LIFE-HISTORY PLASTICITY OF RIPARIAN ANNUAL PLANTS ADAPTED TO EXTREME VARIATIONS IN WATER LEVEL: MESOCOSM EXPERIMENTS

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ABSTRACT

The riparian zones of reservoirs associated with regulated rivers in China experience annual fluctuations in water level of up to 30 m that may vary in timing from year to year. Few plant species can tolerate such hydrological perturbation but short-lived riparian annuals might be evolutionarily pre-adapted to such conditions. This study investigated plasticity of life history in four annual species: one typically associated with free-flowing rivers (*Panicum bisulcatum*) and three that colonize reservoir margins (*Cyperus michelianus, Fimbristylis miliacea* and *Eclipta prostrata*). We found that all four species produced non-dormant seeds that survived prolonged submergence; germination percentage was independent of the time of exposure by receding waters. Although growth was reduced as a result of shorter growing seasons, all four species completed their life cycles and produced seeds before winter. In addition, *P. bisulcatum* and *C. michelianus* allocated biomass to seed production, at the expense of roots and stems, in response to later establishment. All species responded to later establishment with a reduced vegetative growth period before seed production. *C. michelianus, F. miliacea* and *E. prostrata* could also delay the onset of flowering time by up to 2 months. *P. bisulcatum,* a plant that can flower only after exposure to short days, consequently had a fixed flowering time and could accommodate delayed establishment only with a progressively shorter period of vegetative growth. This lower flexibility might explain its absence from reservoir margins. The conceptual framework presented here offers a tool to predict the establishment of vegetation under hydrological disturbance in riparian environments and thereby provides insights into improved restoration practice.

KEY WORDS: hydrology; life-history adaptation; flowering phenology; phenotypic plasticity; water-level fluctuation

INTRODUCTION

Riparian plants on the banks of free-flowing rivers occupy highly dynamic environments, depending on cycles of flooding and drought closely related to the seasonal distribution of precipitation (Lytle and Poff, 2004; Corenblit *et al*., 2009; Greet *et al*., 2011). However, the regulation of rivers has drastically altered natural cycles of flow: over half of the world's largest river systems are regulated by dams and storage reservoirs (Nilsson *et al*., 2005). Changes to flow regimes have induced shifts in plant distribution (Busch and Smith, 1995; Scott *et al*., 1997; Capon, 2003; Barrett *et al*., 2010), community composition (Nilsson *et al.*, 1991; Jansson *et al*., 2000; Beauchamp and Stromberg, 2008), and species diversity (Nilsson *et al*., 1991; Jansson *et al*., 2000; Uowolo *et al*., 2005).

In China, over 87,000 reservoirs with storage capacity greater than 0.1 million m^3 have been constructed for flood control, hydro-electric power generation and irrigation (MWR, 2010). The range of annual water level variation in these reservoirs is much greater than in free-flowing rivers, often as much as 25-30 m (e.g., Zhang and Lou, 2011), and seasonality is different and more variable. For example, in Danjiangkou Reservoir, a hydro-electric power storage reservoir, the water level was lowered gradually in January to reach a minimum in late April, and was then raised from late June to a maximum in late September in 2011; whereas in Huiting Reservoir, an irrigation reservoir, the water level was lowered from late April to its minimum in early September and this was maintained until the next spring (Fig. S1). Furthermore, there is variation in exposure time within a single river system, according to elevation.

The establishment of riparian vegetation is controlled by a combination of the duration of the flooding and the length of resulting growing season after exposure of the sediment by receding waters. In general, perennials are not able to tolerate such prolonged and erratic inundation; consequently attention has focused on short-lived annuals, whose evolutionary adaptations may enable them to complete their life cycles during the period of sediment exposure, for the re-vegetation and stabilization of shores.

Consequently, a better understanding is needed of how such plants respond to variation in exposure date and growing-season length. Adaptation to growing-season length typically involves the synchronization of life-cycle events, such as seed germination, flowering and reproduction, with flow regime (Poff *et al*., 1997; Lytle and Poff, 2004). For example, *Chenopodium rubrum* has been shown to be able to complete its life cycle within the short period of water recession between two floods (Blom *et al*., 1994). Growing-season length is a prime determinant of final size, biomass allocation and fecundity, and therefore of fitness (Galen and Stanton, 1993; Williams and Levine, 2004). Plasticity in phenology and the allocation of biomass, especially to reproduction, may be critical in allowing riparian annuals to complete their life cycles successfully.

