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Ability to recover overrides the negative effects of flooding on growth of tropical grasses *Chloris gayana* and *Panicum coloratum*

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Abstract. This study assessed the flooding tolerance of the tropical grasses *Chloris gayana* Kunth and *Panicum coloratum* L. at different times of the year: (*i*) late winter flooding for 50 days (WF), (*ii*) early spring flooding (SF) for 20 days, and (*iii*) long-term flooding covering both periods (WF + SF, 70 days). A growth period under well-watered conditions was allowed after each flooding event to assess recovery of plant species. Plants were harvested after each flooding event and at the end of the recovery period. *Panicum coloratum* had higher tolerance to WF than *C. gayana*. Treatment WF did not affect biomass in *P. coloratum*, whereas it reduced biomass of flooded plants by 38% in *C. gayana*. Treatment SF did not differentiate the species for tolerance; both registered moderate reduction in their growth (20–30%). Under WF + SF, *C. gayana* showed additional reduction in its growth over that observed when subjected separately to either WF or SF, whereas *P. coloratum* did not. Both species displayed remarkably fast recovery from flooding when temperatures rose during early summer, attaining biomass equivalent to that of non-flooded plants 1 month after water subsided. Therefore, although *P. coloratum* appears slightly more tolerant during flooding than *C. gayana*, both species are promising for introduction in temperate lowland grasslands.

Additional keywords: seasonal flooding, Rhodes grass, Klein grass, plant recovery.

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Introduction

The introduction of new forage species in grassland ecosystems outside their range of origin depends on the possibility of successful establishment and forage productivity in the pasture (Baron and Bélanger 2007). *Chloris gayana* Kunth and *Panicum coloratum* L. are two grass species of African tropical and subtropical origin (Bogdan 1969; Tischler and Ocumpaugh 2004) with incipient incorporation into natural temperate grasslands prone to flooding. This introduction has been facilitated over recent years by the occurrence of warm summers and less restrictive winters with increasing minimum temperatures and shorter freezing periods due to global warming (Long 1999; Chapman *et al*. 2012). In the Flooding Pampa grasslands of Argentina, floods frequently affect plant communities of lowland areas (Paruelo and Sala 1990) where these species are being incorporated with varying degrees of success (Imaz *et al*. 2012). The annual variation of water excess is high; sporadic short floods of up to 2 weeks can occur in summer but prolonged floods of up to 2 months can occur during late winter and early spring (Paruelo and Sala 1990; Striker *et al*. 2011, 2012). In a previous study, we showed that flooding episodes during spring and summer, seasons when these species are sown, could constrain their establishment depending on the depth of the flooding water (Imaz *et al*. 2012). Seedlings of *C. gayana* can tolerate both partial and complete submergence, whereas seedlings of *P. coloratum* perform well under partial submergence (Imaz *et al*. 2012). However, once established, adult plants of both species might tolerate floods during winter dormancy, spring regrowth, or both periods. Therefore, in this work we analysed flooding tolerance of adult plants of *C. gayana* and *P. coloratum* when facing episodes of flooding at different times in their growing cycle.

Plant responses to flooding differ according to the season (Crawford 2003). During winter, escape mechanisms that depend on growth and/or elongation of leaves do not operate in tropical grasses because they are in dormancy phase or under a low growth condition. However, extra reserves (e.g. soluble sugars, starch) stored in the bases of tillers could be utilised to sustain tissue respiration when facing less efficient anaerobic metabolism resulting from flooding (Gibbs and Greenway 2003). Consumption of reserves, reducing the weight of tiller bases as consequence of flooding, might affect post-flooding responses of plants at the beginning of the growing season by reducing their initial growth (Huber *et al*. 2012; Striker 2012). During spring, soil anoxia resulting from flooding imposes on plants a more severe stress condition as they start to grow and consequently demand more oxygen (Kozlowski and Pallardy 1984). In this context, even short-term flooding is expected to be detrimental for plant growth. To overcome this stress, plants can use escape mechanisms such as elongating leaves to increase atmospheric oxygen capture and facilitate root aeration (Bailey-Serres and Voesenek 2010; Striker *et al*. 2008, 2012).

