. 2 Flooding in the Greenbelt Corridor .............................................................. 12
Fig. 3 Greenbelt Corridor sampling site .............................................................. 13
Fig. 4 Greenhouse experiment block schematic ............................................... 17
Fig. 5 Greenhouse experiment shade enclosure specifications .......................... 18
Fig. 6 Greenhouse experiment water level manipulation ................................... 18
Fig. 7 Species richness for each seasonal sampling by wetland indicator status (WIS) 23
Fig. 8 Relative frequency for each seasonal sampling contributed by WIS categories. 26
Fig. 9 Correspondence analysis by sampling plot of all data since the flooding event in the summer of 2007 ................................................................. 28
Fig. 10 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of Carex hyalinolepis ................................................................. 31
Fig. 11 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of Carex hyalinolepis ................................................................. 32
Fig. 12 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of Bromus pubescens ................................................................. 35
Fig. 13 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of Bromus pubescens ................................................................. 36
Fig. 14 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of Elymus virginicus ................................................................. 38
Fig. 15 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of Elymus virginicus ................................................................. 39
Fig. 16 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of *Eupatorium coelestinum* ................................................................. 42

Fig. 17 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Eupatorium coelestinum* ................................................................. 43

Fig. 18 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of *Rumex crispus* ............................................................................................................................................... 46

Fig. 19 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Rumex crispus* ............................................................................................................................................... 47

Fig. 20 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Eclipta prostrata* ............................................................................................................................................... 49

Fig. 21 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Eclipta prostrata* ............................................................................................................................................... 50

Fig. 22 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Dicliptera brachiata* ............................................................................................................................................... 53

Fig. 23 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Dicliptera brachiata* ............................................................................................................................................... 54

Fig. 24 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Cyperus erythrorhizos* ............................................................................................................................................... 56

Fig. 25 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Cyperus erythrorhizos* ............................................................................................................................................... 57

Fig. 26 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Ammannia robusta* ............................................................................................................................................... 60
Fig. 27 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Ammannia robusta* ................................................................. 61

Fig. 28 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Bidens frondosa* ................................................................. 64

Fig. 29 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Bidens frondosa* ................................................................. 65

Fig. 30 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Sorghum halepense* ................................................................. 67

Fig. 31 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Sorghum halepense* ................................................................. 68

Fig. 32 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Solidago sp.* ................................................................. 70

Fig. 33 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Solidago sp.* ................................................................. 72

Fig. 34 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Carex crus-corvi* ................................................................. 74

Fig. 35 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Carex crus-corvi* ................................................................. 75

Fig. 36 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Cardiospermum halicacabum* ................................................................. 78

Fig. 37 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Cardiospermum halicacabum* ................................................................. 79
Fig. 38 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of *Fimbristylis vahlii* ........................................................................................................................................... 82

Fig. 39 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Fimbristylis vahlii* ........................................................................................................................................... 83

Fig. 40 General response pattern illustrating a positive response to shade only with no effect of water or interaction ................................................................................................................. 85

Fig. 41 General response pattern illustrating a positive response to shade and an interaction characterized by the most pronounced differences between water availability treatments at the highest level of shade.............................................. 85

Fig. 42 General response pattern illustrating a positive response to shade and a positive response to substrate saturation with no interaction effect................................. 86

Fig. 43 General response pattern illustrating a positive response to shade and an inhibitory effect of substrate saturation with no interaction effect .......................... 87

Fig. 44 General response pattern illustrating an inhibitory effect of substrate saturation. ......................................................................................................................... 87

Fig. 45 General response pattern illustrating no effect of shade, water or interaction .. 88

Fig. 46 General response pattern illustrating an interaction in which the differences between water treatment means were most pronounced at the intermediate shade level .......................................................................................................................... 88

Fig. 47 General response pattern illustrating a positive response to shade and an interaction characterized the greatest differences between water treatment means in open conditions......................................................................................... 89
**Fig. 48** General response pattern illustrating a positive response to shade in saturated treatments and an interaction characterized by a reversal in the relationship between water treatment means with increasing shade ........................................... 90

**Fig. 49** General response pattern illustrating a negative response to shade and an interaction characterized by the greatest difference between water treatment means under open conditions............................................................................. 90

**Fig. 50** Potential general response pattern characterized by an interaction in which a negative effect of shade is only apparent in saturated treatments.................... 92

**Fig. 51** Amended general response pattern illustrating a negative response to shade with no interaction effect........................................................................................................... 93

**Fig. 52** DCA of all sampling data for species included in the greenhouse study........... 95
INTRODUCTION

Bottomland Hardwood Forests

Since 1950, freshwater forested wetlands in the US have experienced some of the greatest area losses among wetland types (Zedler and Kercher 2005). In the state of Texas, up to 60% of the bottomland hardwood forests (BHF) that existed prior to European settlement have been lost (Frye 1987). Major factors contributing to wetland loss in BHF include clearing for urban and agricultural development and flooding as a result of reservoir construction. By 1987, it was estimated that 600,000 acres of BHF were lost to reservoir construction alone (Frye 1987). Projected impoundment projects are expected to inundate an additional 52,667 acres of bottomland hardwood and riparian forests by the year 2047 (Texas Water Development Board 1997). Additional losses via indirect impacts are also anticipated (TPWD 1997). For example, Johnson et al. (1976) observed decreases in the extent of downstream floodplain forest cover following a dam project on the Missouri River and the collapse of downstream forests was documented in other areas (Rood and Mahoney 1990).

Impoundments and other consequences of rapid urbanization such as increased surface run-off, have resulted in the alteration of historic hydrological patterns. In addition to the inundation of habitat upstream of dam sites, these structures regulate water level fluctuations, alter downstream flow regimes, and result in a falling groundwater table (Nilsson and Berggren 2000). Many studies have shown flow regulation to influence riparian vegetation (e.g. Williams & Wolman 1984; Rood & Mahoney 1990; Nilsson et al. 1991; Friedman et al. 1998; Nilsson & Berggren 2000).
and impoundments are known to result in “long-term biological modification” (TPWD 1997).

BHFs are a type of deciduous hardwood forest found in broad floodplains along rivers and streams of the southeastern and south central United States. They experience occasional or seasonal overbank flooding and commonly consist of *Nyssa* sp., *Quercus* sp., *Taxodium distichum* and other species capable of surviving periodic inundation. These habitats support diverse assemblages of flora and fauna; and perform a variety of valued ecosystem functions including: flood and erosion control, aquifer recharge and contaminant removal (Walbridge 1993; Kellison and Young 1997). Given these crucial roles, restoration and conservation of BHFs is advocated (Stanturf et al. 2001). Because ecosystem processes in wetland habitats are reliant on vegetation (Cronk and Fennessey 2001) and riparian vegetation is susceptible to altered flow regimes, an understanding of vegetation dynamics along regulated rivers is necessary to facilitate restoration and conservation efforts and manage ecosystem functions.

History and Development of the Shade/Flood Tolerance Tradeoff Hypothesis

Shade/flood tolerance tradeoffs represent the most prominent hypothesis currently available to account for the distribution of BHF tree species. And while the inception of the hypothesis dates back to early field studies on herbs, this aspect has been relatively little studied. In fact, the inclusion of these early studies as justification for potential tradeoffs in trees has lead to some ambiguity in the testing of the hypothesis. This, along with gaps in knowledge, will be addressed in terms of the history and development of the hypothesis.
It has been suggested that high stress coupled with frequent disturbance prohibits plant adaptation to a habitat (Grime 1979). In their treatise on BHF's, Wharton et al. (1982) noted the characteristically sparse groundcover vegetation in more frequently inundated areas of the floodplain and described the absence of understory herbs as a function of “hydroperiod and light intensities”. The following year, Menges and Waller (1983) described a smaller proportion of light generalists at lower, compared to higher elevations. They indicated that understory herbs inhabiting the lower elevations were typically high light specialists and thick canopy cover often entirely prevented plant growth in these areas. In support of Grime (1979), they concluded that, together, low light and frequent flooding were too harsh to support plant growth. Multivariate analyses used to correlate species distributions with environmental gradients produced similar findings at the same sites (Menges 1986).

Greater flood induced mortality in shade tolerant tree species (*Acer rubrum* and *Carpinus caroliniana*) than shade intolerant species (*Betula nigra*, *Nyssa aquatica* and *Taxodium distichum*) was observed in a study of seven forests in the southeastern coastal plain, intimating that interactions between shade flood tolerance may be important in structuring these communities (Jones et al. 1994). Additionally, the finding that seedlings of the shade-intolerant canopy dominant *Liquidambar styraciflua* were more common in forests with regular flooding (Jones et al. 1994) lead them to the conclusion that interactions between shade and flooding may produce dominance by shade intolerant species rather than the more shade tolerant community expected in the absence of a large scale disturbance (Hodges 1997).
Hall and Harcombe (1998) cited these and other observations as justification for interactions between shade and flood tolerance in floodplain saplings. In their study, canonical correspondence analysis (CCA) of floodplain saplings revealed relative elevation (a surrogate for flood frequency, intensity and duration) and light availability to be influential in species distribution. However, while published flood tolerance ratings were consistent with species distribution along the ordination axis, there was little agreement with shade tolerance ratings. All but one of the most shade tolerant species were positioned higher on the available light gradient than expected, while some species of intermediate shade tolerance were shifted toward lower light levels. Additionally, observed dominance by shade intolerant species supported the suggestion of Jones et al. (1994) that flooding may preclude successional replacement by shade tolerant species.

Because species found under lower light conditions than expected were among the most flood tolerant and most of the shade tolerant species were found in high or intermediate light conditions, Hall and Harcombe (1998) hypothesized that the disagreement between shade tolerance and observed species distributions was due to species-specific interactions between shade tolerance and flooding. Specifically that flood tolerance may facilitate the persistence of some species in lower light conditions than is typical and, conversely, that flood intolerance may restrict shade tolerant species to canopy gaps.

This statement, in conjunction with the parallels drawn between their study and those of floodplain herbs (Menges and Waller 1983; Menges 1986) has lead to a degree of ambiguity in the subsequent interpretation of shade/flood tolerance tradeoff patterns.
Specifically, it has created a situation in which the lack of a high degree of tolerance to both factors and demonstrated tolerance to both factors can each be considered evidence for a tradeoff. For example, it was suggested that the lack of classification of BHF trees as both highly shade and flood tolerant (McKnight et al. 1981) indicates the importance of tradeoffs in community structure of these forests (Battaglia and Sharitz 2006). This idea conflicts with the specific criteria laid out by Hall and Harcombe (1998) regarding facilitation. The word tradeoff suggests a compromise between two desirable, yet incompatible traits, an implication which is at odds with the idea that flood tolerance may facilitate survival in the shade. And while Hall and Harcombe (1998) did not use “tradeoff” to describe the interactions suggested in their study, it has been referenced and subsequently treated this way in literature.

Battaglia et al. (2004) used published shade and flood tolerance ratings, dispersal mechanisms, and seed size to determine regeneration strategies useful in identifying tradeoffs. Empirical data were compared with PCA derived strategies to test the predictive power of the model. In general, distribution ranges of seedlings with different published tolerance levels exhibited considerable overlap. In the absence of light limitation, highly shade tolerant species with low to moderate published flood tolerance (Celtis laevigata, Diospyros virginiana, Ulmus americana, and Ulmus crassifolia), were found in elevations lower than expected, indicating that some species may be more tolerant of flooding when light availability is not limiting. Data from a separate field site also showed distributions of most shade tolerant species (Acer rubrum, C. laevigata, Ilex decidua, I. opaca, and Ulmus spp.) assessed to be higher on the available light gradient than expected.
Lin et al. (2004) provided evidence that flooding did not modify actual shade tolerance, but instead, imposed additional mortality on individuals of some shade tolerant species. They found unusually high mortality risks in two shade tolerant species (A. rubrum and C. caroliniana) during a period of flooding. Annual death rates for these species were significantly higher than in the periods preceding and following the flooding event. Additionally, comparisons with a proximate mesic site, indicated mortality risk for A. rubrum was greater at the floodplain site in all but the lowest light levels.

Battaglia and Sharitz (2006) found three taxa exhibiting patterns they deemed consistent with the flood/shade tolerance trade-off hypothesis. U. americana appeared tolerant of shade when released from flooding while Fraxinus pennsylvanica and Quercus spp. were more tolerant of flooding when released from shade. A. rubrum was tolerant of a wide range of conditions. In contrast with expectations of the flood/shade tolerance trade-off hypothesis, it was found that occurrence of this species was more probable in higher light conditions at the drier, rather than the wetter end of the distance to water table gradient.

Mann et al. (2008) considered a die-off of ironwood (Carpinus caroliniana) within the framework of the flood shade tolerance trade-off hypothesis. Following a flooding event, C. carolinana was the only important forest species to experience a large decline in abundance and basal area. They assert that its short stature, low flood tolerance and high shade tolerance made it “uniquely susceptible to inundation”. C. carolinana is ranked among the least flood tolerant species in the system and greater mortality due to flooding is expected. Shade intolerant oak species (Q. michauxii and Q. nigra), which
are sometimes given a similar flood tolerance rating, did not show a decline following the flood. This indication of greater flood tolerance, taken with shade intolerance is considered further evidence of a tradeoff.

In a study documenting gap fillers in an Arkansas floodplain forest, King and Antrobus (2005) found results partially in support of flood/shade tolerance tradeoffs. While definitive gap fillers of some shade intolerant species (*Fraxinus spp.*) occurred at lower mean elevations than those of shade tolerant species (*Acer rubrum* and *Ulmus americana*), as a whole, the community is progressing toward dominance by shade tolerant species. They contribute the lack of limitation on shade tolerant species to flooding disturbances of lower frequency, magnitude, or duration at the site.

**Table 1** Comparison of tradeoff patterns reported for species in published literature. Species are listed according to published shade tolerance from most to least tolerant (Burns and Honkala 1990, McKnight et al. 1981). ● = patterns consistent with a tradeoff, o = no tradeoff observed, -- = species not included in study. H&H= Hall and Harcombe (1998), BCS = Battaglia et al. (2004), LHFH = Lin et al. (2004), B&S = Battaglia and Sharitz (2006), MHEH = Mann et al. (2008), K&A = King and Antrobus (2005)

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Though there was disagreement in patterns observed for some species shared between studies, others had indications of tradeoffs which were consistently confirmed (Table 1). *U. americana* and *F. pennsylvanica* were the most notable, with each of four and three studies respectively, confirming patterns which indicate tradeoffs. Complete agreement was also observed in *I. opaca*, however, it was only included in two of the studies. Considerable verification was also found for a tradeoff in *A. rubrum*, but there was disagreement from Battaglia and Sharitz (2006). Indications of a tradeoff for *C. caroliniana* were found in three of four studies, though it is important to note that all in agreement were conducted at the same site.

There also exists disagreement regarding the mechanism by which tradeoffs influence woody vegetation in bottomlands. While some studies have provided evidence that shading may alter flood tolerance and vice versa (Battaglia et al. 2004; Battaglia and Sharitz 2006), others have shown increased mortality under flooded conditions (Lin et al. 2004; Mann et al. 2008) and suggested that actual tolerances are not modified (Lin et al. 2004). These concepts are not mutually exclusive of necessity. For example, a modification of flood tolerance imposed by shading may lead to increased mortality under flooded conditions. However, Lin et al. (2004) did provide evidence that the actual shade tolerance is not modified by flooding in at least some species. The disagreement regarding the action through which tradeoffs manifest, taken with inconsistencies in observed tradeoff patterns and the ambiguity regarding what constitutes a tradeoff indicates the need for further investigation into shade/flood tolerance tradeoff patterns.

Hall and Harcombe (1998) view their hypothesis in the context of a broader growth-survivorship tradeoff proposed by Kobe et al. (1995) which specifically applies to
shade tolerance in long-lived species. However, high-light growth strategies may also allow groundcover species to escape flooding disturbance. This may be accomplished by avoiding it temporally, as in the case of ruderal annuals (Menges and Waller 1983). Or high light may facilitate the rapid shoot elongation shown to allow the escape of flood waters (Osborne 1984; Jackson 1985; Van der Sman et al. 1993).

Despite indications of the importance of elevation and canopy cover on the distribution of floodplain herbs (Wharton et al. 1982; Menges and Waller 1983; Menges 1986) and their treatment as analogues, studies of this nature are relatively rare. There has been only one study corroborating the findings of Menges and Waller (1983) at other sites. And while Siebel and Bouwma (1998) supported their conclusions regarding the inability of tall herb species to tolerate simultaneous shade and flooding, comprehensive field studies which confirm this pattern at other sites are lacking. In addition, there have been relatively few studies addressing the influence of interactions between flooding and shade on herbaceous plant species (Dale and Causton 1992; Lennsen et al. 2003), regardless of the framework in which interactions were viewed. This indicates a need for studies documenting responses of herbaceous species to water and light availability in general. Additionally, these studies were not designed to identify tradeoffs and therefore provide limited insight on their role in wetland herbs. So, while there is growing evidence that shade/flood tolerance tradeoffs may be important in the distributions of some tree species and there are indications that they should also apply to herbaceous species, no studies have definitively explored this possibility.
Objective

The objective of this project was to determine whether BHF herbs comply with the expectations of the flood/shade tolerance tradeoff hypothesis, utilizing field and greenhouse studies. Four years of field data were supplemented with a greenhouse experiment in order to identify patterns congruent with the hypothesis and determine whether its scope should include herbaceous species. Specific questions to be addressed include:

- What changes has the herbaceous plant community in the Lake Lewisville/Ray Roberts Greenbelt Corridor experienced following a major flooding event?
- How do select Greenbelt species respond to shade, water availability and their interaction in a greenhouse environment?
- What response patterns, if any, do these species share?
- Do patterns have predictive power with regard to field distributions?
- Are patterns consistent with the expectations of the flood/shade tolerance tradeoff hypothesis?
- Does the alteration of classical response patterns such as leaf expansion and biomass allocation predict mechanisms for tradeoffs in BHF herbs?

For the hypothesis to be supported in the greenhouse study, species must display interactions which illustrate enhanced flood tolerance in the absence of shade or enhanced shade tolerance in the absence of flooding (Fig. 1). Additionally, interactions which meet the expectation that species are not considered to be highly tolerant of both shade and flooding will also be considered supportive. Interactions indicating an
enhanced tolerance of shade facilitated by flood tolerance will be considered separately. Responses without significant interaction effects will not be considered, as this demonstrates the independence of the two factors.

Observed tradeoff patterns must be consistent with field distributions to corroborate the tradeoff hypothesis in this aspect. Finally, it is anticipated that species exhibiting tradeoff patterns will also be subject to the alteration of classical responses to shade. Morphological changes which have adaptive value under low light such as leaf area expansion and increased allocation to shoot biomass may be prevented or reduced in the presence of substrate saturation. Specifically, it is expected that leaf expansion will be inhibited by flooding.