This study examined life-history and morphological traits of four annual riparian species,

which are able to colonize dynamically exposed riparian zones, and therefore represent suitable models for investigating the survival and adaptation strategy to hydrological variation. Using mesocosms to simulate inundation and exposure periods, we addressed the following questions: (i) what is the effect of growing-season length on growth, and biomass partitioning? We predicted that cumulatively shorter growing-season lengths would decrease plant height, total biomass and seed yield, but might increase reproductive biomass allocation; (ii) what is the effect of growing-season length on flowering phenology and life history? We predicted that cumulatively shorter growing-season lengths would delay the initiation of flowering but might accelerate flower development and fruit maturation; and (iii) are such responses species-specific? We predicted that the two species naturally distributed at lower elevations would have greater evolutionary fitness (expressed as biomass and seed yield) under shorter growing seasons than the two species from higher elevation.

MATERIALS AND METHODS

Material

Four annual species, two typical of lower riparian zones in Chinese rivers and reservoirs (*Panicum bisulcatum* and *Cyperus michelianus*) and two typical of higher zones (*Fimbristylis littoralis* and *Eclipta prostrata*) were identified (Table 1). More than 2000 seeds were collected from at least 30 plants in native populations in Henan Province and Hubei Province, Central China from September to October of 2011.

The seeds were enclosed in 80- mesh nylon bags (5 bags and about 400 seeds per bag for each species), and submerged at the bottoms of five concrete mesocosms (2 m × 2 m × 2 m), filled with tap water on 12 November, at Wuhan Botanical Garden to simulate the flooded condition until they were used in experiments in 2012. We manipulated growing-season length by removing one of the bags of each species on five dates: 27 April, 19 May, 10 June, 12 July, and 17 August. The growing-season length was determined by the onset of senescence in autumn. Seeds from the bags were used for parallel germination and growth experiments.

Germination

Germination tests were carried out in a temperature-controlled (±1°C) growth chamber at a constant temperature of 25°C, using a 12-h photoperiod and a photon irradiance of 25 μmol m^{-2} s^{-1} provided by warm white fluorescent lamps. Thirty seeds were placed in each of five replicate 7-cm diameter Petri dishes containing two layers of filter papers saturated with distilled water. Distilled water was added to the dishes every 1 - 2 days to maintain a moist substrate. Germinated seeds were counted daily for 21 days.

Growth

Growth experiments were carried out in five concrete mesocosms (2 m × 2 m × 0.5 m deep). On each of the five sowing dates, ten seeds of each species were sown per 1.25-L black plastic pot, filled with a soil mixture consisting of 8% sand, 35% silt, 48% clay, and 9% organic matter. Each species had five replicates. On each occasion the pots for the four species were placed randomly in an open mesocosm filled with tap water to cover the surface of soil mixture (a different mescosm for each date). After three weeks, seedlings were thinned to one plant per pot. The plants were grown under full sun conditions, with daily watering, and no fertilization.

Reproductive phenology was recorded for all plants. After bolting, plants were checked daily for the date of first flower. When plants showed signs of senescence, they were harvested, carefully washed to remove soil from the roots. Plant material was oven dried at 60°C to constant weight. Total biomass was partitioned into underground parts (roots), stems, leaves, reproductive parts other than mature seeds or fruits, and mature seeds (fruits), before weighing.

Statistical analysis

Data were analysed using one-way analysis of variance (ANOVA) with sowing date as a factor. Where there were significant treatment effects, post-hoc Tukey tests were used to detect differences between growing periods. Data were first tested for homocedasticity and log-transformed when appropriate to meet this assumption.

RESULTS

Seed germination

Germination was generally high (> 60%) after inundation with tap water for up to 9 months, except for *Cyperus michelianus* (13-22%). *Panicum bisulcatum* maintained germinability > 90%. Germination was not affected by the duration of inundation, with no significant differences among five germination dates for any of the four species (Fig. 1).

Plant growth

Total biomass, maximum stem length and total seed biomass decreased significantly with the reduced growing-season length for all four species, with the exception of the total seed biomass of *Cyperus michelianus*, which was not significantly different (Table 2, Fig. 2). However, the growing-season lengths critical for maintaining final biomass were different among species. *Eclipta prostrata* and *Panicum bisulcatum* showed a reduction in biomass from the third sowing date (10 June), whereas this was evident in *Fimbristylis littoralis* from the fourth sowing date (12 July) and in *C. michelianus* only in the fifth (17 August). Similar trends among species in the minimum growing-season length necessary to maintain seed biomass production were also evident.

Biomass partitioning

The effects of growing-season length on patterns of biomass partitioning among plant parts were most noticeable between the earlier and the later sowing dates in the low-mid ground species, *P. bisulcatum* and *C. michelianus* (Fig. 3). In general, *P. bisulcatum* plants increased biomass partition to seed and leaf at the expense of stem, whereas *C. michelianus* increased seed and leaf biomass at the expense of root biomass, in response to shorter growing-season length. In contrast, biomass partitioning was not affected by growing-season length for the two higher-ground species, *F. littoralis* and *E. prostrata* (Table 2, Fig. 3).