Both of the grass species used in this study present a high amount of constitutive root aerenchyma (>20%; see Imaz *et al*. 2012), which creates a pathway for low-resistance, longitudinal oxygen transport towards root tips through diffusive mechanisms (see review by Colmer 2003). By analysing plant performances under different flooding scenarios throughout the year, it is possible to assess short- and long-term effects of this stress. Therefore, the information generated might help to develop management practices to reduce flooding impact on forage production of these tropical grass species, which are promising for temperate environments.

Information about flooding tolerance of tropical grass species is scarce, and most experiments have been conducted under tropical conditions (Anderson 1972; Cardoso *et al*. 2013, 2014). In addition, recovery period after the water subsides has often been overlooked in flooding experiments, although it is regarded as crucial when aiming to determine true plant tolerance to this stress (Malik *et al*. 2002; Striker *et al*. 2011, 2012; Parad *et al*. 2013). In this paper, we present novel evidence on the importance of the ability to recover from flooding of two promising tropical grass species, *C. gayana* and *P. coloratum*, as well as showing how the effects of flooding on plant performance depend on the season of occurrence. Flooding events in late winter, spring, and both periods were simulated and plant performance was evaluated in terms of biomass of leaves, tiller bases and roots. To our knowledge, this is the first experimental report on the performance of adult plants of tropical forage grasses with potential use in grasslands, when facing flooding in a temperate environment.

Materials and methods

Description of species

Chloris gayana Kunth (Rhodes grass) and *Panicum coloratum* L. var. *coloratum* (Klein grass) are major tropical grasses found worldwide. They are cultivated in the United States (Texas), Africa, Australia, Japan, and South America and under irrigation in the Middle East (Bogdan 1969; Boschma *et al*. 2008). *Chloris gayana* is a stoloniferous, tufted, leafy perennial grass with ascending stems (0.5–1 m) and hairless leaves measuring 10–50 cm long. *Panicum coloratum* is a shortly rhizomatous, tufted perennial, which sometimes displays long, spreading stolons and which has culms measuring 0.3–1.5 m at maturity. Foliage is variable with leaves glabrous to hairy (5–40 cm long), varying in colour from green to glaucous. Both species are used as cultivated pastures for direct grazing to produce hay and silage and also to stabilise sites with erosion problems. In particular, these species are regarded as tolerant to soil salinity and drought (Bogdan 1969; Dear *et al*. 2008; Giles *et al*. 2014), but they are also introduced in areas suffering from flooding (see Boschma *et al*. 2008).

Experimental details

Seeds of *C. gayana* cv. Fine cut and *P. coloratum* cv. Klein verde were sown in summer (February) in 8-L plastic pots filled with sand and topsoil (1 : 1 v : v) from Flooding Pampa grasslands (organic carbon 3.3%; see Soriano 1991) and then transferred to the INFIVE experimental garden (at the Institute of Plant Physiology, La Plata, Buenos Aires). Plants grew outdoors for 6 months, until August, when they were subjected to the following treatments: (*i*) non-flooded control maintained at field capacity; (*ii*) late winter flood (WF) for 50 days; (*iii*) spring flood (SF) for 20 days; and (*iv*) long-lasting flood for 70 days during the late winter and spring flooding (WF + SF) (see Fig. 1*a*). Plants were allowed to grow under well-watered conditions after WF, SF and WF + SF in order to assess their ability to recover from the hypoxic stress (Malik *et al*. 2002; Striker 2012). Flooding intensity was 10 cm above the surface, simulating a frequent flood-level occurrence under field conditions (Paruelo and Sala 1990), similar to previous studies on flooding effects on vegetation in these grasslands (see Grimoldi *et al*. 2005; Striker *et al*. 2005, 2011, 2012). All pots were placed to plastic containers (0.8 by 0.6 by 0.5 m deep, six pots per container) to facilitate the imposition of flooding treatments. Ten replicates were used for each treatment × species combination.

Daily maximum, minimum and mean air temperatures and relative humidity (RH) were registered by a micrometeorological station in the experimental garden. Daily air mean temperature and RH were used to calculate the air-vapour pressure deficit ($\mathrm{VPD_{air}}$; see Fig. 1), in order to characterise the evaporative demand during the different flooding periods (i.e. winter, spring).