Increased root/shoot ratios due to inhibition of shoots by substrate saturation is attributable to the action of roots as a carbohydrate sink in anaerobic respiration. Conversely, root tissue death in the presence of hypoxic conditions may produce further reduction of root/shoot ratios than shading alone, representing a situation in which this response does not constitute an adaptive advantage.
MATERIALS AND METHODS

Field Study

Following heavy rainfall throughout the spring of 2007, the Trinity River watershed experienced record flooding. Peak flooding exceeded 100 year flood levels, reaching depths ca. 2.3 m. Our study area within the Greenbelt Corridor remained inundated for 45 days (from July 8, 2007 to August 10, 2007; Fig. 2). All herbaceous groundcover vegetation apart from a single Carex species experienced mortality. This provided a unique opportunity to assess the composition of herbaceous groundcover species re-colonizing the area.

The study area, a remnant bottomland hardwood forest within the Greenbelt Corridor (GBC) is located between two reservoirs (Lake Ray Roberts and Lake Lewisville) along the Elm Fork of the Trinity River. Historically a bottomland hardwood forest surrounded by oak-savannah uplands, this area is now a patchy mix ranging from open grassy areas to late succession forest (Holcomb 2001) lying within a matrix of suburban and agricultural land uses.

After flood waters receded, fourteen permanent plots (Fig. 3) were established subjectively based on the composition of herbaceous vegetation recolonizing the area.
Fig. 3 Greenbelt Corridor sampling site. The Ray Roberts/Lake Lewisville Greenbelt Corridor lies between two reservoirs along the Elm Fork of the Trinity River. Thirteen of fourteen permanent sampling plots (25m x 25m) lie in the southern reaches of the GBC, just north of Lake Lewisville. The final site is more centrally located between the two reservoirs to the north of this cluster. Map courtesy of Amanda Turley
Plots are GIS (Geographic Information Systems) tagged with a handheld portable GPS device (Trimble Geo XT, GeoExplorer 2008 Series; Trimble Navigation Limited) outfitted with a Hurricane L1 antenna (Trimble Navigation Limited). Plots measure 25m x 25m and are divided into 25 subplots of 5m x 5m each. Within each subplot, a random point was assigned for sampling.

Since the initial sampling in October 2007, plots have been evaluated semiannually in the late spring and early fall to determine long term plant community response to the flooding disturbance. Frequency data were collected using a nested plot design as described in the Bureau of Land Management’s Interagency Technical Reference (ITT 1996). To ensure appropriate quadrat size, data collection was carried out with a square nested quadrat frame with sections measuring 10cm, 20cm, 35cm and 65cm on a side.

In addition to the continuation of vegetation sampling, plots were characterized by environmental factors in the fall of 2010, under the assumption that those chosen will have changed only marginally over time. These measurements are considered applicable since forest structure was little affected by the flood and trees are expected to undergo relatively slow growth. Percent canopy cover was estimated from cover photographs as described by MacFarlane et al. (2007). Cover photographs were obtained with a Nikon D40X digital SLR camera (Nikon Inc.) using a Nikon DX AF-S Nikkor 18-55mm lens (Nikon Inc.) on a leveled tripod with the zoom set to allow maximum information to be captured within the frame. Images were taken during full leaf-out at each of 25 random points per study plot and analyzed using Adobe Photoshop CS4 software (Adobe Systems Inc.). MacFarlane et al. (2007b) also
described a novel approach to cover image analysis utilizing an earlier version of this widely available and comparatively affordable software, yielding similar results to more specialized programs. Additionally, elevation data were extracted from a DEM (Digital Elevation Model) of the Elm Fork watershed for each site using ArcMap 9 GIS software (ESRI, Inc.) Elevation data has long been accepted as a surrogate for hydrological factors such as flooding intensity, duration and distance to water table (Menges 1986 and citations within).

Evaluation was conducted with consideration to wetland indicator status (WIS) in order to better understand the long term impacts of altered hydrology on the study area. Wetland indicator status for region 6 was obtained from the USDA/NRCS PLANTS database (2010). WIS categories indicate the probability of a species being found in a wetland versus upland environment and include five categories (obligate wetland species, facultative wetland species, facultative species, facultative upland species and upland species). These categories range from the highest to lowest probability of being encountered in a wetland habitat.

Ordination of plant community data were generated using R statistics software (R Program Development Team 2010). CA (Correspondence Analysis) was formulated using all community data collected since the flooding event. DCA (Detrended Correspondence Analysis) of field distributions of greenhouse study species was used to evaluate the utility of response patterns uncovered in the greenhouse study. DCA was chosen due to an arc effect in CA analysis of the data. Spearman rank correlations were used to determine if relationships between field distributions and percent canopy
cover and between field distributions and elevation were consistent with response patterns exhibited in the greenhouse study.

Greenhouse Study

Fifteen species (Table 2) were chosen from the community at the long term sampling site located within the GBC. Efforts were made to include species with a range of published tolerances to shade and anaerobic substrate conditions (Table 2). However, since this information is not available for many herb species, temporal field distributions were also used to aide in the selection of species. Therefore, selection of

Table 2 Greenhouse study species and their tolerances to shade and anaerobic conditions (flood) as listed by the USDA (2010). I - intolerant, M - intermediate, T - tolerant, H - high, L - low. Species without values have no published tolerance limits. Nomenclature follows Diggs et al. (1999)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Species</th>
<th>Shade</th>
<th>Flood</th>
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<td>Dicotyledonae</td>
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<td>Acanthaceae</td>
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<td></td>
<td>Dicliptera brachiata (Pursh)</td>
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<td>Asteraceae</td>
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<td>Bidens frondosa (L.)</td>
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<td>Eclipta prostrata (L.)</td>
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<td>Eupatorium coelestinum (L.)</td>
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<td>Solidago sp.</td>
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<td>Lythraceae</td>
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<td>Ammannia robusta (Heer &amp; Regel)</td>
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<td>Polygonaceae</td>
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<td>Rumex crispus (L.)</td>
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<td>Sapindaceae</td>
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<td>Cardiospermum halicacabum (L.)</td>
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<td>Monocotyledonae</td>
<td>Carex crus-corvi (Shuttlew. ex Kunze)</td>
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<td>Carex hyalinolepis (Steu.)</td>
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<td>Cyperus erythrorhizos (Muhl.)</td>
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<td>Fimbristylis vahlii (Lam.)</td>
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<td>Bromus pubescens (Muhl. Ex Willd.)</td>
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<td>Elymus virginicus (L.)</td>
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<td></td>
<td>Sorghum halepense (L.)</td>
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species was contingent upon several factors including: the availability of published
tolerance data, temporal field distributions following the flood, the availability of seed,
and the ability to germinate seed with only physical scarification as pre-treatment. In all
cases, plants were grown from seed collected at the study site in the GBC.

Species, three light availability treatments (80% shade, 40% shade, and open)
two water level treatments (saturated and drained) were crossed in a complete
randomized block design with each of ten blocks housing one replicate of each
treatment (Fig. 4).

The study was carried out under greenhouse conditions with supplemental
lighting (mean PAR ~55 umol m$^{-2}$ sec$^{-2}$) set on a 16/8 light/dark cycle. PAR readings
(Li-Cor model LI-1400) taken on a uniformly overcast day indicate 75% sunlight
transmittance into the greenhouse (outside mean: 252.4 umol m$^{-2}$ sec$^{-2}$, greenhouse
mean: 189.3 umol m$^{-2}$ sec$^{-2}$). On this day, lighting was sufficient to compensate for the
majority of PAR reduction inside the greenhouse, with PAR readings 96.8% of those
recorded outside
(mean 244.3 umol m$^{-2}$ sec$^{-2}$).

Seedlings were
germinated under
uniform light conditions
and transplanted into

**Fig. 4** Greenhouse experiment block schematic (1 of 10). Each block housed a set of three shade treatments (80%, 40%, and open). Shade enclosures contained both a flooded and drained treatment for a randomized set of fifteen species
black 120 ml polypropylene sample vials (Capitol Vial Inc., Thermo Fisher Scientific) with 5 mm drain holes drilled at their base to allow for the manipulation of water levels via treatment reservoirs. Seedlings were grown in a sand substrate supplemented with 1/64 Long Ashton’s nutrient solution (Hewitt 1966), a concentration applicable to levels found within the local watershed (Adhikari, unpublished data).

Shade enclosure framing constructed of wooden dowels supported woven shade fabric (PAK unlimited, Inc.) in 80 and 40% shade values (measured transmittance of ambient light: 20 and 50% respectively). To allow ventilation and maintain ambient temperatures across treatments, the north side of shade enclosures and edges falling below the top of pots were left uncovered (Fig. 5). Open treatments were elevated on PVC frames to ensure they did not lie in the shade of adjacent enclosures. Shade treatments housed two reservoirs each for the institution of water availability treatments.

Reservoirs were constructed from 5.7L clear polypropylene containers and covered with blackout fabric to reduce algal growth. Water level in drained treatment reservoirs was maintained...
8 cm below the substrate surface and saturated treatments at substrate level via 2.5 cm drainage holes at the given water level (Fig. 6).

Stock nutrients were diluted in carbon filtered water to a 1/64 concentration of Long Ashton’s nutrient solution with a MiniDos injection pump (1% series; Hydro USA/International Inc., Carrollton, TX). Initial saturation in designated treatments was achieved with carbon filtered water only, to ensure consistent nutrient availability across all treatments. Nutrients were delivered to treatment reservoirs via drip irrigation and run periodically on a timed cycle to maintain water level.

Consistent delivery of nutrient solution to all treatments was ensured with a closed loop irrigation system. Loop was constructed of ½” (1.3 cm) black polyethylene tubing feeding emitters with a flow rate of 1 gallon (3.79L)/hour. ¼” (0.6 cm) black vinyl distribution tubing (DIG Corp.) supplied each water treatment reservoir for ten minutes, four times daily.

Following a treatment period of 10 weeks, seedlings were harvested. Root and shoot tissues were separated and fresh weights obtained. Roots were preserved in 50% ethanol for further analysis. High resolution images of leaf tissues were obtained at the time of harvest with an Epson Expression 10000XL scanner (Seiko Epson Corporation). Images were analyzed with WinRhizo Pro software (Regent Instruments Inc.). Images were assessed for total leaf surface area. Following image acquisition, tissues were dried to constant mass at 30°C and weights obtained. Total fresh weight (TFW), shoot fresh weight (SFW), and root fresh weight (RFW) were used to indicate plants performance within treatments. Specific shoot height (SSH; final shoot height/shoot dry weight), specific leaf area (SLA; total leaf surface area/total leaf dry weight), and
root/shoot ratios (RAT; root fresh weight/shoot fresh weight) were calculated to uncover potential mechanisms for tradeoffs.

TFW, SFW, RFW, SSH, SLA and RAT were analyzed with a generalized linear mixed model (GLMM) using Proc MIXED (SAS 9.2) to fit the data. The design was a randomized complete block design with ten blocks, two levels of water availability, and three levels of light availability and included the interaction between light and water availability. Blocks were included as random effects. To assess the ANOVA assumptions, comprehensive residual analyses were conducted. This includes formally testing the residuals for normality using the four tests offered by SAS (Kolmogorov-Smirnov, Shapiro-Wilk, Cramer-von Mises, Anderson-Daring). The residuals were plotted against the predicted values and explanatory variables used in the model. Such analyses may reveal outliers or other problems with the data structure. When necessary, data were transformed to meet the requirements of normality and equal variance (Table 3).

If a significant main effect of light was detected multiple comparisons were conducted using unadjusted t-tests. Since there were only two levels of water availability multiple comparisons were not required if a significant main effect of water was detected. If a significant interaction was detected the following analyses were conducted: 1) at each level of light availability the means of drained and undrained plants were compared, 2) within each level of water availability means were compared among levels of light availability, 3) the difference in the performance of drained and undrained plants was compared among levels of light availability. In all cases comparisons were conducted using contrast statements in SAS.
Following statistical analyses, species exhibiting similar response patterns for SFW were qualitatively grouped into general response patterns based on shared significance of main effects, the direction of influence, and the type of interaction, if any were present. Interactions were classified based on shared attributes described by multiple comparisons and analyses of relationships between water treatment means at each level of shade. SFW was chosen as an appropriate measure for these groupings, as it is representative of photosynthetic capacity and reproductive potential. Therefore, it is considered the best approximation of fitness among the biomass measures recorded.

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<tr>
<th>Species</th>
<th>TFW</th>
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<th>RFW</th>
<th>SSH</th>
<th>SLA</th>
<th>RAT</th>
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RESULTS
Field Study Community Dynamics

Over the course of four years of sampling in the GBC, 89 species representing 39 families were encountered within sampling plots (Table A.1). Summary data with species, wetland indicator statuses (WIS), and frequencies for each seasonal sampling are included in the appendix (Tables A.2-A.9). Analyses indicate a distinctly different community structure immediately subsequent to the 2007 flooding event compared to following years.

In the time since the flood, community composition has shifted from more characteristic wetland species to those more typical of upland environments. Greater numbers of obligate (OBL) and facultative wetland species (FACW) were encountered in the fall and spring following the flooding disturbance than have been observed since (Fig. 7). The greatest number of these species, however, was not observed in fall 2007 directly after the flooding event, but in the following spring. However, OBL/FACW species richness is underestimated for the fall 2007 sampling. During this season, Cyperaceae seedlings were widespread (Table 35), but their immaturity made further identification difficult. These seedlings likely represented more than one species from a potential pool of four obligate species (Carex brevior, Carex crus-corvi, Carex hyalinolepis, and Cyperus erythrorhizos), but were counted conservatively as one. The true OBL/FACW species richness for the fall 2007 sampling encountered falls somewhere within a range of 16-20 species, while spring 2008 had 21. The highest OBL/FACW species richness observed since was 15, in the fall 2009, spring 2010 and spring 2011.
Facultative (FAC) species have been increasing in number since the flooding event. This trend was subject to seasonal variability with greater numbers of FAC species encountered in spring samplings for most years. However, the highest FAC species richness was observed in the fall of 2010 with 15 species. This was a sharp increase.

**Fig. 7** Species richness for each seasonal sampling by wetland indicator status (WIS). Wetland indicator status for region 6 was obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). Species of the category NA have no designated WIS. The upper dashed line represents the highest total species richness and the lower dashed line represents the highest combined OBL and FACW species richness. This reflects four years of sampling, from fall 2007- spring 2011 (Fa07-Sp11).
increase from the 7 (fall 2007) or 8 (fall 2008 & 2009) in the preceding years. The spring samplings also had the highest number of FAC species in recent years, with 14 species each in spring 2010 and 2011. This was up from 12 species in the spring of 2008 and only 10 in spring 2009.

Upland (UPL) and facultative upland (FACU) species have contributed comparatively fewer species to total species richness in all seasons. Both categories exhibited variability over time with no apparent trends. FACU species ranged between 2-6 species for all seasons/years and UPL species from 1-2. The low number of listed UPL species does not, however, preclude the presence of upland species, as UPL species only appear on the national WIS list when they have occasional wetland distributions in areas outside the one in question. Typically, upland plants do not appear on the national WIS list and therefore, species without designation are most probably upland species (USDA 2010) which should also be considered. Though there tended to be greater numbers of species with no WIS designation (NA) in recent years, the pattern was inconsistent. For the fall samplings, the number of these species peaked in 2009 with 10 species. In the fall of 2010, the number of NA species dropped to 9. Spring samplings had the greatest number of NA species in 2010. However, there were 9 encountered in 2008. The spring of 2009 and 2011 had 5 and 6 species, respectively. The numbers of these species tended to be greatest in seasons with high overall species richness (spring 2008=9 NA species, fall 2009=10, spring 2010=10, fall 2010=9).

Spring 2008 had the highest total species richness of all sampling seasons with 49 species. This peak in richness appears to be the result of a transition period for the
community, allowing for the persistence of OBL and FACW species while showing increases in FAC, FACU, UPL and species with no WIS designation (NA). The total richness for fall 2007 lies within a range of 33-37 species, which even at the highest value falls below that of all seasons except fall 2008 and spring 2009. The limited richness observed in this season is likely due to the limited duration after the flood to allow for community establishment, coupled with its timing late in the growing season. Fall 2008 showed a sharp decrease in species richness compared to the previous spring. This season had the lowest overall species richness with only 25 species. Over the next two seasons, richness increased, peaking at 47 species in the spring of 2010. Fall 2010 and spring 2011 exhibited slight declines in richness, with 44 and 41 species respectively.

To better understand the contribution of WIS categories to the plant community for each season, relative frequencies for each category were calculated as a percentage of the total plant frequency for each sampling (Fig. 8). The greatest contribution to frequency by OBL and FACW species was encountered directly after recession of flood waters in the fall of 2007. For this season OBL and FACW species contributed approximately 50% of the total plant frequency. These species contributed less than 40% in all subsequent samplings. Percentage OBL/FACW tended to be higher in the fall seasons (except 2010). Fall 2009 had the second highest relative frequency contribution by OBL and FACW species. This coincides with the highest annual total precipitation recorded for the Dallas-Fort Worth area since the year of the flooding disturbance (NOAA and USDC, 2011; 103.86 and 127.13 cm respectively). FAC species contributed the lowest percentage to total plant frequency in the fall of 2007.
Over the next two seasons, this percentage increased, peaking at 61.77% in fall 2008.

Relative FAC frequency decreased through 2009 and then fluctuated between 42-46% over the last three samplings. The most recent sampling, spring 2011, had the highest combined FACU, UPL and NA species at 26.68%. Though the two seasons following the flood had lower percentages at around 19% each, they did not have the lowest value. This occurred in the fall of 2008 with only 6.83%. Combined relative frequency of
these species increased in the next season (spring 2009=24.81%) and then fell to levels similar to those observed following the flood during the wet season, fall 2009 (19.96%). The last three samplings saw increases in the contribution of these species, peaking at the highest observed percentage in spring 2011.

Correspondence Analysis of whole site data revealed a markedly different community in the season immediately following the flood, with a quick “recovery” to the somewhat consistent community structure observed in the area since (Fig. 9). CA yielded two axes which explained 25.7% of the variability in community structure (proportion explained: CA1=0.154, CA2=0.103). The fall 2007 sampling data were separated from the other data along the first CA axis. For this sampling effort, all plots had a score greater than 0.68 on the first axis, while scores for all other samplings were tightly grouped below this threshold. It is important to note that the site with the highest elevation (Site 15) for the fall 2007 sampling was most closely associated with the more recent sampling sites.

