Seasonal timing of inundation affects riparian plant growth and flowering: implications for riparian vegetation composition

Joe Greet^{1,2*}, Roger D. Cousens¹, J. Angus Webb^{1,2}

¹ Department of Resource Management and Geography, The University of Melbourne, VIC 3010, Australia

² eWater Cooperative Research Centre, Australia

*author for correspondence: greetj@unimelb.edu.au

Abstract

Changes to the timing of peak river flows caused by flow regulation affect riparian vegetation composition, but the mechanisms driving such vegetation changes are not well understood. We investigated experimentally the effects of timing of inundation on riparian plant growth and flowering.

We collected 168 sods from 14 sites across five lowland rivers in south-eastern Australia. Plant cover and flowering within the sods was surveyed each season for a year. During this period, sods were inundated for six weeks in either early spring or in summer.

Terrestrial plant taxa (which included most exotic species) senesced in response to inundation, regardless of its timing. In contrast, native amphibious species (particularly amphibious forbs) responded favourably to inundation in spring, but were unaffected by inundation in summer. Native and exotic emergent macrophytes responded favourably to inundation regardless of timing, and flowered frequently in both the spring- and summer-inundation treatments. In contrast, many native annuals flowered only in the spring-inundation treatment, while more exotic grasses flowered in the summer-inundation treatment.

In temperate climates, inundation in early spring followed by non-flooded conditions is likely to be important for promoting the growth of amphibious forbs and the recruitment and flowering of riparian annuals. Without inundation in spring, many terrestrial exotic weeds may flourish and set seed prior to any subsequent inundation (e.g. in summer). We contend that natural seasonal timing (i.e. winter-early spring) of flow peaks is important for the maintenance of native riverbank vegetation and reducing the extent of terrestrial exotic species within the riparian zone.

Keywords

Exotic invasion, Flood timing, Natural flow regime, Riverine vegetation, Sexual reproduction.

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Timing of inundation affects plant growth and reproduction

Introduction

Flow regime is the primary driver of riparian plant community composition (Naiman and Décamps 1997; Poff et al. 1997), and if components of a flow regime are altered, it can be expected that riparian vegetation composition will be affected (Nilsson and Svedmark 2002). For example, some plant species are able to tolerate or respond to inundation events (amphibious species), while others lack adaptations to survive flooding (terrestrial species) (Casanova and Brock 2000). Regulation-induced changes to flooding regimes can be expected to alter the prevalence of plant species in riparian areas accordingly, e.g. reduced flooding favours terrestrial species (Catford et al. 2011). While regulation-induced changes to the seasonality of flooding can also be expected to alter riparian vegetation composition (Ström et al. 2012), the mechanisms of such changes are not well understood (Poff and Zimmerman 2010; Roberts 2002).

Plant growth and/or survival is likely to be sensitive to timing of inundation, but plant responses can be expected to vary (van Eck et al. 2006). Plants are generally more sensitive to flooding while photosynthetically active (during the growing season) because of their greater demand for oxygen at this time (Glenz et al. 2006; Johansson and Nilsson 2002). For example, in a study of ten terrestrial grassland species, all were found to survive winter flooding longer than summer flooding (van Eck et al. 2006). Similarly, woody plant seedlings of temperate environments are typically most sensitive to flooding during the growing season (Glenz et al. 2006; Johnson 2000). Because of their greater impact on plant survival, summer floods can have comparatively greater effects than winter floods on plant distributions (Dixon 2003; van Eck et al. 2006). Responses of plants to inundation also vary depending on their stage of development, with younger plants more sensitive to the timing and duration of inundation (Denton and Ganf 1994; Klimesova 1994). Furthermore, plant species tolerant of inundation may be unaffected by timing of inundation (Bonilla-Warford and Zedler 2002).

