Effects of Different Water Treatments and Density Configurations on Growth and Interspecific Competition between Hemarthria and Cynodon dactylon (Postprint)

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Date: 2018-05-18T00:00:00+00:00

Abstract

To rationally utilize excellent herbaceous plants in the Three Gorges Reservoir drawdown zone for restoring degraded vegetation and to explore the optimal mixed planting ratio of herbaceous plants during the restoration process, we selected two suitable pioneer herbaceous species from the Three Gorges Reservoir drawdown zone, *Hemarthria compressa* (H) and *Cynodon dactylon* (C), as experimental materials. On April 29, 2016, under controlled pot conditions, we established three different water regimes (control group—CK, shallow flooding group—SF, total flooding group—TF) and seven planting ratios, with the number of *H. compressa* and *C. dactylon* plants per pot increasing and decreasing incrementally by 2 plants, respectively. The specific ratios were H0C12, H2C10, H4C8, H6C6, H8C4, H10C2, and H12C0. A comparative study was conducted on the growth of *H. compressa* and *C. dactylon* and their competitive interactions under flooding conditions in mixed plantings. The findings revealed: (1) Regardless of monoculture or mixed planting, water stress significantly reduced the biomass of both *C. dactylon* and *H. compressa*, with *H. compressa* exhibiting greater sensitivity to flooding stress; (2) Both *C. dactylon* and *H. compressa* showed pronounced density-dependent effects on growth, but the response was more intense in *C. dactylon*; (3) Under different water and density conditions, the total relative biomass of the mixed planting system exceeded 1. In the CK group, *C. dactylon* and *H. compressa* exhibited competitive relationships; in the SF and TF groups, the competitive interaction between the two species decreased, demonstrating certain facilitative effects. Through comprehensive analysis of total biomass, root-to-shoot ratio, and competition coefficient (relative total biomass) of *H. compressa* and *C. dactylon* under different water and density conditions in this experiment, we determined that the optimal configuration ratio for *H. compressa* and *C. dactylon* under normal water supply treatment was H2C10, whereas under shallow flooding and deep flooding treatments it was H8C4. These research results can provide a basis for the restoration and management of herbaceous vegetation at different elevation zones in the Three Gorges Reservoir drawdown zone, and also offer theoretical references for artificial restoration of herbaceous vegetation in areas with identical or similar ecological types.

Full Text

Effects of Different Water Conditions and Plant Density on the Growth and Interspecific Competition of *Hemarthria compressa* and *Cynodon dactylon*

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Abstract

To rationally utilize excellent herbaceous plants for degraded vegetation restoration in the riparian zone of the Three Gorges Reservoir and explore optimal mixed planting ratios during restoration, we selected *Hemarthria compressa* (H) and *Cynodon dactylon* (C), two dominant pioneer herbaceous species adapted to the Three Gorges Reservoir drawdown zone, as experimental materials. On April 29, 2016, a pot experiment was conducted using a replacement series design with seven planting ratios (H0C12, H2C10, H4C8, H6C6, H8C4, H10C2, and H12C0) under three water treatments: normal growth conditions (CK), shallow flooding 10 cm above the soil surface (SF), and total flooding 2 m above the soil surface (TF). Results showed that: (1) Regardless of monoculture or mixed planting, water stress significantly reduced biomass production of both species, with *H. compressa* showing greater sensitivity to water stress; (2) Both species exhibited clear density-dependent effects on growth, with *C. dactylon* responding more strongly; (3) Under all three water treatments, the relative yield total (RYT) exceeded 1, indicating that the two species occupied different niches and showed symbiotic relationships. Under CK conditions, the species displayed competitive relationships, whereas under SF and TF treatments, they facilitated each other. Considering biomass production, root:shoot ratio, and competitive ability, we recommend a planting ratio of H2C10 under normal water conditions, whereas H8C4 is optimal under shallow and total flooding conditions. These findings provide a baseline reference for herbaceous vegetation restoration and management at different altitudes in the Three Gorges

Reservoir drawdown zone, and offer theoretical guidance for artificial grassland establishment in ecologically similar regions.

