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RESEARCH ARTICLE

Impact of seasonal water-level fluctuations on autumn vegetation in Poyang Lake wetland, China

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Abstract Water level fluctuations (WLF) are natural patterns that are necessary for the survival of various plants, and WLF guarantee both the productivity and the biodiversity of wetlands. However, the underlying mechanisms of how changes in vegetation are linked to seasonal WLF remain unclear. Using vegetation and hydrological data from 1989 to 2009, we identified the key seasonal fluctuations and their impacts on vegetation in the Poyang Lake wetland by utilizing a tree-based hierarchical model. According to our results: 1) WLF in summer had significant impacts on both sedges and reeds. The severe summer floods promoted the expansion of sedges, while they inhibited the expansion of reeds; 2) WLF in autumn also greatly impacted sedges, while reeds were severely affected in spring. Specifically, we found that low water levels in autumn led to the expansion of sedges, and low water levels in spring led to the expansion of reeds. The results were well corroborated through comparisons of the vegetation distribution patterns over the last two decades (i.e., the 1990s and 2000s), which may shed light on corresponding water resource and wetland management.

Keywords wetland, reeds, sedges, seasonal water-level fluctuations, classification and regression tree model

1 Introduction

Water level fluctuations (WLF) play an essential role in the distribution of vegetation and the composition of wetland environments (Coops et al., 2003; Pennings et al., 2005; Wu and Liu, 2017). Hence, the dispersal of plants within these areas generally shows a clear belt distribution pattern due to the hydrological gradients caused by periodic WLF (Snedden and Steyer, 2013; Sang et al., 2014; You et al., 2017). The cycles of WLF can range from days to centuries; however, seasonal fluctuations are commonly used as the primary factor for understanding biotic processes in wetlands (Hofmann et al., 2008; Jabłońska et al., 2011). In recent decades, hydrological regimes have shifted significantly around the world, and their ecological consequences have been widely recognized, e.g., the changes that have taken place in Lake Chad (Aligeti, 2012), Lake Koronia (Crisman et al., 2014), and the Nile Delta (Darwish et al., 2017). Therefore, it is essential to understand how vegetation distribution is linked to seasonal WLF in wetland ecosystems.

In recent years, increasing interest has been focused on describing the effects of WLF in different seasons on wetland vegetation. In the flood season, changes in the flood stage can not only affect wetland plants directly through mechanical damage (Dienst et al., 2004; Morton and Barras, 2011; Pan et al., 2012; Tan et al., 2016) but also impact them indirectly through the effect of water on other physiochemical parameters, such as the physiochemical properties of light and soil (Spence, 1982; DeBusk and Reddy, 2003; Xu et al., 2015; Li et al., 2017). In the dry season, shallow-rooted aquatic plants in wetland areas are extremely vulnerable to changing WLF (Li et al., 2013; El-Vilaly et al., 2018). Thus, these plants may die and be eliminated from the ecosystem during periods of extreme drought, which dramatically changes the composition of wetland vegetation (Liu et al., 2012). In addition, in the transition seasons with rapid water level changes, plant root mass is impacted by the erosion or accumulation of silt (Weisner and Ekstam, 1993; Gafny and Gasith, 1999), and

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deep water plants may not be able to adjust their morphology as quickly as shallow water plants, causing them to die out (Weisner and Strand, 1996). In sum, seasonal WLF play essential roles in forming the composition of shoreline vegetation (Guo et al., 1998; Luo et al., 2010; Dai et al., 2016). Few studies have revealed scientifically defensible and empirically testable relationships between seasonal WLF and various wetland species (Hofmann et al., 2008). Hence, in view of the fact that extreme floods or droughts can trigger disastrous effects on wetland ecosystems (Pan et al., 2012; Li et al., 2013), it is critical to determine the thresholds of seasonal WLF and how to best maintain these precious ecosystems.

The classification and regression tree (CART) method is a binary recursive partitioning method that yields a class of tree-based models (Qian and Anderson, 1999). The hierarchical structure of the CART model gives its inherent ability to reveal the relative importance of each predictor as well as the interactions among predictors in the fitted tree structure (De'ath and Fabricius, 2000). Therefore, in recent years, the CART model has been applied to ecological studies. For example, Sankaran et al. (2005) detected the determinants of woody cover in African savannas using the CART model; O'Reilly et al. (2015) used the CART model to address the first worldwide synthesis of *in situ* and satellite-derived lake data and found that the surface water warming rates of lakes are dependent on combinations of climate and local characteristics. Humanes et al. (2017) investigated that suspended sediments significantly depressed the growth and survivorship of coral juveniles based on CART model. So far, the CART model has been considered as a powerful tool for identifying the key factors that impact a particular ecosystem, predicting the susceptibility to harm, and measuring the marginality of a system.

Poyang Lake wetland is a hypertrophic Ramsar wetland that experiences dramatic seasonal WLF (Dai, 2015; Dai et al., 2015; The Ramsar Convention, 2017). There are two dominant types of vegetation here, sedges and reeds, which are zonally distributed throughout the littoral area (Liu et al., 2012). In recent years, scholars have observed extreme shifts in the seasonal WLF of the lake and clear degradation of the vegetation (Dai, 2015; Xu et al., 2015; Zhang et al., 2015). Hence, it is critical to identify key seasonal WLF and determine their relationships with various types of vegetation. In our previous research (Dai et al., 2016), we analysed the impact of seasonal WLF on sedge cover during spring, and we found that the continuous presence of high water levels that persisted up to 20 days could often trigger substantial changes in the sedge cover during spring. However, due to the complexity of this unique wetland ecosystem, the key factors that impact the two dominant vegetation types (i.e., sedges and reeds) during autumn are still unclear.