Reproductive phenology

There were considerable differences between the species in the floral development time and the timing of flower production with growing-season length (Table 2, Fig. 4). For *Panicum bisulcatum*, the timing of the onset of flowering was independent of the length of the growing-season, despite its decline from 138 to 24 days. Hence the time to onset of flowering became progressively shorter with delay in sowing date. For the other three species, plants sown earlier flowered earlier, at least up to and including the third sowing date (10 June), and therefore there was no significant change in their development time to flowering. However, plants sown on or after12 July were not able to delay flowering, consequently showing a shorter vegetative period and flowering more rapidly. Thus in the three longer growing-season treatments (starting from April to June), onsets of flowering were 20 - 41 days earlier than for the later-starting growing seasons. By contrast, in the two shorter growing-season treatments (starting in July and August), flowering date was not affected by the delayed start of the growing season.

DISCUSSION

The ability of a plant to colonize the hydrologically extreme and dynamic environments of the riparian zones of regulated reservoirs and rivers depends first on maintaining a viable seed bank that is able to germinate when the exposure of sediment by receding waters occurs. The maintenance of seed viability independent of submergence time found in all four species and their generally high seed germinability after up to 9 months of submergence are clearly appropriate life-history traits. Dormancy was apparently enforced by conditions associated with submergence but no innate dormancy prevented germination on exposure. Seeds of riparian species that are dispersed in autumn and winter have previously been reported as more likely to show dormancy, unlike those dispersed in spring and summer (Boedeltje *et al.*, 2004).

The growth form of the four species is consistent with the reported establishment of seedlings in cohorts associated with successive recession lines, as water levels in rivers dropped (Nilsson *et al.*, 2010). In wetlands that experienced unpredictable water level

fluctuations, Britton and Brock (1994) found germination after wetting was reduced in summer, whereas our results showed no effect of germination timing between April and August.

Shortening of the growing season, by progressively later germination, decreased total plant biomass, plant height and total seed biomass in the four species studied, as would be expected (Sans and Masalles, 1994; Kelly and Levin, 1997; Metcalf *et al*., 2003). Nevertheless, all four species were able to complete their life cycles and produce seed even in the most curtailed season. Changes in the partitioning of biomass between different plant organs in response to growing-season length were only evident in the two low-mid elevation species, *P. bisulcatum* and *C. michelianus*. The greater allocation to seeds and leaves in later-germinating cohorts would tend to maintain fitness (seed production) and the photosynthetic support for seed production (Schutz *et al*., 2009; Wigley *et al*., 2009; Kobe *et al*., 2010). In contrast, greater allocation to roots or stems in earlier-germinating cohorts might provide better adaptation to drought in habitats exposed early in the season (Chapin *et al*., 1993; Kalapos *et al*., 1996; Markesteijn and Poorter, 2009). The two species typical of higher elevations, *F. littoralis* and *E. prostrata,* showed remarkably little flexibility in their biomass allocation and this may reflect the lower probability of shortened growing season in their natural habitats.

As flowering is crucial to the production of progeny (and thus evolutionary fitness), natural selection would be expected to have acted on flowering phenology in these species to maximize evolutionary fitness in unpredictable environments (Fitter and Fitter, 2002; Franks *et al*., 2007; Franks, 2011; Haggerty and Galloway, 2011). *Panicum bisulcatum* was distinctive in that its flowering time in early September was unaffected by germination date and so successively later cohorts showed progressively shorter vegetative periods before reproduction. This indicates a physiological response in which exposure to daylengths below a threshold value (short days) is required for floral initiation; this is typical of tropical grasses (Nada, 1980) and guarantees reproduction in surviving plants before the winter. The early-germinating cohorts of the other three species had an intrinsically shorter life cycle and therefore started flowering earlier. However, they were able to delay flowering up to 2 months in response to later germination, and maintain their vegetative growth periods. There were limits to this phenological plasticity, as cohorts germinating in July and August did not have flowering dates later than those germinating in June and suffered correspondingly reduced vegetative periods. For example, in *C. michelianus*, germination in the August cohort was 111 days later than the April cohort but first flowering was delayed only 58 days, leading to a reduction of the vegetative growing season from 97 to 36 days. This rapid development and reproduction in short growing seasons is similar to that seen in studies of alpine or high-latitude environments (Arroyo *et al*., 1981; Blionis *et al*., 2001; Stinson, 2004; Haggerty and Galloway, 2011), suggesting that there has been natural selection for flowering phenology.

