Responses of an emergent macrophyte, *Zizania latifolia*, to water-level changes in lakes with contrasting hydrological management

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Abstract

Twenty-four lakes associated with the Yangtze floodplain and Huaihe basin, China, with different degrees of disconnection from the river systems, exhibited managed hydrologies ranging from minimally fluctuating reservoir-like lakes, through intermittently fluctuating lakes to those with large, quasi-natural fluctuations in level. We hypothesized that annual water-level fluctuations limit growth and survival of the emergent macrophyte *Zizania latifolia*. We investigated adaptations to submergence and sought to define the tolerances of *Z. latifolia* to the amplitude and timing of water-level fluctuations in these types of lake, at different stages in its phenology and life cycle. Shoots from rhizome buds emerged in early spring and reached maximum extension with high water levels in summer. *Z. latifolia* did not occur in lakes with the highest amplitude (> 5 m) of fluctuation. Height growth in lakes with low amplitude (reservoir-like) was smaller than in lakes with greater amplitude (intermittent to quasi-natural fluctuations), giving the appearance of 'short' and 'tall' phenotypes. Across all lakes, however, maximum height was linearly related to water depth in June and to annual amplitude of water level, indicating a continuous phenotypic response. Peak biomass was weakly affected by these environmental drivers. Field experiments showed that seedlings tolerated water depths of c. twice their height (0.6 m), and submergence rates similar to their maximum extension growth rate (2 $cm.d^{-1}$). Sprouting of rhizome buds was unaffected by submergence to a depth of 0.4 m, but then declined with depth. This study reveals the effects of large-scale hydrological engineering on an emergent macrophyte of economic and conservation importance and informs the management of its populations under seasonally fluctuating water-level regimes.

Key words: annual flooding, plant life-history, phenotypic adaptation, submergence experiment, wetland, Yangtze floodplain

1. Introduction

Macrophytes are important components of many aquatic systems, contributing to biodiversity and helping maintain water quality. Water levels in lakes and rivers fluctuate naturally, largely in response to seasonal rainfall patterns, and such water-level fluctuations have been important selective forces in the evolution of many aquatic macrophytes. This has resulted in a variety of adaptations in morphology, phenology, and life-history strategy that confer fitness in the face of changing water levels (Poff et al., 1997; Liu et al., 2006a,b; Manzur et al., 2009; Song et al., 2015). Hydrological management for water conservation and in response to climate change has greatly modified the water-level fluctuation regimes of many lakes, often leading to significant declines in aquatic vegetation. In particular, engineering projects that necessitated a disconnection between rivers and lakes have tended to stabilize water levels in lakes of the Yangtze floodplain, significantly changing the vegetation types and reducing species diversity (Wang and Wang, 2009; Zhang et al., 2014). Therefore, it is necessary to understand the tolerances and requirements of aquatic macrophytes in relation to water-level fluctuations at different stages in their life histories, in order to carry out ecologically informed water level regulation (Liu et al., 2017).

Studies of adaptations to alternating flood and drought have often focused on riparian systems (Lytle and Poff, 2004; Merritt et al., 2010). For instance, woody species in the flood plains of seasonally flooded riparian systems in arid or semi-arid regions have been of interest, because a sequence of flooding conditions is necessary for seedling establishment e.g. as receding waters expose moist sites suitable for germination (Mahoney and Rood, 1998; Merritt, 2004; Rood et al., 2005). Less is known about the adaptations of emergent macrophytes in lakes with seasonally fluctuating water levels. Different water levels potentially affect growth (Edwards et al., 2003; Deegan et al., 2007) and competitive interactions between species (Kennedy et al., 2003). From a life history perspective, there is evidence that rapidly rising water levels may be deleterious to seedling establishment, as well as to recruitment of shoots from rhizome buds, and ultimate survival of shoots. Similarly, rapidly falling water levels may have adverse effects on established plants.

Zizania latifolia is an emergent, perennial grass (Poaceae) that is endemic to East Asia. It perennates as a rhizome and can grow to a height of 4 m in one growing season, potentially allowing it to withstand large water-level fluctuations (Li et al., 1992; Li, 1995; Zhang et al., 2016; Li et al., 2018). It is widely distributed in the Yangtze floodplain, as a dominant in lakes with a wide range of patterns of water-level fluctuation, representing different hydrological management regimes. *Z. latifolia* provides important ecosystem services, contributing to habitat structure, sedimentation, wave mitigating, and stabilizing the shoreline; it is also of economic value, supplying high-quality raw material for feed and paper and, when infected with the fungus *Ustilago esculenta*, a valuable source of food (Li et al., 1992; Yu and Chen 2008; Guo et al., 2008; Li et al., 2018). However, it can become invasive, leading to lake terrestrialisation and water hypoxia (Li, 1997; Li et al., 2007; Zhang et al., 2016). Although there is experimental evidence concerning the short-term effects of water depth on *Z. latifolia* (Bai et al, 2013; Wang et al., 2014; Li et al., 2018; Wang et al. 2018), we still have little insight into its responses to the seasonal patterns of water-level fluctuation created by different hydrological management strategies (Zhang et al., 2016).

We hypothesized that annual amplitude of submergence, variously affected by different degrees of engineered disconnection from the river, would be an important determinant of the performance of *Z. latifolia.* Thus our overall aim was a systematic investigation of its growth and survival in response to water-level fluctuations, over its annual life history, to elucidate its tolerances and requirements at specific. Specifically, we sought to examine (1) its phenology; (2) its growth and survival in 23 shallow lakes in the Yangtze flood plain (and one lake in the Huaihe basin) with contrasting types of hydrological management and, consequently, different fluctuations in water level; (3) the growth responses of its apical buds and seedlings to changing both water depth and rates of submergence.

2 Materials and methods

2.1 Field investigation

2.1.1 Lakes studied

Twenty-three lakes in the middle-lower Yangtze basin and one lake in the Huaihe basin (Fig. 1) were selected for investigation. They are all in a subtropical monsoon climate with an annual mean temperature of 16.1-17.2 °C and annual precipitation of 996-1600 mm. Lake areas range 2-2933 km^2, water depth 0.4-7.0 m, total nitrogen 0.32-0.88 mg/L, total phosphorus is 0.01-0.06 mg/L, and transparency (Secchi disc) 45-180 cm. The lakes can be classified into three types, according to the characteristics of their water-level fluctuations: reservoir-like, intermittent and quasi-natural (Wang et al., 2016; Yuan et al., 2017; Yuan et al., 2019). Lakes with reservoir-like fluctuations are completely disconnected from the rivers and show relatively little amplitude of fluctuation. The highest water level occurs in the flood season from July to September. However, by the following March, high water level is maintained because the closure of dams for water storage. Water level gradually decreases from April-June to an annual minimum, because of water consumption in the lakes and use for agricultural irrigation (Fig. S1). Lakes with intermittent fluctuations are mainly sub-lakes in flooded areas. During the dry season, flooded areas form many independent sub-lakes, which become connected with the main lakes in the flooding season. Water levels are low from January to May. They rise rapidly to a maximum in June, because of the rapid rise in the main lake area. After this flood, levels remain relatively high in these sub-lakes, and decrease to a minimum gradually after October (Figs S2 & S3). Lakes with quasi-natural fluctuations tend to follow the natural level of the Yangtze River. Generally, the water level is low from January to March, beginning to rise gradually from April to June, reaching the maximum between July and September, and then gradually decreasing (Figs S2 & S3). They include lakes connected to and disconnected from the river.