The main objective of this study was to identify the key seasonal WLF that were associated with the variability of wetland vegetation during autumn in Poyang Lake wetland; additionally, the thresholds necessary for preserving this unique ecosystem were identified using the CART model. To investigate the relative importance of each type of seasonal WLF on both sedges and reeds and to determine how these key hydrological conditions were linked to changes in vegetation during autumn, the following steps were taken: 1) the wetland vegetation was mapped in late autumn using Landsat TM/ETM images; 2) the seasonal water level fluctuation patterns were measured using multi-parameters based on year-round daily hydrological data; and 3) the impact of seasonal WLF on autumn vegetation in this wetland was quantified by combining the vegetation classification maps and the seasonal WLF parameters via the CART model.

2 Data and methods

2.1 Study area

Poyang Lake wetland (115°49′E–116°46′E, 28°24′N–29°46′N) is located at the southern bank of the middle reach of the Yangtze River, China (Fig. 1). The wetland receives drainage from five major tributaries (i.e., Ganjiang River, Fuhe River, Xinjiang River, Raohe River, and Xiushui River) and then flows north into the Yangtze River. The climate in this region is typically warm, humid, subtropical, and prone to monsoons. The mean annual temperature ranges from 16.5°C to 17.8°C, and the mean annual precipitation ranges from 1400 to 1700 mm.

2.1.1 Seasonal water-level fluctuations in Poyang Lake

Seasonal WLF in the lake are caused by its drainage structure and the monsoon climate (Zhang et al., 2013b; Zhang et al., 2014; Li et al., 2015). The average lake water levels in spring (i.e., April – May), summer (i.e., June – September), autumn (i.e., October – November), and winter (i.e., December – March) from 1952 to 2014 were 14, 17, 14, and 10 m, respectively. The mean annual water level amplitude was approximately 11 m (Fig. 2) for the period of 1952 – 2014.

2.1.2 The vegetation pattern and growth period of each vegetation type

Plants within the wetland showed a clear belt distribution pattern along the coastline (Fig. 3). We utilized Zhu and Zhang's three vegetation categories (1997) (Table 1) for this study, as follows: Zone 1 (reeds) includes semi-aquatic emergent tall vegetation (e.g., *Phragmites communis* and *Miscanthus sacchariflorus*); Zone 2 (sedges) includes emergent aquatic vegetation (e.g., *Carex cinerascens* and *Carex argyi*); and Zone 3 (aquatics) includes floating/

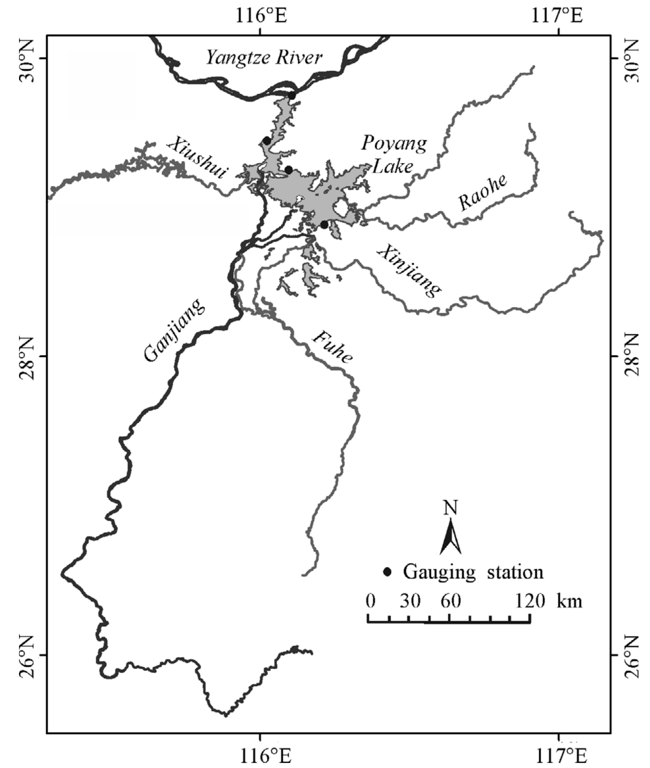

Fig. 1 Map of the Poyang Lake wetland.

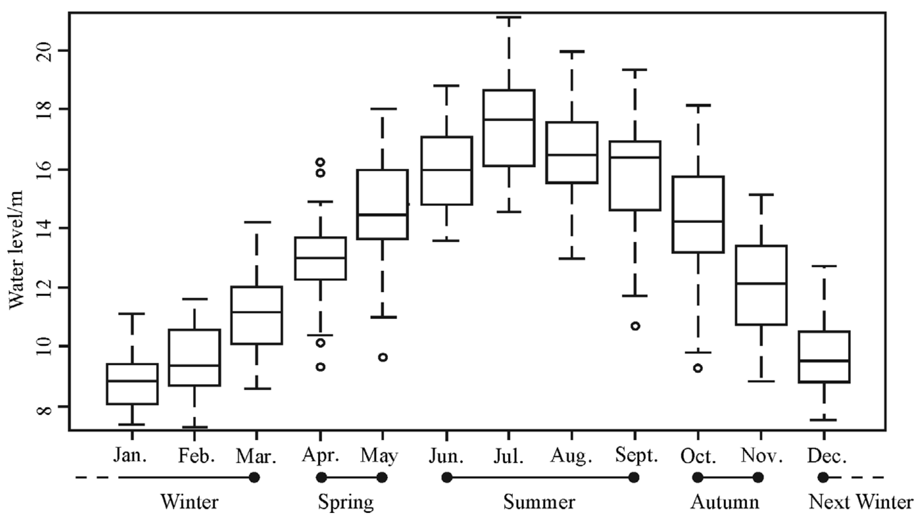

Fig. 2 Inner-annual water level fluctuations of the Poyang Lake during 1952 to 2014.

submerged vegetation (e.g., *Potamogeton malainus* and *Vallisneria natans*). It should be noted that, in this study, we focused only on the two vegetation types found in the marshland in Zone 1 (reeds) and Zone 2 (sedges).

