Temperature and flooding depth thresholds for early recruitment stages in a bulbous plant Bolboschoenus planiculmis

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Abstract

Early recruitment process dominated by vegetation reproduction for wetland plant is a key life-history stage affecting species distribution. Extreme climatic events, such as extreme temperature and heavy rainfall have been predicted to become more intense and frequent under future climate scenarios. To explore the effect of temperature and flooding depth on tubers sprouting and early growth of *Bolboschoenus planiculmis*, we conducted two artificial experiments in the incubator and greenhouse, including ten temperature regimes (8, 10, 12, 14, 16, 19, 22, 25, 28 and 31°C), and ten flooding depth treatments (-5, 0, 3, 6, 9, 12, 16, 20, 30 and 40 cm). The results showed that the temperature and flooding depth had significant effect on the tuber sprouting and ramet early growth. The estimated base temperature for the sprouting is 6.2°C, the final sprouting percentage increased parabolically with increasing temperature and reached a maximum of 61.09% at 25.4°C. The final sprouting percentage increased first and then decreased with increasing flooding depth, and reached a maximum of 96.04% at 3.92 cm. The ramet height increased first and then decreased with increasing flooding depth, and reached a maximum of 61.29 cm at 8.20 cm. Our study will provide a basis for understanding and predicting the influence of climate change on the distribution of *B. planiculmis*.

1. Introduction

Recruitment stages play a particularly important role for species distribution by creating different opportunities for new plant establishment in changing environment (Fraaije et al. 2015). The early recruitment stages of clonal plants was mainly dominated by vegetative reproduction (including radicle emergence, ramet survival and growth) (Vazquez-Ramirez and Venn 2021), and this process was influenced by a variety of environmental factors (Huang et al. 2015). Associated with global change, there has been a rapid increase in frequency and intensity of extreme climatic events (Abernathy et al. 2019). Temperature and flooding, two of the changing environmental factors, are the major determinants of the early life-history stages of plants (Walck et al. 2011). Therefore, understanding the influence of these two factors on the early recruitment stages might allow to predict, and mitigate the effect of future environmental changes on wetland vegetation distribution.

Temperature is a major limiting factor for plant establishment and survival in recruitment stages (Campbell et al. 2018). The response of germination to temperature has three cardinal temperatures: base, optimal, and ceiling temperature. At both, the base and ceiling temperatures germination is zero, whereas, at the optimum temperature, the highest germination rate occurs (Zaferanieh et al. 2020). Generally, the propagules of varied species could not sprout at the temperatures lower than 5°C or higher than 50°C, and the tubers sprouted at the optimum temperature range of 15 ~ 35°C (Hossain et al. 2001, Loddo et al. 2018). These parameters are the basis for models used to predict the timing of sprouting (Kamkar et al. 2012). So more studies on the early plant recruitment stages are required to provide information to maximize the possibilities of their application.

Flooding regime has long been considered as crucial for individual propagule sprouting rates (Greet et al. 2020). Flooding depth is an important occurrence of flooding regime (Mauchamp et al. 2001). At low flooding depth, propagule and ramet can utilize resources, especially carbon dioxide and oxygen in the atmosphere (Vervuren et al. 2003, Deegan et al. 2007). At deep flooding depth, plants can suffer from hypoxia or anoxia because the ability of oxygen to diffuse through the water to the soil is extremely low (Ejiri et al. 2020). Many studies found that sprouting percentage of rhizome of many plants increased first and then decreased with the increasing of flooding depth (Zhan et al. 2010, Dong et al. 2012). However, the effects of flooding on the vegetative structure of wetland plants are very limited and need further study.