Insert Fig. 1 about here

2.1.2 Sampling

The *Z. latifolia* population of each lake was studied over a period of one year between 2011 and 2015. Lakes investigated were: in 2011 (Longkou, Nanfeng, Changyin, Pingfeng, Duchang); in 2012 (Lake Wabuhu); in 2014 (Lake Chaohu, Lake Poganhu, Lake Caizihu, Xingzi, Chenglinji); in 2015 (Lake Honghu, Lake Yandonghu, Lake Changhu, Lake Liangzihu, Lake Nanjishan Changhu, Lake Wuchanghu, Lake Nanjishan Zhanbeihu, Lake Shahuchi, Lake Futouhu, Lake Dahuchi, Lake Shengjinhu, Lake Shimenhu, Hukou). Each population was examined four times to cover the annual life cycle: February-March, May-June, September-October, and December-January. First, the distribution of *Zizania* in the whole lake was determined, and then at least three sites in each lake were selected randomly, including the lowest elevation of its distribution, and the highest elevation of its distribution. At each site 5-8 square, wooden quadrats (0.25 m^2 or 1 m^2) were placed randomly and the percentage plant cover (in vertical projection) and density of *Z. latifolia* recorded. Then we measured its overall height (from the base of the plant to the tip of the topmost unfolded leaf) and its elevation above the water level (vertical distance from water level to the tip of the topmost unfolded leaf) at the centre of the plot. Then above-ground material was harvested and taken back to the laboratory for weighing. Biomass was expressed as fresh mass m^{-2}. The water depth at each sample site, and the monthly average submergence depth from January to December were determined from the relative water surface elevation and annual lake water level data on the day of sampling. From January to December, 2015, the plant height, biomass, cover, and density of *Z. latifolia* were also recorded each month in the lake of the Institute of Hydrobiology in Donghu.

2.1.3 Water level

Daily water level data for the lakes during the survey years were derived from records of local gauge stations, and most were accessible from the relevant hydrological network (219.140.162.169:8800/rw4/report/fa02.asp;www.hbswj.com;61.191.22.157/TYFW/I nfoQuery/Lake.aspx), provided by Hydrology Bureau of Jiangxi Province and Poyang Lake Nature Reserve Administration.

2.2 Pond experiments

Experiments to simulate flooding were carried out in a pond located on the northeast shore of Baoan Lake in Daye City, Hubei Province (N 30°17'26", E 114°43'49"). It had an area of c. 40 m^2 and an average water depth of 1.8 m, with a water temperature of 20-25 °C, a Secchi transparency of 60-98 cm, and a pH 7.6-7.8. Plants were grown in plastic pots (top diameter 25 cm, bottom diameter 15 cm, height 20 cm) suspended at different depths in the water column. The rooting substrate was a 3:1 mixture of lake mud (total nitrogen 1.52 mg/g, total phosphorus 0.58 mg/g, and organic matter 17.52 mg/g) and sand with a depth of 10 cm.

2.2.1 Experiment 1: Effect of water depth on rhizome bud sprouting

In February 2014, Rhizomes were collected from Baoan Lake and trimmed into stem segments, each 8 cm long and with one dormant bud. Five stem segments were randomly planted in each hanging pot, buried 2 cm deep, and pre-cultured for one week. The formal experiment was conducted. The hanging pots were suspended in the pond from 1 to 28 March, at eight submergence depths (distance from the surface of water to the surface of the substrate): 0, 20, 40, 60, 80, 100, 120, 140 cm, with three replicate pots at each depth. The number of rhizome buds sprouting was recorded weekly.

2.2.2 Experiment 2: Effect of water depth on seedling growth

On 25 March, 2014, seedlings were collected from Baoan Lake and those of c. 20 cm were transplanted to suspended pots, with 5 plants per pot. The pots were suspended in the pond at a submergence depth of 0 cm for one week, to allow establishment, until plant height was c. 30 cm. Between 2 and 29 April, the pots were suspended at seven submergence depths: 0, 20, 40, 60, 80, 100, 120 cm, with three replicate pots at each depth. Plant height was measured and the number of deaths recorded weekly.

2.2.3 Experiment 3: Effect of submergence rate on seedlings

The experimental material and pre-culture treatment were the same as above and the experimental treatments was applied from 2 April to 29 April. All the pots were initially submerged at a water depth of 0 cm. Then eight submergence-rate treatments were applied: 0, 1, 2, 3, 4, 5, 6, 7 $cm.d^{-1}$, with three replicate pots in each. Plant height and stem height were measured, and the number of deaths was recorded weekly.

2.3 Data Analysis

Data manipulation and charting were performed using Microsoft Excel 2010. Statistical analysis was performed using SPSS 19.0 software. Statistical analysis of data included Spearman rank corrections, linear regression, and one-way ANOVA. The significance level of regression parameters was tested using the t-test. In the one-way ANOVA, multiple comparisons of means were performed using Tukey's test at 0.05 significance level.

3. Results

3.1 Phenology of growth in *Z. latifolia*

The high-resolution measurements of plant height and biomass throughout 2015 in Lake Donghu revealed an underlying, approximately sigmoidal annual growth curve (Fig. 2). New stems started growth in February, with the fastest growth from March to August before it levelled-off in late summer. Plants had died back completely by November.

Insert Fig. 2 about here

3.2 Water level fluctuations and *Z. latifolia* growth in the field

The six lakes with reservoir-like hydrology showed relatively small annual fluctuations in water level that were not strongly seasonal (c. 1 m) and all supported populations of *Z. latifolia* (Fig. S1). *Z. latifolia* grew to a height of 2-3 m in these lakes, with growth fastest in early summer, although there was some additional growth by September. As previously, plant biomass followed a very similar pattern to height. Shoot density reached a peak in March and declined slightly for the remainder of the growth period.

Z. latifolia populations were also found in eight of the lakes with much greater annual fluctuations in water level (Fig. S2). Three of these were of the intermittent type of hydrology and five were of quasi-natural hydrology. As expected, their water level fluctuations tended to be seasonal, rising rapidly to a peak in July-August that was 3-5 m higher than winter levels. *Z. latifolia* grew very much taller in these lakes, reaching a height of 3.5-6 m, with concomitantly greater biomass. The phenological trends in height, biomass and stem density were, however, rather similar to those in the lakes with smaller fluctuations in water level. The phenological progression of water depths tolerated by *Z. latifolia* in lakes of low (reservoir-like) and high (intermittent and quasi-natural) water-level amplitude are compared in Fig. 3. *Z. latifolia* was not found at all in the remaining 10 lakes with large annual fluctuations in water level, five each with intermittent and quasi-natural hydrologies (Fig. S3). These include the lakes with the greatest annual changes in water level recorded (4.5-12 m).

Insert Fig. 3 about here

Correlations between *Z. latifolia* performance (height and biomass) at its annual peak at the end of the growing season (autumn) and submergence depths in different lakes during the year revealed some striking trends (Table 1). During winter and early spring there was negative or no significant correlation between autumn height and submergence depth. From May to November, however, there were significant positive correlations, those for June and July submergence being the strongest. There was an even greater correlation between autumn height and annual water level amplitude. In contrast, such relationships were not found for autumn biomass, which was generally weakly negatively correlated with submergence for most of the year, and also with annual amplitude of submergence.

Insert Table 1 about here

The relationships between autumn plant height and both June water depth or annual amplitude of depth are essentally linear across all lakes supporting *Z. latifolia,* including those of all three hydrological types (Fig. 4), even though data for low- and high-amplitude lakes form distinct clusters along the regression lines. Annual amplitude proved an extremely good predictor of autumn height in *Z. latifolia* (Fig. 4B). Autumn biomass cannot be explained consistently by submergence depth or annual water-level amplitude.

Insert Fig. 4 about here

3.3 Effect of submergence depth on rhizome bud sprouting (experiment 1)

The proportion of *Z. latifolia* rhizomes able to sprout buds (Fig. 5) was entirely unaffected by submergence to a depth of 0.4 m. Beyond this depth, it declined rapidly to 20% by a depth of 1 m but showed no further reduction after that.

Insert Fig. 5 about here

3.4. Effect of submergence depth on seedling growth (experiment 2)

Submergence stimulated seedling elongation growth of *Z. latifolia* progressively up to c. 1m at a water depth of 0.6 m (Fig. 6). Beyond that depth, all the seedlings died. However, height growth was partly at the expense of stem diameter, which was progressively reduced with greater water depth.