The reeds in Zone 1 generally wither and turn yellow in late autumn, while the sedges in Zone 2 remain vibrant and green. The reeds of Zone 1 and the sedges of Zone 2 can be easily distinguished by a sharp boundary that becomes evident in the emergent marsh areas in late autumn, as shown in Fig. 3(c). However, within each zone, such as Zone 2, the non-dominant species, i.e., *Phalaris arundinacea*, is difficult to distinguish from the primary *Carex* spp. (including *Carex cinerascens*, *Carex argyi*, and *Carex unisexualis*) via remote sensing imagery. Therefore, both were classified as sedges in this study. Similarly, *Phragmites*, the major wetland community in Zone 1 (reeds), is usually mixed with *Triarrhena lutarioriparia* and *Artemisia selengensis*. Thus, all of these species were

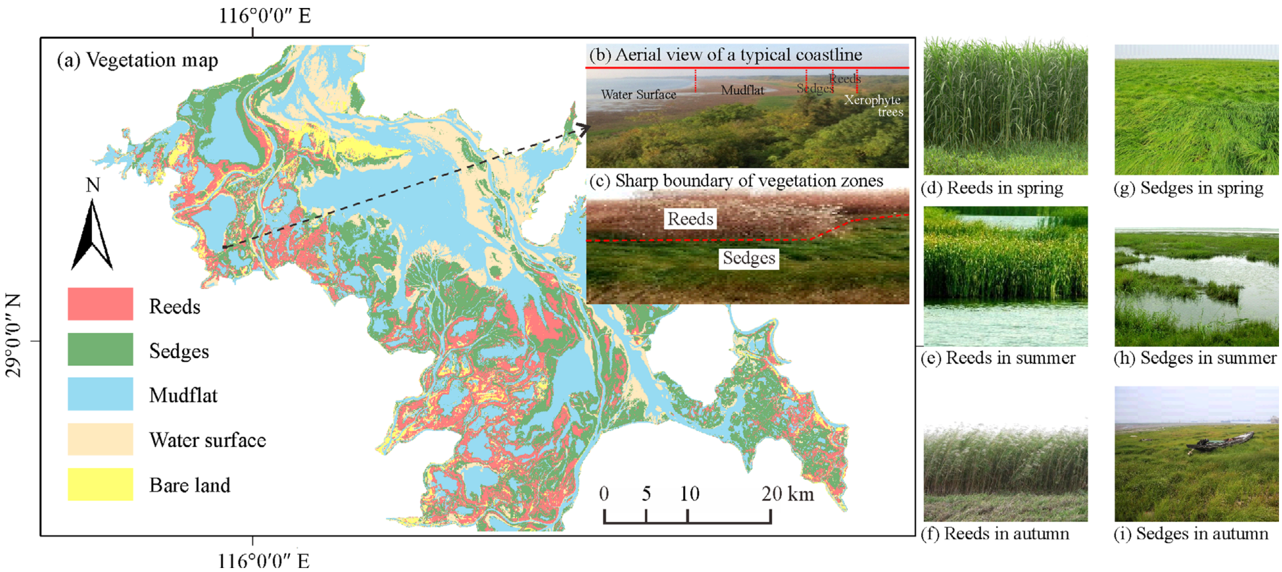

Fig. 3 Vegetation distribution pattern of Poyang Lake wetland and seasonal variations of various vegetation zones. (a) Vegetation map. (b) An aerial view of a typical coastline of Poyang Lake with reed and sedge zones changing with elevation from high to low on the emergent marsh areas. (c) The sharp boundary between the two distinctive vegetation zones. (d), (e), and (f) reeds in spring, summer, and autumn, respectively. (g), (h), and (i) sedges in spring, early summer, and autumn.

classified as reeds in this study. The reeds dominate the higher-elevation positions (15 – 17 m), and the sedges dominate the lower-elevation niches (13 – 15 m); this characteristic further differentiates their life history characters in this area (Zhu and Zhang, 1997; Sang et al., 2014).

The reed zone is primarily composed of flood-intolerant species, as shown in Table 1 (Liu and Ye, 2000; Wang et al., 2004). In the reed zone, the floods last for two or three months at most (Sang et al., 2014). Thus, reeds can tolerate much drier conditions than most other vegetation types. Additionally, in this area, the life cycle of reeds can be divided into four distinct periods: the reproduction period (in spring), the maturity period (in summer), the senescent period (in autumn), and the dormancy period (in winter). The appended drawings in Figs. 3(d), 3(e), and 3(f) show the seasonal changes in the reed zone.

The sedge zone is primarily composed of flood-tolerant species (Table 1), and sedges are the most abundant vegetation type in the Poyang Lake wetland (Guan et al., 1987; Liu and Ye, 2000; Wang et al., 2004). Sedges reside in the relatively low-elevation areas, i.e., 13 – 15 m. Unlike reeds, sedges can tolerate much wetter conditions. However, during peak flooding, the lake water levels can completely inundate this zone and stimulate a summer dormancy period that is specific to sedges. Thus, the life cycle of sedges in Poyang Lake is divided into four periods: the first re-growth period (in spring), the summer dormancy period, the second re-growth period (in autumn), and the winter dormancy period. The appended drawings in Figs. 3(f), 3(h), and 3(i) show the seasonal changes in the sedge zone. Note that the partial submersion of sedges, shown in Fig. 3(g), occurs at the very beginning of summer when the lake water spreads over these surfaces; however, the water eventually completely covers the plants.

Table 1 List of taxa in each vegetation zone in Poyang Lake wetland

Vegetation type	Dominant species	Surface elevation
Reeds	*Phragmites communis* *Triarrhena lutarioriparia* *Artemisia selengensis* *Artemisia rubripes* *Polygonum caespitosum*	15−17 m
Sedges	*Carex cinerascens* *Carex brevicuspis* *Carex scabrifolia* *Carex argyi* *Carex doniana* *Phalaris arundinacea* *Polygonum orientale*	13−15 m
Aquatics	*Vallisneria natans* *Potamogeton malaianus* *Potamogeton crispus* *Trapa maximowiczii* *Hydrilla verticillata var. rosburghii* *Najas minor*	< 13 m

In this study, we focused only on the impact of seasonal WLF on vegetation during autumn to elaborate on our previous findings (Dai et al., 2016).