Nineteen species were associated with the fall 2007 sampling, having CA1 scores greater than 0.68 (Table 4). Of these, eight species were only encountered during the fall 2007 sampling (Acalypha ostryifolia, Amaranthus sp., Ammannia robusta, Eclipta prostrata, Heliotropium indicum, Leucospora multifida, Ludwigia decurrens, and Physalis turbinata). Several of these species are still present in the area, but are restricted to mudflats along the river channel (e.g. A. robusta, E. prostrata, and L. multifida). Fimbristylis vahlii is also now typically found in these areas, but was found in low numbers within sampling plots in a few seasons since the fall of 2007. Aster praealtus, Cyperus erythrorhizos, Lemna sp. and Physalis longifolia were encountered.
only in fall 2007 and spring 2008, but their abundance was reduced in the spring. The floating aquatic species of the genus *Lemna* was encountered in five plots in the fall following the flood, but in spring was only present in a single plot commonly associated with standing water. *Campsis radicans* was associated with the fall 2007 sampling due

![Fig. 9 Correspondence analysis by sampling plot of all data since the flooding event in the summer of 2007. Biannual sampling was carried out in the spring and fall from the fall of 2007 through spring 2011. Labels indicate year (first two digits), season (FA=fall, SP=spring), and sampling plot number (final number). Plots for the sampling immediately following the flood are distributed along the positive end of axis one, while plot data for all of the other sampling efforts cluster closely near zero.](image)
to broader distribution during this period, as frequency was greater in spring 2009 but
confined to a single plot. *C. halicacabum* was present in every sampling, but with lower
frequencies than those encountered in fall 2007. The remaining species (*Melothria
pendula, Rivina humilis, Rorippa sessiliflora*, and *Sicyos angulatus*) were encountered
in two or more sampling seasons outside of fall 2007, but at comparatively lower
frequencies.

Therefore, species included in the greenhouse study are of three types with
regard to their temporal field distributions: those only associated with the sampling
following the flood (*A. robusta* and
*E. prostrata*), those closely
associated with the sampling
following the flood but also found
in other seasons (*C. halicacabum,
*C. erythrorhizos* and *F. vahlii*), and
those associated with more recent
sampling seasons (*B. frondosa, B.
pubescens, C. crus-corvi, C.
hyalinolepis, D. brachiata, E.
coelestinum, E. virginicus, R.
crispus, S. halepense*, and
*Solidago* sp.).

**Table 4** CA scores for species associated with the
fall 2007 sampling along the first and second
ordination axes. Species in bold were only
encountered during this sampling, while the others
were associated due to higher frequencies and/or
broader distributions during this period

<table>
<thead>
<tr>
<th>Species</th>
<th>CA1</th>
<th>CA2</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acalypha ostryifolia</em></td>
<td>3.2078</td>
<td>-0.6374</td>
</tr>
<tr>
<td><em>Amaranthus</em> sp.</td>
<td>2.4864</td>
<td>0.9939</td>
</tr>
<tr>
<td><em>Ammannia robusta</em></td>
<td>1.9949</td>
<td>0.9258</td>
</tr>
<tr>
<td><em>Aster praealtus</em></td>
<td>1.5504</td>
<td>-1.0225</td>
</tr>
<tr>
<td><em>Campsis radicans</em></td>
<td>0.7172</td>
<td>-0.6368</td>
</tr>
<tr>
<td><em>Cardiospermum halicacabum</em></td>
<td>1.5980</td>
<td>0.7360</td>
</tr>
<tr>
<td><em>Cyperus erythrorhizos</em></td>
<td>0.8173</td>
<td>1.1402</td>
</tr>
<tr>
<td><em>Eclipta prostrata</em></td>
<td>1.9949</td>
<td>0.9258</td>
</tr>
<tr>
<td><em>Fimbristylis vahlii</em></td>
<td>1.0314</td>
<td>0.6252</td>
</tr>
<tr>
<td><em>Heliotropium indicum</em></td>
<td>2.5410</td>
<td>1.0015</td>
</tr>
<tr>
<td><em>Lemna</em> sp.</td>
<td>3.9957</td>
<td>-0.5959</td>
</tr>
<tr>
<td><em>Leucospora multifida</em></td>
<td>1.5325</td>
<td>-1.9521</td>
</tr>
<tr>
<td><em>Ludwigia decurrens</em></td>
<td>2.1997</td>
<td>0.9542</td>
</tr>
<tr>
<td><em>Melothria pendula</em></td>
<td>1.6055</td>
<td>-0.6238</td>
</tr>
<tr>
<td><em>Physalis longifolia</em></td>
<td>2.5251</td>
<td>0.3791</td>
</tr>
<tr>
<td><em>Physalis turbinata</em></td>
<td>3.7165</td>
<td>-0.3738</td>
</tr>
<tr>
<td><em>Rivina humilis</em></td>
<td>0.9574</td>
<td>-0.9870</td>
</tr>
<tr>
<td><em>Rorippa sessiliflora</em></td>
<td>1.0735</td>
<td>0.5557</td>
</tr>
<tr>
<td><em>Sicyos angulatus</em></td>
<td>0.8528</td>
<td>-0.9045</td>
</tr>
</tbody>
</table>
Greenhouse Study

Individual response graphs are presented for each species and variable, regardless of significant effects. Graphs are furnished to allow the reader to visualize responses and to contribute tolerance data since available information for these species is limited. Significant interaction effects are presented on the figures themselves, while independent effects are addressed in tables and the text body.

*Carex hyalinolepis*

**Table 5** Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Carex hyalinolepis*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>Water</th>
<th>Shade x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>9.79</td>
<td>0.0004</td>
<td>0.16</td>
</tr>
<tr>
<td>SFW</td>
<td>18.98</td>
<td>&lt;.0001</td>
<td>0.30</td>
</tr>
<tr>
<td>RFW</td>
<td>3.38</td>
<td>0.0460</td>
<td>0.14</td>
</tr>
<tr>
<td>SSH</td>
<td>5.20</td>
<td>0.0096</td>
<td>7.48</td>
</tr>
<tr>
<td>SLA</td>
<td>54.21</td>
<td>&lt;.0001</td>
<td>3.77</td>
</tr>
<tr>
<td>RAT</td>
<td>13.18</td>
<td>&lt;.0001</td>
<td>1.77</td>
</tr>
</tbody>
</table>

*Significant effects (p=<0.05) are in bold*

Biomass responses of *C. hyalinolepis* are presented as raw means ± SE in figure 10. All measures of biomass were influenced by shade only (Table 5). There was no significant effect of water or interaction for total fresh weight (TFW), shoot fresh weight (SFW), or root fresh weight (RFW). All measures of biomass responded positively to increasing shade (Fig. 10). Means for each shade treatment indicate that all biomass measures were significantly higher in the 80% shade treatment compared to the 0 and 40% shade treatments respectively (Table 6).
Fig. 10 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of Carex hyalinolepis grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
Fig. 11 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Carex hyalinolepis* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
Table 6 Effects of shade on the performance of *Carex hyalinolepis*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT). Means are presented ± SE. Letters indicate significant differences (p<0.05) between means.

<table>
<thead>
<tr>
<th>Response variable</th>
<th>0% shade</th>
<th>40% shade</th>
<th>80% shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>0.527 ± 0.068 g A</td>
<td>0.535 ± 0.078 g A</td>
<td>0.944 ± 0.108 g B</td>
</tr>
<tr>
<td>SFW</td>
<td>0.191 ± 0.027 g A</td>
<td>0.200 ± 0.035 g A</td>
<td>0.418 ± 0.079 g B</td>
</tr>
<tr>
<td>RFW</td>
<td>0.358 ± 0.050 g A</td>
<td>0.334 ± 0.053 g A</td>
<td>0.505 ± 0.057 g B</td>
</tr>
<tr>
<td>SSH</td>
<td>216.97 ± 14.28 cm g⁻¹ A</td>
<td>272.28 ± 21.76 cm g⁻¹ B</td>
<td>253.10 ± 15.34 cm g⁻¹ B</td>
</tr>
<tr>
<td>SLA</td>
<td>129.57 ± 3.72 cm² g⁻¹ A</td>
<td>160.16 ± 5.37 cm² g⁻¹ B</td>
<td>206.89 ± 6.47 cm² g⁻¹ C</td>
</tr>
<tr>
<td>RAT</td>
<td>2.146 ± 0.142 A</td>
<td>1.705 ± 0.123 B</td>
<td>1.180 ± 0.131 C</td>
</tr>
</tbody>
</table>

Raw means ± SE for specific shoot height (SSH; cm shoot height / g shoot dry weight), specific leaf area (SLA; cm² leaf surface area / g leaf dry weight), and fresh weight root / shoot ratio (RAT) are presented in figure 11. SSH was independently influenced by both shade and water availability, but had no interaction effect (Table 5). Mean SSH was significantly lower under open conditions as compared to the 40 and 80% shade treatments respectively (Table 6). Mean SSH was significantly lower in drained treatments (225.01 ± 9.25 cm g⁻¹) compared to saturated treatments (268.84 ± 17.66 cm g⁻¹).

SLA showed an effect of shade but no effect of water or interaction (Table 5). Mean SLA increased successively at each level of shade (Table 6). RAT was influenced by shade, but had no effect of water or interaction. As expected, RAT (Fig. 11.c) had an inverse relationship with increasing shade. Mean RAT was significantly lowered at each increasing level of shade (Table 6).

*Bromus pubescens*

Biomass responses of *B. pubescens* are presented as raw means ± SE in figure 12. All measures of biomass were affected by shade, but there was no effect of water or
interaction (Table 7). All biomass measures responded positively to shade (Fig. 12).

Mean TFW was significantly higher than the open treatment in both the 40 and 80% treatments, with the 40 and 80% shade treatments remaining similar (Table 8). SFW increased across all shade levels, while mean RFW was only different in comparisons of the 0 and 80% shade treatments (Table 8).

Table 7 Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of Bromus pubescens. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade F</th>
<th>Shade p value</th>
<th>Water F</th>
<th>Water p value</th>
<th>Shade x Water F</th>
<th>Shade x Water p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>6.33</td>
<td><strong>0.0046</strong></td>
<td>1.01</td>
<td>0.3218</td>
<td>0.50</td>
<td>0.6136</td>
</tr>
<tr>
<td>SFW</td>
<td>10.56</td>
<td><strong>0.0002</strong></td>
<td>0.14</td>
<td>0.7082</td>
<td>0.58</td>
<td>0.5652</td>
</tr>
<tr>
<td>RFW</td>
<td>4.15</td>
<td><strong>0.0243</strong></td>
<td>1.69</td>
<td>0.2020</td>
<td>0.57</td>
<td>0.5693</td>
</tr>
<tr>
<td>SSH</td>
<td>0.27</td>
<td>0.7637</td>
<td>0.91</td>
<td>0.3448</td>
<td>0.30</td>
<td>0.7433</td>
</tr>
<tr>
<td>SLA</td>
<td>19.54</td>
<td>&lt;.0001</td>
<td>0.01</td>
<td>0.9094</td>
<td>0.00</td>
<td>0.9989</td>
</tr>
<tr>
<td>RAT</td>
<td>0.28</td>
<td>0.7553</td>
<td>5.36</td>
<td><strong>0.0268</strong></td>
<td>0.31</td>
<td>0.7364</td>
</tr>
</tbody>
</table>

*Significant effects (p=<0.05) are in bold

Raw means ± SE for SSH, SLA, and RAT are presented in figure 13. SSH was not affected by shade, water, or their interaction (Table 7). SLA, was affected by shade, but had no effects of water or interaction (Table 7). SLA was similar between the 0 and 40% shade treatments and both means were significantly lower than that of the 80% shade treatment (Table 8). RAT was influenced by water only, with no effect of shade or

Table 8 Effects of shade on the performance of Bromus pubescens. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), and specific leaf area (SLA). Means are presented ± SE. Letters indicate significant differences (p<0.05) between means.

<table>
<thead>
<tr>
<th></th>
<th>0% shade</th>
<th>40% shade</th>
<th>80% shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>5.375 ± 1.322 g A</td>
<td>11.812 ± 2.210 g B</td>
<td>15.357 ± 2.330 g B</td>
</tr>
<tr>
<td>SFW</td>
<td>1.666 ± 0.295 g A</td>
<td>3.853 ± 0.603 g B</td>
<td>5.493 ± 0.679 g C</td>
</tr>
<tr>
<td>RFW</td>
<td>3.689 ± 1.009 g A</td>
<td>7.802 ± 1.573 g AB</td>
<td>9.545 ± 1.819 g B</td>
</tr>
<tr>
<td>SLA</td>
<td>81.80 ± 9.10 cm² g⁻¹ A</td>
<td>97.92 ± 11.56 cm² g⁻¹ A</td>
<td>165.01 ± 9.28 cm² g⁻¹ B</td>
</tr>
</tbody>
</table>
Fig. 12 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of *Bromus pubescens* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE
Fig. 13 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Bromus pubescens* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE
interaction (Table 7). Mean RAT was significantly lower in the saturated treatment (1.612 ± 0.210) compared to the drained treatment (2.527 ± 0.443).

_Elymus virginicus_

**Table 9** Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of _Elymus virginicus_. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>$p$ value</th>
<th>Water</th>
<th>$p$ value</th>
<th>Shade x Water</th>
<th>$p$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>4.32</td>
<td><strong>0.0212</strong></td>
<td>0.79</td>
<td>0.3789</td>
<td>0.73</td>
<td>0.4904</td>
</tr>
<tr>
<td>SFW</td>
<td>16.68</td>
<td><strong>&lt;0.0001</strong></td>
<td>0.04</td>
<td>0.8464</td>
<td>3.22</td>
<td><strong>0.0495</strong></td>
</tr>
<tr>
<td>RFW</td>
<td>1.96</td>
<td>0.1564</td>
<td>1.72</td>
<td>0.1988</td>
<td>0.20</td>
<td>0.8183</td>
</tr>
<tr>
<td>SSH</td>
<td>8.06</td>
<td><strong>0.0010</strong></td>
<td>0.09</td>
<td>0.7621</td>
<td>3.21</td>
<td>0.0501</td>
</tr>
<tr>
<td>SLA</td>
<td>40.76</td>
<td><strong>&lt;0.0001</strong></td>
<td>4.11</td>
<td><strong>0.0488</strong></td>
<td>0.04</td>
<td>0.9633</td>
</tr>
<tr>
<td>RAT</td>
<td>15.79</td>
<td><strong>&lt;0.0001</strong></td>
<td>0.96</td>
<td>0.3339</td>
<td>2.51</td>
<td>0.0969</td>
</tr>
</tbody>
</table>

*Significant effects ($p$=<0.05) are in bold

Biomass responses of _E. virginicus_ are presented as raw means ± SE in figure 14. This species exhibited a complex biomass response. TFW was affected by shade, but had no effect of water or interaction (Table 9). TFW responded positively to shade. Mean TFW for the 80% shade treatment was significantly higher than the open treatment, while mean TFW of the intermediate level of shade was similar to both the open and the 80% shade treatment (Table 10). SFW exhibited an effect of shade and an interaction effect (Table 9). Shoot biomass responded positively to shade in both drained and saturated treatments. In drained conditions, mean SFW was significantly higher in the 80% shade treatment compared to the open treatment, while mean SFWs in each of these treatments were similar to the 40% shade treatment (Fig. 14.b). Under saturated conditions, mean SFWs of the 0 and 40% shade treatments were similar and significantly lower than that of the 80% shade treatment (Fig. 14.b). SFW means were
Fig. 14 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of *Elymus virginicus* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 9). Differences between shade treatments (p<0.05) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers.
Fig. 15 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Elymus virginicus* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
similar between drained and saturated treatments for all shade treatments except 80%, where mean SFW was significantly higher in the saturated treatment (Fig. 14.b). The relationship between means of flooded and drained treatments at 80% shade was different from that of the 0 and 40% shade treatments respectively (Fig. 14.b). RFW had no significant effect of shade, water, or their interaction (Table 9).

Raw means ± SE for SSH, SLA, and RAT are presented in figure 15. SSH was influenced by shade, but showed no effect of water or interaction (Table 9). SSH exhibited a positive relationship with increasing shade, with successively higher means across shade treatments (Table 10). SLA was influenced independently by both shading and water availability, with no interaction effect (Table 9). SLA exhibited a positive relationship with increasing shade in both drained and saturated treatments (Fig. 15.b). Mean SLA was successively higher with increasing shade (Table 10). In the saturated treatment (99.07 ± 9.26 cm² g⁻¹) mean SLA was significantly lower compared to the drained treatment (116.66 ± 8.56 cm² g⁻¹). RAT was influenced by shade, but had no effect of water or interaction (Table 9). As expected, this response exhibited a negative relationship with increasing shade (Fig. 15.c). In the open and 40% shade treatments, mean RATs were similar and significantly higher than that of the 80% shade treatment.

Table 10 Effects of shade on the performance of Elymus virginicus. Response variables include total fresh weight (TFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT). Means are presented ± SE. Letters indicate significant differences (p<0.05) between means.

<table>
<thead>
<tr>
<th></th>
<th>0% shade</th>
<th>40% shade</th>
<th>80% shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>0.259 ± 0.039 g</td>
<td>0.359 ± 0.045 g</td>
<td>0.443 ± 0.061 g</td>
</tr>
<tr>
<td>SSH</td>
<td>292.24 ± 29.18 cm g⁻¹</td>
<td>417.84 ± 27.81 cm g⁻¹</td>
<td>472.71 ± 49.22 cm g⁻¹</td>
</tr>
<tr>
<td>SLA</td>
<td>65.57 ± 5.21 cm² g⁻¹</td>
<td>101.70 ± 6.18 cm² g⁻¹</td>
<td>156.33 ± 9.54 cm² g⁻¹</td>
</tr>
<tr>
<td>RAT</td>
<td>3.075 ± 0.217 A</td>
<td>3.959 ± 1.025 A</td>
<td>1.760 ± 0.248 B</td>
</tr>
</tbody>
</table>
**Eupatorium coelestinum**

**Table 11** Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Eupatorium coelestinum*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>Water</th>
<th>Shade x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>3.45</td>
<td><strong>0.0432</strong></td>
<td>0.79</td>
</tr>
<tr>
<td>SFW</td>
<td>9.41</td>
<td><strong>0.0004</strong></td>
<td>0.08</td>
</tr>
<tr>
<td>RFW</td>
<td>2.81</td>
<td>0.0740</td>
<td>0.27</td>
</tr>
<tr>
<td>SSH</td>
<td>4.04</td>
<td><strong>0.0257</strong></td>
<td>2.06</td>
</tr>
<tr>
<td>SLA</td>
<td>4.08</td>
<td><strong>0.0252</strong></td>
<td>0.81</td>
</tr>
<tr>
<td>RAT</td>
<td>12.64</td>
<td><strong>0.0001</strong></td>
<td>1.81</td>
</tr>
</tbody>
</table>

*Significant effects (p<0.05) are in bold

Biomass responses of *E. coelestinum* are presented as raw means ± SE in figure 16. TFW was affected by shade, but showed no influence of water or interaction (Table 11). Mean TFWs of 0 (0.363 ± 0.094 g) and 40% (0.400 ± 0.073 g) shade treatments were similar and significantly lower than that of the 80% shade treatment (0.876 ± 0.220 g). SFW exhibited an effect of shade and an interaction effect (Table 11). Shoot biomass in the saturated treatment was significantly greater in the 80% shade treatment compared to the 0 and 40% shade treatments, while the relationship between means of saturated and drained treatments was significantly different in the 80% shade treatment compared to the 0 and 40% shade treatments (Fig. 16.b). There were no significant effects of shade, water, or their interaction on RFW (Table 11).