Bolboschoenus planiculmis, a perennial helophyte with tuber propagation, is distributed in East Asia, Central Asia and Central Europe (Ding et al. 2021). It forms a monodominant or mixed community in salt marshes, reclaimed paddy fields and lagoons (Yang et al. 2020). Meanwhile, this species provides food for endangered migratory birds like swan geese (*Anser cygnoides*) and cranes (*Grus leucogeranus*) (Yang et al. 2020, 2021). Generally, *B. planiculmis* lives at low elevations, and it is one of the most vulnerable species to seasonal flooding conditions and temperature (Kim et al. 2013). The effects of temperature, flooding state, salinity, and interspecific interactions on *B. planiculmis* have been discovered by several scholars (Kim et al. 2013, Liu et al. 2018, Yang et al. 2020). However, there were few studies on the response of the early plant recruitment stages to environmental factors.

The study was to investigate how the tubers of *B. planiculmis* adapt to the environment of temperature and flooding depth change during the early plant recruitment. The purposes of the current study were (1) to investigate the effects of different temperatures and flooding depths on *B. planiculmi* tuber sprouting performance, and (2) to estimate the temperature and flooding depth thresholds for bud sprouting of *B. planiculmi*.

2. Materials And Methods

2.1. Study area

The Momoge National Nature Reserve (45°45’–46°10’N, 122°27’–124°04’E) is located in the northern part of Songliao settlement area and the western edge of Songnen Plain in China. The climate is a temperate continental monsoon climate with annual average temperature at 4.2°C. The annual average precipitation is 392 mm, 50–70% of which is mainly concentrated in the summer months between July and August (Ban et al. 2019). The terrain is flat, and the relative elevation is only 2–10m (Wei et al. 2019). It covers an area of 1440 km^2, of which the saline-alkaline wetland covers nearly 80%. The dominant species are *Phragmites australis, Bolboschoenus planiculmis* and *Schoenoplectus nipponicus* et al (Liu et al. 2018). Predominant soil types include marsh, meadow, alkali, sandy, alluvial soil and chernozem (Jiang et al. 2007).

2.2 Materials collection and preliminary treatments

Tubers of *B. planiculmis* without damage or necrosis were collected in late April 2020 from Momoge National Nature Reserve. They were put into ziplock bags and stored at 4°C until the start of the experiment. Healthy tubers were selected and sterilized by immersion in sodium hypochlorite solution (5%) for five minutes. They were washed carefully with distilled water and used for biometric measurement. Fresh weight and diameter were measured of each tuber piece. The tubers averaged 1.12 ± 0.56g in weight and 9.85 ± 1.9mm in diameter.

Two experiments were carried out in late April 2021. The incubator experiment examined the responses of tuber sprouting to the constant temperature. The greenhouse experiment was designed to investigate the effect of flooding depth on tuber sprouting.

2.3. Experimental design

Incubator experiment: Trays (length of 47 cm, width of 45 cm) with 5*6 small pots (length of 6.5 cm, width of 6.5 cm, depth of 6.5 cm) was selected as experiment equipment. Each pot was filled with river sand (washing repeatedly and autoclave before using). The treatment consisted of ten temperatures (8, 10, 12, 14, 16, 19, 22, 25, 28 and 31°C). Three replicates of 10 tubers were placed on a tray for one treatment in an incubator. Each pot contained only 1 tuber and was covered with a shallow layer of sand (1cm). The humidity was controlled in 40–50% and photoperiod was controlled at 12h light/12h dark conditions. Distilled water was added every day to maintain an adequate moisture level for sprouting.

Greenhouse experiment: The randomly selected tubers were placed in plastic basins (length of 50 cm, width of 38 cm, depth of 20 cm) filled with10 cm of river sand. Five drainage holes were made in the bottom of the basins so that tubers could be inserted at the desired flooding depth. Tubers were covered with a shallow layer of sand (1cm). The flooding depths consisted of ten treatments: -5, 0, 3, 6, 9, 12, 16, 20, 30 and 40cm. Each treatment consisted of four replications of 10 tubers. An appropriate amount of water was added every day to maintain a constant flooding depth. The temperature was set at about 25 ± 3℃ and the humidity was controlled at 40–50%.

Tubers were considered to have sprouted with the emergence of the radicle. No sprouting of new tubers for seven consecutive days was considered as the end of the sprouting experiment. The number of regenerated ramet was counted every day until the end of the experiment. All plants were measured for their ramet height above the sediment surface. The experiment lasted for 30 days.