2.2 Vegetation mapping

We mapped the annual vegetation of the Poyang Lake wetland using Landsat TM/ETM images acquired in late autumn; this time period was selected because the surface areas are relatively stable and experience the most significant level of exposure at this time (Ye et al., 2013). Table 2 lists when the selected Landsat TM/ETM images were acquired. All images were processed using the following three steps: 1) pre-processing, 2) hierarchical classification, and 3) accuracy assessment.

Table 2 Dates of Landsat TM/ETM images used in the current research

Year	Date	Year	Date
1989	November 20th	2004	November 29th
1991	December 10th	2005	October 31st
1995	December 17th	2006	November 3rd
1996	November 23rd	2007	November 30th
1999	December 10th	2008	December 10th
2001	November 21st	2009	December 6th
2003	November 3rd		

For the image pre-processing step, we utilized the ENVI 4.7 software for map registration by choosing ground-control points on a geo-referenced Landsat image of the wetland. The root mean square errors were < 0.3 pixels for all images from 1989 to 2009. We then selected a spatial subset to extract images of the entire wetland.

Then, we delineated the following vegetation and land cover types using a hierarchical classification method (You et al., 2017): water, mudflat, aquatics, sedges, and reeds. Specifically, the normalized difference vegetation index (NDVI) was first calculated by ENVI 4.7 using the formula (NIR – RED)/(NIR + RED) to obtain the areas covered in vegetation; thus, we identified the first levels of classification, i.e., the vegetation, water, and mudflat zones. Next, we delineated each vegetation type from the whole vegetated area, i.e., the second level of classification, which included the three types of wetland vegetations, i.e., aquatics, sedges, and reeds. Each classification type was extracted from the remote sensing images based on the spectral curve characteristics of various marks. We applied the wetland inventory data that are annually collected by the Poyang Lake Marsh Field Station as the ground reference data for our analyses.

A standard error matrix, overall classification accuracies, and kappa chance correction statistics were applied to the images to determine the accuracy of the hierarchical classifications. The overall accuracies of the classification were over 80% when compared to the ground truth data and the Kappa indexes, which were greater than 0.89.

2.3 Hydrological data

Year-round daily hydrological data corresponding to the vegetation maps were obtained from the Hydrological Bureau of Jiangxi Province. Each seasonal WLF hydrograph was measured via three parameters: the seasonal average water level, the seasonal maximum water level, and the seasonal minimum water level (Dai et al., 2016). The parameters of WLF in all four seasons were calculated prior to the acquisition time of the remote sensing images, as shown in Table 3.

Table 3 Hydrological parameters reflecting seasonal water level fluctuation patterns*

Seasonal WLF	Parameters for measuring the corresponding WLF
WLF in spring	The average\maximum\minimum value
WLF in summer	The average\maximum\minimum value
WLF in autumn	The average\maximum\minimum value
WLF in winter	The average\maximum\minimum value

*WLF is the abbreviation of water-level fluctuations.

2.4 The classification and regression tree model

The CART model is a binary recursive partitioning method that recursively separate values of a dependent variable into different subsets based on predictive variables; this process continues until the observations in each subset reach a criterion of homogeneity (Fig. 4(a)) (Qian and Anderson, 1999). The hierarchical structure of the fitted tree reveals the relative importance of each predictive variable. In this study, this process was conducted using the package *rpart* (Therneau et al., 2017) in the R environment (www.r-project.org).

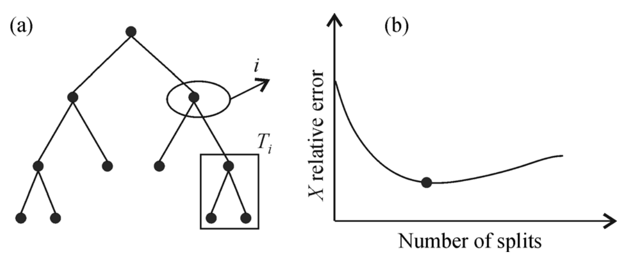

Fig. 4 An example of a CART Tree model (the child node and the sub tree) (a) and the plot of the cross-validated deviance versus tree size for pruning a CART tree (b).

The recursive partitioning CART model can be described as a process that reduces the level of "impurity" (Qian and Anderson, 1999). The impurity of each node is measured by the deviance, which is defined as:

$$D_i = -\sum_{k=1}^{g_i} P_k \log(P_k), \quad (1)$$

where g_i represents the number of classes in node i, and P_k represents the proportion of observations in class k. The deviance is 0 for a homogenous node, in which all observations belong to the same class. The deviation after the split is defined as below:

$$D_{i,\text{child}} = D_{i,L} + D_{i,R}. \tag{2}$$

The split that maximizes the reduction in the deviance $\Delta D = D_i - D_{i,\text{child}}$ is the one chosen at a given node.

If there are no stopping rules, the binary splitting can continue until each final node has only one data point. To avoid overfitting, we used a plot of the cross-validated deviance (or the X relative error) versus the tree size to determine the appropriate size for the model. As Fig. 4(b) shows, the associated relative valley value of both the cross-validated deviance and the tree size occurred in the area depicted by the grey spot when the CART tree reached the appropriate size.

3 Results

3.1 Seasonal water level fluctuations of Poyang Lake in 1989–2009

Figure 5 shows the water level changes in Poyang Lake for each season from 1989 to 2009. These trends can be measured by observing the three linear regressions of the respective maximum, average, and minimum water levels in each season. As illustrated in Fig. 5, all WLF variables in all four seasons showed declining trends in 1989–2009, as characterized by the different slopes and intercepts. The slopes varied between −0.04 and −0.16, while the intercepts varied between 9.42 and 21.26. The two most significant declines occurred during the lowest water level in spring (*slope*: −0.16 $\text{m}\cdot\text{yr}^{-1}$, $P < 0.01$) and the highest water level in summer (*slope*: −0.16 $\text{m}\cdot\text{yr}^{-1}$, $P < 0.01$). Additionally, the downward trends of the lowest and average water levels in autumn were also significant (*slope*: −0.14 $\text{m}\cdot\text{yr}^{-1}$ and −0.12 $\text{m}\cdot\text{yr}^{-1}$, respectively).