Raw means ± SE for SSH, SLA, and RAT are presented in figure 17. SSH exhibited a main effect of shade in addition to an interaction effect (Table 11). In the saturated treatment, mean SSHs for the 0 and 80% shade treatment were similar and significantly lower than that of the 40% shade treatment (Fig. 17.a). Under drained
Fig. 16 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of *Eupatorium coelestinum* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 11). Differences between shade treatments (p<0.05) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers.
Fig. 17 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Eupatorium coelestinum* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 11). Differences between shade treatments (p<0.05) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers.
conditions, treatment means were similar across all levels of shade (Fig. 17.a). Mean SSH was significantly higher in the saturated treatment than the drained treatment at the intermediate shade level, with similar water treatment means in the open and 80% shade treatments (Fig. 17.a). Differences between water treatment means were significantly greater in the 40% shade treatment (Fig. 17.a). SLA was also affected by shade and its interaction with water availability (Table 11). In saturated treatments, mean SLA was significantly higher than the open treatment under 40 and 80% shade respectively (Fig. 17.b). There were no significant differences between shade treatment means under drained conditions (Fig. 17.b). Though there were no significant differences between drained and saturated means at any one level of shade, the divergence between water treatments in open conditions was significantly greater than that in the 40 and 80% shade treatments (Fig. 17.b). RAT was influenced by shade, but had no effect of water or interaction (Table 11). RAT decreased with increasing shade (Fig. 17.c). Mean RATs in 0 (1.641 ± 0.122 \(^A\)) and 40% shade (1.341 ± 0.117 \(^A\)) were similar and significantly higher than that of 80% shade (0.874 ± 0.132 \(^B\)).

*Rumex crispus*

Biomass responses of *R. crispus* are presented as raw means ± SE in figure 18. TFW and SFW were affected by shade, water availability, and their interaction (Table 12). These responses were nearly identical, with the exception of significantly higher mean SFW in the 80% shade/drained treatment compared to the drained treatments exposed to higher light levels (Figs. 18.a and 18.b). Mean TFWs for the drained treatment were similar across all levels of shade (Fig. 18.a). In saturated treatments, for both TFW and SFW, means in 0 and 40% shade treatments were similar and
Table 12 Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Rumex crispus*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>Water</th>
<th>Shade x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>( p ) value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>12.99</td>
<td>(&lt;.0001)</td>
<td>4.86</td>
</tr>
<tr>
<td>SFW</td>
<td>26.83</td>
<td>(&lt;.0001)</td>
<td>4.74</td>
</tr>
<tr>
<td>RFW</td>
<td>5.13</td>
<td>(0.0113)</td>
<td>0.58</td>
</tr>
<tr>
<td>SSH</td>
<td>0.23</td>
<td>0.7944</td>
<td>1.32</td>
</tr>
<tr>
<td>SLA</td>
<td>37.51</td>
<td>(&lt;.0001)</td>
<td>1.22</td>
</tr>
<tr>
<td>RAT</td>
<td>11.47</td>
<td>(0.0002)</td>
<td>1.49</td>
</tr>
</tbody>
</table>

*Significant effects \((p=\leq0.05)\) are in bold

significantly lower than that of the 80% shade treatment (Figs. 18.a and 18.b). For both TFW and SFW, water availability treatment means were similar at 0 and 40% shade, while the mean of the saturated treatment was significantly higher compared to the drained treatment (Figs. 18.a and 18.b). Differences in the water treatment means were also significantly greater in the 80% shade treatment compared the 0 and 40% shade treatments respectively (Figs. 18.a and 18.b). RFW was influenced by shade, but had no effect of water or interaction (Table 12). Shade treatment means were similar in the 0 and 40% shade treatments and significantly lower than mean RFW in the 80% shade treatment (Table 13).

Raw means ± SE for SSH, SLA, and RAT are presented in figure 19. SSH had no effect of shade, water, or their interaction (Table 12). SLA was influenced by shade, but had no effect of water or interaction (Table 12). Mean SLA increased successively with increasing shade (Table 13). RAT was influenced by shade, but had no effect of water or interaction (Table 12). Shade treatment means were similar under 0 and 40% shade and significantly lower than that of the 80% shade treatment (Table 13).
Fig. 18 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) of *Rumex crispus* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 12). Differences between shade treatments ($p<0.05$) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers.
Fig. 19 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Rumex crispus* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
Biomass responses of *Eclipta prostrata* are presented as raw means ± SE in figure 20. TFW and SFW were independently influenced by shade and water, but had no interaction effect (Table 14). Shade treatment means for both TFW and SFW under 0 and 40% shade were similar and significantly lower than that of the 80% shade treatment (Table 15). For TFW, the saturated treatment mean (4.290 ± 0.954 g) was significantly higher than that of the drained treatment (2.260 ± 0.380 g). Similarly, the SFW saturated treatment mean (1.731 ± 0.502 g) was significantly higher than that of

### Table 13

Effects of shade on the performance of *Rumex crispus*. Response variables include root fresh weight (RFW), specific leaf area (SLA), and root/shoot ratio (RAT). Means are presented ± SE. Letters indicate significant differences (*p*<0.05) between means.

<table>
<thead>
<tr>
<th></th>
<th>0% shade</th>
<th>40% shade</th>
<th>80% shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>RFW</td>
<td>0.443 ± 0.072 g A</td>
<td>0.644 ± 0.170 g A</td>
<td>1.029 ± 0.187 g B</td>
</tr>
<tr>
<td>SLA</td>
<td>184.19 ± 8.07 cm² g⁻¹ A</td>
<td>243.75 ± 17.06 cm² g⁻¹ B</td>
<td>358.18 ± 12.43 cm² g⁻¹ C</td>
</tr>
<tr>
<td>RAT</td>
<td>2.357 ± 0.208 A</td>
<td>2.208 ± 0.262 A</td>
<td>1.073 ± 0.118 B</td>
</tr>
</tbody>
</table>

### Table 14

Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Eclipta prostrata*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>Water</th>
<th>Shade x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td><em>p</em> value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>6.39</td>
<td><strong>&lt;0.0044</strong></td>
<td>4.72</td>
</tr>
<tr>
<td>SFW</td>
<td>18.04</td>
<td><strong>&lt;0.0001</strong></td>
<td>5.03</td>
</tr>
<tr>
<td>RFW</td>
<td>2.84</td>
<td>0.0725</td>
<td>4.27</td>
</tr>
<tr>
<td>SSH</td>
<td>1.82</td>
<td>0.1741</td>
<td>0.45</td>
</tr>
<tr>
<td>SLA</td>
<td>46.26</td>
<td><strong>&lt;0.0001</strong></td>
<td>8.52</td>
</tr>
<tr>
<td>RAT</td>
<td>32.92</td>
<td><strong>&lt;0.0001</strong></td>
<td>0.04</td>
</tr>
</tbody>
</table>

*Significant effects (*p*=<0.05) are in bold.
Fig. 20 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) Eclipta prostrata grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE
Fig. 21 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Eclipta prostrata* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
the drained treatment (0.767 ± 0.134 g). RFW was affected by water, but had no effect of shade or interaction (Table 14). For this response variable, the saturated treatment mean (2.389 ± 0.388 g) was also significantly higher than that of the drained treatment (1.467 ± 0.231 g).

Raw means ± SE for SSH, SLA, and RAT are presented in figure 21. SSH had no effect of shade, water, or their interaction (Table 14). SLA was influenced independently by shade and water, but had no interaction effect (Table 14). Mean SLA in the 0 and 40% shade treatments were similar and significantly lower than that of the 80% shade treatment (Table 15). The saturated treatment mean SLA (300.31 ± 20.31 cm² g⁻¹) was significantly higher than that of the drained treatment (255.45 ± 12.70 cm² g⁻¹). RAT was influenced by shade, but had no effect of water or interaction (Table 14). Treatment means under 0 and 40% shade were similar and significantly higher than that of the 80% shade treatment (Table 15).

**Table 15** Effects of shade on the performance of *Eclipta prostrata*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), specific leaf area (SLA), and root/shoot ratio (RAT). Means are presented ± SE. Letters indicate significant differences (p<0.05) between means

<table>
<thead>
<tr>
<th></th>
<th>0% shade</th>
<th>40% shade</th>
<th>80% shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>2.375 ± 0.384 g^A</td>
<td>1.827 ± 0.384 g^A</td>
<td>5.624 ± 1.332 g^B</td>
</tr>
<tr>
<td>SFW</td>
<td>0.525 ± 0.074 g^A</td>
<td>0.501 ± 0.102 g^A</td>
<td>2.721 ± 0.684 g^B</td>
</tr>
<tr>
<td>SLA</td>
<td>225.79 ± 8.31 cm² g⁻¹^A</td>
<td>228.48 ± 14.67 cm² g⁻¹^A</td>
<td>370.85 ± 17.63 cm² g⁻¹^B</td>
</tr>
<tr>
<td>RAT</td>
<td>3.307 ± 0.258^A</td>
<td>2.895 ± 0.215^A</td>
<td>1.179 ± 0.126^B</td>
</tr>
</tbody>
</table>

Biomass responses for *D. brachiata* are presented as raw means ± SE in figure 22. All measures of biomass had main effects of shade and water, but no interaction effect (Table 16). TFW, SFW, and RFW treatment means were significantly lower under
**Table 16** Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Dicliptera brachiata*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Shade F</th>
<th>Shade p value</th>
<th>Water F</th>
<th>Water p value</th>
<th>Shade x Water F</th>
<th>Shade x Water p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>3.75</td>
<td><strong>0.0336</strong></td>
<td>10.76</td>
<td><strong>0.0024</strong></td>
<td>0.01</td>
<td>0.9890</td>
</tr>
<tr>
<td>SFW</td>
<td>4.32</td>
<td><strong>0.0193</strong></td>
<td>5.81</td>
<td><strong>0.0202</strong></td>
<td>0.14</td>
<td>0.8728</td>
</tr>
<tr>
<td>RFW</td>
<td>3.58</td>
<td><strong>0.0388</strong></td>
<td>13.25</td>
<td><strong>0.0009</strong></td>
<td>0.00</td>
<td>0.9992</td>
</tr>
<tr>
<td>SSH</td>
<td>1.11</td>
<td>0.3402</td>
<td>1.37</td>
<td>0.2503</td>
<td>0.37</td>
<td>0.6943</td>
</tr>
<tr>
<td>SLA</td>
<td>6.57</td>
<td><strong>0.0041</strong></td>
<td>0.34</td>
<td>0.5635</td>
<td>0.43</td>
<td>0.6546</td>
</tr>
<tr>
<td>RAT</td>
<td>0.40</td>
<td>0.6736</td>
<td>4.29</td>
<td><strong>0.0484</strong></td>
<td>0.61</td>
<td>0.5501</td>
</tr>
</tbody>
</table>

*Significant effects (p<=0.05) are in bold

Open conditions compared to the 80% shade treatment, while the intermediate treatment was similar to both 0 and 80% shade (Table 17). All saturated treatment means were significantly lower than those of the drained treatment, for all measures of biomass (Table 18).

Raw means ± SE for SSH, SLA, and RAT are presented in figure 23. SSH had no effect of shade, water, or their interaction (Table 16). SLA was influenced by shade, but had no effect of water or interaction (Table 16). Treatment means of the 0 and 40% shade levels were similar and significantly lower than that of the 80% shade treatment (Table 17). RAT was influenced by water, but had no effect of shade or interaction.

**Table 17** Effects of shade on the performance of *Dicliptera brachiata*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), and specific leaf area (SLA). Means are presented ± SE. Letters indicate significant differences (p<0.05) between means.

<table>
<thead>
<tr>
<th></th>
<th>0% shade</th>
<th>40% shade</th>
<th>80% shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>0.147 ± 0.034 g^A</td>
<td>0.217 ± 0.044 g^AB</td>
<td>0.313 ± 0.062 g^B</td>
</tr>
<tr>
<td>SFW</td>
<td>0.040 ± 0.007 g^A</td>
<td>0.061 ± 0.011 g^AB</td>
<td>0.090 ± 0.019 g^B</td>
</tr>
<tr>
<td>RFW</td>
<td>0.110 ± 0.027 g^A</td>
<td>0.154 ± 0.032 g^AB</td>
<td>0.220 ± 0.040 g^B</td>
</tr>
<tr>
<td>SLA</td>
<td>211.71 ± 24.88 cm^2 g^{-1}^A</td>
<td>201.44 ± 25.50 cm^2 g^{-1}^A</td>
<td>323.06 ± 24.98 cm^2 g^{-1}^B</td>
</tr>
</tbody>
</table>
Fig. 22 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Diciptera brachiata* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
Fig. 23 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Dicliptera brachiata* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
(Table 16), with a significantly lower mean in the saturated compared to the drained treatment (Table 18).

**Table 18** Effects of water availability on the performance of *Dicliptera brachiata*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), and root/shoot ratio (RAT). Means are presented ± SE. All means presented were significantly different (*p<0.05*)

<table>
<thead>
<tr>
<th></th>
<th>Drained</th>
<th>Saturated</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>0.286 ± 0.032 g</td>
<td>0.164 ± 0.045 g</td>
</tr>
<tr>
<td>SFW</td>
<td>0.074 ±0.008 g</td>
<td>0.053 ± 0.014 g</td>
</tr>
<tr>
<td>RFW</td>
<td>0.213 ± 0.024 g</td>
<td>0.110 ± 0.029 g</td>
</tr>
<tr>
<td>RAT</td>
<td>3.038 ± 0.193</td>
<td>2.342 ± 0.302</td>
</tr>
</tbody>
</table>

*Cyperus erythrorhizos*

Biomass responses for *C. erythrorhizos* are presented as raw means ± SE in figure 24. TFW and RFW were affected by water availability, but had no effect of shade or interaction (Table 19). For both of these measures, mean biomass was significantly lower in the saturated treatment, compared to that of the drained (Table 20). SFW was independently influenced by shade and water, but had no interaction effect (Table 19). Shoot biomass in the 40 and 80% shade treatments was similar and significantly higher than that of the open treatment (Table 21). The saturated treatment mean for SFW was

**Table 19** Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Cyperus erythrorhizos*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT)

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>Water</th>
<th>Shade x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td><em>p</em> value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>1.16</td>
<td>0.3245</td>
<td>10.36</td>
</tr>
<tr>
<td>SFW</td>
<td>4.58</td>
<td><strong>0.0157</strong></td>
<td>18.88</td>
</tr>
<tr>
<td>RFW</td>
<td>2.71</td>
<td>0.0810</td>
<td>16.66</td>
</tr>
<tr>
<td>SSH</td>
<td>11.51</td>
<td><strong>0.0001</strong></td>
<td>11.12</td>
</tr>
<tr>
<td>SLA</td>
<td>18.96</td>
<td><strong>&lt;0.0001</strong></td>
<td>0.02</td>
</tr>
<tr>
<td>RAT</td>
<td>9.95</td>
<td><strong>0.0006</strong></td>
<td>0.59</td>
</tr>
</tbody>
</table>

*Significant effects (*p*=<0.05) are in bold
Fig. 24 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Cyperus erythrorhizos* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
Fig. 25 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Cyperus erythrorhizos* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
significantly lower than the drained treatment (Table 20).

Raw means ± SE for SSH, SLA, and RAT are presented in figure 25. Shade and water availability affected SSH, but there was no interaction effect (Table 19). SSH increased successively with increasing shade (Table 21), while the saturated treatment mean was significantly higher than that of the drained (Table 20). SLA was showed an effect of shade, but not of water or interaction (Table 19). Mean SLA in the open and

Table 20 Effects of water availability on the performance of *Cyperus erythrorhizos*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), and specific shoot height (SSH). Means are presented ± SE. All means presented were significantly different (p<0.05)

<table>
<thead>
<tr>
<th></th>
<th>Drained</th>
<th>Saturated</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>0.979 ± 0.125 g</td>
<td>0.535 ± 0.143 g</td>
</tr>
<tr>
<td>SFW</td>
<td>0.345 ± 0.045 g</td>
<td>0.202 ± 0.057 g</td>
</tr>
<tr>
<td>RFW</td>
<td>0.604 ± 0.081 g</td>
<td>0.297 ± 0.092 g</td>
</tr>
<tr>
<td>SSH</td>
<td>285.20 ± 30.21 cm g⁻¹</td>
<td>506.90 ± 54.46 cm g⁻¹</td>
</tr>
</tbody>
</table>

40% shade treatments were similar and significantly lower than that of the 80% shade treatment (Table 21). RAT was influenced by shade, but had no effect of water or interaction (Table 19). Treatment means were successively lower with increasing shade (Table 21).

Table 21 Effects of shade on the performance of *Cyperus erythrorhizos*. Response variables include shoot fresh weight (SFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT). Means are presented ± SE. Letters indicate significant differences (p<0.05) between means

<table>
<thead>
<tr>
<th></th>
<th>0% shade</th>
<th>40% shade</th>
<th>80% shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>SFW</td>
<td>0.177 ± 0.041 g</td>
<td>0.274 ± 0.043 g</td>
<td>0.369 ± 0.089 g</td>
</tr>
<tr>
<td>SSH</td>
<td>203.67 ± 12.13 cm g⁻¹</td>
<td>361.51 ± 56.50 cm g⁻¹</td>
<td>509.71 ± 48.45 cm g⁻¹</td>
</tr>
<tr>
<td>SLA</td>
<td>123.18 ± 8.15 cm² g⁻¹</td>
<td>148.34 ± 9.97 cm² g⁻¹</td>
<td>207.11 ± 10.45 cm² g⁻¹</td>
</tr>
<tr>
<td>RAT</td>
<td>2.201 ± 0.253</td>
<td>1.741 ± 0.145</td>
<td>1.104 ± 0.161</td>
</tr>
</tbody>
</table>

58
**Ammannia robusta**

**Table 22** Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Ammannia robusta*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>Water</th>
<th>Shade × Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>0.81</td>
<td>0.4515</td>
<td>8.51</td>
</tr>
<tr>
<td>SFW</td>
<td>0.16</td>
<td>0.8487</td>
<td>13.11</td>
</tr>
<tr>
<td>RFW</td>
<td>5.75</td>
<td><strong>0.0072</strong></td>
<td>3.95</td>
</tr>
<tr>
<td>SSH</td>
<td>11.63</td>
<td><strong>0.0001</strong></td>
<td>8.19</td>
</tr>
<tr>
<td>SLA</td>
<td>13.37</td>
<td>&lt;<strong>0.0001</strong></td>
<td>4.89</td>
</tr>
<tr>
<td>RAT</td>
<td>38.08</td>
<td>&lt;<strong>0.0001</strong></td>
<td>3.66</td>
</tr>
</tbody>
</table>

*Significant effects (p<0.05) are in bold

Biomass responses for *A. robusta* are presented as raw means ± SE in figure 26.