2.4. Statistical analyses

Estimation of base temperature for incubator experiment

Earlier estimation methods were based on sprouting assays at suboptimal temperatures, while the most robust estimates were provided by the X-intercept of a linear regression of median sprouting time to the reciprocal of temperature (Masin et al. 2017). The time necessary for the sprouting of half of the total sprouting tubers (t_{50}) was calculated for each replicate, and the sprouting percentage was estimated as $1/t_{50}$.

A logistic model was fitted for tubers sprouting relating the percentage of sprouting to time of incubation at each temperature. The equation was:

$y = A_2 + (A_1-A_2)/(1 + (x/x_0)^p)$,

where y was the cumulative sprouting percentage, A_1, A_2 and p were parameters from the equation and x was the accumulated incubation time (days). From the equation, the number of days required to reach 50% of sprouting (t_{50}) was obtained for each treatment. The base temperature was determined as the temperature at which the sprouting rate of development was equal to zero by extrapolating from the liner relation between the sprouting rate ($1/t_{50}$) and temperature.

Tuber sprouting and ramet growth

Five parameters of sprouting and early growth were determined for temperature and flooding depth: final sprouting percentage (FSP), sprouting rate (SR), survival rate of sprouts (SRS), relative growth rate (RGR) and mean time to sprout (MST).

The final sprouting percentage (FSP) was calculated using the following equation:

$FSP = N_g /N_t \times 100$,

where N_g is number of buds sprouting and N_t is the total number of tubers evaluated (Braziene et al. 2021). The survival rate of sprouts (SRS) was calculated using the following equation:

$SRS = N_s /N_t \times 100$,

where N_s is the number of survival buds sprouting. The relative growth rate (RGR) was calculated using the following equation:

$RGR = (\ln H_2-\ln H_1)/(t_2-t_1)$,

where H_2 is the natural of ramet height; H_1 is the initial of ramet height; t_2 is the final time; t_1 is the initial sprouting time (Tsetsegmaa et al. 2018). The mean time to sprout (MTS) was calculated using the following equation:

$MTS = \Sigma(n_i \times d_i)/N$,

where n_i is the number of tubers sprouting per day, d_i is the incubation period in days, and N is the total number of tuber sprouting in the treatment (Tompsett and Pritchard 1998).

The data (final sprouting percentage, sprouting rate, ramet height, survival rate sprouts, relative growth rate, $1/t_{50}$ and mean time to sprouting) was subjected to one-way analysis of variance (ANOVA) to evaluate the effect of the main factor (temperature and flooding depth). Duncan's multiple range test was used for statistical analyses. In order to ensure homogeneity of variance, mean time to sprout and ramet

height was log-transformed. The relationships between these parameters and two factors (temperature and flooding depth) were evaluated using polynomial regression. The relationship between the final sprouting percentage and flooding depth was evaluated using non-linear Gaussian regression.

3. Results

3.1. Effects of temperature on tubers sprouting

Final sprouting percentage, mean time to sprout and sprout rate of *B. planiculmis* were significantly affected by temperature (Table 1, P 0.001). The longest sprouting time was 23 days at 8°C, and the shortest sprouting time was 4 days at 28°C (Fig. 1a). The final sprouting percentage increased parabolically with increasing temperature and reached a maximum of 61.09% at 25.4°C (R^2 = 0.79, P< 0.001, Fig. 2a). The mean time to sprout decreased with the increase in temperature (R^2=0.42, P< 0.001, Fig. 2b). There was a significant positive correlation between the sprout rate and temperature (R^2=0.96, P < 0.001, Fig. 2c). The estimated base temperature for the bud-sprouting of *B. planiculmis* was 6.2°C, and the optimum temperature is 25.4°C.