Riparian habitats represent a clear gradient of growing-season length, as flood duration decreases almost linearly with increasing elevation. The observed differences in plant performance among the species studied were generally in accordance with the natural distribution patterns along riverbank elevation gradients observed in the field. *Cyperus michelianus* responded flexibly to growing season length, increasing biomass allocation to seed production even in the shortest growing season treatment; it is generally, the most tolerant species, and often colonizes newly exposed riparian zones rapidly (Fig. 1). *F. littoralis* and *E. prostrata* were flexible with respect to flowering time, but not so in terms of biomass allocation; however they maintained generally high biomass allocation to seed production and hence perform well at higher elevations in the field. Although *P. bisulcatum* increased allocation to seed production under a shorter growing season. As the only species showing photoperiod sensitivity, it experienced the greatest reduction in vegetative growth after late establishment, which reduced overall seed production. This reduced flexibility might explain its restriction to free-flowing rivers, and absence from regulated reservoirs; its preference for low elevations in the river profile may be related to sensitivity to drought stress (Alfonso and Brueggemann, 2012).

Very few species are able to tolerate the extreme and relatively unpredictable fluctuations in water level imposed on the riparian zone of reservoirs and regulated rivers (Nilsson *et al*., 1991; Johansson and Nilsson, 2002). The results of this study support the three initial predictions and largely explain how these short-lived annuals are able to accommodate such extreme hydrologies. All four species produce non-dormant seeds that can survive prolonged submergence to ensure the potential for germination whenever conditions are favourable (emergence from flooding). They can complete their life cycles in relatively short period and respond flexibly when establishment is delayed by up to four months, by means of later flowering and/or shortened vegetative period in order to maintain seed production. Two of the species can also allocate more biomass to seed production, at the expense of roots and stems, in response to late recession of flood waters. The conceptual framework presented here offers a tool to predict the establishment of vegetation under hydrological variation in riparian environments and thereby provides insights that can be used to improve restoration practice and interpret the effect of changes in flow regulation.

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Supporting Information

Fig S1. Hydrographs for two hydropower reservoirs (a) Three Gorges Reservoir and (b) Danjiangkou Reservoir; and two irrigation reservoirs (c) Huiting Reservoir and (d) Yinghe Reservoir I in Hubei Province in 2011and 2012.

Table 1. Frequency of occurrence of four annual plant species on the margins of 29 free-flowing rivers and 22 reservoirs in Central China in 2012

Species	Frequency (%)		Elevational range
	Rivers	Reservoirs	
Panicum bisulcatum Thunberg (Poaceae)	24.1	0.0	Low to Mid
Cyperus michelianus (L.) Link (Cyperaceae)	13.8	40.9	Low to Mid
Fimbristylis littoralis Gaudichaud (Cyperaceae)	24.1	40.9	Mid to high
Eclipta prostrata L (Asteraceae)	27.6	50.0	High

Table 2 Results of ANOVA for the effects of initial growing period of *Panicum bisulcatum*, *Cyperus michelianus*, *Fimbristylis littoralis* and *Eclipta prostrata* plants on life history traits and percentage allocation

	P. bisulcatum	*C. michelianus*	*F. littoralis*	*E. prostrata*
d.f.	4	4	4	4
F –value and significant levels				
1. Life history traits				
Total biomass	32.33***	11.67***	30.33***	36.47***
Maximum stem length	28.67***	5.30**	3.17*	17.76***
Total seed biomass	11.05***	1.37 ns	30.49***	4.80**
2. Partitioning				
Seeds	7.20***	4.08*	1.38 ns	0.75 ns
Leaf and reproductive supports	19.42***	3.69*	1.66 ns	1.11 ns
Stems	6.93***	0.29 ns	1.73 ns	0.19 ns
Roots	1.72 ns	6.91***	0.51 ns	0.70 ns
3. Reproductive phenology				
Date of first flowering	2.45 ns	7.59***	6.88***	50.46***
Days until flowering	2011.00***	11.91***	9.39***	24.50***