TFW and SFW exhibited an effect of water availability, but had no effect of shade or interaction (Table 22). For both measures, mean biomass was significantly lower in the saturated treatment compared to the drained (Table 23). RFW was affected by shade, but had no effect of water or interaction (Table 22). Treatment means at the 40 and 80% shade levels were similar and significantly lower than the open treatment (Table 24).

Raw means ± SE for SSH, SLA, and RAT are presented in figure 27. SSH was influenced independently by shade and water, but had no interaction effect (Table 22).

**Table 23** Effects of water availability on the performance of *Ammannia robusta*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), specific shoot height (SSH), and specific leaf area (SLA). Means are presented ± SE. All means presented were significantly different (p<0.05).

<table>
<thead>
<tr>
<th></th>
<th>Drained</th>
<th>Saturated</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>0.398 ± 0.060 g</td>
<td>0.239 ± 0.061 g</td>
</tr>
<tr>
<td>SFW</td>
<td>0.186 ± 0.028 g</td>
<td>0.094 ± 0.023 g</td>
</tr>
<tr>
<td>SSH</td>
<td>269.34 ± 56.06 cm g⁻¹</td>
<td>449.78 ± 75.04 cm g⁻¹</td>
</tr>
<tr>
<td>SLA</td>
<td>227.65 ± 22.08 cm² g⁻¹</td>
<td>350.33 ± 52.33 cm² g⁻¹</td>
</tr>
</tbody>
</table>
Fig. 26 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Ammannia robusta* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE
Fig. 27 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of Ammannia robusta grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 22). Differences between shade treatments (p<0.05) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers.
For this response variable, treatment means increased successively with increasing shade (Table 24), while the saturated treatment mean was significantly higher than the drained (Table 23). SLA showed an effect of shade and water, but no interaction effect (Table 22). Mean SLA also increased successively in response to increased shading (Table 24), while the saturated treatment mean was significantly higher than that of the drained (Table 23). RAT showed an effect of shade and interaction (Table 22). Under drained conditions, 40 and 80% shade treatment means were similar and significantly lower than that of the open treatment, while in saturated treatments, RAT successively decreased with increasing shade (Fig. 27.c). The drained treatment mean was significantly lower than that of the saturated at the intermediate shade level, while water treatment means were similar under 0 and 80% shade (Fig. 27.c). However, the relationship between water treatment means in the 80% shade treatment was significantly different than this relationship in the 0 and 40% shade treatments respectively (Fig. 27.c).

Table 24 Effects of shade on the performance of *Ammannia robusta*. Response variables include root fresh weight (RFW), specific shoot height (SSH), and specific leaf area (SLA). Means are presented ± SE. Letters indicate significant differences (*p*<0.05) between means.

<table>
<thead>
<tr>
<th></th>
<th>0% shade</th>
<th>40% shade</th>
<th>80% shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>RFW</td>
<td>0.263 ± 0.050 g A</td>
<td>0.138 ± 0.031 g B</td>
<td>0.082 ± 0.020 g B</td>
</tr>
<tr>
<td>SSH</td>
<td>147.96 ± 13.63 cm g⁻¹ A</td>
<td>350.04 ± 82.64 cm g⁻¹ B</td>
<td>519.35 ± 88.95 cm g⁻¹ C</td>
</tr>
<tr>
<td>SLA</td>
<td>160.24 ± 6.42 cm² g⁻¹ A</td>
<td>262.04 ± 37.80 cm² g⁻¹ B</td>
<td>417.48 ± 56.92 cm² g⁻¹ C</td>
</tr>
</tbody>
</table>
B. frondosa

Biomass responses for *B. frondosa* are presented as raw means ± SE in figure 28. There were no effects of shade, water or their interaction on any measure of biomass for this species (Table 25). Raw means ± SE for SSH, SLA, and RAT are presented in figure 29. Neither shade, water nor their interaction had an effect on SSH (Table 25). SLA was influenced by shade, but had no effect of water or interaction (Table 25). Treatment means under 0 (198.72 ± 10.54 cm² g⁻¹ A) and 40% shade (231.06 ± 16.94 cm² g⁻¹ A) were similar and significantly lower than the 80% shade mean(416.12 ± 36.77 cm² g⁻¹ B). RAT was also affected by shade, but had no effect of water or interaction (Table 25). Mean RAT in the 0 (3.483 ± 0.519 A) and 40% shade (3.111 ± 0.391 A) treatments was similar and significantly higher than that of the 80% shade treatment (1.820 ± 0.187 B).

**Table 25** Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Bidens frondosa*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>Water</th>
<th>Shade x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>0.51</td>
<td>0.6036</td>
<td>0.32</td>
</tr>
<tr>
<td>SFW</td>
<td>1.10</td>
<td>0.3421</td>
<td>0.01</td>
</tr>
<tr>
<td>RFW</td>
<td>0.41</td>
<td>0.6693</td>
<td>0.33</td>
</tr>
<tr>
<td>SSH</td>
<td>0.71</td>
<td>0.4996</td>
<td>1.60</td>
</tr>
<tr>
<td>SLA</td>
<td>19.7</td>
<td>&lt;.0001</td>
<td>0.10</td>
</tr>
<tr>
<td>RAT</td>
<td>4.90</td>
<td>0.0144</td>
<td>0.00</td>
</tr>
</tbody>
</table>

*Significant effects (p=<0.05) are in bold*
Fig. 28 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Bidens frondosa* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
Fig. 29 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Bidens frondosa* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
**Sorghum halepense**

Table 26 Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Sorghum halepense*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>p value</th>
<th>Water</th>
<th>p value</th>
<th>Shade x Water</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>0.06</td>
<td>0.9424</td>
<td>1.15</td>
<td>0.2911</td>
<td>1.18</td>
<td>0.3183</td>
</tr>
<tr>
<td>SFW</td>
<td>1.58</td>
<td>0.2178</td>
<td>0.44</td>
<td>0.5128</td>
<td>2.63</td>
<td>0.0837</td>
</tr>
<tr>
<td>RFW</td>
<td>0.36</td>
<td>0.7023</td>
<td>1.71</td>
<td>0.1997</td>
<td>1.13</td>
<td>0.3341</td>
</tr>
<tr>
<td>SSH</td>
<td>0.36</td>
<td>0.6999</td>
<td>4.09</td>
<td><strong>0.0491</strong></td>
<td>2.14</td>
<td>0.1296</td>
</tr>
<tr>
<td>SLA</td>
<td>10.07</td>
<td><strong>0.0003</strong></td>
<td>0.95</td>
<td>0.3340</td>
<td>5.11</td>
<td><strong>0.0101</strong></td>
</tr>
<tr>
<td>RAT</td>
<td>8.96</td>
<td><strong>0.0008</strong></td>
<td>13.24</td>
<td><strong>0.0009</strong></td>
<td>7.44</td>
<td><strong>0.0021</strong></td>
</tr>
</tbody>
</table>

*Significant effects (p=<0.05) are in bold

Biomass responses for *S. halepense* are presented as raw means ± SE in figure 30. All measures of biomass showed no effects of shade, water or their interaction (Table 26). Raw means ± SE for SSH, SLA, and RAT are presented in figure 31. SSH was affected independently by water, but had no effect of shade or interaction (Table 26). The saturated treatment mean (161.26 ± 17.51 cm g⁻¹) was significantly higher than that of the drained treatment (116.10 ± 10.41 cm g⁻¹). SLA was affected by shade and an interaction (Table 26). In drained conditions, mean SLA was significantly higher in the 80% shade treatment compared to the 40% shade treatment, while the open treatment mean was intermediate and similar to both (Fig. 31.b). In saturated substrate conditions, mean SLAs of the 40 and 80% shade treatments were similar and significantly higher than that of the open treatment (Fig. 31.b). Under intermediate levels of shade, mean SLA was significantly higher than that of the drained treatment, while water treatment means were similar at 0 and 80% shade levels (Fig. 31.b). However, the relationship between water treatment means at 40 and 80% shade were similar.
Fig. 30 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Sorghum halepense* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE
Fig. 31 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of Sorghum halepense grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 26). Differences between shade treatments ($p<0.05$) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers.
and significantly different from that of the open treatment (Fig. 31.b). RAT showed effects of shade, water and their interaction (Table 26). Shade treatment means of the 40 and 80% levels were similar and significantly lower than the open treatment under drained conditions (Fig. 31.c). In saturated treatments, mean RAT under 80% shade was significantly lower than that of the 40% treatment, while the mean in open conditions was intermediate and similar to both (Fig. 31.c). In open conditions, the drained treatment mean was significantly higher than that of the saturated treatment, while water treatment means were similar under 40 and 80% shade (Fig. 31.c). The difference between water treatment means was significantly greater in the open treatment compared to the 40 and 80% shade treatments respectively (Fig. 31.c).

Solidago sp.

Biomass responses for Solidago sp. are presented as raw means ± SE in figure 32. TFW, SFW and RFW were each affected by water availability and an interaction (Table 27). These responses were similar, but had subtle differences. Mean TFW in the 40% shade treatment was significantly higher than that of the open treatment in drained conditions, while the 80% treatment mean was intermediate and similar to both (Fig. 32.a). Under saturated conditions, the 80% shade treatment mean was significantly higher than that of the intermediate shade treatment, while the open treatment mean was intermediate to and similar to both (Fig. 32.a). In the intermediate shade treatment, the saturated treatment mean was significantly lower than that of the drained, while water treatment means were similar at the other two shade levels (Fig. 32.a). For this response variable, the difference between water treatment means was greater at the
Fig. 32 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) Solidago sp. grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 27). Differences between shade treatments ($p<0.05$) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers...
**Table 27** Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Solidago* sp. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Shade</th>
<th>Water</th>
<th>Shade x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>1.72</td>
<td>0.1947</td>
<td>6.59</td>
</tr>
<tr>
<td>SFW</td>
<td>2.92</td>
<td>0.0643</td>
<td>6.72</td>
</tr>
<tr>
<td>RFW</td>
<td>0.90</td>
<td>0.4176</td>
<td>5.78</td>
</tr>
<tr>
<td>SSH</td>
<td>3.84</td>
<td><strong>0.0301</strong></td>
<td>4.30</td>
</tr>
<tr>
<td>SLA</td>
<td>17.21</td>
<td>&lt;.0001</td>
<td>0.53</td>
</tr>
<tr>
<td>RAT</td>
<td>1.02</td>
<td>0.3727</td>
<td>1.90</td>
</tr>
</tbody>
</table>

*Significant effects (p<=0.05) are in bold.*

Intermediate level of shade than at the other two levels of shade (Fig. 32.a). Drained treatment means for SFW under 40 and 80% shade were similar and significantly higher than that of the open treatment (Fig. 32.b). In saturated conditions, 0 and 40% shade treatment means were similar and significantly lower than that of the 80% shade treatment (Fig. 32.b). In the intermediate shade level, the saturated treatment mean was significantly lower than that of the drained (Fig. 32.b). The relationship between water treatment means at the 40 and 80% shade levels were significantly different, while that of the open treatment was similar to both (Fig. 32.b). RFW in drained conditions was similar in the 0 and 80% shade treatments, while these were significantly lower than that of the 40% shade treatment. There was no difference in mean RFW across shade treatments under saturated conditions (Fig. 32.c). The saturated treatment mean was significantly lower than the drained at the intermediate shade level, while water treatment means were similar in open and 80% shade treatments (Fig. 32.c).

Differences between water treatments were significantly greater in the intermediate level of shade compared to both the open and 80% treatments (Fig. 32.c).
Fig. 33 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Solidago* sp. grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 27). Differences between shade treatments (p<0.05) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers.
Raw means ± SE for SSH, SLA, and RAT are presented in figure 33. SSH was affected by shade, water and their interaction (Table 27). In drained water treatments, mean SSH was significantly higher in the 80 compared to the 40% shade treatment, while the mean was intermediate and similar to both in open conditions (Fig. 33.a). Shade treatment means were similar across all levels under saturated conditions (Fig. 33.a). The saturated treatment mean was significantly higher under 40% shade, while water treatment means were similar at the other two shade levels (Fig. 33.a). Differences between water treatment means were significantly greater at the intermediate shade level than the 0 and 80% treatments respectively (Fig. 33.a). SLA was influenced by shade, but had no effect of water or interaction (Table 27). Mean SLA increased successively with increasing shade (0%: 147.14 ± 15.21 cm² g⁻¹ A, 40%: 204.47 ± 19.64 cm² g⁻¹ B, 80%: 257.65 ± 9.66 cm² g⁻¹ C). RAT had no effect of shade, water or their interaction (Table 27).

Carex crus-corvi

Biomass responses for C. crus-corvi are presented as raw means ± SE in figure 34. TFW was influenced by shade, but had no effect of water or interaction (Table 28). In the 40 and 80% shade treatments, mean TFW was similar and significantly higher than the open treatment (Table 29). SFW was affected by shade and an interaction (Table 28). Under drained conditions shade treatment mean SFW was similar across all levels of shade (Fig. 34.b). Treatment means under 40 and 80% shade were similar and significantly higher than the open treatment under saturated condition (Fig. 34.b). Water treatment means were similar at all levels of shade, however the relationship between these means in open conditions was significantly different than that at the 40 and 80%
Fig. 34 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Carex crus-corvi* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 28). Differences between shade treatments ($p<0.05$) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers.
Fig. 35 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of Carex crus-corvi grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
Table 28 Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Carex crus-corvi*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>Water</th>
<th>Shade x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>8.65</td>
<td><strong>0.0009</strong></td>
<td>0.55</td>
</tr>
<tr>
<td>SFW</td>
<td>12.2</td>
<td><strong>&lt;.0001</strong></td>
<td>1.29</td>
</tr>
<tr>
<td>RFW</td>
<td>8.07</td>
<td><strong>0.0014</strong></td>
<td>2.04</td>
</tr>
<tr>
<td>SSH</td>
<td>1.58</td>
<td>0.2194</td>
<td>0.70</td>
</tr>
<tr>
<td>SLA</td>
<td>28.93</td>
<td><strong>&lt;.0001</strong></td>
<td>0.00</td>
</tr>
<tr>
<td>RAT</td>
<td>3.89</td>
<td><strong>0.0320</strong></td>
<td>3.76</td>
</tr>
</tbody>
</table>

*Significant effects (p=<0.05) are in bold

shade treatments respectively (Fig. 34.b). RFW was affected by shade and an interaction (Table 28). In drained treatments, means were similar across all levels of shading (Fig. 34.c). Under saturated conditions, means of the 40 and 80% shade treatments were similar and significantly higher than that of the open treatment (Fig. 34.c). The saturated treatment mean was significantly lower than the drained in open conditions, while water treatment means were similar at the other two levels of shade (Fig. 34.c).

Raw means ± SE for SSH, SLA, and RAT are presented in figure 35. SSH showed no effect of shade, water or their interaction (Table 28). SLA was influenced by

Table 29 Effects of shade on the performance of *Carex crus-corvi*. Response variables include total fresh weight (TFW), specific leaf area (SLA), and root/shoot ratio (RAT). Means are presented ± SE. Letters indicate significant differences (p<0.05) between means.

<table>
<thead>
<tr>
<th></th>
<th>0% shade</th>
<th>40% shade</th>
<th>80% shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>0.262 ± 0.068 g&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.419 ± 0.087 g&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.730 ± 0.182 g&lt;sup&gt;B&lt;/sup&gt;</td>
</tr>
<tr>
<td>SLA</td>
<td>155.75 ± 8.77 cm&lt;sup&gt;2&lt;/sup&gt; g&lt;sup&gt;−1&lt;/sup&gt; A&lt;sup&gt;A&lt;/sup&gt;</td>
<td>199.71 ± 11.81 cm&lt;sup&gt;2&lt;/sup&gt; g&lt;sup&gt;−1&lt;/sup&gt; B&lt;sup&gt;B&lt;/sup&gt;</td>
<td>291.06 ± 12.30 cm&lt;sup&gt;2&lt;/sup&gt; g&lt;sup&gt;−1&lt;/sup&gt; C&lt;sup&gt;C&lt;/sup&gt;</td>
</tr>
<tr>
<td>RAT</td>
<td>1.862 ± 0.170&lt;sup&gt;AB&lt;/sup&gt;</td>
<td>2.016 ± 0.246&lt;sup&gt;A&lt;/sup&gt;</td>
<td>1.368 ± 0.149&lt;sup&gt;B&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
shade, but had no effect of water or interaction (Table 28). With increasing shade, mean SLA increased successively (Table 29). RAT had an effect of shade, but no effect of water or interaction (Table 28). The mean of the 80% shade treatment was significantly lower compared to that of the 40% shade treatment, while the mean of the open treatment was intermediate and similar to both (Table 29).

*Cardiospermum halicacabum*

**Table 30** Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Cardiospermum halicacabum*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response</th>
<th>Shade</th>
<th>Water</th>
<th>Shade x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>13.74</td>
<td>&lt;.0001</td>
<td>0.02</td>
</tr>
<tr>
<td>SFW</td>
<td>24.28</td>
<td>&lt;.0001</td>
<td>3.38</td>
</tr>
<tr>
<td>RFW</td>
<td>2.06</td>
<td>0.1431</td>
<td>0.00</td>
</tr>
<tr>
<td>SSH</td>
<td>9.70</td>
<td>0.0003</td>
<td>20.02</td>
</tr>
<tr>
<td>SLA</td>
<td>37.00</td>
<td>&lt;.0001</td>
<td>9.18</td>
</tr>
<tr>
<td>RAT</td>
<td>2.96</td>
<td>0.0653</td>
<td>1.02</td>
</tr>
</tbody>
</table>

*Significant effects (p<=0.05) are in bold

Biomass responses for *C. halicacabum* are presented as raw means ± SE in figure 36. TFW and SFW each had effects of shade and interaction (Table 30). These responses were nearly identical, however in saturated conditions, SFW showed a successive increase in biomass with increasing shade while TFW means in the 0 and 40% shade treatment were similar and significantly lower than under 80% shade (Figs. 36.a and 36.b). For both measures, all shade treatment means were similar under drained conditions (Figs. 36.a and 36.b). Saturated treatment means were significantly lower than the drained in open conditions for both TFW and SFW (Figs. 36.a and 36.b).
**Fig. 36** Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Cardiospermum halicacabum* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 30). Differences between shade treatments (*p*<0.05) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers.
Fig. 37 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Cardiospermum halicacabum* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE.
However, this relationship was reversed in the 80% shade treatment, and water availability treatments were similar in the intermediate shade treatment (Figs. 36.a and 36.b). For each of these response variables, the relationship between water availability treatments was different at each level of shading (Figs. 36.a and 36.b). RFW had no effects of shade, water or their interaction (Table 30).