Keywords: *Hemarthria compressa*; *Cynodon dactylon*; growth; biomass allocation; interspecific competition; water stress; density

Introduction

Following impoundment of the Three Gorges Reservoir, water levels undergo periodic fluctuations between 145 m and 175 m, causing severe ecological degradation in the drawdown zone [1-2]. Many native plants cannot survive these extreme water level changes, leading to serious soil erosion and declining landscape quality [3]. Constructing vegetation communities has proven to be a rational and effective strategy for bank restoration [5], with herbaceous plants serving as pioneer species due to their survival and expansion capabilities. However, protection and rational utilization of herbaceous vegetation in the Three Gorges drawdown zone remain underdeveloped, partly due to insufficient understanding of how native dominant grasses adapt ecologically to flooding and compete under varying conditions.

Competition profoundly shapes plant morphology, life history, and population adaptation, representing a primary force determining community composition, structure, and dynamics [6-7]. In the Three Gorges drawdown zone, flooding acts as a key stress factor altering competitive relationships, while competitive ability serves as an important indicator of plant adaptation to stressful environments [8]. When establishing artificial grasslands for effective restoration, planting ratios can effectively regulate intraspecific and interspecific competition [9]. However, scientific questions remain unanswered regarding how native grasses adapt ecologically to flooding at different mixing ratios, how intra- and interspecific competition changes, and which ratios are optimal under varying flood conditions. Addressing these questions is crucial for establishing and restoring functional grassland ecosystems in the Three Gorges Reservoir region.

Both *Cynodon dactylon* and *Hemarthria compressa* are perennial Poaceae herbs [10-11] that commonly co-occur in the upper Yangtze region [12]. Their rapid expansion capabilities make them suitable for vegetation reconstruction in the drawdown zone. Although previous studies examined interspecific competition between these species [13-14], they focused only on single density configurations, limiting predictive power for other configurations. This study employs a replacement series design with gradient density configurations to investigate growth and interspecific competition under different flooding conditions, thereby overcoming limitations of single-density studies and providing theoretical support for vegetation restoration.

Materials and Methods

Experimental Materials

The experiment used annual cuttings of *C. dactylon* and *H. compressa* as research materials. Pot experiments were conducted using containers measuring 30 cm in diameter and 25 cm in height. On April 29, 2016, *C. dactylon* was cut into segments with 2-3 nodes, while *H. compressa* was cut into 10 cm segments containing buds. Plants were cultivated according to experimental design ratios and placed under a rain shelter at the Southwest University Ecological Experimental Garden for acclimation with regular weeding. Initial plant height and basal stem diameter measurements are shown in .

Experimental Design

Three water treatments were established: (1) Control (CK) with soil moisture at 60-63% of field capacity; (2) Shallow flooding (SF) with water 10 cm above the soil surface; and (3) Total flooding (TF) with water 2 m above the soil surface. Density configurations used a replacement series design [15] with total planting density of 12 plants per pot. The seven ratios were: H0C12, H2C10, H4C8, H6C6, H8C4, H10C2, and H12C0. A completely randomized block design was employed, with planting diagrams shown in [Figure 1: see original paper]. Daily observations began from the first treatment day to ensure maintained soil moisture conditions [16], with indices measured after treatment completion.

Measurement Indices

Biomass. Biomass was calculated as dry weight. At harvest, roots and shoots were separated, oven-dried at 80°C to constant weight, and weighed. Total biomass, aboveground biomass, belowground biomass, and root:shoot ratio were determined.

Growth and Morphological Indices. These included main stem length, basal stem diameter, branch number, total root length, and root diameter. Main stem length was measured with a ruler, basal diameter with vernier calipers, and root systems were scanned using a WinRHIZO La2400 root scanner.

Data Processing and Analysis

Plant competitive ability was assessed using competition indices matched to the experimental design [17-18]. In replacement series experiments, commonly used indices include Relative Yield Total (RYT), Relative Competition Intensity (RCI), and Aggressivity (A).

RYT evaluates biological efficiency in mixed planting systems. $RYT > 1$ indicates species occupy different niches with symbiotic relationships; $RYT = 1$ indicates shared resources with neutral relationships; $RYT < 1$ indicates antagonistic competition. The formula is:

$RYT = (Yab/Yaa) + (Yba/Ybb)$

where Yaa is monoculture biomass of *H. compressa*, Ybb is monoculture biomass of *C. dactylon*, Yab is mixed biomass of *H. compressa*, and Yba is mixed biomass of *C. dactylon*.