Insert Fig. 6 about here

3.5 Effect of rate of submergence on seedling growth (experiment 3)

As in the previous experiment, seedlings generally responded to increasing submergence with greater growth in height (Fig. 7). However the rate of subergence also proved to be important. Plants survived and continued to grow to the end of the experiment at subergence rates up to 2 $cm.d^{-1}$, because the tops of them were able to remain emergent. When the increasing water level exceeded the plant's height, they ceased growth and then died. Seedlings died after 21 days at submergence rates of 3-4 $cm.d^{-1}$, after 14 days at 5 $cm.d^{-1}$ and after only 7 days at 6-7 $cm.d^{-1}$.

Insert Fig. 7 about here

4. Discussion

The hydrological diversity of managed lakes in the Yangtze basin (Zhang, 2013) has provided a range of environmental conditions that effectively encompassed the tolerances of *Zizania latifolia* to water-level fluctuations. All of the lakes were characterized by shallow water in early spring but their water levels exhibited different amplitudes and timing of change during the growing season. Low water levels early in the year have previously been associated with invasive spread in *Z. latifolia* (Zhang et al., 2016). Although water conservation projects often reduce the annual amplitude of water level (Poff et al., 1997; Nilsson and Berggren, 2000), it was lakes with intermittent and quasi-natural fluctuations that revealed its ultimate limits, as *Z. latifolia* was conspicuously absent from the lakes with the largest annual amplitude of water level (i.e. >5 m). This amount of submergence is consistent with the greatest height recorded for this species (Li, 1995) and presumably represents the limit beyond which adequate contact with the atmosphere for gas exchange via aerenchyma could be maintained (Yamasaki, 1984). However, it was lakes of these same types, albeit with rather smaller annual water-level amplitudes, that yielded the most vigorous height growth of *Z. latifolia*. The most modified lakes, those with reservoir-like hydrology, were consistent in that all supported populations of *Z. latifolia*. Nevertheless, the plants were of shorter stature in them.

In the 14 lakes that supported populations of Z. *latifolia*, its annual growth tended to track rising water levels during the growing season. In reservoir-like lakes, this appeared to limit upward growth, as its height rarely exceeded the water level by more than 20-30 cm. This gives the impression of a 'short' form of the plant, ranging in maximum height from 0.9 to 2.5 m in height, depending on the lake. Nevertheless, in the deeper lakes it was able to grow much taller (and attain correspondingly greater biomass), again tending to exceed peak water levels by a small margin. This gives the impression of a 'tall' form of the plant, ranging in maximum height from 3.4-6.3 m. It is not clear how upward growth is limited by water level but it is possible that structural support from the water column is necessary. Our experiments showed that height growth with increasing inundation depth was partly at the expense of reduced stem diameter, as was also previously. An experiment by Li et al. (2018) showed that the stem diameter decreased from 4.5 mm to 2.5 mm linearly when water depth was 0-0.9 m. Another experiment by Wang et al. (2018) found that the stem diameter decreased from 7 mm to 4.5 mm linearly when water depth was 0-0.36 m. Lignification of the culms is limited to a sclerenchyma ring and three rings of vascular bundles (Sumanon et al., 2018), which is probably insufficient to support such tall plants.

Perhaps our most striking finding was that the clear dependence of final, autumn height on submergence applied to all of the lakes in which *Z. latifolia* could survive, irrespective of their hydrological type. Interestingly the water depth (ranging from -0.4 m to 3.3 m) in June was the best monthly predictor of final height, even though the highest water levels were in July. However, it appears that the annual amplitude in water level was the ultimate determinant of final plant height, as demonstrated by the highly significant linear relationship them. This suggests that the height response to water level is essentially continuous and that the apparent segregation between short and tall phenotypes is simply a reflection of the hydrological discontinuity between reservoir-like lakes and the other two types of lake. The apparent absence of genotypic differentiation is in conformity with the low genetic diversity reported by Xu et al. (2008) for this species and the importance of clonal, asexual reproduction in its life history (Yang et al., 1999).

The seasonal progression of height growth in Lake Donghu was similar in form to that reported for *Z. latifolia* by Yamasaki and Tange (1981) in experiments in Japan and Li et al. (1992) in the study in China. Our phenological observations support the division the life history of the *Z. latifolia* into five periods (Zhang, 2013; Liu et al., 2017): the rhizome bud (RB) period (February-March), a period of early growth (April-May), a rapid growth period (June-August), a flowering and fruiting period (September-October), and a dormant period (November-January). Plant height and biomass yield in autumn were generally negatively correlated with submergence depth in the early part of the growing season, until April and this result was consistent with the short-term experimental results of Bai et al. (2013), Wang et al. (2014), Li et al. (2018) and Wang et al. (2018). After this time, we found the switch to a strong positive correlation, discussed above. Increasing height and biomass over the later part of the growing season was associated with declining stem densities, suggesting self-thinning and an element of intra-specific competition for resources, probably light (Li, 1995).

The pond experiments using seedlings and rhizome buds emphasize the importance of submergence at the early phenological stages (Bai et al., 2013; Wang et al., 2014; Zhang et al., 2016; Li et al., 2018). The response of seedlings to water depth mirrored the results from the field measurements of mature plants. Height growth responded progressively to increasing depth of submergence up to 80 cm but maintained an ever-declining aerial portion of 20-40 cm above the water level. Experiments by Wang et al. (2018) showed that the seedlings of this species could achieve normal growth out of the water surface after initial conditions of 100% submergence. However, at a submergence of 1 m and beyond we observed a catastrophic switch, with no plant survival. Plants could survive total submergence for only about a week. The triggering of this catastrophe also appears to be related to the rate of submergence. Although seedlings grew taller with increasing rates of submergence, this was only as long as they could maintain an aerial portion and plants died when overtaken by the water level. As noted earlier, increased height with submergence was at the expense of stem diameter and excessive weakening of the stems at this stage may ultimately reduce autumn height in the Poaceae (Qiang, 2006). We could not study tolerance to the rate of water level rise at later life history periods, but speculate that it should not exceed the maximum rate of plant growth, as Yuan et al. (2019) found in a study of *Carex species*. All of the evidence points the fact that actively growing *Z. latifolia* plants cannot survive sustained total submergence. This is presumably because of the need to maintain gas exchange with the atmosphere to oxygenate tissues via aerenchyma (Yamasaki, 1984; Wang et al., 2012; Wang et al., 2014).

The same is not true of dormant, carbohydrate-rich rhizomes and their buds, which can withstand prolonged anoxia, as in many submerged species (Crawford and Braendle, 1996). Our experiment with this phenological stage was no exception and the sprouting of rhizome buds was not affected by submergence of 0.4 m; even though the numbers sprouting declined with deeper submergence, a fraction of about 20% of buds was not inhibited below 1 m. The experiment by Li et al. (2018) similarly showed that the RBS percentage decreased to less than 20% linearly when water depth was 0-0.9 m. In contrast, an investigation by Zhang et al. (2016) in Wuchang lake found no evidence of this species when water depth was beyond 0.7 m during the RSB.

5. Conclusion

The examination of numerous lakes with contrasting hydrologies, arising from different degrees of engineered disconnection from the river, across the Yangtze (and Huaihe) basins has revealed the ranges of tolerance of submergence shown by *Zizania latifolia* throughout its annual life history in detail and allowed critical stages to be identified (summarized in Fig. 8). Our phenological measurements support the division the approximately sigmoidal annual growth curve of *Z. latifolia* into five periods. As hypothesised, the annual amplitude of water level, itself substantially influenced by water levels in June, was the strongest determinant of final plant height, irrespective of lake management regime. The remarkable phenotypic plasticity of *Z. latifolia* allowed it respond to increasing annual submergence up to c. 5 m, which proved to be its limit for survival. These findings should serve to inform the management of both wild and crop populations of this ecologically significant aquatic species and may provide guidance for the management of other emergent macrophytes. Given the importance of *Z. latifolia* in different types of lake ecosystem, its successful management also has implications for the restoration and conservation of lakes whose water levels need to be managed for multiple purposes.