Biomass responses and plant growth

Plant biomass was determined at the beginning of the experiment (day 0), at the end of the late winter flood (day 50, flooded and non-flooded plants), at the end of the spring flood (day 70, flooded and non- flooded plants), and at the end of the recovery period (day 100). Biomass was separated into shoot and roots. Subsequently, shoot biomass was divided into leaves (blades and sheaths) and tiller bases, which contain the carbohydrate reserves to sustain plant regrowth (Bertrand *et al*. 2003). Examination of root distribution in plastic pots at final harvest revealed no accumulation of roots at the bottom of the pot and helped us to discount potential constraints on plant growth due to pot size (Poorter *et al*. 2012). In addition, the relative growth rates

(RGR) of plants after flooding during winter, spring, both periods, and after the recovery period were calculated following the classical approach by Hunt (1982), which is based on the equation:

$$\mathrm{RGR}(\mathrm{g\,g^{-1}day^{-1}}) = [\ln(\mathrm{W}_2) - \ln(\mathrm{W}_1)]/(\mathrm{t}_2 - \mathrm{t}_1)$$

where W_2 and W_1 are the average plant weights of the corresponding treatment at times 2 and 1 (respectively), and $t_2 - t_1$ is the number of days between harvests.

Statistical analyses

Biomass data were analysed separately for each period (late winter, spring and recovery period harvests) by two-way analysis of variance (ANOVA), with species and flooding treatment as main factors. When significant interactions were detected, *a posteriori* Tukey tests were applied to determine the effect of each combination of species and treatments. RGR comparisons among treatments within species for each period were made by one-way ANOVAs and subsequent Tukey tests. Normality and the homogeneity of variances were previously verified. Statistical analyses were performed using the package STATISTICA for Windows (StatSoft; Tulsa, OK, USA). All results are presented as mean values of 10 replicates ± standard error.

Results and discussion

Environmental conditions during flood in late winter (WF) registered mean minimum temperatures of 6.5°C ± 4.0°C, mean maximum temperatures 17.6°C ± 4.2°C, and average mean temperatures 11.0°C ± 3.5°C (Fig. 1*b*; see also Soriano 1991). The atmospheric evaporative demand estimated through the $\mathrm{VPD_{air}}$ increased until spring, and ranged from 0.54 to 1.55 kPa (mean 0.97 kPa; Fig. 1*c*). WF determined a differential response in total biomass accumulation between species, as indicated by the flooding × species interaction (Table 1). In this regard, at day 50, flooded plants of *C. gayana* attained 62% of the total biomass of the respective controls, whereas in *P. coloratum*, flooding did not affect biomass per plant (although a lower biomass of tiller bases, a proportionally small compartment, was also recorded; Fig. 2). These responses were the result of lower RGR of *C. gayana* plants when subjected to WF with respect to controls, whereas RGR of *P. coloratum* plants was unaffected by WF (Table 2). The lower biomass of *C. gayana* plants after WF was a result of reductions in the biomass of all plant compartments: leaves (by 43%), tiller bases (49%) and roots (57%) (Fig. 2).

The lower tolerance to flooding during winter of *C. gayana* than *P. coloratum* does not seem completely attributable to the well-known higher tolerance to low temperatures of the latter species (Tischler and Ocumpaugh 2004), because both species grew at similar rates under control conditions (Table 2). Hence, it is possible that adult plants of *P. coloratum* possess a slightly better metabolic adaptation to flooding than *C. gayana*, being able not only to maintain their biomass but also to grow. For practical purposes, a long-term rest period should be considered from grazing of both species after winter flood to facilitate recovery of plants during early summer before intense biomass removal by defoliation (Oesterheld and McNaughton 1991), especially if it is expected that flooding might reduce plant reserves (e.g. lower weight of tiller bases in both species; see Bertrand *et al.* 2003), which can compromise initial regrowth.