RCI measures competition intensity, with RCI < 0 indicating the species is disadvantaged and may be excluded, RCI $= 0$ indicating no effect, and RCI > 0 indicating facilitation. The formulas are:

RCIh = (Yaa - Yab)/Yaa RCIc = (Ybb - Yba)/Ybb

Aggressivity (A) compares competitive abilities between species, with A > 0 indicating species a is dominant, A $= 0$ indicating equal competitive ability, and A < 0 indicating species a is subordinate. The formulas are:

Ah = (Yab/Yaa) - (Yba/Ybb) Ac = (Yba/Ybb) - (Yab/Yaa)

Data were analyzed using SPSS 18.0 software with two-way ANOVA. Duncan' s test was used to examine significant differences among treatments ($P < 0.05$).

Results

Effects of Water Stress and Density on Morphology and Growth

All *C. dactylon* survived (100% survival rate) across treatments. Water treatment significantly affected plant height and total root length ($P < 0.05$), with average height under SF higher than CK but lower under TF. Branch number decreased with increasing flood depth. *H. compressa* also showed 100% survival. Water treatment extremely significantly affected all morphological indices ($P < 0.01$). Plant height increased under SF but decreased under TF. Basal stem diameter and root length followed similar patterns, while root diameter was greater under TF than SF. Density configuration significantly affected *C. dactylon* height, basal diameter, and root diameter ($P < 0.05$), but not root length. For *H. compressa*, density configuration extremely significantly affected all morphological indices ($P < 0.01$). The interaction between water and density significantly affected *C. dactylon* height and root length ($P < 0.05$) and extremely significantly affected all *H. compressa* indices except basal stem diameter ($P < 0.01$). Detailed statistical results are presented in and , with morphological responses illustrated in [Figure 2: see original paper] and [Figure 3: see original paper].

Effects of Water Stress and Density on Biomass

Water treatment extremely significantly affected total, aboveground, belowground biomass and root:shoot ratio of *C. dactylon* ($P < 0.01$), with all biomass components decreasing as flood depth increased while root:shoot ratio increased. Similar patterns occurred for *H. compressa* ($P < 0.05$). Density configuration extremely significantly affected total and belowground biomass of *C. dactylon* ($P < 0.01$), with maximum total biomass occurring at H0C12 under CK, but at H8C4 under SF and TF. For *H. compressa*, maximum biomass occurred at H2C10. The water × density interaction extremely significantly affected most biomass parameters for both species ($P < 0.01$). Detailed results are shown in and , with biomass responses illustrated in [Figure 4: see original paper] and [Figure 5: see original paper].

Relative Yield Total (RYT)

Across all water treatments and density configurations, RYT values exceeded 1 . Under CK, RYT at H2C10 was significantly higher than at H10C2 ($P < 0.05$). Under SF, no significant differences existed among density configurations. Under TF, RYT showed no significant differences among ratios, indicating consistent symbiotic relationships.

Relative Competition Intensity (RCI)

For *C. dactylon*, RCIc was greatest at H10C2 and exceeded 0, while minimal at H2C10. For *H. compressa*, RCIh was less than 0 at H8C4 and H2C10 but greater than 0 at other ratios, with maximum at H10C2. RCIh generally decreased as the proportion of *H. compressa* increased .

Aggressivity of *H. compressa*

Aggressivity values were positive only at H4C8 and H6C6 under CK (0.18 and 0.70 respectively) and at H2C10 under SF (1.97). All other values were negative, indicating *C. dactylon* was generally more competitive. Aggressivity decreased as the proportion of *H. compressa* increased across water treatments .

Discussion

Effects of Water Treatments on Both Species

When environmental factors like water availability change, plants exhibit altered morphology, biomass accumulation, and root:shoot ratios [20], adjusting biomass allocation strategies to adapt [21]. Hypoxia is the primary constraint in flooded environments, causing shifts from aerobic to anaerobic respiration and reducing photosynthetic product assimilation [22]. Plants respond through stem elongation to reach the water surface and access atmospheric oxygen, thereby mitigating flood damage [23]. In this study, both species showed greater height under shallow flooding than control conditions (H8C4, H10C2, H12C0), demonstrating this escape strategy.

Under total flooding, the species showed different responses. *H. compressa* maintained pre-flood height, reflecting a quiescence strategy that conserves nutrients for prolonged energy supply [24]. Conversely, *C. dactylon* continued elongating underwater, representing an active adaptive response that benefits underwater oxygen and light acquisition [25-26]. These contrasting strategies suggest potential for targeted restoration at different reservoir elevations.