Raw means ± SE for SSH, SLA, and RAT are presented in figure 37. SSH was independently influenced by shade and water, but had no interaction effect (Table 30). In the 0 (111.82 ± 8.65 cm g⁻¹ A) and 40% shade (120.54 ± 8.13 cm g⁻¹ A) treatments, means were similar and significantly lower compared to the 80% shade treatment (148.46 ± 8.27 cm g⁻¹ B). The drained treatment mean (111.83 ± 7.00 cm g⁻¹) was significantly lower than that of the saturated treatment (142.05 ± 6.60 cm g⁻¹). SLA was affected by shade and water, but had no interaction effect (Table 30). Mean SLA in the 40% shade treatment (263.33 ± 8.83 cm² g⁻¹ B) was significantly higher than the open treatment mean (235.18 ± 8.66 cm² g⁻¹ A), while that of the 80% shade treatment (363.69 ± 17.49 cm² g⁻¹ A) was significantly higher than both. The drained treatment mean (269.68 ± 12.80 cm² g⁻¹) was significantly lower than the saturated (305.11 ± 14.99 cm² g⁻¹). RAT was not affected by shade, water or their interaction (Table 30).

**Fimbristylis vahlii**

Biomass responses for *F. vahlii* are presented as raw means ± SE in figure 38. TFW and RFW were affected by shade, but had no effects of water or interaction (Table 31). Both of these response variables decreased successively with increasing shade
Table 31 Summary table of two-way ANOVA assessing the effects of shade, water availability (Water), and their interaction on the performance of *Fimbristylis vahlii*. Response variables include total fresh weight (TFW), shoot fresh weight (SFW), root fresh weight (RFW), specific shoot height (SSH), specific leaf area (SLA), and root/shoot ratio (RAT).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Shade</th>
<th>Water</th>
<th>Shade x Water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p value</td>
<td>F</td>
</tr>
<tr>
<td>TFW</td>
<td>32.99</td>
<td>&lt;.0001</td>
<td>0.16</td>
</tr>
<tr>
<td>SFW</td>
<td>23.80</td>
<td>&lt;.0001</td>
<td>1.61</td>
</tr>
<tr>
<td>RFW</td>
<td>52.10</td>
<td>&lt;.0001</td>
<td>0.04</td>
</tr>
<tr>
<td>SSH</td>
<td>35.52</td>
<td>&lt;.0001</td>
<td>15.42</td>
</tr>
<tr>
<td>SLA</td>
<td>3.06</td>
<td>0.0582</td>
<td>8.34</td>
</tr>
<tr>
<td>RAT</td>
<td>20.45</td>
<td>&lt;.0001</td>
<td>1.62</td>
</tr>
</tbody>
</table>

*Significant effects (p<0.05) are in bold

(Table 32). SFW was influenced by shade and an interaction (Table 31). In drained treatments, mean SFW of the 0 and 40% shade treatments were similar and significantly higher than the 80% shade treatment (Fig. 38). Shade treatment means decreased successively with increasing shade under saturated conditions (Fig. 38.b).

The saturated treatment mean was higher than the drained in open conditions, while water treatment means were similar under 40 and 80% shade (Fig. 38.b). The difference between water treatment means was significantly greater in the open treatments, compared to that in the 40 and 80% shade treatments respectively (Fig. 38.b).

Raw means ± SE for SSH, SLA, and RAT are presented in figure 39. SSH was

Table 32 Effects of shade on the performance of *Fimbristylis vahlii*. Response variables include total fresh weight (TFW), root fresh weight (RFW), specific shoot height (SSH), and root/shoot ratio (RAT). Means are presented ± SE. Letters indicate significant differences (p<0.05) between means.

<table>
<thead>
<tr>
<th></th>
<th>0% shade</th>
<th>40% shade</th>
<th>80% shade</th>
</tr>
</thead>
<tbody>
<tr>
<td>TFW</td>
<td>0.861 ± 0.197 g&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.317 ± 0.049 g&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.084 ± 0.022 g&lt;sup&gt;C&lt;/sup&gt;</td>
</tr>
<tr>
<td>RFW</td>
<td>0.536 ± 0.146 g&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.141 ± 0.025 g&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.021 ± 0.008 g&lt;sup&gt;C&lt;/sup&gt;</td>
</tr>
<tr>
<td>SSH</td>
<td>61.11 ± 8.70 cm g&lt;sup&gt;-1&lt;/sup&gt;&lt;sup&gt;A&lt;/sup&gt;</td>
<td>161.91 ± 36.10 cm g&lt;sup&gt;-1&lt;/sup&gt;&lt;sup&gt;B&lt;/sup&gt;</td>
<td>709.08 ± 179.45 cm g&lt;sup&gt;-1&lt;/sup&gt;&lt;sup&gt;C&lt;/sup&gt;</td>
</tr>
<tr>
<td>RAT</td>
<td>1.725 ± 0.237&lt;sup&gt;A&lt;/sup&gt;</td>
<td>0.818 ± 0.098&lt;sup&gt;B&lt;/sup&gt;</td>
<td>0.369 ± 0.087&lt;sup&gt;C&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Fig. 38 Total fresh weight (a), shoot fresh weight (b), and root fresh weight (c) *Fimbristylis vahlii* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE. Multiple comparisons were run on responses with main interaction effects (Table 31). Differences between shade treatments ($p<0.05$) are identified with upper-case letters; between water availability treatments with lower-case letters. Relationships between water treatments were also compared at each level of shading. Differences are indicated with numbers.
Fig. 39 Specific shoot height (a), specific leaf area (b), and root/shoot ratio (c) of *Fimbristylis vahlii* grown under two levels of water availability (drained - dashed line, saturated - solid line) and three levels of shade. Means are presented ± SE
independently influenced by shade and water, but had no interaction effect (Table 31). SSH increased successively across increasing levels of shade (Table 32), while the drained treatment mean (142.49 ± 44.71 cm g⁻¹) was significantly lower compared to the saturated treatment (441.14 ± 117.98 cm g⁻¹). SLA was affected by water, but not by shade or an interaction (Table 31). The saturated treatment mean (244.17 ± 19.49 cm² g⁻¹) was significantly higher compared to the drained (172.49 ± 13.88 cm² g⁻¹). RAT was influenced by shade, but had no effect of water or interaction (Table 31). Shade treatment means decreased successively with increasing shade (Table 32).

**General Response Patterns**

Consideration of the fifteen species included in the study yielded ten distinct response patterns. These included a broad range of tolerance combinations to shaded, lighted, saturated and drained conditions from a potential sixteen (Table 33). For taxa with interaction effects, tolerance of substrate saturation was often dependent on the shade level in which plants were grown.

**Table 33** All possible seedling tolerance combinations to shaded (S), lighted (L), saturated (SA) and drained (DR) conditions. Species were considered either tolerant (T) or intolerant (I) of these conditions to varying degrees. In some cases, tolerance of saturation was highly dependent on the level of shade

<table>
<thead>
<tr>
<th>Shade tolerance</th>
<th>Tolerant of saturation</th>
<th>Intolerant of saturation</th>
<th>Tolerant of draining</th>
<th>Intolerant of draining</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shade tolerant</td>
<td>S-T/SA-T</td>
<td>S-T/SA-I</td>
<td>S-T/DR-T</td>
<td>S-T/DR-I</td>
</tr>
<tr>
<td>Shade intolerant</td>
<td>S-I/SA-T</td>
<td>S-I/SA-I</td>
<td>S-I/DR-T</td>
<td>S-I/DR-I</td>
</tr>
<tr>
<td>Light tolerant</td>
<td>L-T/SA-T</td>
<td>L-T/SA-I</td>
<td>L-T/DR-T</td>
<td>L-T/DR-I</td>
</tr>
<tr>
<td>Light intolerant</td>
<td>L-I/SA-T</td>
<td>L-I/SA-I</td>
<td>L-I/DR-T</td>
<td>L-I/DR-I</td>
</tr>
</tbody>
</table>
C. hyalinolepis and B. pubescens are considered to be intolerant of light and tolerant of saturation in the seedling stage. They were each affected independently by shade, but had no effects of water or interaction (Tables 5 & 7). These species shared a response characterized by a positive effect of increasing shade (Fig. 40). Only the highest shade level was sufficient to elicit this response in C. hyalinolepis (Table 6), while mean SFW for B. pubescens was successively higher in each level of shade (Table 8).

E. virginicus, E. coelestinum and R. crispus were each affected by shade and an interaction (Tables 9, 11 & 12) characterized by the most pronounced differences in water treatment means at the highest level of shade (Fig. 41). These species responded positively to shade and

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**Fig. 40** General response pattern illustrating a positive response to shade only with no effect of water or interaction. This response was shared by C. hyalinolepis and B. pubescens. The dashed line represents drained treatments and the solid line represents saturated treatments.

**Fig. 41** General response pattern illustrating a positive response to shade and an interaction characterized by the most pronounced differences between water availability treatments at the highest level of shade. This response was shared by E. virginicus, E. coelestinum, and R. crispus. The dashed line represents drained treatments and the solid line represents saturated treatments.
each produced the greatest mean shoot biomass in the 80% shade/saturated treatment (Figs. 14.b, 16.b & 18.b). Though *R. crispus* also had a main effect of water (Table 12), it was assigned with this grouping on the basis of the interaction displayed. For all three species, the relationship between water treatment means was significantly different under 80% shade than in the open or 40% shade treatment (Figs. 14.b, 16.b & 18.b), though, multiple comparisons did not detect a difference between the 80/drained and the 80/saturated treatments for *E. coelestinum* (Fig. 16.b). *E. virginicus* and *E. coelestinum* are each considered to be light intolerant and tolerant of saturation in the seedling stage. But based on the more pronounced response of *R. crispus*, it is categorized as intolerant of both light and draining. For these species, performance in saturated conditions was dependent on the level of shade.

*E. prostrata* is considered to be intolerant of light and draining in the seedling stage. It was affected independently by shade and water but had no interaction effect (Table 14). This species was characterized by a positive effect of both shade and substrate saturation (Fig. 42), with the highest mean SFW in the 80/saturated treatment (Fig. 20.b).

![Fig. 42 General response pattern illustrating a positive response to shade and a positive response to substrate saturation with no interaction effect. This response was exhibited by *E. prostrata*. The dashed line represents drained treatments and the solid line represents saturated treatments](image-url)
**D. brachiata** and **C. erythrorhizos** were also influenced independently by shade and water availability with no interaction effect (Tables 16 & 19). These species were characterized by a positive effect of shade and an inhibitory effect of substrate saturation (Fig. 43), with the highest mean SFW in the 80/drained treatment (Figs. 22.b and 24.b). **C. erythrorhizos** responded positively to shading even in the intermediate treatment (Table 21), while only 80% shade was sufficient to elicit a response in **D. brachiata** (Table 17). Because of this **C. erythrorhizos** is considered to be moderately intolerant of light and intolerant of saturation and **D. brachiata** is intolerant of light and saturation in the seedling stage.

**A. robusta** exhibited an independent effect of water availability with no effect of shade or interaction.
(Table 22). For this species, substrate saturation inhibited performance (Fig. 44). Therefore, it is considered to be tolerant of shade and intolerant of substrate saturation in the seedling stage.

*B. frondosa* and *S. halepense* are considered to be tolerant of shade and saturation. Each had no effect of shade, water or interaction (Tables 25 & 26). For each of these species, performance was highly variable within treatments and, therefore, all treatments were found to be similar (Fig. 45).

*Solidago* sp. exhibited an effect of water and an interaction (Table 27) characterized by the most pronounced differences between water treatment means in the intermediate shade treatment (Fig. 46). This species performed poorly in open conditions, regardless of water availability and was inhibited by substrate saturation in substrate saturation in
intermediate shade conditions (Fig. 32.b). Mean SFW was highest and similar in the 40/drained, 80/drained and 80/saturated treatments (Fig. 32.b). Therefore, this species is considered to be moderately intolerant of light and generally intolerant of saturation in the seedling stage. However, performance was improved under 80% shade in the saturated treatment.

*C. crus-corvi* was light intolerant and tolerant of saturation. However, performance in saturated conditions was improved by shading. It exhibited an effect of shade and an interaction (Table 28) characterized by the greatest differences between water availability treatments in open conditions (Fig. 47). This species responded positively to increasing shade (Fig. 34.b). Though multiple comparisons did not uncover differences between water treatment means at any level of shade, analysis of the relationship between water treatment means at each level of shade uncovered an interaction in which this relationship was significantly different in open conditions compared to 40% and 80% shade respectively (Fig. 34.b).

![Shade vs. Shoot Fresh Weight](image)

**Fig. 47** General response pattern illustrating a positive response to shade and an interaction characterized the greatest differences between water treatment means in open conditions. This response was exhibited by *C. crus-corvi*. The dashed line represents drained treatments and the solid line represents saturated treatments.
*C. halicacabum* was tolerant of shade and its tolerance of saturation was highly dependent on the level of shade. This species was affected by shade and an interaction (Table 30) characterized by a reversal in the relationship between water treatment means with increasing shade (Fig. 48). For this species, SFW was inhibited by substrate saturation in open conditions (Fig. 36.b). However, water treatment means were similar in the intermediate level of shade and the saturated treatment mean was significantly higher than that of the drained under 80% shade (Fig. 36.b).

*F. vahlii* was intolerant of shade and drained conditions. Its tolerance of saturation was dependent upon the shade level. This species exhibited an effect of shade and an interaction effect (Table 31) characterized by the greatest differences between water

**Fig. 48** General response pattern illustrating a positive response to shade in saturated treatments and an interaction characterized by a reversal in the relationship between water treatment means with increasing shade. This response was exhibited by *C. halicacabum*. The dashed line represents drained treatments and the solid line represents saturated treatments.

**Fig. 49** General response pattern illustrating a negative response to shade and an interaction characterized by the greatest difference between water treatment means under open conditions. This response was exhibited by *F. vahlii*. The dashed line represents drained treatments and the solid line represents saturated treatments.
treatment means under open conditions (Fig. 49). This species was affected negatively by shade and accumulated the greatest shoot biomass in open/saturated conditions (Fig. 38.b). Multiple comparisons uncovered differences in water treatment means in the full sun treatments only, and the comparison of relationships between water treatment means at each level of shade agreed that this relationship in open conditions was significantly different than in the 40 and 80% shade treatments (Fig. 38.b).

**Consideration of Total Fresh Weight in General Responses**

Some may consider TFW to be a better indicator of performance than SFW, as it incorporates both shoot biomass (indicative of both photosynthetic capacity and reproductive potential) as well as root biomass (indicative of the ability to exploit soil water and nutrients). Additionally, belowground biomass is a better indicator of reproductive potential for plants which propagate vegetatively. Some plants would be regrouped in the consideration of this response variable. For these it was typically the interaction effect that was inconsistent.

The consideration of TFW indicates some overlap between the first (Fig. 40) and second groupings (Fig. 41). The grouping of *C. hyalinolepis* and *B. pubescens* is supported by the TFW response. These species would remain in the first group (Fig. 40). Additionally, *E. virginicus* would be moved to this group, as it showed no interaction in TFW due to similarities in RFW across treatments (Table 9). *E. coelestinum* could also potentially be moved to group one, due again to a lack of response in RFW (Table 11). Though, its interaction effect was not significant at $p<0.05$ it would be significant at a threshold of 10% (Table 11) and, therefore, could be considered intermediary to groups one (Fig. 40) and two (Fig. 41). The TFW response for *R. crispus* was consistent
with that of SFW (Table 12) and therefore, it would remain in group two (Fig. 41).

*E. prostrata* would remain in group three (Fig. 42) and *D. brachiata* would remain in group four (Fig. 43) based on consistent TFW responses (Tables 14 & 16). However, *C. erythrorhizos* did not display an effect of shade on TFW (Table 19) and would be moved from group four (Fig. 43) to group five (Fig. 44). Based on a 5% significance threshold, *A. robusta* would remain in group five (Fig. 44). However, it is important to note that an interaction effect for TFW would be considered significant at $p<0.10$ (Table 22), thus putting it in the realm of a shade/flood tolerance tradeoff. This interaction, illustrated by the response pattern shown in Fig. 50 is identical to the hypothetical response (Fig. 1). For this measure, *A. robusta* demonstrated an ability to tolerate saturation in open conditions and an ability to tolerate shade in drained conditions.

*B. frondosa* and *S. halepense* had no significant effects on TFW (Tables 25 & 26) and would be retained in group six (Fig. 45). *Solidago* sp. would remain in group seven (Fig. 46) based on a consistent TFW response (Table 27). *C. crus-corvi* had only a weak interaction effect for TFW, considered significant only at $p<0.10$ (Table 28).
Therefore, similarly to *E. coelestinum* it could be moved to group one (Fig. 40), or retained in its original group, eight (Fig. 47).

TFW response of *C. halicacabum* was similar to that of SFW (Table 30) and would remain in group nine (Fig. 48). *F. vahlii* would be retained in a group of its own, as it was the only species to exhibit a negative response to shade, however, TFW had no interaction effect (Table 30), due to a high degree of variability in the open treatments for RFW (Fig. 38.c).

Therefore, its response pattern would be amended as shown in Fig. 51. For this measure, *F. vahlii* is considered to be intolerant of shade and tolerant of saturation.

Therefore, grouping by TFW response would result in nine groups if TFW alone were considered or ten if SFW were an additional consideration. If a significance threshold of 5% were strictly adhered to, group one (Fig. 40) would consist of *C. hyalinolepis, B. pubescens, E. virginicus, E. coelestinum*, and *C. crus-corvi*. However, *E. coelestinum* could be retained in group two (Fig. 41) if an allowance were made to consider an interaction effect significant at $p<0.10$ based on the interaction observed in SFW. Similarly, *C. crus-corvi* could be retained in group eight (Fig. 47) based on these same criteria. Group two (Fig. 41) would include *R. crispus* and potentially *E.*
coelestinum. *E. prostrata* would remain in group three alone (Fig. 42). *D. brachiata* would become the sole member of group four (Fig. 43). Group five (Fig. 44) would include *C. erythrorhizos* and *A. robusta*. *B. frondosa* and *S. halepense* would remain in group six (Fig. 45). *Solidago* sp. would remain the sole member of group seven (Fig. 46). Group eight (Fig. 47) could be dissolved and *C. crus-corvi* moved to group one (Fig. 40) or retained for the reasons stated above. *C. halicacabum* would be retained with its original response pattern, nine (Fig. 48). *F. vahlii* would remain the sole member of group ten. However, its response pattern would be amended to reflect the lack of interaction effect on TFW (Fig. 51).

Field Distributions and General Response Patterns

Field data were analyzed to determine whether species exhibiting similar response patterns in the greenhouse experiment were associated in analysis of data from the field study. Detrended Correspondence Analysis (DCA; Fig. 52) of species included in the greenhouse study revealed two axes, which together explained almost 66% of the variability in species distributions (41.09 and 24.66%). Four distinct clusters were revealed. Most species were clustered in the upper half of the ordination, though some species were more closely associated than others. Though there was some clustering of species by the response pattern established, there was a high degree of overlap between groupings. Only in groups one and six did all members cluster closely in the ordination. Two of three members of the second grouping were associated. And while species exhibiting distinct response patterns were often far removed from most species, they were also closely associated with a member from another group. Species
cluster somewhat better with regard to TFW response pattern groupings, due to most of
the first group being associated with the large cluster in the upper half of the ordination.