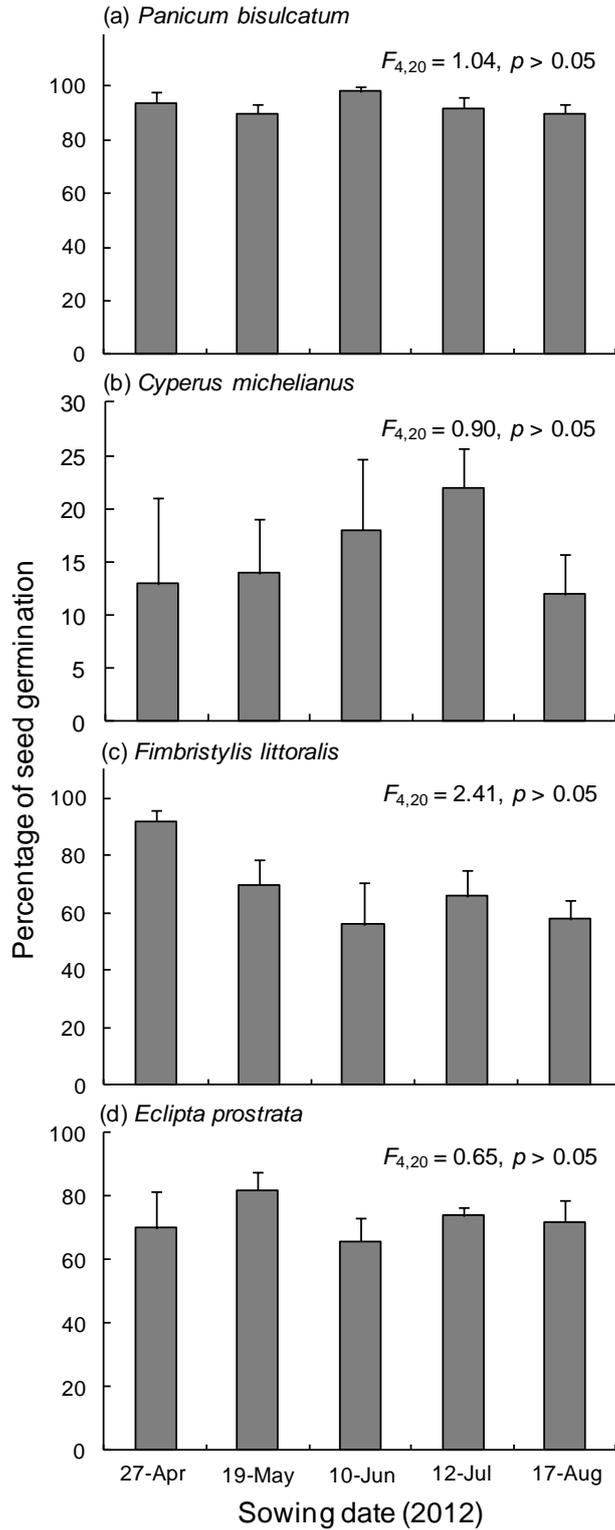ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