Insert Fig. 8 about here

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Figure captions

Fig. 1 The location of the 24 lakes studied in the Yangtze floodplain (23) and the Huaihe basin (1), China.

Fig. 2 Phenology of growth in height and biomass of *Zizania latifolia* at Lake Donghu in 2015. Bars indicate one standard error (n = 10).

Fig. 3 Distribution of upper and lower tolerance limits of water depth for *Zizania latifolia* in each month across all lake in which it was found. (A) Lakes of low water-level amplitude; (B) Lakes of high water-level amplitude.

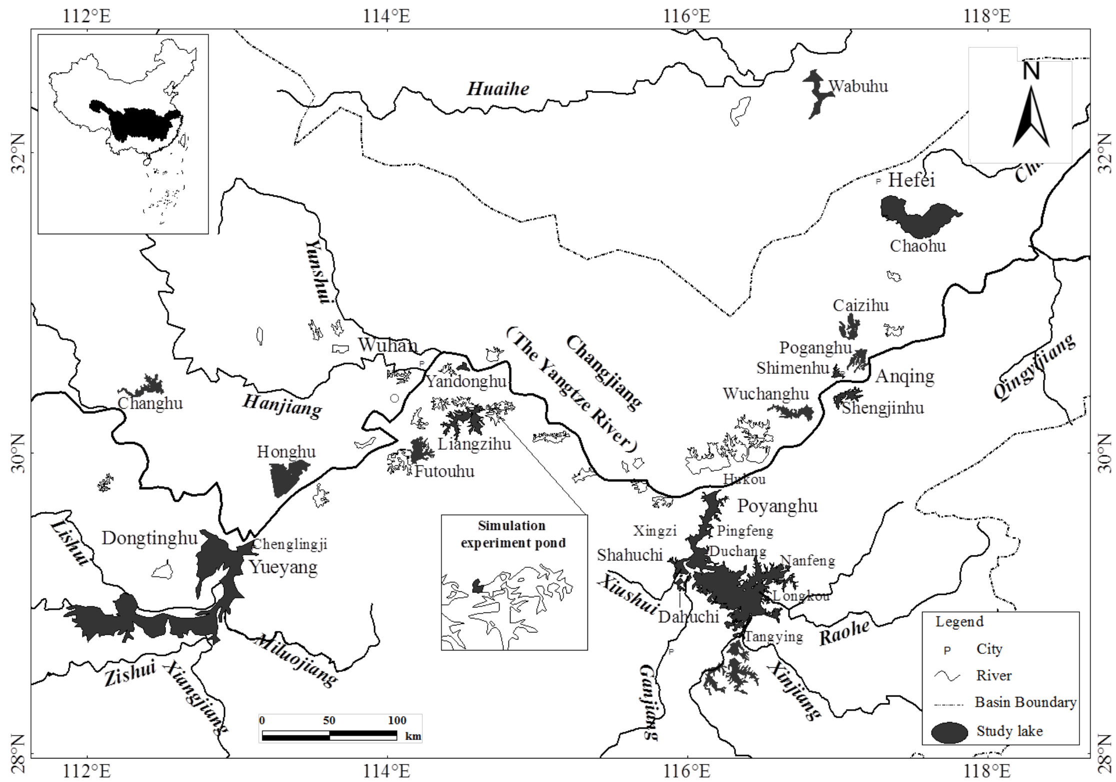
Fig. 4 Relationships between plant autumn height of *Zizania latifolia* and (A) water depth in June, and (B) annual water-level amplitude in all study lakes in which it occurred. Autumn height represents the maximum at the end of the growing season (September or October).

Fig. 5 Effect of submergence depth on rhizome bud sprouting (RBS) percentage in *Zizania latifolia.* The bars indicate one standard error. Different letters indicate significant differences between treatments ($P < 0.05$).

Fig. 6 Effect of submergence depth on seedlings of *Zizania latifolia* over 28 days in a pond experiment. Submergence depths: A, 0 m; B, 0.2 m; C, 0.4 m; D, 0.6 m; E, 0.8 m; F, 1.0 m; G, 1.2 m. Stem diameters (diam) at the end of the experiment are also shown. The bars indicates ±standard error.

Fig. 7 Effect of rate of submergence (A-H: 0-7 $cm.d^{-1}$, interval 1 $cm.d^{-1}$) on seedlings of *Zizania latifolia*. Submergence rates: A, 0 $cm.d^{-1}$; B, 1 $cm.d^{-1}$; C, 2 $cm.d^{-1}$; D, 3 $cm.d^{-1}$; E, 4 $cm.d^{-1}$; F, 5 $cm.d^{-1}$; G, 6 $cm.d^{-1}$; H, 7 $cm.d^{-1}$. The bars indicate ± standard error. Height represents the length from the base of the plant to the tip of the topmost unfolded leaf. Stem height represents the length from the base of the plant to the top of uppermost leaf sheath. The dotted line shows the cumulative water level.

Fig. 8 Conceptual summary of water level fluctuations tolerances and requirements of *Zizania latifolia* in (A) Lakes of low water-level amplitude; (B) Lakes of high water-level amplitude. D, dormant period; RB, rhizome bud period; EG, early growth period; RG, rapid growth period; FF, flowering and fruiting period.



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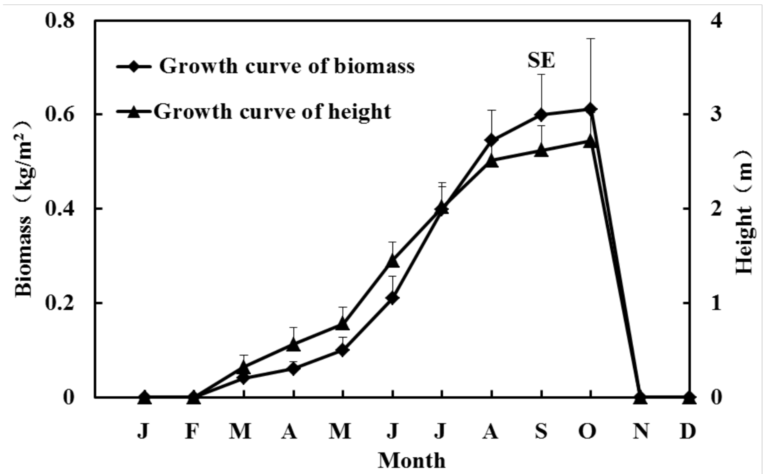

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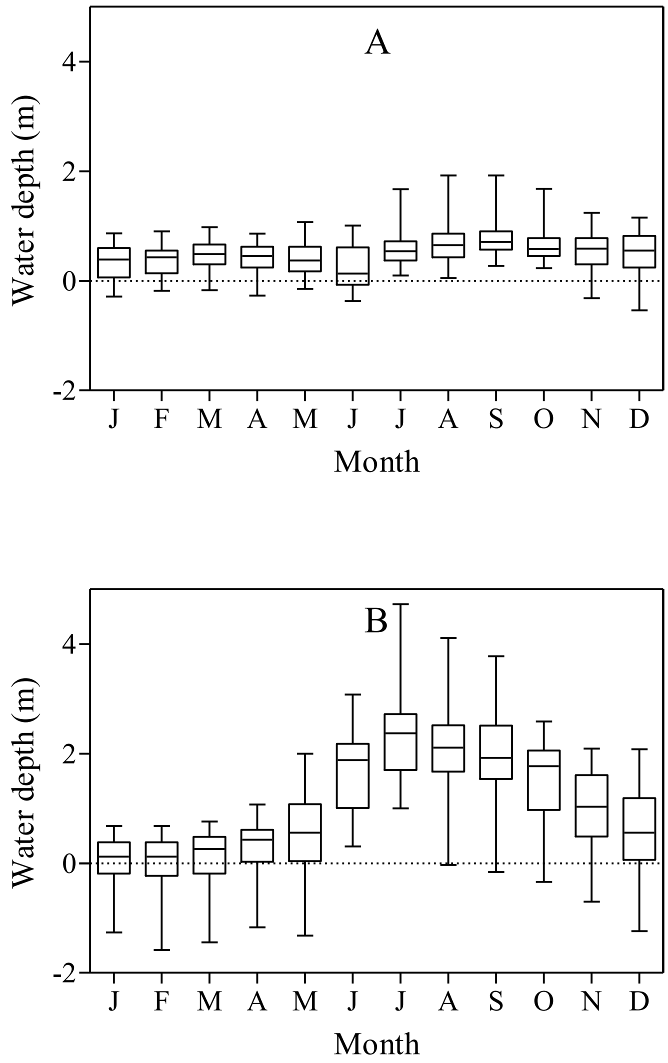