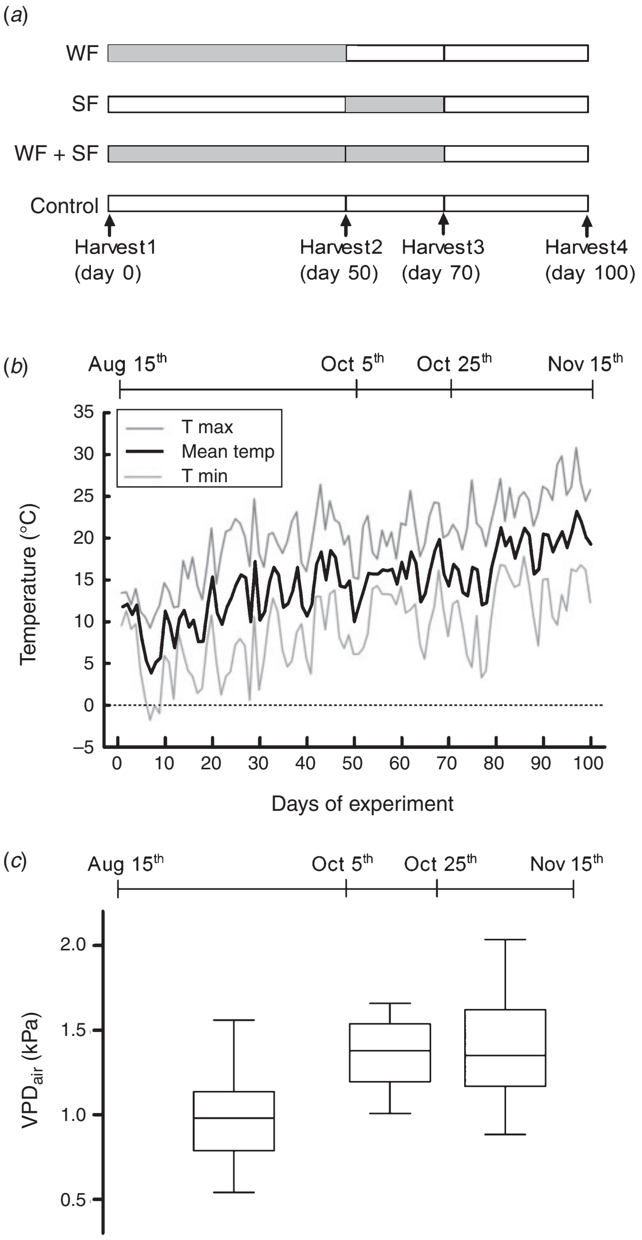

Fig. 1. (*a*) Scheme of treatments applied on 6-month-old plants of *Chloris gayana* and *Panicum coloratum*: a winter flooding (WF) for 50 days, an early spring flooding (SF) for 20 days, and a long-lasting flood (WF + SF, winter plus spring) for 70 days. Four harvests were carried out corresponding to the end of each flooding period, and at the end of the recovery phase as indicated by arrows. (*b*) Daily maximum, mean and minimum air temperature. (*c*) Air-vapour pressure deficit ($\mathrm{VPD_{air}}$) for each experimental period as a measure of atmospheric evaporative demand.

During spring flood (SF), mean minimum temperature was 11.1°C ± 3.1°C, mean maximum temperature 22.7°C ± 2.6°C, and average mean temperature 16.7°C ± 1.9°C (Fig. 1*b*). Temperatures were still below the optimum for photosynthesis and growth of tropical grasses with the C_4 carbon-fixation

Table 1. Results of two-way ANOVAs for the effects of flooding treatment and species on biomass (total, leaves, tiller bases and roots) of *Chloris gayana* and *Panicum coloratum* plants

Harvests were collected after winter flooding (day 50), after spring flooding (day 70), and at the end of the recovery period (day 100). *F*-values of the ANOVAs are presented; $*P<0.05$; $**P<0.01$; $***P<0.001$; n.s, $P>0.05$