Fig. 1. Seed germination of (a) *Panicum bisulcatum*, (b) *Cyperus michelianus*, (c) *Fimbristylis littoralis*, and (d) *Eclipta prostrata* plants on five sowing dates, after prolonged storage under water. Results of one-way ANOVA are indicated.
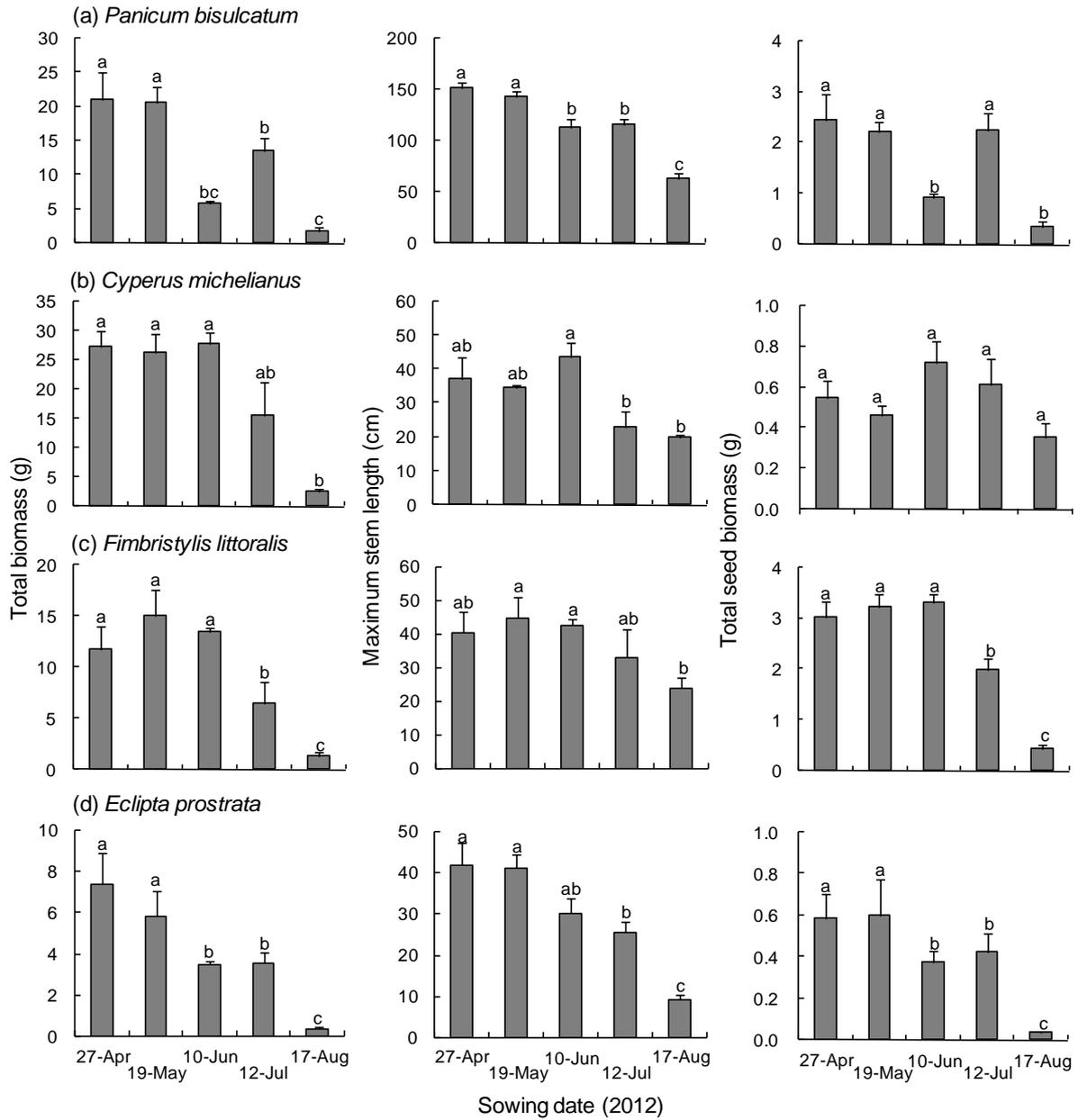
Fig. 2. Total biomass, maximum stem length and total seed biomass for (a) *Panicum bisulcatum*, (b) *Cyperus michelianus*, (c) *Fimbristylis littoralis*, and (d) *Eclipta prostrata* plants in response to growing-season length, as determined by five sowing dates. The bars indicate standard errors. Different letters indicate significant ($p < 0.05$) differences according to Tukey multiple comparisons.