Understanding plant responses to seasonal timing of inundation requires consideration of their life-history strategies. Some plants may avoid the adverse effects of inundation through timing of important life-history events (Blom and Voisenek 1996). Indeed, many riparian plants have life-histories adapted to the seasonal timing of natural flow regimes through their seasonal sequence of germination, growth and flowering (Lytle and Poff 2004; Poff et al. 1997). For example, for wetland plants along the River Murray, Australia, flooding in spring (when natural flooding typically occurs) is critical for their growth and maintenance (Robertson et al. 2001). Similarly, in the US, winter-spring peak flows have been shown to be important for riparian tree species with vernal growth patterns (Reily and Johnson 1982; Stromberg and Patten 1990). Changes to natural seasonal flow timing caused by flow regulation are thus likely to adversely affect species with life-histories adapted to natural flow regimes (Bunn and Arthington 2002; Lytle and Poff 2004). Conversely, some plants may be advantaged by changes to seasonal flow timing if non-flooded conditions correspond with periods favourable for their growth and reproduction. Thus, the success of non-native (exotic) species in riparian areas can only be predicted if flow regime is considered in tandem with their phenology (e.g. timing of flowering and seed release)(Richardson et al. 2007).

In contrast to research on plant growth, there have been very few studies on the effect of timing of inundation on plant reproduction (Greet et al. 2011). However, these studies suggest that timing of

inundation has important consequences for plant reproduction. Reinundation has been reported to stimulate flowering in the ephemeral wetland species *Rhynchospora inundata*, but only when this occurs at particular times of year (Gerritsen and Greening 1989). Timing of inundation and subsequent emersion has also been shown to be important for several riparian annuals and biennials. Plants germinating in response to inundation earlier in the growing season are able to flower and set seed, but plants germinating following inundation later in growing season are unlikely to develop sufficiently to enable flowering (Van der Sman et al. 1992; Warwick and Brock 2003).

In this study, we assess the effect of seasonal timing of inundation on the growth and sexual reproduction of the riparian plant species of five lowland rivers of the Murray-Darling Basin, south-eastern Australia. In previous work, we found that regulation-induced changes in seasonal flow timing were associated with differences in riparian vegetation composition, with seasonal flow inversion (high summer-autumn flows and low winter-spring flows) associated with more exotic taxa (mostly terrestrial weeds) and lower native plant diversity than natural flow regimes (high winter-spring flows and low summer-autumn flows) (Greet et al. 2012a). The aim of this study was to determine whether experimental manipulation of inundation timing would affect plant growth and reproduction, and help to explain these vegetation patterns. Specifically, we predicted that natural timing of inundation (early spring) would encourage greater growth and reproduction of native taxa than summer inundation, because such taxa are likely to have life-histories adapted to natural flow regimes (Bunn and Arthington 2002). Conversely, we predicted that a lack of inundation in spring (i.e. summer inundation) would favour exotic taxa that grow in the cooler months and flower in spring.

Methods

Study area

We collected sods of topsoil from 14 sites across the Acheron, Broken, Campaspe, Goulburn, and Ovens rivers (Figure 1). These five rivers are in northern Victoria, south-eastern Australia. The region has a warm temperate climate and average annual rainfall in the study area ranges from around 550 to 700 mm (Bureau of Meteorology, unpublished data). Within the study area, floodplains have been extensively cleared for agriculture. Remnant riparian vegetation is typically restricted to a narrow band (one or two trees wide) of mature River Red Gums (*Eucalyptus camaldulensis*). The mid-storey is typically sparse, with the native Silver Wattle (*Acacia dealbata*), exotic Willows (*Salix* spp.*; exotic species indicated by an asterisk throughout the paper) and Blackberries (*Rubus* spp.*) most common. The understorey is typically dominated by exotic grasses and forbs, with native forbs, rushes (*Juncus* spp.), sedges (e.g. *Isolepis inundata*), and reeds (*Phragmites australis*) common along the river margins.

Sod collection

Sites consisted of a 200 m reach of riverbank, and were selected where native overstorey was present and there was no stock access. Twelve sods were collected at each site (168 sods in total) in May 2010 (austral autumn) when flows were low in all rivers. The longitudinal location of sod collection along a site was selected randomly. At each location, sods were removed from the bank at an elevation of 10 cm above the water level. Collected sods generally consisted of bare substrate, seedlings and/or young or

low-growing herbaceous plants. In cases where sod collection was not possible (e.g. tree-fall, large vegetation, etc) another random location was selected. Sods were removed using a hollow metal pipe of 10 cm diameter to a depth of 10 cm and then placed in pots of similar dimensions with holes for drainage. The pots were later placed in an unheated greenhouse with automated overhead watering on water-filled 2 cm deep trays such that the drainage holes were submerged and the sods prevented from drying out.