Fig. 52 DCA of all sampling data for species included in the greenhouse study. Labels are species abbreviations followed by numbered general response patterns (amm_rob=Ammannia robusta, bid_fro=Bidens frondosa, bro_pub=Bromus pubescens, car_hal=Cardiospermum halicacabum, car_cru=Carex crus-crovi, car_hya=Carex hyalinolepis, cyp_ery=Cyperus erythrorhizos, dic_bra=Dicliptera brachiata, ecl_pro=Eclipta prostrata, ely_vir=Elymus virginicus, eup_coe=Eupatorium coelestinum, fim_val=Fimbristylis vahlii, rum_cri=Rumex crispus, soli_sp=Solidago sp., sor_hal=Sorghum halepense)

Species field distributions were also correlated with percent cover and elevation
data to determine if distributions were consistent with the general response patterns
established in the greenhouse study (Table 34). Due to the limited distribution of some species, and therefore limited data, only seven species from the greenhouse study were suitable for correlation analysis. Of the species tested, all but C. crus-corvi were significantly correlated with percent canopy cover. Of these, all but E. virginicus exhibited a negative correlation with percent canopy cover. This tendency toward more open areas is in contrast to what the greenhouse response for most species would predict. Only C. crus-corvi and E. virginicus were found to have field distributions consistent with the response to shade shown in the greenhouse study. S. halepense was the only species to exhibit a significant correlation which is also in disagreement with the greenhouse study results.

Table 34 Results summary of Spearman rank correlation of field distribution for select greenhouse study species with regard to percent canopy cover (Cover) and elevation (a surrogate for flood intensity/duration and water availability). Field data for all seasons/years were analyzed.

<table>
<thead>
<tr>
<th>Species</th>
<th>Cover r</th>
<th>p value</th>
<th>Elevation r</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bromus pubescens</td>
<td>-0.4423</td>
<td>&lt; 0.0001</td>
<td>-0.1169</td>
<td>0.2195</td>
</tr>
<tr>
<td>Cardiospermum halicacabum</td>
<td>-0.5329</td>
<td>&lt; 0.0001</td>
<td>0.1699</td>
<td>0.0732</td>
</tr>
<tr>
<td>Carex crus-corvi</td>
<td>-0.0010</td>
<td>0.9913</td>
<td>-0.0147</td>
<td>0.8781</td>
</tr>
<tr>
<td>Carex hyalinolepis</td>
<td>-0.4116</td>
<td>&lt; 0.0001</td>
<td>0.0625</td>
<td>0.5126</td>
</tr>
<tr>
<td>Elymus virginicus</td>
<td>0.4094</td>
<td>&lt; 0.0001</td>
<td>-0.0783</td>
<td>0.4118</td>
</tr>
<tr>
<td>Rumex crispus</td>
<td>-0.2646</td>
<td>0.0048</td>
<td>0.0958</td>
<td>0.3153</td>
</tr>
<tr>
<td>Sorghum halepense</td>
<td>-0.5812</td>
<td>&lt; 0.0001</td>
<td>-0.5389</td>
<td>&lt; 0.0001</td>
</tr>
</tbody>
</table>

*Significant effects (p=<0.05) are in bold
DISCUSSION

General Responses and the Shade/Flood Tolerance Tradeoff Hypothesis

Criteria for identifying tradeoffs included pinpointing interaction effects suggestive of an enhanced ability to tolerate shade in the absence of substrate saturation or an enhanced tolerance of saturation in the absence of shade. Interactions indicating an enhanced ability to tolerate shade, facilitated by flood tolerance were to be considered separately. However, no interactions of this type were encountered.

In general, results do not suggest the broad application of the flood/shade tolerance trade-offs to herbaceous BHF species. Instead, several unique response patterns were observed. Of these, conservative interpretation indicates that only one, represented by a single species, supports the hypothesis that species should not be highly tolerant of both shade and flooding. The response of *F. vahlii* displayed an enhanced tolerance of substrate saturation in the absence of shade. Though *A. robusta* did not support the hypothesis at the chosen threshold, some may consider its TFW response to be consistent with a tradeoff. Similar to *F. vahlii*, this interaction also represented an enhanced tolerance of saturation in the absence of shade. However, this interaction represents a modification of shade tolerance while *F. vahlii* merely demonstrated a high degree of flood tolerance coupled with shade intolerance. Unfortunately, limited field distribution data for these species did not allow for correlation analysis. However, their association with the sampling directly following the flood, taken with the affinity of these species to sunny flats along the river channel in more recent years (personal observation) suggests that water availability is important in their distribution.
The indication of potential tradeoffs in these two species suggests that tradeoffs may be important in ephemeral mudflat species. A high-light growth strategy may allow them to exist in regularly flooded areas despite indications of anoxic sensitivity (Menges and Waller 1983). For example, *A. robusta* was classified as a damp ground annual pioneer species characteristic of exposed soil surfaces (Watt et al. 2007) in spite of its limited tolerance to substrate saturation. Additionally, riparian pioneer species have been associated with characteristic seed, germination and dispersal traits which appear to confine them to river adjacent habitats except in times of overbank flooding (Leyer and Pross 2009). This suggests that a reliance on flooding disturbance for seed dispersal and exposure of substrates may confine mudflat ephemerals with anoxic sensitivity to open habitats regardless of their physiological shade tolerance.

Only *F. vahlii* conformed to the generalization that species are not expected to be highly tolerant of both flooding and shade (Hall and Harcombe 1998, Battaglia and Sharitz 2006), the majority of species did not support this assumption. Other species had positive or no effects of shade and all but three (*A. robusta, D. brachiata, and C. erythrorhizos*) had at least similar performance between water treatments at the highest level of shade. Additionally, shading facilitated improved tolerance of substrate saturation in several species. And while this does demonstrate the potential of interactions between these factors to modify accepted tolerances, the concept is antithetical to the idea of a tradeoff. For *E. coelestinum* and *C. crus-corti*, this was represented by subtle interactions, while *E. virginicus, Solidago* sp. and *C. halicacabum* showed more pronounced effects. These species (with the exception of *Solidago* sp.) are considered to display limited tolerance to anaerobic conditions (USDA/NRCS 2010,
Hypoxia is the ultimate adversity plants face in saturated soils (Jackson and Colmer 2005) and without effective adaptations to oxygenate root tissues, aerobic respiration ceases, eventually leading to the loss of cell integrity and tissue death (Vartapetian and Jackson 1997; Cronk and Fennessey 2001). Though limited effects on root biomass were shown here, the energy deficits associated with anaerobic respiration alone can reduce root function (Colmer and Greenway 2011). In plants with compromised root systems, shading likely provides an advantage for water conservation similar to the benefits of epinasty in flooded upland plants (Cronk and Fennessey 2001) by reducing the direct insolation of leaf surfaces. In addition, this may represent an enhanced flood escape response (Osborne 1984; Jackson 1985; Van der Sman et al. 1993) facilitated by shade avoidance (Taiz and Zeiger 2006). And though this apparently imparts some advantage in the tolerance of simple substrate saturation, plants with a high degree of internode elongation may not fare so well in the physical disturbance characteristic of flooding. *R. crispus* was grouped with *E. virginicus* and *E. coelestinum* based on its interaction, but the nature of its response suggests an affinity for shade and waterlogging rather than facilitation of flood tolerance by shade. Furthermore, the response is consistent with published tolerances, as *R. crispus* is both highly flood and shade tolerant (Visser et al. 1996; Vervuren et al. 1999), capable of surviving complete submergence in low light for more than two years (Vervuren et al. 2003).

The hypothesis that shade and flood tolerances interact to produce tradeoffs was rejected for several species based on the lack of interaction effects (*C. hyalinolepis*, *B. pubescens*, *E. prostrata*, *D. brachiata*, *C. erythrorhizos*, *B. frondosa*, and *S.*).
halepense). Some may be well suited for survival in the presence of both flooding and shade (C. hyalinolepis, B. pubescens, E. prostrata). Though responses indicate greater shade tolerance than expected coupled with high published flood tolerance in the species with ratings available (C. hyalinolepis and E. prostrata), there is no evidence that this was facilitated by flood tolerance. Similarly, demonstrated shade tolerance in conjunction with limitation by waterlogging is suggestive of nothing more than the tolerance to each individual factor.

Tolerance ratings from the USDA (2010) PLANTS database are tenuous assignments based on field observations and estimates from literature and are best viewed as approximations. However, the departure from published tolerance ratings in the responses of some species (C. hyalinolepis, E. prostrata, C. erythrorhizos, and S. halepense) should still be considered. Each exhibited a higher degree of shade tolerance than expected, while S. halepense also displayed greater tolerance to substrate saturation. In addition, species generally performed better in the shade. There are a few potential explanations for this observation. First, abnormal greenhouse conditions may have produced biased results. However, there were no signs of herbivory, disease or nutrient deficiency and temperatures fluctuated within normal ranges. And no morphologies or growth patterns observed were beyond the range of expectations. Secondly, light reflected off surfaces into the open side of shade enclosures may have been sufficient to alleviate light limitation in shaded species. However, phototropism would be expected in this circumstance and none was observed. Thirdly, light availability may not have been sufficiently reduced. However, the highest shade treatment value was selected based on cover estimates for field
sampling plots. Estimated % PAR reduction in sampling plots based on canopy cover (Lhotka and Loewenstein 2006) is applicable to measured % PAR reduction for shade enclosures. Given these considerations, it is more probable that results demonstrate shade avoidance responses coupled with photoinhibition of some species in open treatments by the high irradiance typical of Texas summers. Species characteristic of open habitats are known to exhibit more pronounced shade avoidance responses than species normally found in a shaded environment (Taiz and Zeiger 2006; Lambers et al 2006). Rapid internode elongation provides an adaptive advantage by increasing a plant’s chances to outgrow adjacent plants and compete more effectively for light, though it is often costly in terms of leaf expansion (Taiz and Zeiger 2006). Although these plants were unable to escape light limitation, the significantly higher biomass often observed in the shade indicates adaptive value. However, the longer, thinner stems associated with this response have been shown to enhance the risk of mechanical failure (Huber et al. 2011), which would place individuals at a distinct disadvantage to survive a flooding disturbance. So while responses are consistent with adaptations suggestive of the ability to tolerate shade and hypoxia, caution must be exercised in the interpretation of tradeoffs, as physical disturbance may be significantly more important for them in a number of species. Furthermore, the photoinhibition observed for some species indicates that the scale upon which shading is considered may be important when studying tradeoffs in herb seedlings; especially the warm season species that were inhibited by full sun in this study. Even in areas devoid of overstory canopy cover, shading by existing herbs may potentially facilitate seedling establishment for these species.
Field distributions indicated by correlation analysis were inconsistent with observed responses in all but a few species (C. crus-corvi and E. virginicus). However, this is to be expected with shade avoidance responses. Other than S. halepense, species negatively correlated with canopy cover exhibited some of the most pronounced responses to shade. While they have demonstrated the ability to tolerate shading, there are indications that germination rather than growth requirements for light may restrict some species to open environments: R. crispus: (e.g. Cavers and Harper 1966, Baskin and Baskin 1978, Van Assche et al. 2002), E. prostrata: (Altom and Murray 1996, Chauhan and Johnson 2008). The tolerance of substrate saturation displayed in the greenhouse study by S. halepense may partially explain its distribution in lower elevations. However, overbank flooding is infrequent in the area due to regulation of the river and low elevations do not necessitate flood tolerance in this situation.

Specific Shoot Height

About half of the species tested responded to shade, water or their interaction with taller, less dense shoot tissues. However, these responses were not uniform with regard to response pattern, published tolerance or observed field distribution. Effects of saturated soil conditions were likely due to a combination of escape response (Osborne 1984; Jackson 1985; Van der Sman et al. 1993) and/or aerenchymatous tissue formation (Jackson and Colmer 2005), though cross sections of stem tissue were not collected for analysis. Effects of shade can be contributed to shade avoidance strategy (Taiz and Zeiger 2006). Results for species with positive biomass responses to saturation or shade in conjunction with increased SSH (C. hyalinolepis, E. virginicus, E. coelestinum, C. erythrorhizos, and C. halicacabum) should be cautiously interpreted
due to the potential for increased susceptibility to physical disturbance. Conversely, plants without significant effects on SSH (B. pubescens, R. crispus, E. prostrata, D. brachiata, B. frondosa, and C. crus-corvi) would be similarly equipped to tolerate flooding disturbance under any of the conditions represented.

Specific Leaf Area

Leaf expansion is a common acclimation to shaded conditions, increasing surface area for light interception (Chapin et al. 1987; Rice and Bazzaz 1989; Barbour et al. 1999). There are indications that some herbaceous species may exhibit reduced leaf surface area under saturated soil conditions (Dale and Causton 1992), a response which may inhibit a plant’s ability to thrive in the shade. As expected, leaf area expansion was observed with increased shading. Every species except F. vahlia experienced a positive effect of shade on SLA. Notably, this was the only species to exhibit negative biomass responses to increasing shade. However, even then it was very close to a significant effect of shade on SLA though, any leaf area expansion by this species appears to have had little adaptive value. Some species were more sensitive and intermediate shade was sufficient to elicit a significant increase (C. hyalinolepis, E. virginicus, R. crispus, A. robusta, Solidago sp., C. crus-corvi, and C. halicacabum). For other species (B. pubescens, E. prostrata, D. brachiata, C. erythrorhizos, and B. frondosa), only the highest level of shade induced leaf expansion.

The hypothesis that inhibition of SLA by saturation would limit shade tolerance and coincide with tradeoff patterns was not fully supported for any species. Of the five species exhibiting a main effect of water, only E. virginicus was limited. This response was consistent with the findings of Dale and Causton (1992), as SLA was consistently
lower in saturated treatments across both open and shaded conditions. However, biomass responses did not support the suggestion that reduced SLA by saturation would limit shade tolerance. Contrary to the findings of Dale and Causton (1992) and Lennsen et al. (2003), saturation promoted leaf expansion in each of the other species affected (E. prostrata, A. robusta, C. halicacabum, and F. vahlii). Promotion of leaf expansion by saturation in the two species with response patterns attributable to tradeoffs directly conflicts with predictions. E. coelestinum and S. halepense exhibited interaction effects with patterns suggestive of the observations of Lennsen et al. (2003), in which species SLAs were found to be inhibited by saturation in open but not shaded conditions.

There was no consistency observed in SLA responses within groupings containing more than one member, other than the consistently higher SLAs observed for all species under shaded conditions. Increased leaf area expansion under saturated conditions was observed in species with both positive (E. prostrata) and negative (A. robusta) effects of substrate saturation on shoot biomass. Additionally, higher mean SLAs in saturated treatments were observed for species with interaction effects. For these species, both poor (F. vahlii) and the highest mean biomass measures (C. halicacabum) were observed in the saturated/80% shade treatments. Thus, a positive response of SLA to saturation does not necessarily confer an adaptive advantage in dealing with a combination of shade and substrate saturation. However, limited leaf area expansion under shaded conditions in F. vahlii may have contributed to its generally poor performance in the shade.
SLA responses were also not predicted by published tolerance in the species for which they were available. Increased leaf expansion was observed over a range of shade tolerance. SLA was reduced in the moderately flood tolerant, *E. virginicus*, and increased in highly tolerant, *E. prostrata*. These responses were somewhat consistent with their published tolerances. However, other species of low, moderate and high tolerance to anaerobic substrate conditions each showed no effect of water availability. Two of the three species listed with low flood tolerance exhibited an interaction effect, though saturation did not significantly reduce SLA, even in open conditions. And, this interaction was shared between species with low (*S. halepense*) and high (*E. coelestinum*) shade tolerance.

**Root to Shoot Ratios**

Roots function in the acquisition of water and nutrients, anchorage and storage (Evert and Eichhorn 2006). Soil saturation creates hypoxic conditions in the root zone, inducing anaerobic respiration (Cronk and Fennessey 2001). Under these circumstances, roots may act as a carbohydrate sink (Laan et al. 1990, Vartapetian and Jackson 1997, Blom et al. 1990), reducing allocation to above ground biomass. And though root aerenchyma formation may mitigate oxygen deficits in some bottomland species, inhibition of shoot performance under saturated conditions has also been shown in species with high root porosities (Visser et al. 2000). Conversely, flooded plants may also exhibit lowered root/shoot ratios as a consequence of reduced root tissues (Cronk and Fennessey 2001; Kozlowski 1984) or as an effect of pronounced flood escape responses (Osborne 1984; Jackson 1985; Van der Sman et al. 1993).
Consequently, substrate saturation has the potential to either inhibit or enhance allocation to aboveground biomass in the presence of shade.

Reduced RAT in the presence of substrate saturation for *B. pubescens* and *D. brachiata* was due to inhibition of root biomass and is therefore consistent with classical allocation of resources in response to flood. Additionally, general reduction of RAT in response to shade was observed for the majority of species (*C. hyalinolepis, E. virginicus, E. coelestinum, R. crispus, E. prostrata, C. erythrorhizos, A. robusta, B. frondosa, S. halepense, C. crus-corvi, and F. vahlii*). Most exhibited a general decrease in RAT with increasing shade. All but *A. robusta* and *S. halepense* were inconsistent with the expectation that saturation may alter characteristic allocation to shoot biomass in the presence of shade. Insignificant effects on biomass preclude the interpretation of the interaction displayed by *S. halepense*. In *A. robusta*, a subtle interaction represented inhibition of shoot biomass by substrate saturation coupled with inhibition of roots by shading. So, while it seems that carbohydrate consumption by roots for anaerobic respiration inhibited shoot growth for this species, light limitation also inhibited root growth. Reduction in photosynthetic capacity by light limitation reduces carbohydrate status of plants, producing a respiratory burden in root tissues (Lambers et al. 2006). Therefore, the apparent action of the roots as a carbohydrate sink in limiting shoot performance coupled with the inability of shoots to support the carbohydrate burden of anaerobic respiration in saturated root tissues produced a self-reinforcing inhibition resulting in the subtle tradeoff response exhibited for TFW. And though both of these responses were contingent on subtle interactions, their
consistency supports the hypothesis that modification of classical biomass allocation patterns may indicate mechanisms for tradeoffs in BHF herbs.

Conclusions

Only *F. vahlii* demonstrated a tradeoff in the context of SFW response patterns. However, the modified allometry of *A. robusta* in conjunction with its subtle TFW tradeoff suggests that it should also support the tradeoff hypothesis. Furthermore, the nature of its inclusion represents the potential importance of TFW response in uncovering tradeoff patterns. Only one species exhibited consistent inhibition of SLA by substrate saturation across shade treatments and this did not coincide with a tradeoff. In fact, saturation improved leaf area expansion in the two species exhibiting tradeoffs. Results indicate that tradeoffs involving simple substrate saturation may be important in ruderal annuals, as suggested by Menges and Waller (1983). However, the indication that the response of some plants to concurrent shade and substrate saturation may make them particularly susceptible to the physical disturbance of flooding also deserves further investigation. Species produced highly individualized responses, both in the ten shoot biomass response patterns observed and within response patterns for measures such as SSH, SLA and RAT. Only increased leaf expansion and allocation to shoot biomass were displayed by most species in response to shade.