Consequently, the patterns of WLF shifted dramatically during the last two decades. As shown in Fig. 6, Poyang Lake was in a relatively wet period during the 1990s, especially in spring and summer. However, the lake experienced a relatively dry period during the 2000s, especially in spring, summer, and autumn.

3.2 Vegetation succession of the wetland in 1989–2009

Figure 7 shows the changes in the coverage area of each vegetation type in the Poyang Lake wetland from 1989 to 2009. The linear regression of reed cover indicates a significant upward trend from 1989 to 2009 (*slope*: 14.05 $\text{km}^2\cdot\text{yr}^{-1}$, $P < 0.01$), while the linear regression of sedge cover shows a general downward trend for 1989–2009 (*slope*: −5.98 $\text{km}^2\cdot\text{yr}^{-1}$). Specifically, the coverage area of

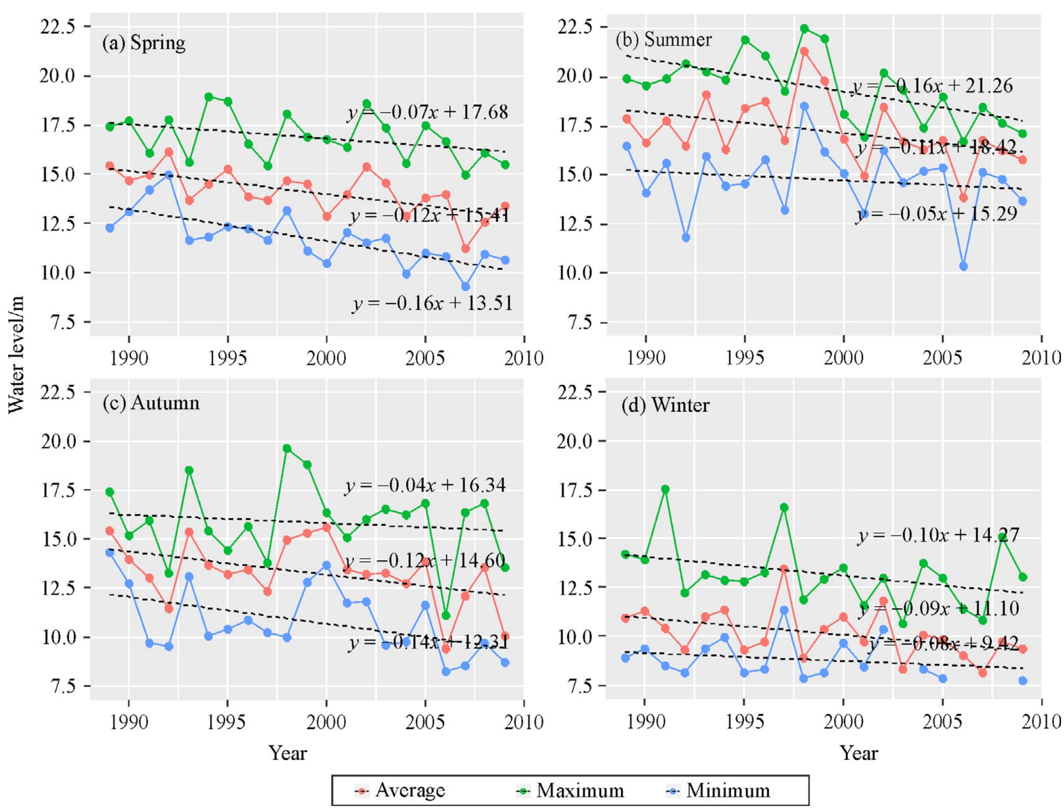

Fig. 5 Changes in seasonal water level fluctuations in 1989 to 2009.

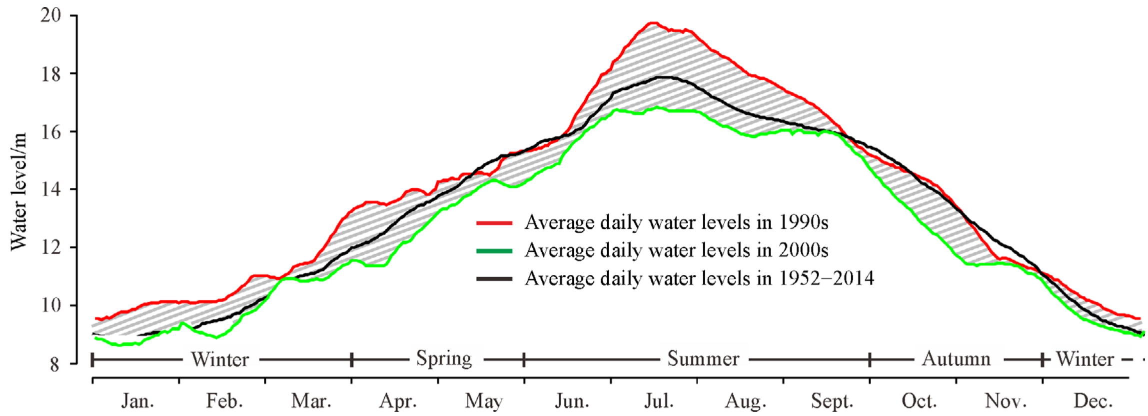

Fig. 6 Comparison of seasonal water level fluctuations in the Poyang Lake during the 1990s and the 2000s, as compared to the average for 1952 to 2014.