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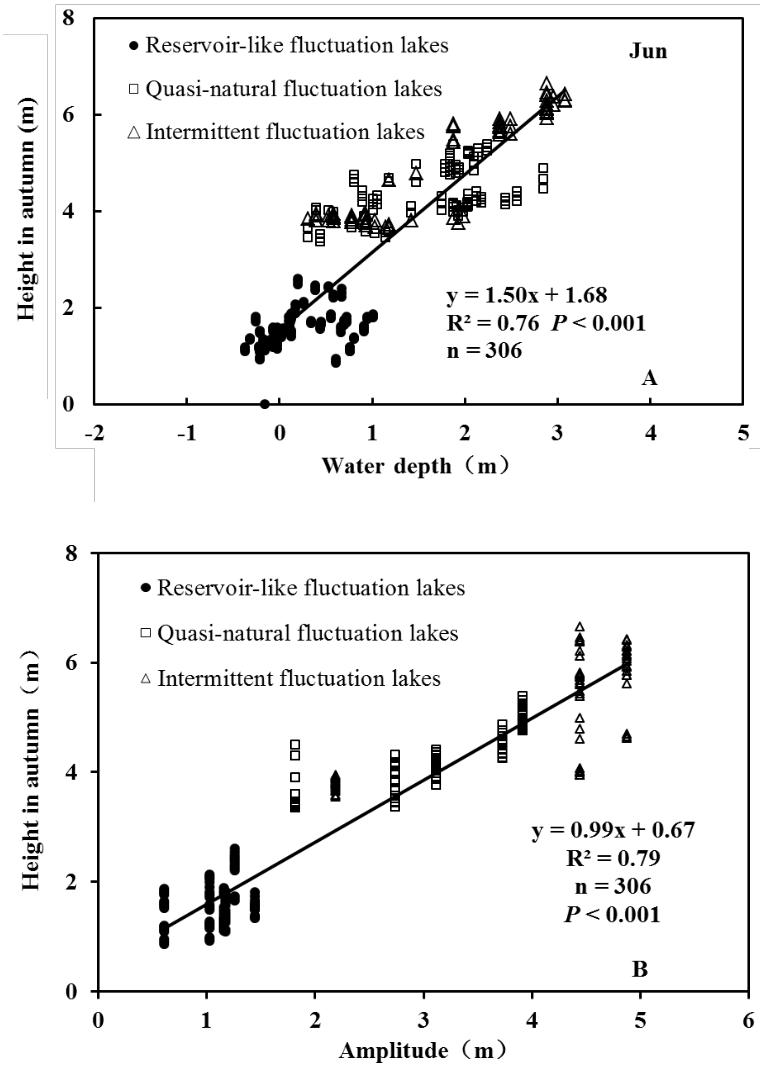

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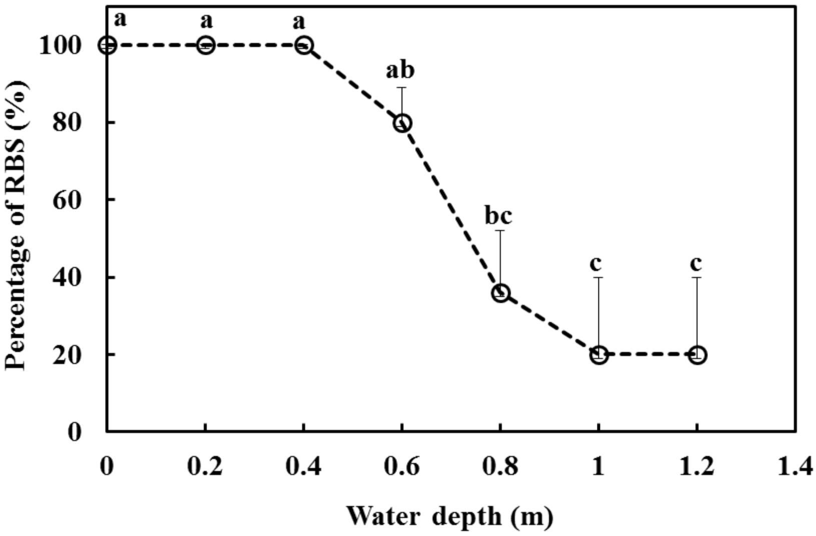

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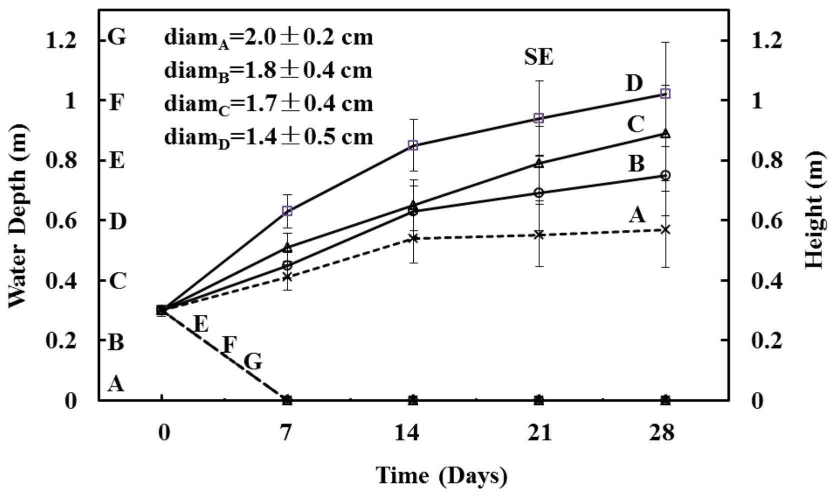