Inundation treatment

Six sods from each site were randomly allocated to each of two treatments: inundation in early spring or inundation in summer. The spring inundation commenced at the beginning of the austral spring (1 Sep 2010), whereas summer inundation commenced in the middle of summer (7 Feb 2011). These timings were intended to reflect typical peak flow periods of the natural and regulated flow regimes, respectively, of the region (Greet et al. 2012a). Inundation involved submerging sods in large black plastic tubs to a depth of 20 cm for six weeks (a period most terrestrial herbaceous plants were expected to be unable to survive; van Eck et al. 2006). Continuous inundation for at least 6 weeks is likely to be a realistic flood duration for the elevation from which the sods were collected. Prior to inundation, a few individual plants (mostly *Phragmites australis*) greater than 10 cm tall were trimmed at 10 cm in height such that all vegetation was submerged by at least 10 cm. While clipping may affect plant growth and reproduction (Crossle and Brock 2002), the number of plants that were trimmed was small, and trimmed plants were species that were not expected to flower over the course of the experiment. Immediately following inundation, the surface of the water was sieved to remove any flotsam. The tubs were then covered with shade cloth to prevent the water from heating up. Water temperatures in the tubs were monitored and maintained below 18°C for both the spring and summer inundation treatments. After six weeks of inundation, the sods were removed from the tubs and placed back on the trays in the greenhouse.

The vegetation growing in the sods was surveyed on four occasions: in mid-winter (prior to spring inundation), mid-spring (one week following removal of the spring-inundated sods), mid-summer (just prior to inundation of the summer-inundated sods), and mid-autumn (two months following removal of the summer-inundated sods). This timing was intended to maximise the observation of phenological events. For each survey and sod, taxa were identified and given a cover score based on the proportion of the sod it covered: 1 = 0-25%; 2 = 25-50%; 3 = 50-75%; 4 = 75-100%. The number of individual plants of each taxon that were flowering was also recorded. Plants were identified to the lowest taxonomic level possible. Some taxa were grouped for practical reasons. For example, seedlings of native *Juncus* spp. from the subgenus *genuini* are difficult to identify to species-level. Similarly, exotic *Rumex* spp.* and *Conyza* spp.* were not separated. All taxa were classified as native or exotic according to Walsh and Stajsic (2007), from which the taxonomic nomenclature used in this study was also sourced.

Data analysis

We tested the effects of timing of inundation on plant cover and reproduction using ANOVA in GenStat version 13. For univariate analyses, plant taxa were grouped according to origin (native or exotic), plant

type (rush, sedge, grass, forb or woody) and moisture affinity (amphibious or terrestrial) (see Appendix 1 for further explanation). For each survey and sod, we determined the total cover of native and exotic taxa, as well as the cover of native and exotic taxa within each of the plant groupings. Similarly, the numbers of flowering native and exotic taxa, and numbers of flowering native and exotic taxa within each of the plant groupings were determined. For analyses involving cover data, we used the mid-points of the cover scores for each taxon (e.g. cover score 1 = .125; 2 = .375; etc.) summed across all taxa within the respective plant groupings. 'Timing of inundation', 'Season of survey' and their interaction were treated as fixed effects, while 'River', 'Site' nested within 'River', and 'Sod' nested within 'Site' were treated as random effects. Similarity percentage (SIMPER; Clarke and Gorley 2001) analyses were used to examine assemblage-level differences in plant growth and reproduction associated with timing of inundation. SIMPER analyses were conducted using PRIMER Version 6 and the Bray-Curtis similarity measure.

Results

Over the course of the experiment, 117 taxa were observed growing in the sods, of which 54 were native and 62 exotic. Exotic taxa were mostly terrestrial forbs and grasses, and about half were annuals or biennials (Table 1). Native taxa were mostly forbs, while several native rushes and sedges were also common. Native taxa were mostly perennial, with more amphibious species than terrestrial (Table 1). The most commonly observed taxa were *Juncus* subgenus *genuini* (present in 44% of all sod surveys), *Isolepis inundata* (42%), *Cyperus eragrostis** (29%), *Persicaria decipiens* (24%), *Persicaria hydropiper* (21%), and *Verbena bonariensis** (16%).