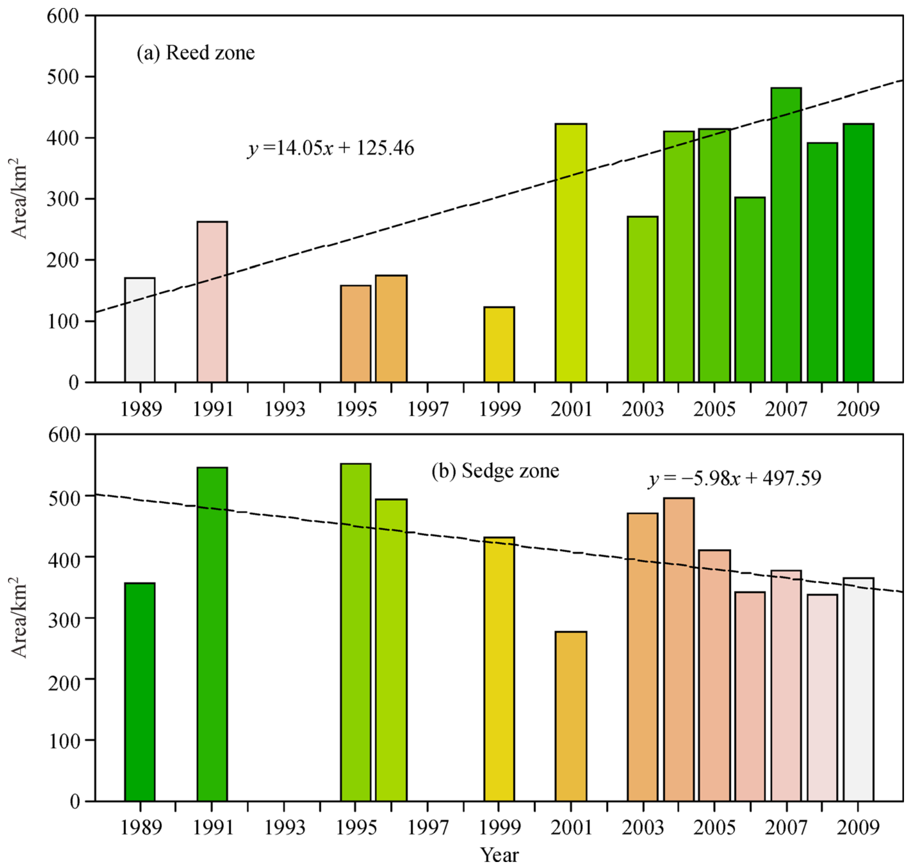

Fig. 7 Changes in coverage area of the two typical vegetation types (reeds and sedges) from 1989 to 2009.

reeds increased dramatically in the 2000s after experiencing a period of decline throughout the 1990s. There was a general downward trend in coverage area of sedges in the 2000s after a period with very high values throughout the 1990s.

3.3 Response of sedge distribution to seasonal WLF

The CART tree in the top panel of Fig. 8 shows the response of sedges to seasonal WLF. In the graphic of the CART tree, the text above each split explains which variable was split and the condition of the left branch. The mean value of the response variable, i.e., the average coverage area of sedges, is shown below each split. As seen in Fig. 8 (top panel), the final model for the sedges has two splits. The first occurred during the average water level in summer, which indicated that the variability of sedge cover was largely determined by WLF in summer. In years

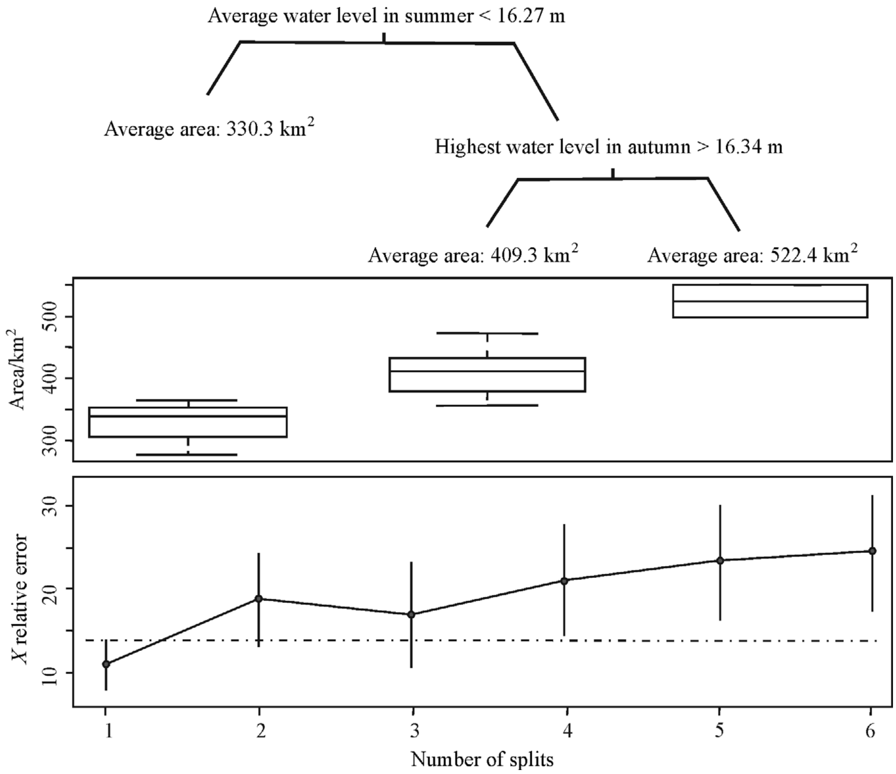

Fig. 8 The final CART model for the coverage area of sedges.

when the average water level in summer was less than 16.27 m, the coverage area of sedges most likely shrinks to 330.4 km^2. If the average water level in summer was not less than 16.27 m, the CART tree checks the second split, which was recorded at the highest water level in autumn. The second split indicated that, during the years in which the average water level in summer was not less than 16.27 m, the WLF of autumn were essential for the distribution of sedges. If the highest water level in autumn was higher than 16.34 m, the coverage area of sedges would most likely be 409.3 km^2; otherwise, it would likely expand to 522.4 km^2. The middle panel in Fig. 8 shows the boxplots for the coverage area of sedges within each of the three nodes.

