

Effects of *Cynodon dactylon*-*Hemarthria altissima* Intercropping on Plant Biomass under Different Flooding Conditions: Postprint

Authors: Chen Jinping, Zeng Chengcheng, Wei Hong, Liu Yuan, Wang Zhenxia, Jia Zhongmin

Date: 2017-03-08T00:00:00+00:00

Abstract

Understanding the optimal planting configurations of *Cynodon dactylon* and *Hemarthria altissima* under varying waterlogging regimes is crucial for vegetation restoration in degraded wetlands. Four water treatments were established: control (CK), flooding-drought alternation (FD), soil surface flooding (FL), and complete submergence (SM), combined with four planting densities (1, 2, 4, or 12 plants per pot) and two planting patterns (monoculture and mixed culture), to investigate biomass variations in both species under different waterlogging conditions, planting methods, and densities. The results showed that water regime, planting density, and planting pattern all significantly affected the aboveground biomass and total biomass of both species ($P < 0.05$). Under CK and FD conditions, mixed culture at medium and high densities significantly reduced the aboveground and total biomass of *C. dactylon* compared to monoculture ($P < 0.05$), whereas *H. altissima* biomass in mixed culture showed a certain increase relative to monoculture, with significant enhancement under high-density mixed culture ($P < 0.05$). Under FL conditions, mixed culture at medium and low densities enhanced the biomass of both *C. dactylon* and *H. altissima* to varying degrees. Under complete submergence, medium- and low-density mixed culture significantly promoted the aboveground and total biomass of *C. dactylon* ($P < 0.05$), but exhibited no significant effect on *H. altissima* ($P > 0.05$); high-density mixed culture showed no significant influence on the biomass of either species ($P > 0.05$). As the degree of waterlogging increased, the growth inhibition imposed by mixed culture on *C. dactylon* gradually diminished. In regions experiencing long-term shallow waterlogging, medium- and low-density mixed culture would be more favorable for the long-term coexistence of *H. altissima* and *C. dactylon*. In completely submerged areas at lower elevations, high-density mixed culture of *H. altissima* and *C. dactylon* represents a more optimal strategy.

Full Text

Effects of Mixed Intercropping of *Cynodon dactylon* and *Hemarthria altissima* on Plant Biomass Under Different Flooding Conditions

CHEN Jinping¹, ZENG Chengcheng¹, WEI Hong¹, LIU Yuan¹,
WANG Zhenxia¹, JIA Zhongmin¹

¹Key Laboratory of Eco-environments in Three Gorges Reservoir Region, Ministry of Education; Chongqing Key Laboratory of Plant Ecology and Resources; School of Life Sciences, Southwest University, Chongqing 400715, China

²Institute of Agricultural Resources and Environment, Guangxi Academy of Agricultural Sciences, Nanning 530007, China

³Southeast Sichuan Geological Group, Chongqing Bureau of Geology and Minerals Exploration, Chongqing 400038, China

Abstract

The water-level fluctuation zone of the Three Gorges Reservoir has experienced severe ecological degradation, particularly vegetation loss. Revegetation projects using riparian species such as *Cynodon dactylon* and *Hemarthria altissima* have been implemented as a key restoration strategy. Understanding plant growth responses to different flooding regimes and identifying suitable planting patterns are critical for improving wetland management strategies. This study investigated the optimal planting patterns for these two species under four flooding conditions: control (CK), flooding-dry alternating (FD), soil surface flooding (FL), and submergence (SM). Four planting densities were established (1, 2, 4, or 12 plants per experimental pot), with mixed intercropping applied at a 1:1 ratio in pots containing 2, 4, or 12 plants.

Results indicated that water treatment, planting density, and planting pattern significantly influenced the aboveground and total biomass of both species ($P < 0.05$). Under CK and FD conditions, *C. dactylon* biomass significantly decreased in mixed intercropping at medium and high densities ($P < 0.05$), whereas *H. altissima* biomass significantly increased at high density ($P < 0.05$). Under FL conditions, low- and medium-density mixed intercropping enhanced *C. dactylon* biomass ($P < 0.05$), while *H. altissima* biomass increased across all densities. Under SM conditions, low- and medium-density mixed intercropping significantly increased *C. dactylon* biomass ($P < 0.05$) but did not affect *H. altissima* biomass ($P > 0.05$). The inhibitory effect of mixed intercropping on *C. dactylon* diminished with increasing flooding stress. These findings suggest that low- and medium-density mixed intercropping promotes long-term coexistence in areas with prolonged shallow flooding, while high-density mixed intercropping is optimal for completely submerged low-altitude areas in the Three Gorges Reservoir region.