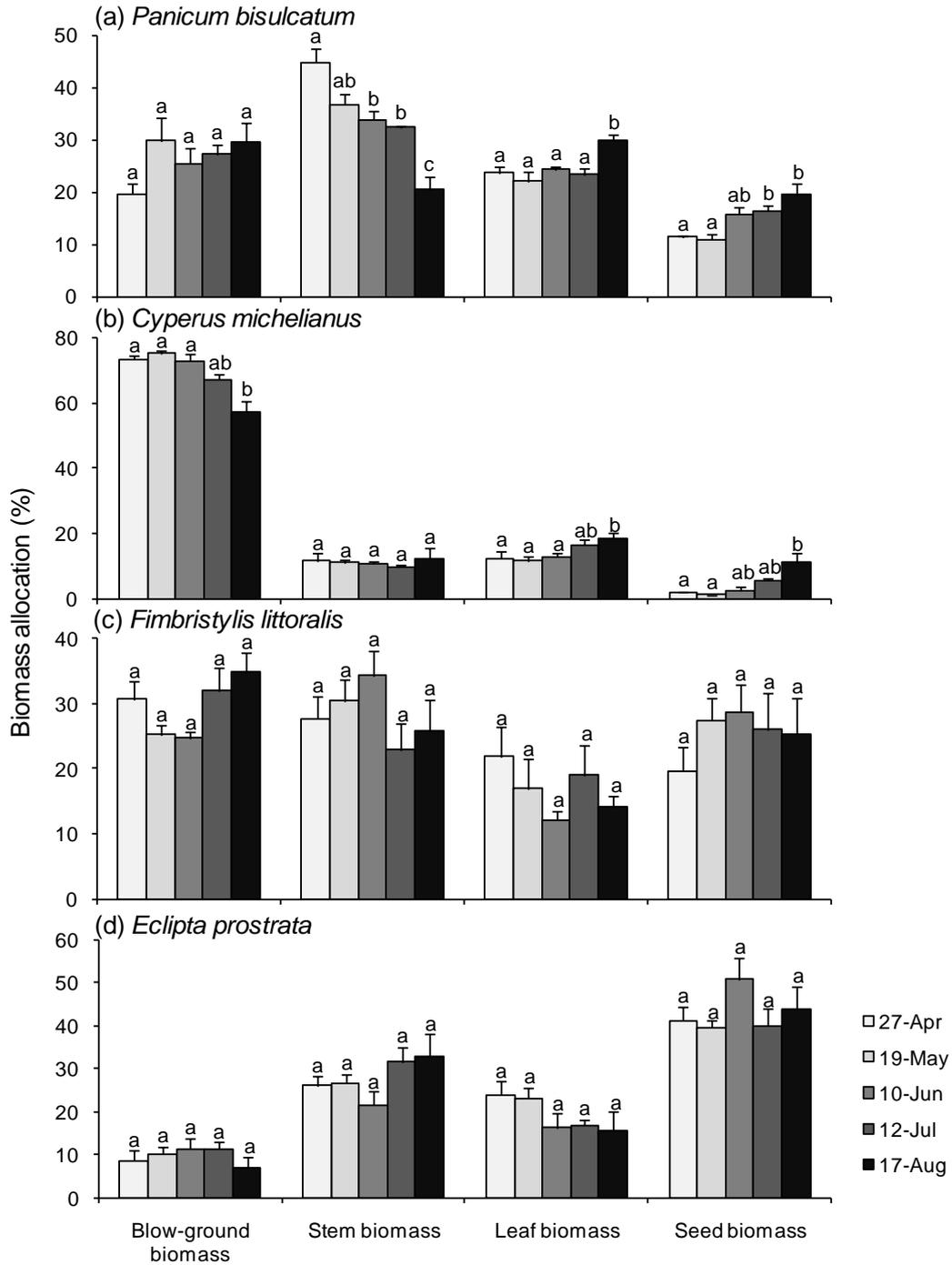
Fig. 3. Allocation of biomass to the different plant fractions for (a) *Panicum bisulcatum*, (b) *Cyperus michelianus*, (c) *Fimbristylis littoralis*, and (d) *Eclipta prostrata* plants in response to growing-season length, as determined by five sowing dates. The bars indicate standard errors. Different letters indicate significant differences between treatments for each fraction ($p < 0.05$).
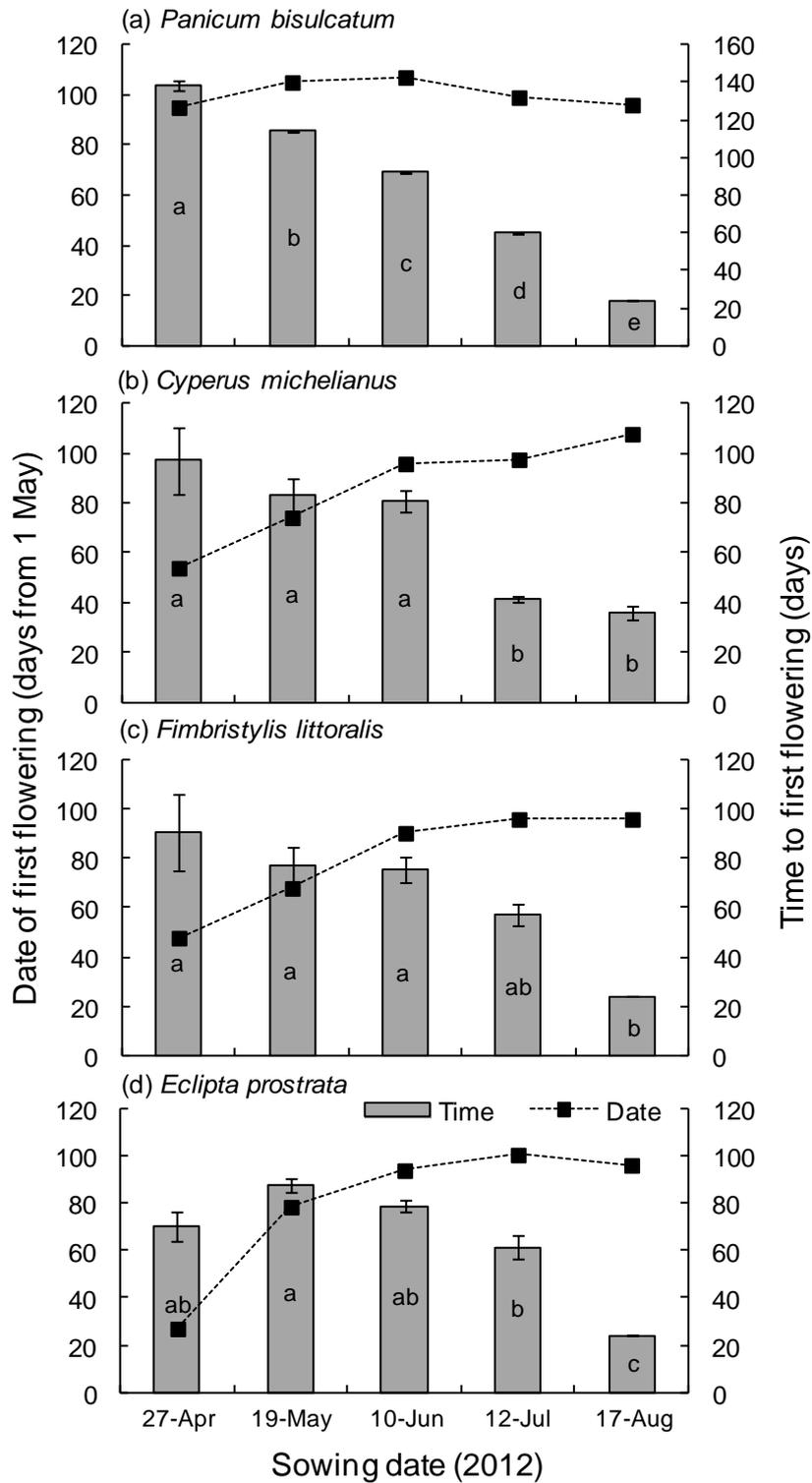