3.2. Effects of temperature on regenerated ramet from tubers

Significant effects of temperature were found on the regenerated ramet early growth of *B. planiculmis* (Table 1). The ramet height linearly increased with the temperature increasing (R^2=0.74, P< 0.001, Fig. 3a). The survival rate of sprouting increased parabolically with increasing temperature and reached its maximum value (100%) at 22.9°C (R^2=0.93, P< 0.001, Fig. 3b). There was a significant positive correlation between the relative growth rate and temperature (R^2=0.46, P< 0.001, Fig. 3c).

3.3. Effects of flooding depth on tubers sprouting

The tubers sprouting of *B. planiculmis* were significantly affected by flooding depth (Table 1). The longest sprouting time was 17 days at 40 cm, and the shortest time to sprouting was 12 days at 0 cm (Fig. 1b). The final sprouting percentage of *B. planiculmis* increased first and then decreased with increasing flooding depth, and reached a maximum of 96.04% at 3.92 cm (R^2 = 0.63, P< 0.001, Fig. 4a). The mean time to sprout increased as the increasing flooding depth (R^2 = 0.49, P< 0.001, Fig. 4b). The sprouting rate showed a significant decrease as the flooding depth increased from − 5 cm to 40 cm (R^2 = 0.93, P< 0.001, Fig. 4c).

3.4. Effects of flooding depth on regenerated ramet from tubers

Under each treatment, all the regenerated ramet remained alive. The one-away ANOVA indicated that the ramet height and relative growth rate were significantly affected by flooding depth (Table 1). The ramet height increased first and then decreased with increasing flooding depth, and reached a maximum of

61.29 cm at 8.20 cm (R^2 = 0.51, P< 0.001, Fig. 5a). The relative growth rate was negatively correlated with the increasing flooding depth (R^2 = 0.37, P< 0.001, Fig. 5b).

4. Discussion

4.1. Responses of tubers sprouting to temperature

In this study, the final sprouting percentage increased first and then decreased with the increasing temperature, and 25°C is the optimum temperature for *B. planiculmis* tubers sprouting. A similar trend was also reported by Hossain et al. (2001), who found that the rhizomatous sprouting of *Panicum repens* also has a unimodal pattern, and the optimum temperature is 25°C. This may be due to the fact that both too high and too low temperatures lead to secondary tuber dormancy (Andersson et al. 2013, Mollaee et al. 2020). We also found that the mean time to sprout decreased with the increasing in temperature from 8°C to 31°C. Similar to our results, Retana-Cordero et al. (2021) found that the mean time to rhizome sprouting of turmeric decreased with the temperature increasing from 20°C to 30°C. This may be because tubers could not regulate endogenous hormone content in the low temperature, and lack enough energy to accumulate to break dormancy (Kawabata and Nishimoto 2003, Naor et al. 2006).

The estimated base temperature for the sprouting of *B. planiculmis* tubers is 6.2°C. The value was similar to the estimated value of 5.8°C reported by Holt and Orcutt (1996) for population of *Cyperus esculentus* in California, but lower than estimated value of 11.2°C proposed by for *Cyperus rotundus* population in California. Although these three species are members of the *Cyperaceae*, factors such as the origin of the population, reproductive age, and storage time before experimentation affect the interspecific response to temperature (Holt and Orcutt 1996, Loddo et al. 2012). In addition, the difference of average annual temperature between the area where the three populations are located also affected the base temperature. The annual average temperature in California is 21°C, which is higher than the average annual temperature 4.2°C of Momoge National Nature Reserve. In general, the base temperature of a plant is proportional to the annual average temperature of the region in which it is located (Loddo et al. 2018). The rate of *B. planiculmis* sprouting increased with the increasing in temperature from 8°C to 31°C. Similar to our results, Loddo et al. (2018) found that the sprouting rate of all studied species such as *Echinochloa crus-galli* and *Sorghum halepense* increased with increasing temperature. This may be because that the metabolic activity decreases, and physiological reaction cannot take place at low temperatures (Zaferanieh et al. 2020).