Keywords: *Cynodon dactylon*; *Hemarthria altissima*; flooding; mixed intercropping; biomass

1. Materials

The experimental materials consisted of *Hemarthria altissima* and *Cynodon dactylon*. Cuttings were collected from the Beibei section of the Jialing River on May 16, 2015, and cut into 5 cm segments for propagation. Uniform, healthy cuttings were transplanted into plastic pots measuring 22 cm × 15 cm × 17 cm (top diameter × bottom diameter × height). All potted plants were maintained in an ecological experimental garden at 249 m elevation under identical light and water conditions for acclimation prior to treatment. Only main stems were retained, and all plants exhibited vigorous growth with new roots and shoots before treatment initiation. The basic physicochemical properties of the experimental soil are presented in .

**** Basic physicochemical characteristics of the soil

Parameter	Value
pH	7.82
Organic matter (%)	1.32
Total N (g/kg)	0.82
Total P (g/kg)	0.31
Total K (g/kg)	7.72
Alkali-hydrolyzable N (mg/kg)	129.54
Available P (mg/kg)	31.72
Available K (mg/kg)	33.6
Field capacity	33.6%

2. Experimental Design

Hemarthria altissima seedlings approximately 35 cm tall and *C. dactylon* seedlings approximately 32 cm tall were randomly assigned to experimental groups based on three factors: water treatment, planting density, and planting pattern. The experimental design is summarized in .

Four water treatments were established: - **CK (Control)**: Maintained at 70–80% field capacity (33.6%) - **FD (Flooding-Dry Alternating)**: Alternating between soil surface flooding (5 cm depth) and mild drought (50–55% field capacity) - **FL (Soil-Flooding)**: Continuous soil surface flooding at 5 cm depth - **SM (Submergence)**: Water level maintained 5 cm above plant tops, adjusted as plants grew

Treatment intensity increased in the order: CK < FD < FL < SM. Pots were randomly positioned and regularly rearranged to minimize environmental heterogeneity, with sufficient spacing to prevent interference.

Three planting densities were implemented: - **Low density:** 1 plant per pot - **Medium density:** 2 or 4 plants per pot - **High density:** 12 plants per pot

For mixed intercropping, *C. dactylon* and *H. altissima* were planted in alternating arrangements at a 1:1 ratio. Single-crop controls were established for each species at each density.

4. Statistical Analysis

SPSS 20.0 software was used for three-factor analysis of variance (ANOVA) to examine the effects of water treatment, planting density, and planting pattern on root biomass, aboveground biomass, and total biomass. Post-hoc tests compared differences between sole and mixed cropping under identical water and density conditions. All biomass values were calculated as the average of individual plants within each treatment group. Plant material was separated into root and shoot components, oven-dried at 75°C to constant weight, and weighed using an electronic balance.

Results

1. Effects of Flooding and Planting Patterns on *Cynodon dactylon* Biomass All *C. dactylon* plants survived across treatments (100% survival). Three-factor ANOVA revealed that water treatment and planting density had extremely significant effects on root, aboveground, and total biomass ($P < 0.01$). Planting pattern and all two-way and three-way interactions significantly affected aboveground and total biomass ($P < 0.05$).

**** Effects of water treatment, planting density, and planting pattern on *C. dactylon* biomass

Source	Root biomass	Aboveground biomass	Total biomass
Water treatment	**	**	**
Planting density	**	**	**
Planting pattern	ns	*	*
Water × Density	**	**	**
Water × Pattern	ns	*	*
Density × Pattern	ns	*	*
Water × Density × Pattern	ns	*	*

Note: **P < 0.01, *P < 0.05, ns = not significant

Under CK and FD conditions, mixed intercropping at medium and high densities significantly reduced *C. dactylon* aboveground and total biomass compared to sole cropping ($P < 0.05$). In contrast, low-density mixed intercropping produced biomass values comparable to sole cropping ($P > 0.05$). Under FL conditions, low- and medium-density mixed intercropping significantly increased biomass ($P < 0.05$), while high-density mixed intercropping showed no significant difference from sole cropping ($P > 0.05$). Under SM conditions, low- and medium-density mixed intercropping significantly enhanced aboveground and total biomass ($P < 0.05$), but high-density mixing showed no significant effect. Under complete submergence, all *C. dactylon* leaves withered, but rhizomes remained viable.

2. Effects of Flooding and Planting Patterns on *Hemarthria altissima* Biomass *Hemarthria altissima* also exhibited 100% survival. Water treatment and planting density had extremely significant effects on all biomass parameters ($P < 0.01$). The water \times density interaction and planting pattern significantly affected aboveground and total biomass ($P < 0.05$), while other interactions were not significant .