Biomass responses	Main effects		Interaction
	Flooding (F)	Species (S)	F × S
	Harvest, day 50		
Total biomass	39.56***	0.014n.s.	17.47***
Leaves (blades + sheaths)	19.26***	6.68*	24.37***
Tiller bases	35.27***	1.54n.s.	3.45n.s.
Root	17.1***	12.36**	0.163n.s.
	Harvest, day 70		
Total biomass	15.90***	6.89*	6.34*
Leaves (blades + sheaths)	22.46***	9.10**	5.84*
Tiller bases	2.47n.s.	41.39***	7.48***
Root	11.89***	0.013n.s.	0.49n.s.
	Harvest, day 100		
Total biomass	1.314n.s.	3.66n.s.	1.48n.s.
Leaves (blades + sheaths)	1.22n.s.	6.86*	1.80n.s.
Tiller bases	5.05**	19.03***	6.1**
Root	2.57n.s.	0.02n.s.	1.79n.s.

pathway (Sweeney and Hopkinson 1975; Sage and Pearcy 2000), but clearly higher than those registered during WF. The VPD_{air} reached an average of 1.37 ± 0.2 kPa (range 1.01–1.75 kPa), a higher value, as expected, than in winter (Fig. 1*c*). Plant growth of both species was reduced by SF when analysed for total biomass compared with their controls, in accordance to the reduction in RGR provoked by SF in both species (from 0.016–0.023 $g\,g^{-1}\,day^{-1}$ to 0.03–0.05 $g\,g^{-1}\,day^{-1}$; see Table 2 and Fig. 2). In *C. gayana*, at day 70, the biomass reductions in leaves and roots were equivalent to 21% and 32%, respectively, of non-flooded control plants (Fig. 2). In *P. coloratum*, the reduction in leaf and root biomass was slightly higher than in *C. gayana*, representing 32% and 34% of controls, respectively. In both species, the biomass of tiller bases did not change with SF relative to their respective controls (Fig. 2).

These results suggest that plants of both species do not appear to rely on consumption of tiller base mass (related to potential carbohydrate reserves; see also Bertrand *et al*. 2003) to grow during spring with more favourable temperatures (mean 16.7°C for SF *v*. 11.0°C for WF) where the current photosynthesis is expected to be sufficient for biomass accumulation (in contrast to the observed response during winter when flooded plants registered a lower biomass of tiller bases). In these species, the impact of hypoxia during spring determined a 20–30% lower biomass per plant than under control conditions, which concurs with the reductions observed in a comprehensive study of 12 accessions of the tropical grass *Brachiaria humidicola* (Cardoso *et al*. 2013, 2014). Further evidence is lacking of the tolerance to flooding of tropical grasses under temperate environments, so opportunities for comparison are minimal. Nevertheless, some contrasts can be made of the performance of these new introduced grasses with that of native C_4 grasses inhabiting temperate grasslands. In this regard, *Paspalum dilatatum*, a grass of broad distribution in South American grasslands, showed a similar tolerance to spring flooding to that of both species tested here (see Rubio *et al*. 1995; Striker *et al*. 2006, 2011).

Interestingly, when plants were flooded during winter and spring (WF + SF), the response in biomass accumulation differed between species as indicated by the flooding × species interaction for the harvest at day 70 (Table 1). Plants of *C. gayana* subjected to WF + SF had 27% lower biomass than under either WF or SF (and 42% lower biomass than controls; Fig. 2), in line with the lowest RGR registered for this species during the experiment (see RGR of plants subjected to WF + SF in Table 2). By contrast, in *P. coloratum*, WF + SF did not provoke any further negative effect on biomass accumulation over that caused by either WF or SF as a single event (i.e. ~33% reduction in growth compared with controls; Fig. 2), as confirmed by the similar RGR between plants subjected to WF + SF and either WF or SF (Table 2). The lack of additive detrimental effects of long-term flooding on *P. coloratum* growth suggests a better tolerance of this species to prolonged root-zone hypoxia. In forage grass species, no comparisons are available to contrast the effects on growth between long-term flooding events and shorter ones during different seasons. However, a recent report on cereal crops (wheat and barley) revealed a higher sensitivity to flooding during mid-spring than during winter (de San Celedonio *et al*. 2014), as *P. coloratum* showed in our study. In the case of *C. gayana*, compared with *P. coloratum*, the relatively poor tolerance exhibited when flooded during winter (see RGR of plants subjected to WF at day 50 in Table 2) might be partially responsible for the negative additive effect on growth when flooding was extended until spring (WF + SF). This is supported by the fact that plants subjected to an additional period of flooding during spring did not accumulate biomass (30.5 ± 1.8 g $plant^{-1}$ at day 70 in WF + SF treatment *v*. 29.7 ± 1.7 g $plant^{-1}$ at day 50 in WF treatment; Fig. 2, upper panel).