The individualistic nature of responses in this study made the establishment of functional biomass response groups difficult and sheds light on a fundamental problem with functional group community assembly hypotheses (e.g. Boutin and Keddy 1993; Keddy 1992): the integral assumption that component species of a functional group will respond to all stressors in the same way. These approaches seek to generalize
responses to environmental variables based on traits, regardless of taxonomic composition. Assembly rules, for example, use hierarchical filters to predict the presence of plants within a habitat. These do not consider interactions or amplified effects of factors in combination, which produced many of the distinct responses observed here. Furthermore, the species-specific nature of these responses precludes broad generalization and any attempt to do so would be considered gross oversimplification. And though models with power to predict community composition are certainly the goal, oversimplification can be misleading. Even the indication that ruderal species may be more susceptible to the type of tradeoffs tested for here was tempered by disparate individual responses.

The individualistic responses exhibited typify the Gleasonian continuum concept (Gleason 1926). And the broad range of tolerances displayed by most species indicates the potential for a considerable amount of overlap along gradients of light and water availability. Certainly though, drastic environmental discontinuities such as those found in the highly disturbed habitat adjacent to the river channel may produce abrupt changes in plant community composition that could be viewed as a distinct association.

However, as noted, species common to mudflats are not truly confined there. Flooding disturbances allow these species to colonize areas where they are less typical and often compose the “pioneer” species in secondary succession of the floodplain (Leyer and Pross 2009); contributing to species richness and relative frequency of typical riparian species. Furthermore, the transition toward a community composed of more facultative and upland species since the flooding of the GBC indicates the importance of these disturbances in the maintenance of healthy BHF herb communities.
Recommendations

Direct testing of soil moisture levels would be preferable, due to the problematic nature of using elevation as a surrogate, especially in areas with limited overbank flooding. Elevation appeared to be a poor surrogate for flood tolerance in the field, due to several potential factors. Elevation data were extracted from a 9m resolution DEM for the floodplain, the finest resolution available. The scale of the data was insufficient to account for the full degree of variability between sampling plots. For example, a creek bed running directly through plot ten (commonly associated with standing water) was not represented on the map and the greater soil moisture present was not accounted for. Additionally, elevation would only be expected to correlate with flood tolerance in times of abundant precipitation, a characteristic not present throughout the field study. Regulation of the river subjects it to reduced flow variability (Cowell and Stoudt 2002) which may also minimize elevation effects. Finally, elevation may be a better predictor of tree species flood tolerance, especially along impounded rivers, as distance to water table would be expected to exert more influence over them than shallower rooted ground cover species.

Also, the test of flood tolerance applied in the greenhouse study, was instituted as more of a physiological stress (root zone O\textsuperscript{2} deprivation) than the physical disturbance which may be more influential on groundcover BHF communities. For example, species such as *A. robusta* and *F. vahlii* appear to rely on the scouring and sedimentation effects of flooding and/or drawdown along the river channel for exposed substrate on which to colonize. Additionally, *C. hyalinolepis* has been linked to sites with a high degree of sediment deposition (Sluis and Tandarich 2004). They found that the
prolific vegetative reproduction of this species allowed it to dominate these habitats, presumably due to the ability of vegetative shoots to escape burial and capitalize on the reduced competition present. So while tradeoffs do not seem to be important for most of the species tested, at least with flooding treated simply as hypoxic substrates, consideration of the physical disturbance of a flood may produce different results.

Hall and Harcombe (1998) presented their hypothesis as being potentially influential in several aspects of life history: germination, growth and mortality. And while this study only considered growth and mortality aspects, there are indications in the literature that light and water requirements for germination may be influential in structuring BHF herb communities. Additionally, flooding is important for seed dispersal in many riparian plant species. Therefore, studies utilizing a comprehensive approach (e.g. Battaglia et al. 2004) to test for tradeoffs with regard to germination, growth, mortality and dispersal characteristics are recommended.

An understanding of the effects of flood on dispersal in BHF species is necessary to predict which species are likely to colonize following a flooding disturbance. For example hydrochorus seeds are likely to be deposited by a flood while seeds of species with other dispersal mechanisms may be buried too deeply by sediment to germinate. Germination rates at various soil depths are an important consideration as burial depth is directly related to light availability. Seed characteristics such as size and buoyancy should be considered. Interaction effects between shade and flood on germination are important, as tolerance of shade and flooding in terms of growth and mortality is unimportant for a species unable to colonize in these areas. Seed bank studies which incorporate the influence of shade and water availability are also recommended.
Additionally, the indication that shading by existing herbs may facilitate seedling establishment should be explored.

To better understand the role of tradeoffs on existing plant communities, the effect of flooding disturbance on plants first grown in the shade should be evaluated. These studies should incorporate shoot density measures and evaluate the role of mechanical failure in species exhibiting both high and low shoot densities. Studies considering interactions between shade and substrate saturation may be a better predictor of tradeoff effects in species recolonizing after a flood. Taken in conjunction, these approaches have the potential to better illustrate the influence flooding on BHF communities.

The progression of the field study community toward one composed of more upland species in the absence of subsequent flooding indicates the importance of floods in maintaining healthy BHF communities. Therefore, management practices along regulated river reaches should allow seasonal or at least occasional overbank flooding within BHF wetlands. Plant community dynamics and seed bank composition should be monitored to ensure diverse community structure. However, further research is required to determine proper integration of tradeoffs into management techniques.
APPENDIX

SPECIES AND FREQUENCY DATA FOR THE LAKE LEWISVILLE/RAY ROBERTS GREENBELT CORRIDOR OVER FOUR YEARS OF SAMPLING
**Table A.1** List of all species represented over four years of sampling in the Lake Lewisville/Ray Roberts Greenbelt Corridor. Wetland indicator status for region 6 (WIS-Reg 6) and native/introduced status (N/I) were obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). + following WIS indicates a greater tendency toward wetland environments; - to upland environments. * indicates a tentative WIS assignment based on limited information. Species with missing values have no WIS designation. Nomenclature follows Diggs et al. (1999).

<table>
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<th>Species</th>
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<td><em>Carex crus-corvi</em> (Shuttiew. ex Kunze)</td>
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113
Sanicula canadensis (L.) UPL N
Torilis arvensis (Huds.) NI I

Asteraceae
Ambrosia trifida (Scheele) FAC N
Aster praealtus (Poir.) FACW- N
Aster subulatus (Michx.) OBL N
Bidens frondosa (L.) FACW N
Conyza canadensis (L.) UPL N
Dracopis amplexicaulis (Vahl) FAC+ N
Eclipta prostrata (L.) FACW N
Eupatorium coelestinum (L.) FACW- N
Eupatorium serotinum (Michx.) FAC- N
Grindelia papposa (GL Nesom & YB Suh) FAC N
Iva annua (L.) FAC N
Solidago sp. N/A N/A

Bignoniaceae
Campsis radicans (L.) FAC N

Boraginaceae
Heliotropium indicum (L.) FACW I
Myosotis macrosperma (Engelm.) FAC N

Brassicaceae
Rorippa sessiliflora (Nutt.) OBL N

Caprifoliaceae
Symphoricarpos orbiculatus (Moench) FACU* N
Chenopodiaceae
Chenopodium pallescens (Standl.) - N

Convolvulaceae
Dichondra recurvata (Tharp & MC Johnst.) FAC N
Ipomoea lacunosa (L.) FACW N

Cucurbitaceae
Melothria pendula (L.) FAC N
Sicyos angulatus (L.) FACW- N

Euphorbiaceae
Acalypha ostryifolia (Riddell) - N
Chamaesyce prostrata (Alton) - N
Chamaesyce serpens (Kunth) UPL N
Croton monanthogynus (Michx.) - N
Tragia urticifolia (Michx.) - N

Fabaceae
Apios americana (Medik.) FAC N
Lathyrus hirsutus (L.) - I
Medicago orbicularis (L.) - I
Senna marilandica (L.) FAC N
Vicia sativa (L.) FAC I

Geraniaceae
Geranium carolinianum (L.) - N

Lamiaceae
Teucrium canadense (L.) FACW- N

Lythraceae
Ammannia robusta (Heer & Regel) OBL N

Malvaceae
Hibiscus laevis (All.) OBL N

Menispermaceae
Cocculus carolinus (L.) FACU N

Onagraceae
Ludwigia decurrens (Walter) OBL N

Oxalidaceae
Oxalis corniculata (L.) FACU N
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<td><em>Rubus trivialis</em> (Michx.)</td>
<td>FAC</td>
<td>N</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td><em>Galium aparine</em> (L.)</td>
<td>FAC-</td>
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</tr>
<tr>
<td>Sapindaceae</td>
<td><em>Cardiospermum halicacabum</em> (L.)</td>
<td>FAC</td>
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<td>Scrophulariaceae</td>
<td><em>Leucospora multifida</em> (Michx.)</td>
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<td><em>Physalis turbinata</em> (Medik.)</td>
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<td></td>
<td><em>Solanum carolinense</em> (L.)</td>
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<td>N</td>
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<tr>
<td></td>
<td><em>Solanum ptychanthum</em> (Dunal.)</td>
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<td></td>
<td><em>Solanum rostratum</em> (Dunal.)</td>
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<tr>
<td>Verbenaceae</td>
<td><em>Lippia lanceolata</em> (Michx.)</td>
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</tr>
<tr>
<td></td>
<td><em>Lippia nodiflora</em> (Michx.)</td>
<td>FACW</td>
<td>N</td>
</tr>
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<td></td>
<td><em>Verbena scabra</em> (Vahl)</td>
<td>FAC</td>
<td>N</td>
</tr>
<tr>
<td>Violaceae</td>
<td><em>Viola missouriensis</em> (Greene)</td>
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<td>Vitaceae</td>
<td><em>Parthenocissus quinquefolia</em> (L.)</td>
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**Table A.2** Fall 2007 sampling summary with species, wetland indicator status (WIS) and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor. The unknown Cyperaceae listed consisted of seedlings which were unable to be identified further. Seedlings consisted of the following potential species: *Carex brevior, Carex crus-corvi, Carex hyalinolepis* and *Cyperus erythrorhizos*. Wetland indicator statuses for region 6 were obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). + following WIS indicates a greater tendency toward wetland environments; - to upland environments. * indicates a tentative WIS assignment based on limited information. Species with missing values have no WIS designation. Nomenclature follows Diggs et al. (1999)

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<th>Sampling plots</th>
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<td>Acalypha ostryifolia</td>
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<td>Amaranthus sp.</td>
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<td>Ammannia robusta</td>
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<td>Aster praealtus</td>
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</tr>
<tr>
<td>Campsis radicans</td>
<td>FAC</td>
<td>.00</td>
</tr>
<tr>
<td>Cardiospermum halicacabum</td>
<td>FAC</td>
<td>.00</td>
</tr>
<tr>
<td>Chamaesyce serpens</td>
<td>UPL</td>
<td>.00</td>
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<td>Cocculus carolinus</td>
<td>FACU</td>
<td>.00</td>
</tr>
<tr>
<td>Cyperus erythrorhizos</td>
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</tr>
<tr>
<td>Dicliptera brachiata</td>
<td>FACW</td>
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</tr>
<tr>
<td>Eclipta prostrata</td>
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</tr>
<tr>
<td>Eupatorium coelestinum</td>
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</tr>
<tr>
<td>Fimbristylis vahlii</td>
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<td>Heliotropium indicum</td>
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<td>Lemna sp.</td>
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Table A.3 Spring 2008 sampling summary with species, wetland indicator status (WIS) and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor. Wetland indicator statuses for region 6 were obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). + following WIS indicates a greater tendency toward wetland environments; - to upland environments. * indicates a tentative WIS assignment based on limited information. Species with missing values have no WIS designation. Nomenclature follows Diggs et al. (1999)

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<th>Sampling plots</th>
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<tr>
<td>Bromus secalinus</td>
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<tr>
<td>Carex bulbostylis</td>
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<td>.00</td>
</tr>
<tr>
<td>Carex crus-corvi</td>
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<td>.00</td>
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<td>Ipomoea lacunosa</td>
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<td>Lippia sp.</td>
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<td>Phalaris caroliniana</td>
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<td>Rumex crispus</td>
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Table A.4 Fall 2008 sampling summary with species, wetland indicator status (WIS) and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor. Wetland indicator statuses for region 6 were obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). + following WIS indicates a greater tendency toward wetland environments; - to upland environments. * indicates a tentative WIS assignment based on limited information. Species with missing values have no WIS designation. Nomenclature follows Diggs et al. (1999)
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<thead>
<tr>
<th>Species</th>
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<th>Percent Presence</th>
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<tr>
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120
Table A.5 Spring 2009 sampling summary with species, wetland indicator status (WIS) and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor. Wetland indicator statuses for region 6 were obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). + following WIS indicates a greater tendency toward wetland environments; - to upland environments. * indicates a tentative WIS assignment based on limited information. Species with missing values have no WIS designation. Nomenclature follows Diggs et al. (1999)

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<tr>
<th>Species</th>
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**Table A.6** Fall 2009 sampling summary with species, wetland indicator status (WIS) and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor. Wetland indicator statuses for region 6 were obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). *+ following WIS indicates a greater tendency toward wetland environments; - to upland environments. * indicates a tentative WIS assignment based on limited information. Species with missing values have no WIS designation. Nomenclature follows Diggs et al. (1999)
| Species                              | FAC   | OBL   | Rubus trivialis | Cardiospermum halicacabum | Carex brevior | Carex bulbosyllis | Carex crus-corvi | Carex hyalinolepis | Chamaesyce prostrata | Chenopodium pallescens | Cocculus carolinus | Conyza canadensis | Croton monanthogynus | Dichondra recurvata | Dicliptera brachiata | Elymus virginius | Eupatorium coelestinum | Eupatorium serotinum | Hibiscus laevis | Iva annua | Juncus effusus | Lathyrus hirsutus | Lippia sp. | Oxalis corniculata | Rivina humilis | Rorippa sessiliflora | Rubus trivialis | Rumex altissimus | Rumex crispus | Smilax sp. | Solanum ptychanthum | Solanum rostratum | Sorghum halepense | Symphoricarpos orbiculatus |
|-------------------------------------|-------|-------|----------------|---------------------------|---------------|--------------------|-----------------|--------------------|---------------------|-----------------------|--------------------|-----------------|---------------------|---------------------|---------------------|-----------------|---------------------|----------------------|----------------|----------|-------------|------------------|----------|---------------------|-----------|----------------------|----------------|---------------------|----------------|-----------------|----------------|-----------------|---------------------|-----------------|----------------------|-----------------|
|                                     | .00   | .00   | .48            | .48                       | .00           | .00                | .48             | .48                | .64                 | .00                   | .48                | .00              | .00                 | .48                | .04                 | .00            | .00                 | .00                 | .00          | .00     | .00    | .00     | .00     | .00     |
| Cardiospermum halicacabum          |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Carex brevior                      |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Carex bulbosyllis                  |       | .12   | .28            | .20                       | .04           | .04                | .00             | .04                | .20                 | .12                   | .12                | .16              | .12                 | .08                | .40                 | .04            | .04                 | .00                 | .00          | .00     | .00    | .00     | .00     | .00     |
| Carex crus-corvi                   |       | .16   | .48            | .24                       | .08           | .04                | .00             | .04                | .20                 | .16                   | .48                | .00              | .48                 | .16                | .08                 | .00            | .00                 | .00                 | .00          | .00     | .00    | .00     | .00     | .00     |
| Carex hyalinolepis                 |       | .00   | .00            | .04                       | .48           | .48                | .64             | 1.00               | .76                 | .40                   | .92                | .04              | .92                 | .28                | .00                 | .00            | .00                 | .00                 | .00          | .00     | .00    | .00     | .00     | .00     |
| Chamaesyce prostrata               |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Chenopodium pallescens             |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Cocculus carolinus                 |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Conyza canadensis                  |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Croton monanthogynus               |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Dichondra recurvata                |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Dicliptera brachiata               |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Elymus virginius                   |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Eupatorium coelestinum             |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Eupatorium serotinum               |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Hibiscus laevis                    |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Iva annua                          |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Juncus effusus                     |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Lathyrus hirsutus                  |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Lippia sp.                         |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Oxalis corniculata                 |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Rivina humilis                     |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Rorippa sessiliflora               |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Rubus trivialis                    |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Rumex altissimus                   |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Rumex crispus                      |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Smilax sp.                         |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Solanum ptychanthum                |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Solanum rostratum                  |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Sorghum halepense                  |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
| Symphoricarpos orbiculatus         |       |       |                |                           |               |                    |                 |                    |                     |                       |                    |                 |                     |                     |                    |                |                     |                     |               |         |       |       |       |       |
Table A.7 Spring 2010 sampling summary with species, wetland indicator status (WIS) and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor. Wetland indicator statuses for region 6 were obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). + following WIS indicates a greater tendency toward wetland environments; - to upland environments. * indicates a tentative WIS assignment based on limited information. Species with missing values have no WIS designation. Nomenclature follows Diggs et al. (1999)

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Table A.7 Spring 2010 sampling summary with species, wetland indicator status (WIS) and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor. Wetland indicator statuses for region 6 were obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). + following WIS indicates a greater tendency toward wetland environments; - to upland environments. * indicates a tentative WIS assignment based on limited information. Species with missing values have no WIS designation. Nomenclature follows Diggs et al. (1999)
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Table A.8 Fall 2010 sampling summary with species, wetland indicator status (WIS) and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor. Wetland indicator statuses for region 6 were obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). + following WIS indicates a greater tendency toward wetland environments; - to upland environments. * indicates a tentative WIS assignment based on limited information. Species with missing values have no WIS designation. Nomenclature follows Diggs et al. (1999)

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Table A.9 Spring 2011 sampling summary with species, wetland indicator status (WIS) and frequency for each of fourteen permanent sampling plots in the Greenbelt Corridor. Wetland indicator statuses for region 6 were obtained from the USDA/NRCS PLANTS database. WIS categories include OBL (obligate wetland species; estimated probability 99% occurrence in wetlands), FACW (facultative wetland species; 67-99% occurrence in wetlands), FAC (facultative species; equally likely to occur in wetland or upland environments with an estimated probability of 34-66% occurrence in wetlands), FACU (facultative upland species; 67-99% estimated probability of occurrence in uplands), and UPL (upland species; 99% upland). + following WIS indicates a greater tendency toward wetland environments; - to upland environments. * indicates a tentative WIS assignment based on limited information. Species with missing values have no WIS designation. Nomenclature follows Diggs et al. (1999)

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REFERENCES


Dempsey MA (2011) Anatomical and morphological responses of Cardiospermum halicacabum (balloon vine) to four levels of water availability. MS Thesis, University of North Texas, Denton, TX


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