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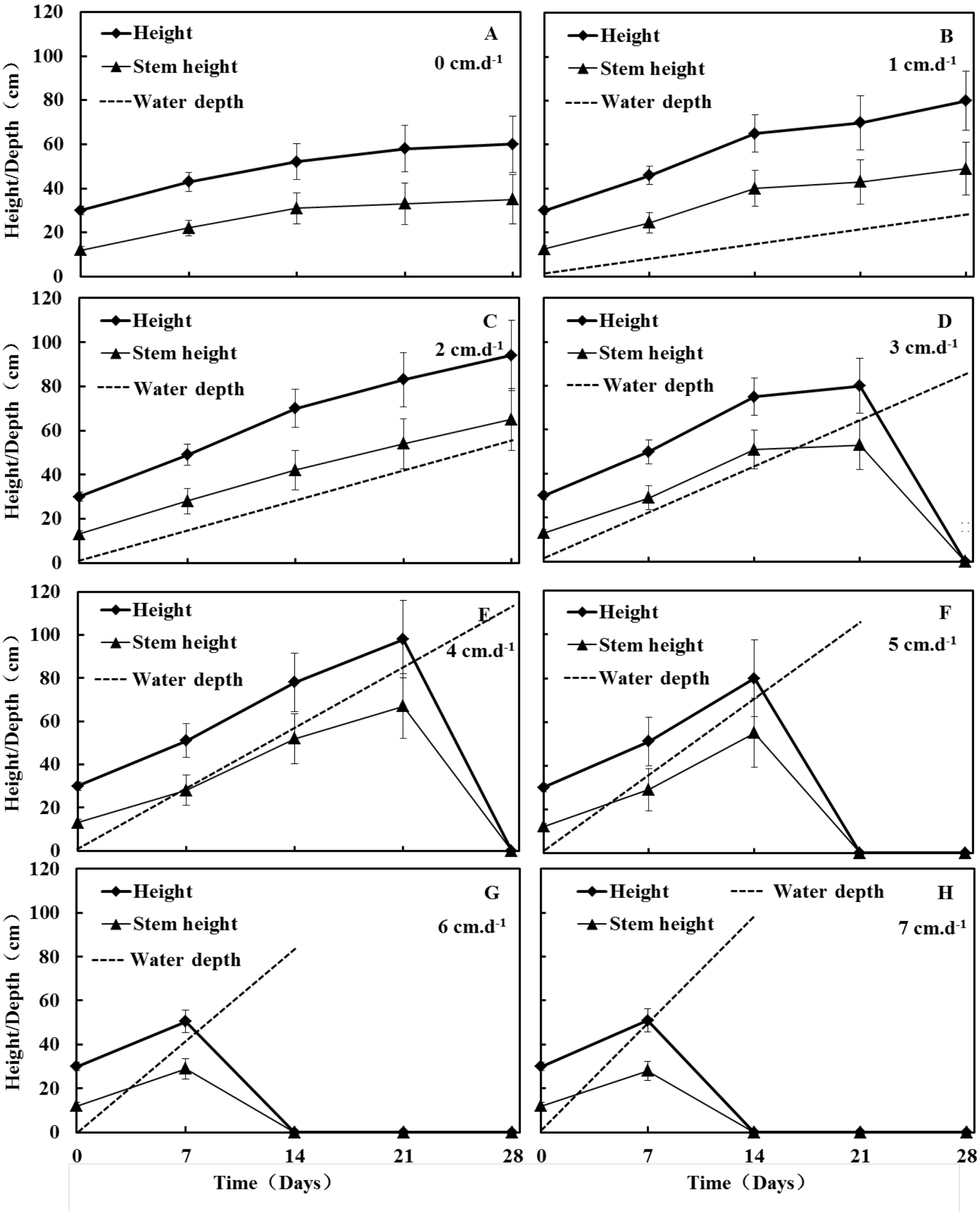

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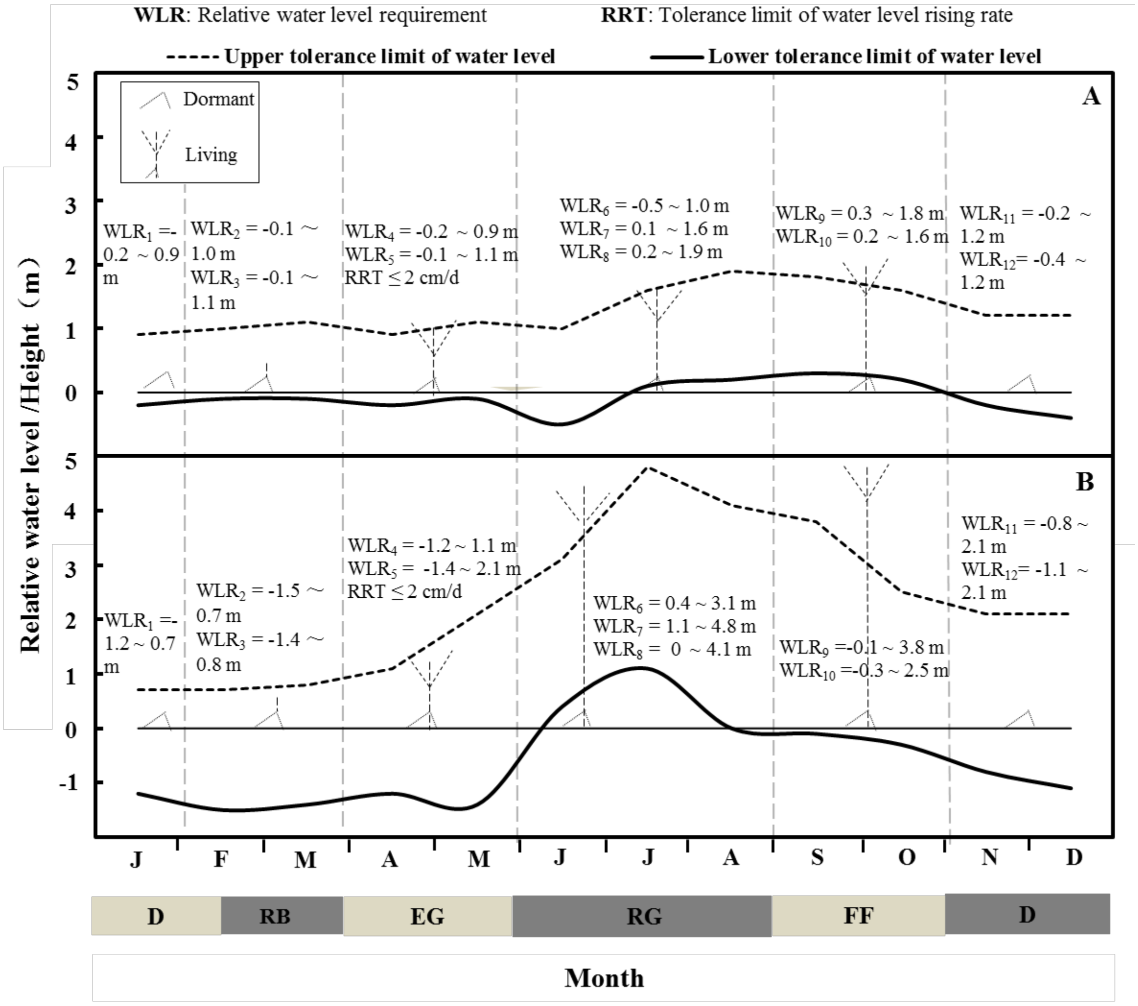

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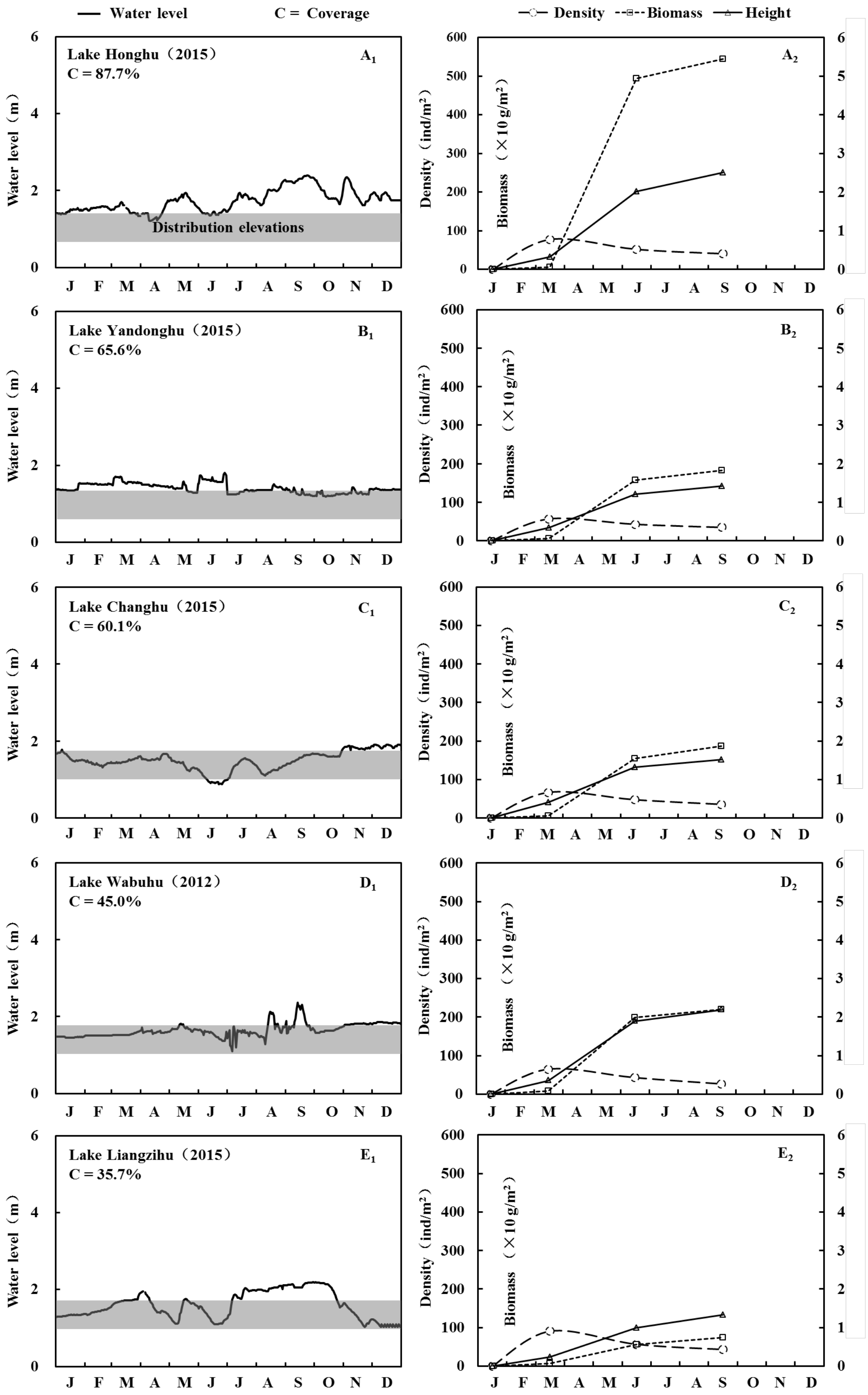
Supplementary information