4.2. Responses of regenerated ramet from tubers to temperature

Ramet height of *B. planiculmis* increased with increasing temperature. Similar results have also been demonstrated by the study of Heide (2011), who found that ramet height of *Sorbus* was lower at 9°C than that at 15°C and 21°C. This may because higher temperature is conducive to photosynthesis and plant growth (Tang et al. 2021). The survival rate of sprouting increased first and decreased then with

increasing temperature and reached its maximum value (100%) at 22.9°C. This is similar with the result of Pinheiro et al. (2021), who found that the survival rate of *Hedychium coronarium* was the optimal at 25°C. Gibberellin regulates stem elongation, and its transport rate on tubers decreases with increasing temperature (Wu et al. 2020). Relative growth rate of *B. planiculmis* increased with increasing temperature form 8°C to 31°C. The rate of ramet elongation of *B. planiculmis* in the period of low temperature showed slower initially, and faster elongation when the temperature was above 25°C. Similar to our results, Retana-Cordero et al. (2021) reported an increasing trend in relative growth rate formed 17.2°C to 30.1°C. Hossain et al. (2001) have been observed that elongation of ramet occurred faster with increased temperature. This may because the high temperature increased the physiological activity, protein and enzyme synthesis, and accelerated the metabolism of rhizome (Ishimine et al. 2004).

4.3. Responses of tubers sprouting to flooding depth

The final sprouting percentage of *B. planiculmis* was increased first and then decreased with increasing flooding depth, and reached a maximum of 96% at 3.9 cm. Similar results were demonstrated by (Zhan et al. 2010), who found that the *Myriophyllum oguraense* Miki subsp. *yangtzense* sprouting percentage increased first and then decreased with the increasing water depth. This may be due to that high water depth reduces oxygen availability in the root zone (An et al. 2018, Song et al. 2021) and enhanced ethanol production which is hazardous to plants (Ferreira et al. 2009). *B. planiculmis* may need to remain dormant to reduce energy consumption to provide and maintain normal physiological functions in deep flooding levels (Matsui and Tsuchiya 2006, Song 2021)

The mean time to sprout of *B. planiculmis* increased with the increasing flooding depth. Similar to our result, Zhou and Wang (2012) found that the mean time to sprout of macrophyte *Myriophyllum oguraense* increased with the increase of flooding depth. This may because the large amount of ethylene produced in the tubers under flooding stress alter the metabolic pathways in the sprouting of tuber (Kouighat et al. 2021). The sprouting rate decreased with the increasing flooding depth. A similar trend was reported in the rhizomatous sprouting rate of a *Carex cinerascens* hygrophyte by Yuan et al. (2019), who found that the rate of emergence showed negative trends with the increase of flooding depth. Min et al. (2019) also found that the sprouting rate was reduced and the mean time to sprout was prolonged for *Vallisneria natans* and *Hydrilla verticillate* at 2 m flooding depth. Because the extremely low light levels can be an additional stress when the tubers were completely submerged. Low light and low CO_2 efficiency greatly impede underwater photosynthesis (Colmer and Voesenek 2009).

4.4. Responses of regenerated ramet from tubers to flooding depth

Flooding depth is very important in influencing protophase growth of aquatic macrophytes (Zhan et al. 2010). In this study, with the flooding depth increasing, regenerated ramet height of *B. planiculmis* increased first and then decreased, and reached a maximum of 61.3 cm at 8.2 cm. This can be explained that deeper flooding constrains plant growth by limiting the availability of resources such as light and oxygen (Chen et al. 2010), when the flooding depth was low, the plant adopted ‘escape’ strategy to

increase ramet height (Liu et al. 2018, Bai et al. 2021). Meanwhile, our result was consistent with the previous finding that the height of ramet sprouting from rhizomes of *Acorus calamus* is firstly increased and then decreased as the water level increased (Cao et al. 2015). The final average plant height of *Acorus calamus* reached a maximum of 75.1 cm at a water level of 49.6 cm, is higher than *B. planiculmis*. This may be the reason why the rhizomes of *Acorus calamus* are more tolerant to low oxygen and low light environments under water. The relative growth rate was decreased with increasing flooding depth. Vretare et al. (2001) also found that the relative growth rate of *Phragmites australis* was significantly higher in 5 cm water depth compared to 75 cm depth. This may be because that higher flooding depth may affect the support degree of plant tissue structure, resulting in aerenchyma obstruction of gas exchange and slow growth (Zhang et al. 2014).