The cross-validation results for the sedge model are shown in the bottom panel, which indicates the relative predictive error that was determined via the same cross-validation simulation (or *X* relative error) at each split (within one standard deviation). This process explains why only the first two splits were included in the final model. As shown in Fig. 8 (bottom panel), after the second split, further splits would not have reduced the relative predictive error of the model.

3.4 Response of reed distribution to seasonal WLF

The CART tree in the top panel of Fig. 9 shows the response of reeds to seasonal WLF. Similar to the results of the CART tree for sedges, the CART tree for reeds also had two splits. The first occurred at the peak water level in summer. The second occurred at the average water level in spring. In other words, the distribution of reeds was most significantly influenced by WLF in summer. In the years in which the highest water level was greater than 19.21 m, the coverage area of reeds likely shrinks to a mere 193.3 km^2. If the highest water level in summer was lower than 19.21 m, the average water level in spring was the most important variable affecting the distribution of reeds. In years in which the average water level in spring was higher than 13.97 m, the average coverage area of reeds was likely 301.5 km^2. Otherwise, their average coverage area would most likely expand to approximately 424.0 km^2. As mentioned above, the middle panel shows the boxplots of the coverage area for reeds within each of the final nodes. The reason for including only the first two splits in the final model is presented in the lower panel (Fig. 9).

In summary, the results from the CART model indicated that WLF in summer significantly affected both sedges and reeds. Severe summer floods promoted the expansion of sedges, while they inhibited the expansion of reeds. WLF in autumn affected sedges to a lesser degree. For example, dry autumns generally caused an expansion in sedge cover. However, reeds were more severely affected by fluctuations in spring. Dry springs generally caused an expansion in reed cover.

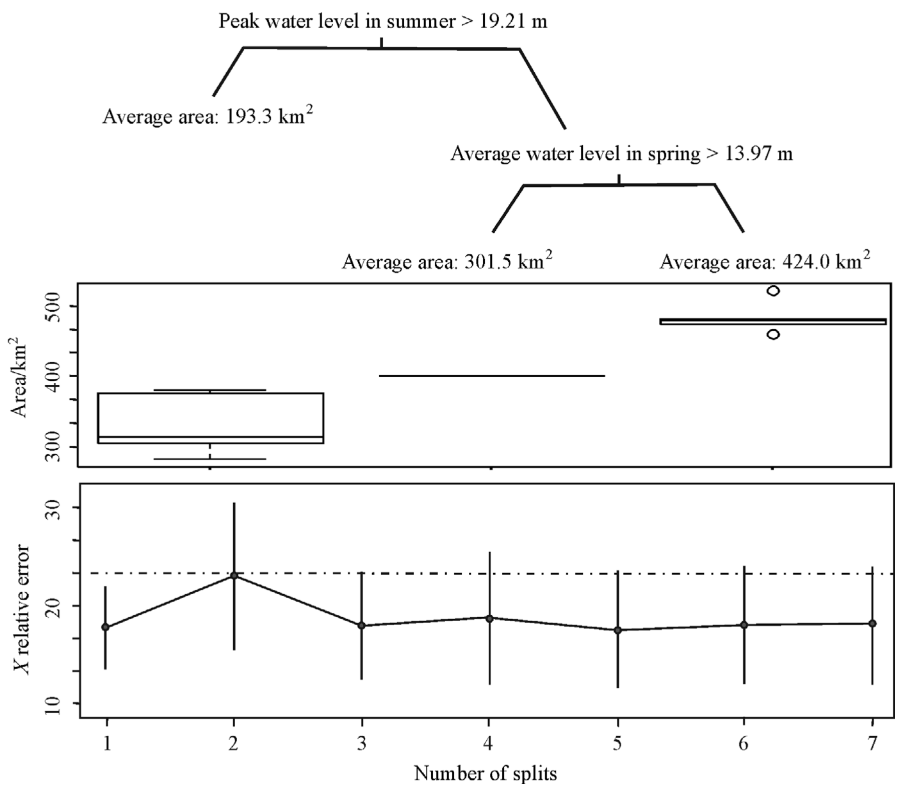

Fig. 9 The final CART model for the coverage area of reeds.

4 Discussion

4.1 Vegetation succession under specific WLF during the last two decades

According to the results of our CART model, in the 1990s which were characterized by extremely high water levels in both summer and spring (Fig. 6) the wetland would be expected to exhibit declining reed cover and expanding sedge cover. In contrast, in the 2000s which were characterized by extremely low water levels in spring

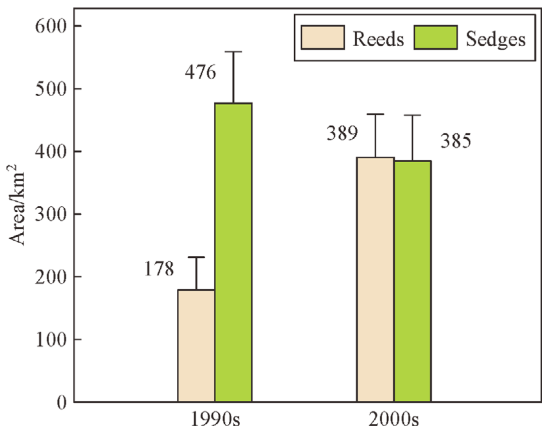

Fig. 10 Comparison of coverage area of each vegetation type in the Poyang Lake wetland during the 1990s and the 2000s.

and summer the reed coverage would be expected to expand and the sedge cover would be expected to shrink. However, the following low water levels in autumn in the 2000s would have promoted the expansion of sedges to some extent. Hence, there would have been no significant shrinkage in sedge cover during the 2000s.

As shown in Fig. 10, the CART model results were well corroborated by the distribution patterns of vegetation over the last two decades. In the 1990s, the coverage area of reeds did indeed shrink dramatically to just 178 $km^2 \cdot yr^{-1}$. In contrast, the coverage area of sedges substantially expanded to 476 $km^2 \cdot yr^{-1}$. In other words, in the 1990s the structure of the Poyang Lake wetland featured a dramatic reduction in reeds which was offset by a correspondingly dramatic increase in sedges. In the 2000s, the reeds expanded their coverage area to 389 $km^2 \cdot yr^{-1}$, while the sedge cover showed a general decline to approximately 385 $km^2 \cdot yr^{-1}$. Overall, in the 2000s the Poyang Lake wetland experienced an increase in reeds and a slight decrease in sedges.