In both species, regardless of the differences in growth provoked by WF and SF among different plant compartments (see above), plants fully regained total biomass during the recovery phase; that is, there were no differences in total biomass among plants subjected to any previous flooding treatment (see day 100 in Fig. 2) and no interaction or flooding effects on that harvest date (Table 1), in accordance with the high RGR registered by plants previously flooded at either period (see RGR values after recovery in Table 2). Remarkably, previous differences in biomass accumulation determined by root-zone hypoxia were overridden by the ability of these grasses to recover from flooding. Two factors might help to explain such high recovery capacity. First, flooding resulted in in proportional reductions in growth of shoots and roots in both species (Fig. 2, at day 70), therefore, the shoot : root ratio remained similar to that under control conditions, allowing an adequate balance between water uptake (root mass) and transpiration (leaves mass) after flooding subsided (see also Striker *et al*. 2012). Second, the increasing temperatures during the recovery period (average mean temperature 18.2°C ± 2.9°C and maximum temperatures with peaks of 27–30°C; (Fig. 1*a*) might have helped to sustain high growing rates in these tropical grass species (Sweeney and

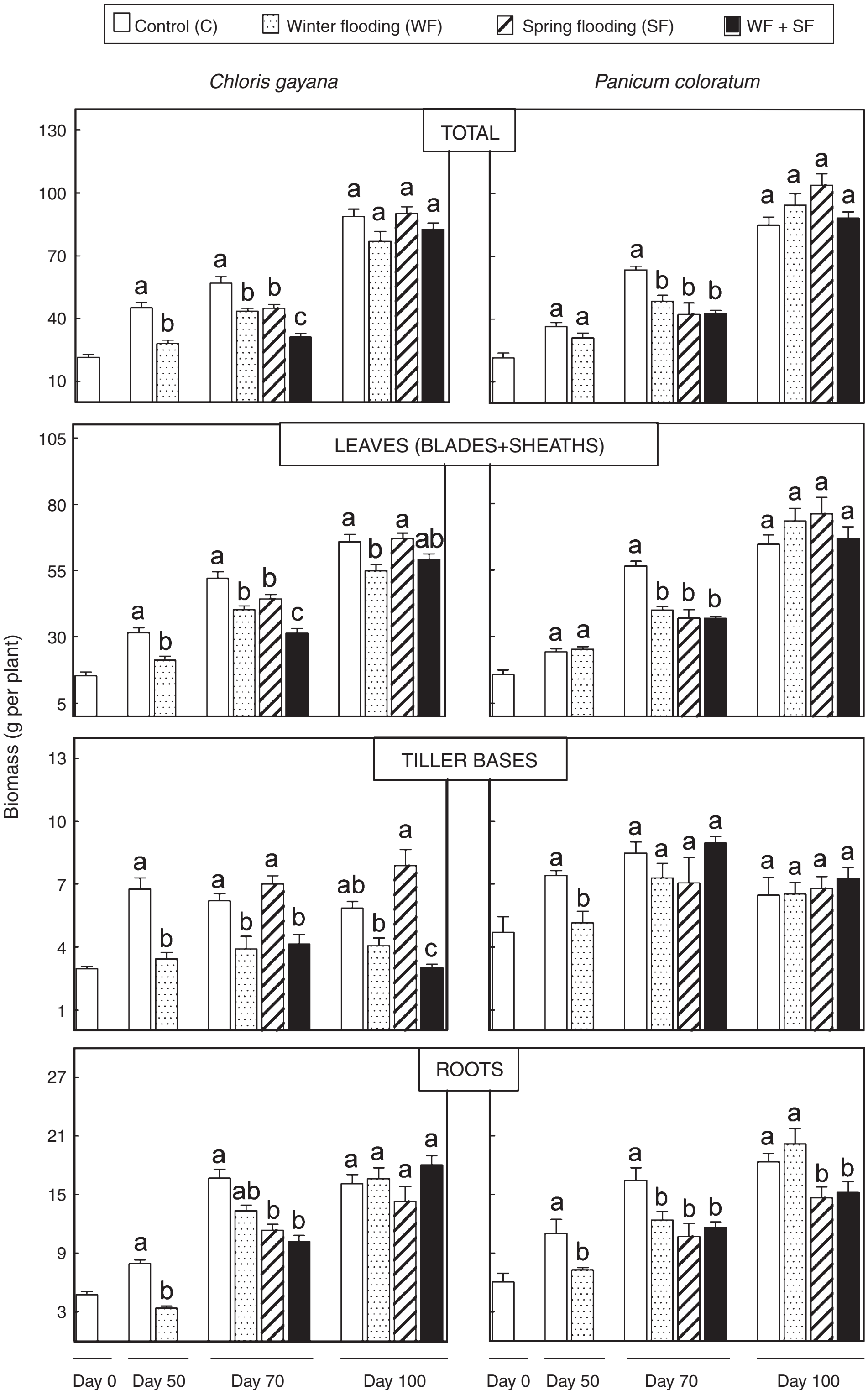

Fig. 2. Biomass of *Chloris gayana* and *Panicum coloratum* plants subjected to flooding during winter, spring, or both periods. Harvests were gathered at the end of winter (day 50), mid-spring (day 70), and after 1 month of recovery period (day 100). Total biomass per plant, and divided into leaves (blades plus sheaths), tiller bases and roots is shown. Initial biomass (day 0) is given for comparison. Bars within parameter and harvest date with the same letter are not significantly different between treatments based on Tukey tests. Values are means ± s.e. of 10 replicates.

Table 2. Relative growth rate (RGR) of plants of *Chloris gayana* and *Panicum coloratum* subjected to flooding during winter, spring or both periods