Conclusion

The present study demonstrates that temperature and flooding significantly affect the early plant recruitment stages of *B. planiculmis*. The optimum temperature and flooding depth for tuber sprouting and early growth is ranging from 25°C to 28°C and from 3 cm to 9 cm, respectively. Our results will provide a basis for predicting species distribution trends under global climate change. However, increasing fluctuations in temperature (the term thermoperiodicity) and timing of precipitation are likely to occur due to ongoing global warming and changes in rainfall patterns (Heffelfinger et al. 2018), future studies will explore the effect of diurnal fluctuating temperature and flooding duration on tuber sprouting of *B. planiculmis.*

Declarations

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Conflict of interest

The authors declare no conflict of interest.

Data availability statement

All data used for analyses are available from the corresponding author upon request.

Authors' contributions

Dongjia Yu: methodology, contributed to conceptualization, writing-original draft preparation, writing-review and editing.

Haoran Tang: experimental design and implementation.

Pangwei Li: formal analysis, writing-review and editing.

Mengdie Zhou: contributed to experimental design and implementation

Guangying Zhao: conceptualization, writing-review and editing,

Yanjing Lou: conceptualization, methodology, writing-review and editing, funding acquisition and supervision.

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Tables

Table 1 Summary of one-away ANOVAs to test the effects of temperature and flooding depth on final sprouting percentage, sprouting rate, mean time to sprout, ramet height, survival rate sprouts, and relative growth rate.

Variables	Parameters	DF	F-value	*P*
Temperature	Final sprouting percentage	9	132.07	< 0.001***
	Sprouting rate	9	2201.98	< 0.001***
	Mean time to sprout	9	14.68	< 0.001***
	Ramet height	9	19.90	< 0.001***
	Survival rate sprouts	9	2.30	< 0.001***
	Relative growth rate	9	33.29	< 0.001***
Flooding depth	Final sprouting percentage	9	94.90	< 0.001***
	Sprouting rate	9	128.86	< 0.001***
	Mean time to sprout	9	17.07	< 0.001***
	Ramet height	9	6.75	< 0.001***
	Relative growth rate	9	9.31	< 0.001***

***p<0.001

Figures

Figure 1

Cumulative sprouting percentage of *B. planiculmis* tubers during 30 days under different temperature regimes (a) and flooding depth treatments (b).

Figure 2

Variation of the final sprouting percentage (a), mean time to sprout (b) and sprouting rate (c) of *B. planiculmis* according to the temperature regimes (8, 10, 12, 14, 16, 19, 22, 25, 28, and 31 °C).

Figure 3

Variation of ramet height (a), survival rate of sprouts (b), relative growth rate (c) of *B. planiculmis* according to the temperature regimes (8, 10, 12, 14, 16, 19, 22, 25, 28, and 31 °C).