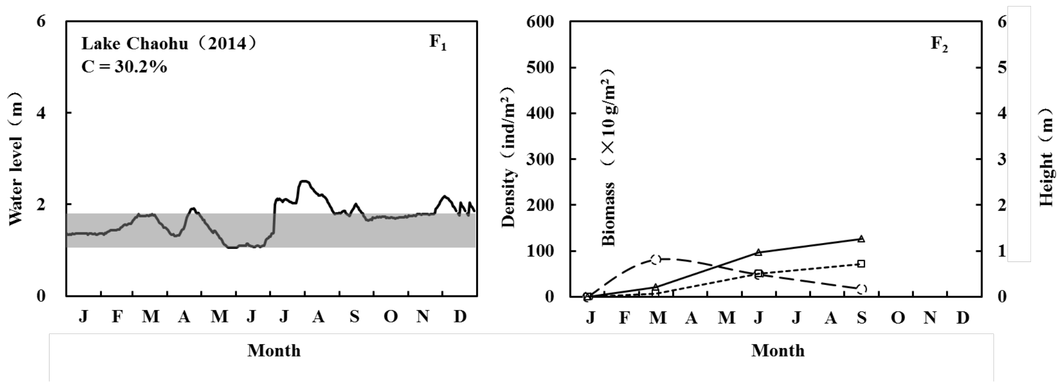


Fig. S1 Annual changes in water level (A_1-F_1) and height, biomass and density of *Zizania latifolia* (A_2-F_2) in all the lakes of low water-level amplitude (reservoir-like fluctuations). Water level represents standardized water level (= observed water level data – mean water level between Jan and Mar + 1.5 m). The shaded area represents the distribution range of *Zizania latifolia*.

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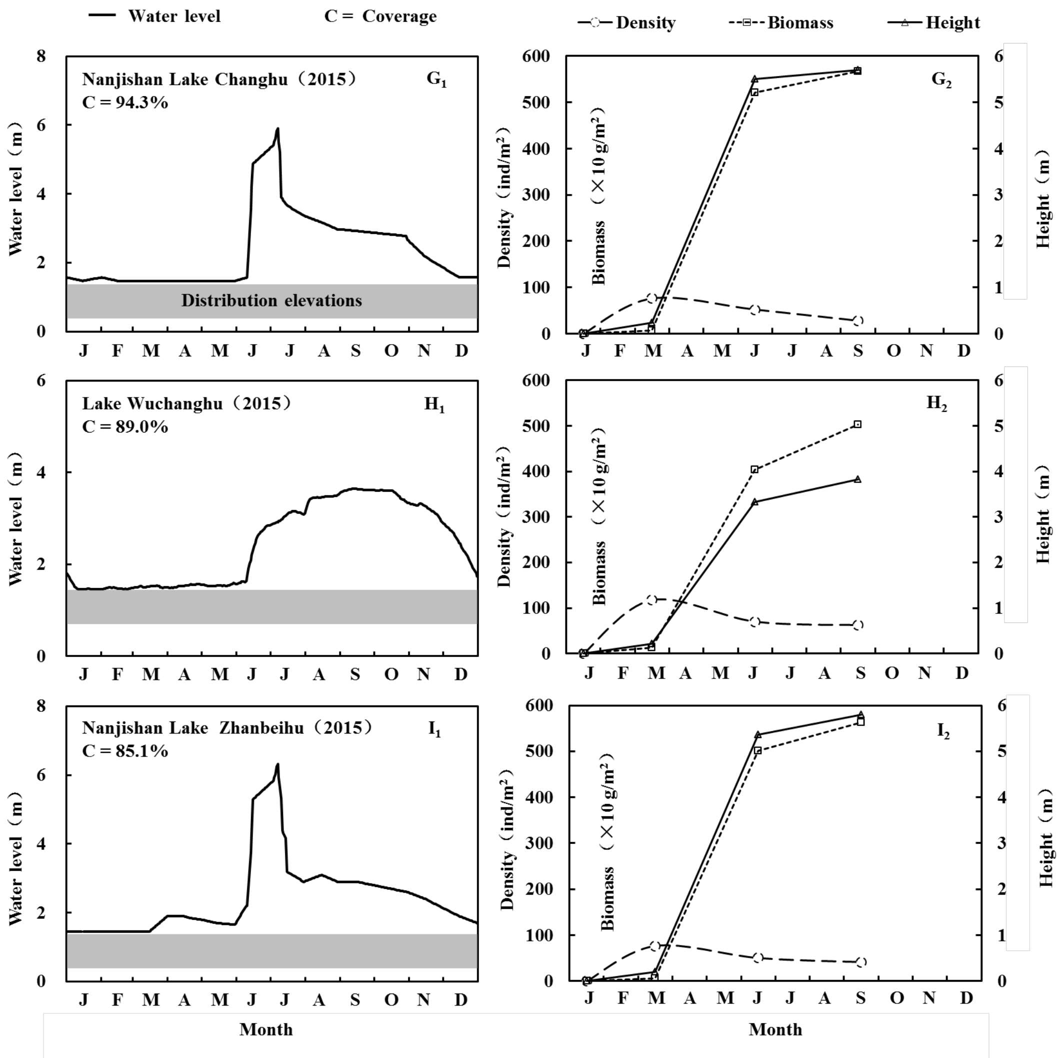

Water level
C = Coverage
Density
Biomass
Height
Nanjishan Lake Changhu（2015）
C = 94.3%
G1
Distribution elevations
G2
Lake Wuchanghu（2015）
C = 89.0%
H1
H2
Nanjishan Lake Zhanbeihu（2015）
C = 85.1%
I1
I2
Water level（m）
Density（ind/m²）
Biomass （×10 g/m²）
Height（m）
J F M A M J J A S O N D
Month