Calculations were based on the equation: RGR = $[\ln(W_2) - \ln(W_1)]$/(no. of days between harvests). Within species and time, means followed by the same letter are not significantly different ($P > 0.05$) among treatments based on Tukey's tests

RGR ($g\,g^{-1}\,day^{-1}$)	*Chloris gayana*	*Panicum coloratum*
	After winter flood (day 50)	
Control	0.015 ± 0.002a	0.011 ± 0.002a
WF	0.005 ± 0.001b	0.009 ± 0.002a
	After spring flood (day 70)	
Control	0.016 ± 0.002b	0.023 ± 0.002a
WF	0.024 ± 0.002a	0.008 ± 0.001b
SF	0.003 ± 0.001c	0.005 ± 0.002b
WF + SF	0.001 ± 0.001c	0.007 ± 0.002b
	After recovery period (day 100)	
Control	0.015 ± 0.002c	0.012 ± 0.003c
WF	0.019 ± 0.003bc	0.022 ± 0.002b
SF	0.023 ± 0.002b	0.030 ± 0.003a
WF + SF	0.033 ± 0.002a	0.024 ± 0.002ab

Hopkinson 1975; Sage and Pearcy 2000). Finally, these results demonstrate the importance of considering a recovery period when assessing plant flooding-tolerance as highlighted by Striker (2012) and Parad *et al*. (2013).

Conclusion

Panicum coloratum showed better tolerance to late-winter flooding than *C. gayana*. However, when both grasses were flooded for 20 days in spring, there were no differences in flooding tolerance between them, as shown by a similar reduction in their growth. Under long-term flooding (winter and spring), *C. gayana* showed a more pronounced reduction in its growth than when subjected to either winter or spring flood separately. By contrast, *P. coloratum* did not exhibit an additional reduction in its growth when under long-term flooding, which suggests this species as more tolerant to prolonged root-zone hypoxia. Both grass species displayed outstandingly fast recovery from flooding when temperatures rose during early summer, attaining a biomass equivalent to non-flooded controls only 1 month after water subsided (although *C. gayana* did not fully recover the weight of tiller bases, where reserves are located). It is concluded that, although *P. coloratum* appears slightly more tolerant during flooding than *C. gayana*, both species seem promising as forage species to be introduced in temperate, lowland areas prone to soil flooding. However, a rest period before grazing is recommended in order to allow plants full recovery and to ensure their persistence within the pasture.

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