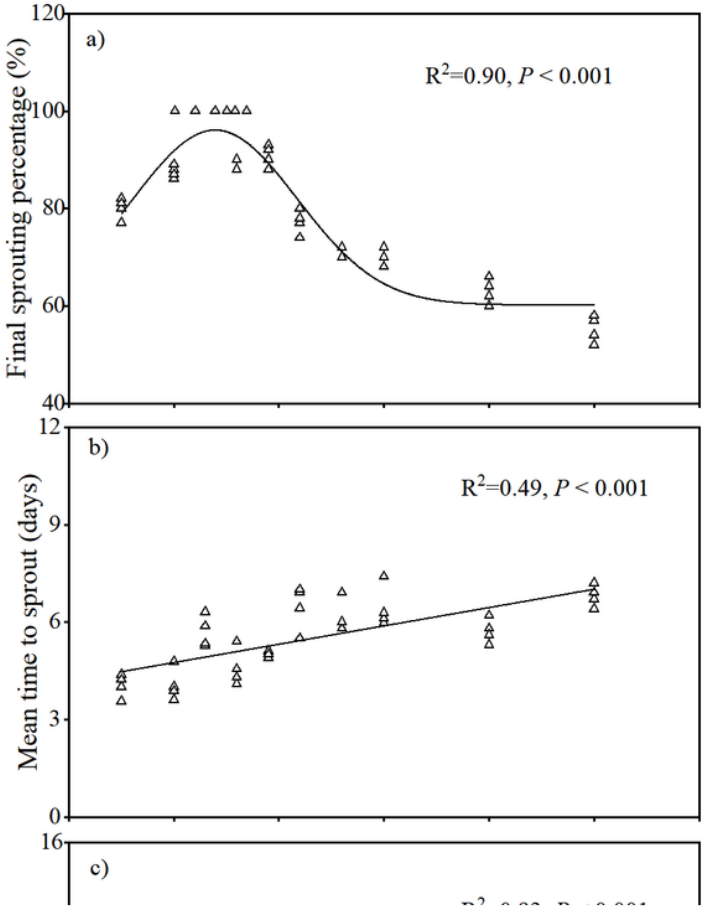

Figure 4

Variation of the final sprouting percentage (a), mean time to sprout (b) and sprouting rate (c) of *B. planiculmis* according to flooding depth regimes (-5, 0, 3, 6, 9, 12, 16, 20, 30 and 40 cm).

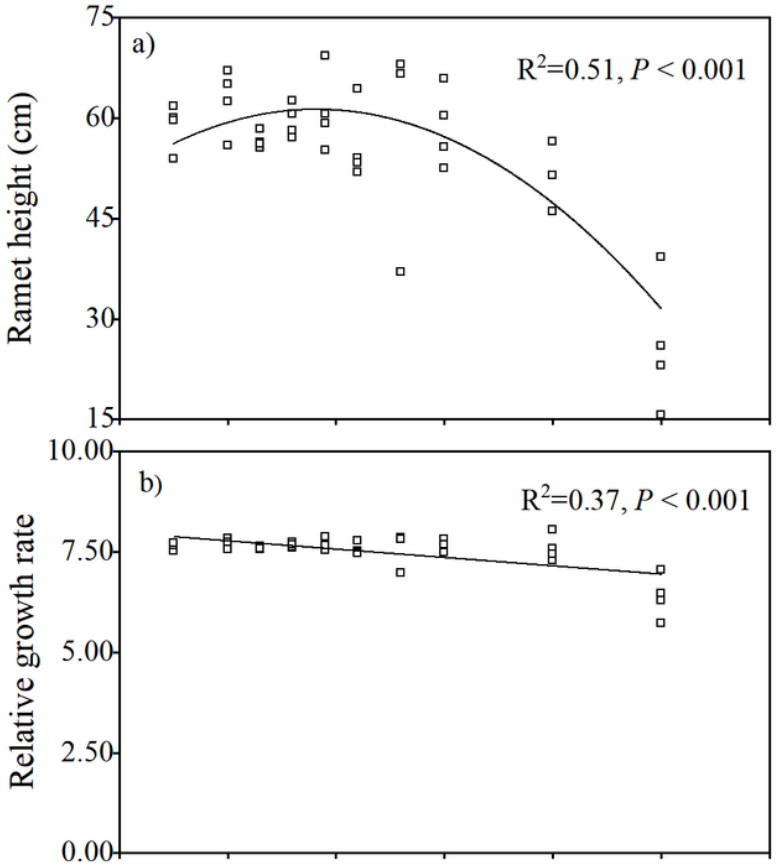

Figure 5

Variation of ramet height (a), relative growth rate (b) of *B. planiculmis* according to flooding depth regimes (-5, 0, 3, 6, 9, 12, 16, 20, 30 and 40 cm).