**** Effects of water treatment, planting density, and planting pattern on *H. altissima* biomass

Source	Root biomass	Aboveground biomass	Total biomass
Water treatment	**	**	**
Planting density	**	**	**
Planting pattern	ns	*	*
Water \times Density	**	**	**
Water \times Pattern	ns	ns	ns
Density \times Pattern	ns	ns	ns
Water \times Density \times Pattern	ns	ns	ns

Note: ** $P < 0.01$, * $P < 0.05$, ns = not significant

Under non-submergence conditions (CK, FD, FL), low-density mixed intercropping did not significantly affect *H. altissima* biomass compared to sole cropping ($P > 0.05$). However, high-density mixed intercropping significantly increased total and aboveground biomass under CK and FD conditions ($P < 0.05$). Under SM conditions, low-density mixed intercropping enhanced biomass but without statistical significance ($P > 0.05$), while high-density mixing showed no significant difference from sole cropping.

[Figure 1: see original paper] Effects of water treatment, planting density, and planting pattern on *C. dactylon* biomass. Values are means; different lower-case letters indicate significant differences between planting patterns under the same water treatment and density ($P < 0.05$).

[Figure 2: see original paper] Effects of flooding and planting pattern on *H. altissima* biomass.

Across all treatments, *H. altissima* generally produced higher biomass than *C. dactylon*. *Cynodon dactylon* biomass declined with increasing water stress, whereas *H. altissima* maintained high biomass under non-submergence conditions but decreased sharply under complete submergence. Under non-submergence conditions, both species showed decreasing biomass with increasing density in both cropping systems. Mixed intercropping generally enhanced *H. altissima* biomass across all parameters, while benefiting *C. dactylon* only under FL and SM conditions.

Discussion and Conclusion

Mixed intercropping can improve root physiological metabolism and promote soil microbial activity, maintaining high levels of microbial quantity and enzyme activity [20-21]. It can also yield significant production benefits [22], improve plant nutrition [23-24], and coordinate inter-plant interactions [25]. However, intra- and interspecific competition represents a major limiting factor for plant growth. Species sensitive to interspecific competition may face exclusion if they remain at a competitive disadvantage.

Under normal water conditions, mixed intercropping significantly reduced *C. dactylon* total and aboveground biomass at medium and high densities, while *H. altissima* biomass increased at high density but showed no difference at medium density. This indicates that *C. dactylon* growth was suppressed by interspecific competition under non-flooded conditions. Inappropriate species combinations can lead to yield reductions, consistent with previous findings [27]. Plant competition is complex and sensitive, influenced by multiple factors including rhizobium inoculation [28-29] and abiotic stresses such as salinity [30].

Research on *Alternanthera philoxeroides* demonstrated that competition intensity decreased with increasing water level, shifting to facilitation when water levels exceeded 40 cm above plant tops [31]. Flooding stress is thus an important factor affecting competition intensity, which is species-specific [32] and closely related to environmental conditions [33]. In this study, mixed *C. dactylon* remained suppressed under alternating wet-dry conditions, while *H. altissima* biomass increased across all mixed densities, particularly at high density. This differential response likely reflects species-specific flooding adaptations: *H. altissima* employs escape strategies (stem elongation, leaf area expansion) to maintain high biomass under non-submergence stress [4], whereas *C. dactylon* growth declines with increasing water stress [5]. The larger biomass of *H. altissima* may shade *C. dactylon*, reducing its competitive ability under low-stress conditions, as evidenced under FL conditions at high density.

Under continuous soil flooding, low-density mixed intercropping promoted biomass in both species, suggesting that flooding mitigated *C. dactylon*'s competitive disadvantage. Therefore, low- and medium-density mixed intercropping would favor long-term species coexistence in such conditions. Under

complete submergence, high-density mixing had no significant effect on either species, while low-density mixing significantly increased *C. dactylon* biomass and moderately enhanced *H. altissima* growth. This may occur because submergence suppresses growth in both species, reducing *H. altissima*'s competitive advantage and allowing facilitation to become more prominent [34–36]. Species interactions can shift from competition to facilitation under high environmental stress [36], and mixed cropping often outperforms monoculture by alleviating intense intraspecific competition [13, 37].

Biodiversity positively correlates with stability [38], and positive species interactions can extend community coexistence and enhance species richness [39]. Under submergence, high-density mixed intercropping of *H. altissima* and *C. dactylon* is recommended to improve vegetation coverage and soil retention [40].