639

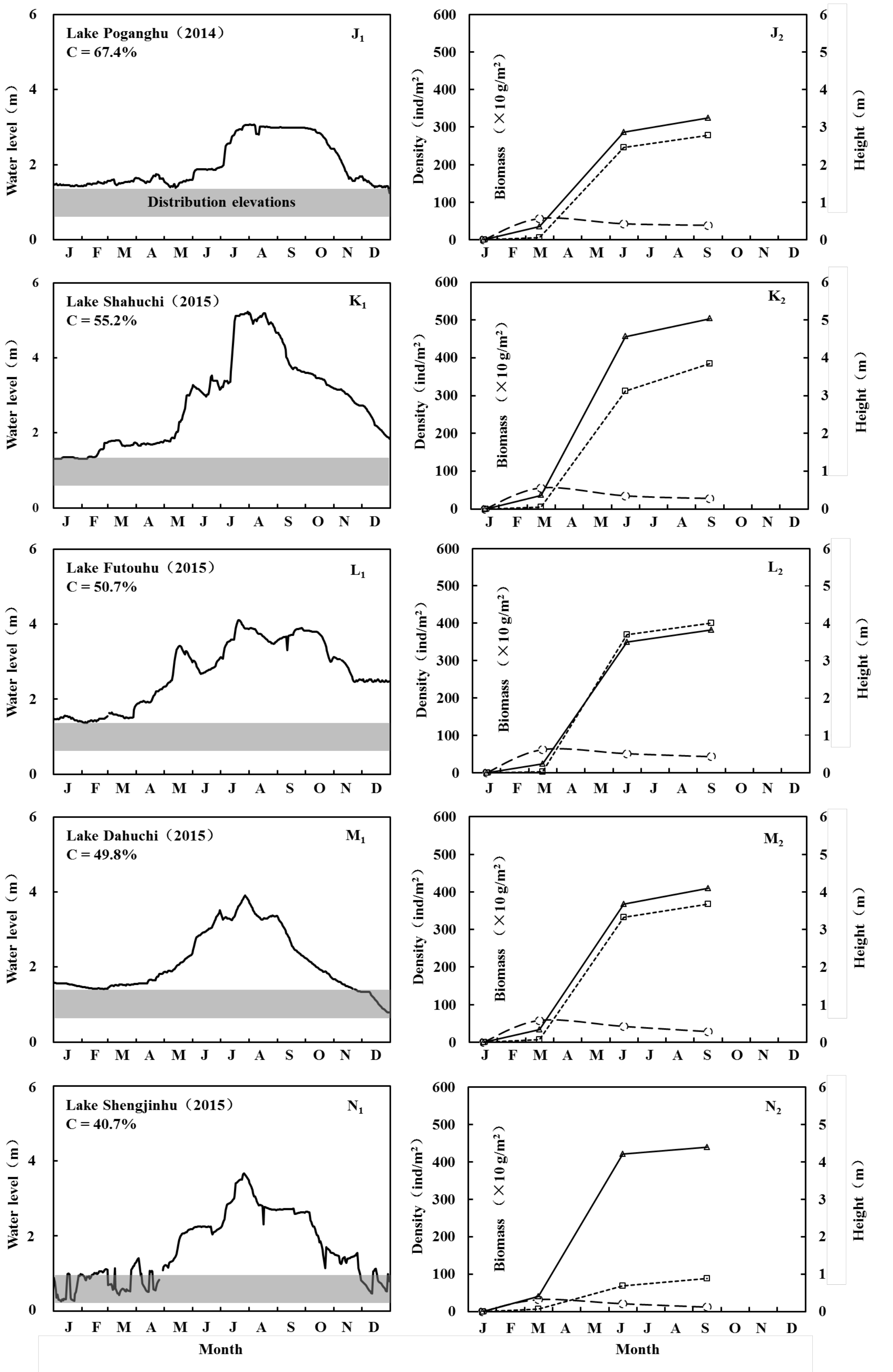

Fig. S2 Annual changes in water level (G_1-N_1) and height, biomass and density of *Zizania latifolia* (G_2-N_2) in lakes of high water-level amplitude (with intermittent or quasi-natural fluctuations).

Water level represents standardized water level (= observed water level data – mean water level between Jan and Mar + 1.5 m). The shaded area represents the distribution range of *Zizania latifolia*.

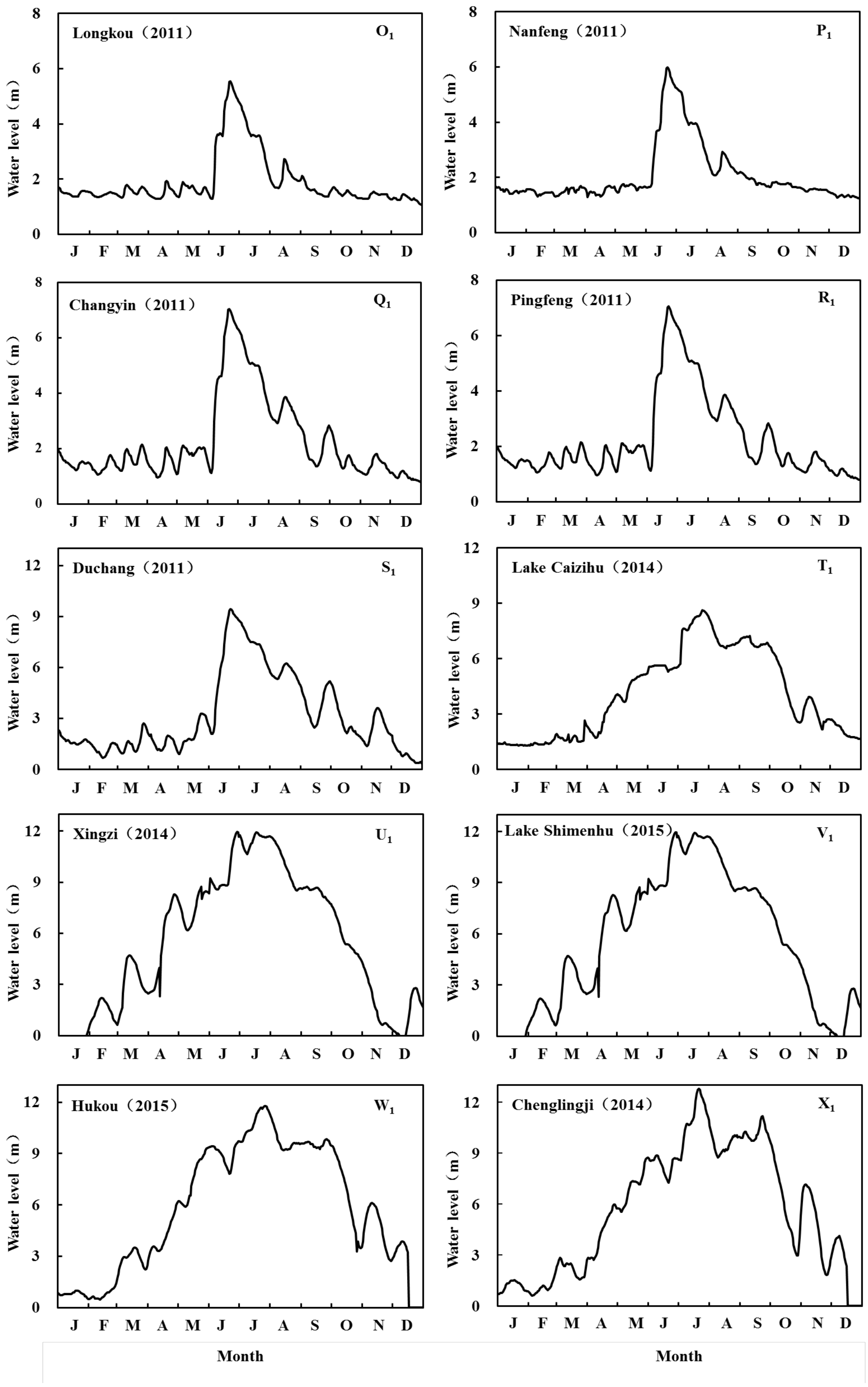

Fig. S3 Annual changes in water level in lakes of high water-level amplitude lacking *Zizania latifolia*, with intermittent (O_1-S1) or quasi-natural fluctuations (T_1-X_1). Water level represents standardized water level (= observed water level data – mean water level between Jan and Mar + 1.5 m).