Fig. 4. Date of first flower production and time to flowering for (a) *Panicum bisulcatum*, (b) *Cyperus michelianus*, (c) *Fimbristylis littoralis*, and (d) *Eclipta prostrata* plants in response to growing-season length, as determined by five sowing dates. The bars indicate standard errors. Different letters indicate significant ($p < 0.05$) differences according to Tukey multiple comparisons.
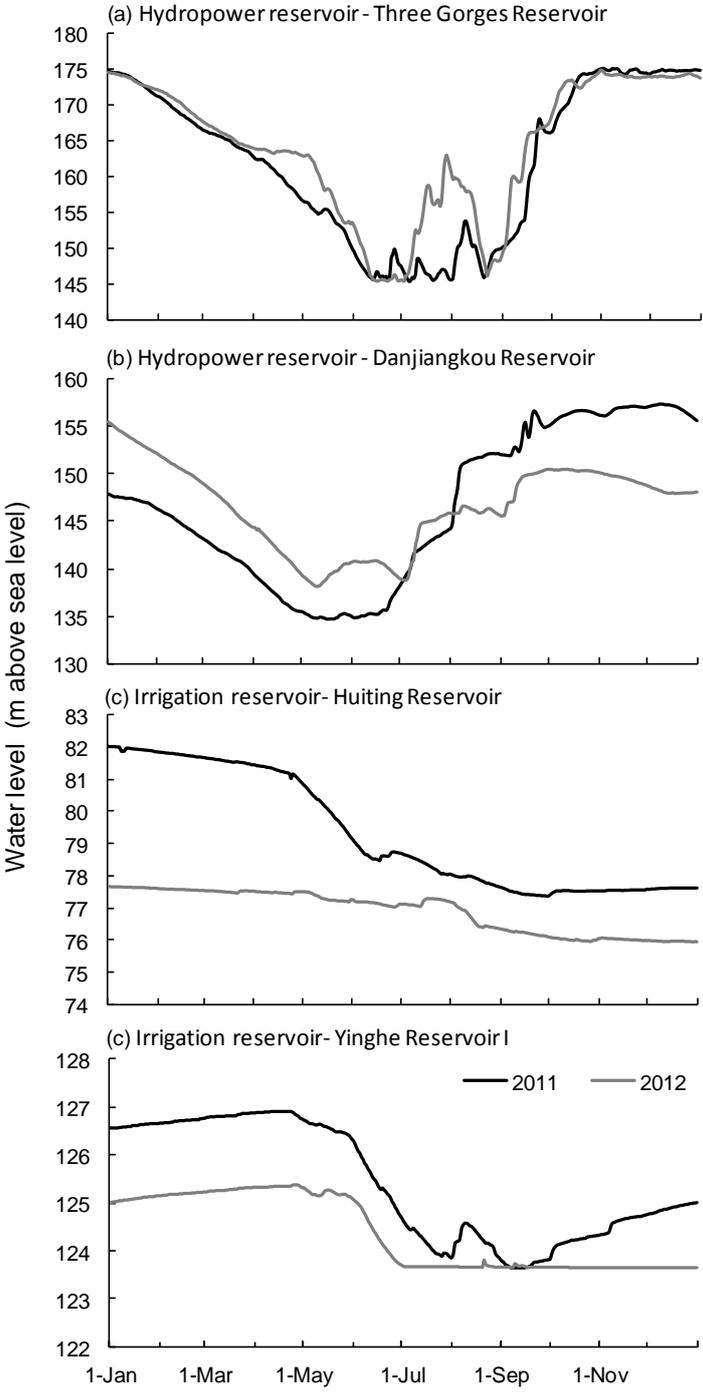
Fig. S1

Fig. S1 Hydrographs for two hydropower reservoirs (a) Three Gorges Reservoir and (b) Danjiangkou Reservoir; and two irrigation reservoirs (c) Huiting Reservoir and (d) Yinghe Reservoir I in Hubei Province in 2011and 2012.