In summary, optimal planting strategies vary with flooding conditions in the Three Gorges Reservoir region: - **High-altitude, non-flooded or wet-dry alternating zones:** Mixed cropping disadvantages *C. dactylon*; sole cropping is recommended. - **Long-term shallow-flooded zones:** Low- and medium-density mixed intercropping promotes coexistence. - **Low-altitude, completely submerged zones:** High-density mixed intercropping is optimal for restoration outcomes.

These findings provide practical guidance for vegetation restoration in reservoir wetlands and other degraded ecosystems.

References

- [1] Colmer TD, Voesenek L. Flooding tolerance: suites of plant traits in variable environments. *Functional Plant Biology*, 2009, 36(8): 665–681.
- [2] [Citation text appears incomplete in original]
- [3] Ye C, Cheng XL, Zhang YL, Wang ZX, Zhang QF. Soil nitrogen dynamics following short-term revegetation in the water level fluctuation zone of the Three Gorges Reservoir, China. *Ecological Engineering*, 2012, 38(1): 37–44.
- [4] [Citation text appears incomplete in original]
- [5] [Citation text appears incomplete in original]
- [6] Yang CD, Zhang X, Zhou CY, Seago JL Jr. Root and stem anatomy and histochemistry of four grasses from the Jiangnan Floodplain along the Yangtze River, China. *Flora*, 2011, 206(7): 653–661.
- [7] [Citation text appears incomplete in original]
- [8] Callaway RM. Positive interactions among plants. *The Botanical Review*, 1995, 61(4): 306–349.
- [9] Babikova Z, Gilbert L, Bruce TJA, Birkett M, Caulfield JC, Woodcock C, Pickett JA, Johnson D. Underground signals carried through common mycelial networks warn neighboring plants of aphid attack. *Ecology Letters*, 2013, 16(7): 835–843.
- [10] [Citation text appears incomplete in original]

- [11] [Citation text appears incomplete in original]
- [12] [Citation text appears incomplete in original]
- [13] Neumann A, Schmidtke K, Rauber R. Effects of crop density and tillage system on grain yield and N uptake from soil and atmosphere of sole and intercropped pea and oat. *Field Crops Research*, 2007, 100(2-3): 285-293.
- [14] [Citation text appears incomplete in original]
- [15] [Citation text appears incomplete in original]
- [16] [Citation text appears incomplete in original]
- [17] [Citation text appears incomplete in original]
- [18] [Citation text appears incomplete in original]
- [19] [Citation text appears incomplete in original]
- [20] Niemi RM, Vepsäläinen M, Wallenius K, Simpanen S, Alakukku L, Pietola L. Temporal and soil depth-related variation in soil enzyme activities and in root growth of red clover and timothy in the field. *Applied Soil Ecology*, 2005, 30(2): 113-125.
- [21] [Citation text appears incomplete in original]
- [22] [Citation text appears incomplete in original]
- [23] [Citation text appears incomplete in original]
- [24] [Citation text appears incomplete in original]
- [25] Jolliffe PA, Wanja FM. Competition and productivity in crop mixtures: some properties of productive intercrops. *Journal of Agricultural Science*, 2000, 132(4): 425-435.
- [26] [Citation text appears incomplete in original]
- [27] [Citation text appears incomplete in original]
- [28] [Citation text appears incomplete in original]
- [29] [Citation text appears incomplete in original]
- [30] [Citation text appears incomplete in original]
- [31] [Citation text appears incomplete in original]
- [32] [Citation text appears incomplete in original]
- [33] Eskelinen A. Herbivore and neighbour effects on tundra plants depend on species identity, nutrient availability and local environmental conditions. *Journal of Ecology*, 2008, 96(1): 155-165.
- [34] Luo FL, Nagel KA, Scharr H, Zeng B, Schurr U, Matsubara S. Recovery dynamics of growth, photosynthesis and carbohydrate accumulation after de-submergence: a comparison between two wetland plants showing escape and quiescence strategies. *Annals of Botany*, 2011, 107(1): 49-63.
- [35] Tan SD, Zhu MY, Zhang QF. Physiological responses of bermudagrass (*Cynodon dactylon*) to submergence. *Acta Physiologiae Plantarum*, 2010, 32(1): 133-140.
- [36] Crain CM. Interactions between marsh plant species vary in direction and strength depending on environmental and consumer context. *Journal of Ecology*, 2008, 96(1): 166-173.
- [37] [Citation text appears incomplete in original]
- [38] [Citation text appears incomplete in original]
- [39] Lin K, Zhang DY, He F. Demographic tradeoffs in a neutral model explain death-rate abundance-rank relationship. *Ecology*, 2009, 90(1): 31-38.

[40] [Citation text appears incomplete in original]

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

Source: ChinaXiv – Machine translation. Verify with original.