4.2 Potential reasons for differences in the responses to seasonal WLF of each vegetation type

The characteristics and requirements of reeds and sedges are very different. Varying hydrological demands and the adaptability of different species throughout their stages of growth have led to succession in the Poyang Lake wetland under specific conditions of WLF over the last two decades.

In spring, WLF cause a stage of re-growth for both reeds and sedges. According to Xie and Yang (2009), generic soil with a volumetric water content of approximately 35% is ideal for the germination and tilling of reeds. Thus, the springtime submersion that occurs during unusually wet years may suppress their growth. However, sedges grow best in wet soil on exposed sites during spring. Wetter conditions are more favourable for the development of stands of sedges rather than reeds (Wang et al., 2008, 2009a). Therefore, lower seasonal mean water levels in spring will result in reeds having a larger coverage area. Additionally, Xie and Yang (2009) found that, in the most favourable sites, reeds could grow 3 – 6 cm per day in spring, which was more rapid than the growth rate of sedges. Therefore, even under relatively mild hydrological conditions where sedges and reeds can share dominance, reeds can gain a competitive advantage over sedges in the spring. Overall, drier springs promote the growth of reeds and discourage the growth of sedges, which is not only a result of the hydrological adaptability of the species but also the result of species competition.

In summer, high lake levels accompanied by other environmental limitations (e.g., oxygen deficiency due to long periods of submersion and physical damage caused by hydrodynamic forces) have dramatically destructive effects on wetland plants, especially on flood-intolerant reeds. However, high water levels in summer have had both negative and positive impacts on sedges. On one hand, prolonged submersion throughout the summer flooding season causes severe withering in the above-ground portions of sedges, which promotes the start of a summer dormancy stage (Wu et al., 2012; Zhang et al., 2013a). On the other hand, alternating between inundation and exposure promotes the tilling of sedges in autumn. Therefore, sedges begin to rapidly expand immediately after the recession of water in autumn (Wang et al., 2009b). In summary, although the summer submergence forces sedges into dormancy, the relief from submersion in autumn could lead to a re-growth period for sedges (Dai, 2015). Hence, severe summer flooding promotes the expansion of sedges and inhibits the development of reeds. In addition, a severe summer flood may kill reeds growing near their lower elevational limits. After summer flooding, sites previously dominated by reeds will be taken over by sedges at the beginning of their second growth period in autumn. This phenomenon also explains why severe summer flooding promotes the expansion of sedges while it inhibits the development of reeds.

Reeds undergo their senescent period in autumn. During this time, their tilling ability generally decreases; thus, it becomes difficult for reeds to expand their areas of growth. As a result, WLF during autumn do not significantly interfere with the distribution of reeds. During this time, sedges begin their second stage of growth on the fertile re-exposed alluvial plains. Because the highest water level in autumn determines the boundary of the re-exposed areas, i.e., the growth sites for sedges, the highest water level at this time is the second most important hydrological parameter for the distribution of sedges as they compete with reeds.

In conclusion, we determined that the influence of WLF on vegetation succession in the Poyang Lake wetland was due to the differing needs and characteristics of the different species and their varying hydrological demands and adaptability. Variations in the life cycles of reeds and sedges are caused by summer floods. Specifically, most reeds can survive these occurrences as well as the senescence phase in autumn. Most sedges are submerged; therefore, they are dormant during the summer floods. However, in autumn, they begin a period of active growth on the exposed fertile alluvial plains. Hence, after summer flooding, sites that were previously dominated by reeds could be taken over by sedges. Note that in Poyang Lake wetland sedges have developed a unique adaptation to environments that quickly change from aquatic to littoral. In other words, sedges have two growth cycles each year which gives them a huge inter-species competitive advantage in years with extreme summer flooding; these results provide a glimpse into how different species development and characteristics can affect the distribution of vegetation under specific conditions of WLF.

5 Conclusions

In this study, we presented examples of the seasonal WLF in Poyang Lake and discussed their implications for the wetland ecosystem; furthermore, we placed specific emphasis on the distribution patterns of vegetation in autumn. We found that both sedges and reeds were greatly affected by WLF in summer. Severe summer flooding promoted the expansion of sedges; however, it inhibited the development of reeds. In the years with severe summer floods (i.e., when the highest water level was greater than 19.2 m), the coverage area of reeds shrinks by 37%, to a mere 193.3 km^2. However, in years with no severe summer floods (i.e., when the average water level is less than 16.3 m), the coverage area of sedges shrinks by 21%, to 330.4 km^2. WLF in autumn are the second most important hydrological condition that affect the growth of sedges. If the highest water level is lower than 16.3 m, the coverage area of sedges can expand by 24%, to 522.4 km^2. The second most important hydrological condition for reeds are WLF in spring. Dry springs result in the expansion of reeds. In years when the average water level in spring is lower than 14.0 m, the average coverage area of reeds can expand by 38%, to 424.0 km^2. This finding shows that the shift in the seasonal WLF over the last two decades is responsible for the changes in the distribution dynamics of sedges and reeds in the Poyang Lake wetland.

This paper provides valuable information for the future ecological management of the Poyang Lake wetland. As noted, many scholars have attributed the significant shift in the hydrological regime observed in the 2000s to the operation of the Three Gorges Dam (TGD) (Zhang et al., 2011; Liu et al., 2013; Lai et al., 2014; Mei et al., 2015; Zhang et al., 2015). Thus, an eco-regulation process should be proposed for the dam with the goal of creating more suitable and sustainable hydrological and hydro-dynamic conditions to prevent the ecological and structural breakdown or physical degradation of the Poyang Lake wetland.

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