Flooded environments feature weak light and oxygen deficiency, prompting wetland plants to reduce root length, increase root diameter, and expand root:shoot ratios to overcome oxygen limitation [27]. In this study, both species significantly reduced root length under total flooding while increasing root diameter, enhancing gas transport capacity [28-29]. The increased root:shoot ratio resulted from asynchronous impacts of water stress on above- and below-ground parts [30], with underwater leaf senescence reducing aboveground biomass while nutrient translocation to roots increased belowground biomass [31]. Both species reduced biomass under flooding, but *C. dactylon*' s stem elongation consumed substantial nutrient reserves, while *H. compressa* translocated aboveground nutrients underground for survival [32].

Effects of Density Configuration

Planting density affects growth by altering light and nutrient availability. In mixed cultures, the taller *H. compressa* canopy reduced light availability for *C. dactylon*, which responded by increasing height to compete [33]. However, *C. dactylon* total biomass in mixtures was lower than in monoculture (H0C12) because *H. compressa*' s dense canopy created shaded conditions that *C. dactylon* could not penetrate, reducing its aboveground biomass. Additionally, *H. compressa*' s longer roots gave it competitive advantage for soil nutrients, reducing *C. dactylon* belowground biomass.

H. compressa height and total biomass were greatest at low proportions (H2C10) under CK, but at high proportions (H12C0) under flooding. This reflects intense intraspecific competition at high densities in the confined pot environment, where resource niche overlap caused intense light competition, prompting height increases to acquire more resources [34-35].

Effects on Interspecific Competition

RYT precisely evaluates maximum biological efficiency in mixed systems [36]. RYT > 1 in all treatments indicated that *C. dactylon* and *H. compressa* occupied different niches, with *H. compressa*' s upright growth habit and *C. dactylon*' s prostrate form creating spatial niche separation [35]. However, RYT alone cannot indicate competition intensity, requiring RCI for assessment [37].

Biomass is the best indicator of relative competitiveness [38]. Under CK, *C. dactylon* individual biomass in mixtures decreased by 45.8%, 33.9%, 35.8%, 26.1%, and 52.1% at H2C10, H4C8, H6C6, H8C4, and H10C2 respectively, while *H. compressa* individual biomass decreased by 26.8%, 33.5%, 15.5%, 19.6%, and 23.3%. Both species showed density-dependent effects, but *C. dactylon* responded more strongly, indicating predominant competition under suitable conditions [39]. The pot environment limited resources, and *H. compressa*' s rapid growth, extensive root system, and broad leaves enabled it to capture resources more effectively, giving it competitive advantage [40].

Competition intensity in wetland plants correlates with water level. Under suitable water conditions, competition is intense, but increases in flooding depth reduce competition and may facilitate neighboring species [41]. In the Sanjiang Plain, *Glyceria spiculosa* promoted *Carex lasiocarpa* and *Deyeuxia angustifolia* biomass accumulation at 40 cm water depth, whereas it inhibited them at lower depths [42]. Similarly, this study found *C. dactylon* RCI < 0 (indicating facilitation) at most ratios under flooding, with biomass exceeding monoculture levels, suggesting *H. compressa* presence enhanced its productivity. Under SF, *C. dactylon* RCI was mostly < 0, indicating minimal *H. compressa* impact, while

H. compressa RCI was mostly > 0, showing strong *C. dactylon* impact. Under TF, *C. dactylon* aggressivity values were mostly negative, indicating its competitive advantage, likely related to species-specific flood tolerance [43]. The trade-off between stress tolerance and competitive ability may shift with environmental severity [44], though this relationship requires further investigation for these species.

Conclusion

This study demonstrates that both *C. dactylon* and *H. compressa* exhibit sensitivity and plasticity to water stress and density configurations. All plants survived (100%) and responded actively through biomass allocation adjustments, reduced branch number and root length, and increased root diameter. Density configurations created significant differences between treatments. Under CK, the species showed competitive relationships, with *C. dactylon* individual biomass decreasing as *H. compressa* proportion increased. Under flooding, interspecific competition decreased and facilitation emerged. Mixed planting was superior to monoculture under certain conditions. Considering total relative biomass, we recommend a planting ratio of H2C10 under normal water conditions and H8C4 under flooding conditions for artificial grassland establishment in the Three Gorges Reservoir drawdown zone.

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Note: Figure translations are in progress. See original paper for figures.