Plant cover

In general, the cover of both native and exotic taxa varied seasonally, with seasonal effects differing between the two treatments (i.e. there were significant effects of Season, and a Timing x Season interaction; Table 2). Within the sods, the cover of native taxa increased from mid-winter to mid-summer in both the spring- and summer-inundation treatments (i.e. whether inundated or not during that period), but increased more so in the spring-inundation treatment. The cover of native taxa remained fairly stable from summer to autumn in both treatments, i.e. it was unaffected by inundation in summer (Figure 2a). In contrast, inundation, whether in early spring or summer, reduced the overall cover of exotic taxa, while during periods without inundation, the cover of exotic taxa generally increased (Figure 2b). More specifically, the cover of native amphibious forb taxa was greater in the spring-inundation treatment than in the summer-inundation treatment; the cover of native amphibious forbs responded positively to inundation in spring, but not to inundation in summer (Figure 2c; Table 2). In contrast, the cover of exotic grass taxa was much greater in the summer-inundation treatment than in the spring-inundation treatment in both spring and summer (Figure 2d; Table 2). The cover of exotic grass taxa responded similarly to exotic taxa in general: it varied seasonally and was reduced by inundation (whether in spring or summer).

At the species-level, terrestrial taxa (including most exotic grass and forb taxa) typically senesced (thus reduced in cover) in response to inundation in either spring or summer (Table 3). Most exotic grasses, particularly the tufted cool-season annuals *Holcus lanatus** and *Bromus diandrus**, were sensitive to

inundation. Exotic rhizomatous exotic grasses such as *Paspalum distichum** and *Agrostis stolonifera** were relatively flood-tolerant; these grasses often regrew from rhizomes following emersion. Moreover, *P. distichum**, a summer-growing semi-aquatic grass, increased in cover in response to inundation in summer. Short-lived (annual and biennial) exotic terrestrial forbs such as *Conyza* spp.*, *Cirsium vulgare** and *Sonchus oleraceus** were also particularly flood-sensitive (Table 3). Native terrestrial forbs (e.g. *Senecio glomeratus* and *Epilobium hirtigerum*) and seedlings of native woody taxa (e.g. *Acacia dealbata* and *Eucalyptus camaldulensis*) also typically senesced in response to inundation in either spring or summer. The native terrestrial forbs *Helichrysum luteoalbum* and *Euchiton* spp. senesced in response to inundation but germinated in large numbers following emersion, particularly in summer.

In contrast, several native amphibious forbs (e.g. *Persicaria* spp. and *Crassula helmsii*) increased in cover in response to inundation, and particularly to inundation in spring. Notably, the native annual forb *Persicaria hydropiper* germinated and grew prolifically following inundation in spring, but was susceptible to desiccation and reduced in cover following inundation in summer. Native and exotic emergent macrophytes, i.e. rushes and sedges (e.g. *Juncus* spp. and *Cyperus eragrostis**) generally increased in cover in response to inundation in either spring or summer. The exotic amphibious forbs *Callitriche stagnalis** and *Ludwigia palustris** responded similarly.

Plant reproduction

In total, 60 plant taxa (23 native and 37 exotic) flowered over the course of the experiment. These included five rushes, six sedges, 15 grasses (12 exotic), and 34 forbs (21 exotic) (see Appendix 1). The emergent macrophytes *Isolepis inundata* (flowering in 21% of all sod surveys), *Cyperus eragrostis** (6%) and *Juncus articulatus** (4%), and the native amphibious forbs *Persicaria hydropiper* (9%), *P. praetermissa* and *P. decipiens* (3% each) flowered most frequently.

Native taxa flowered most abundantly in summer in both treatments; timing of inundation did not affect the numbers of native taxa that flowered (Figure 3a; Table 4). In contrast, timing of inundation affected the flowering patterns of exotic taxa. More exotic taxa flowered in spring and summer in the summer-inundation treatment than in the spring-inundation treatment. In contrast, more exotic taxa flowered in autumn in the spring-inundation treatment than in the summer-inundation treatment (Figure 3b; Table 4). More exotic grass taxa flowered in the summer-inundation treatment than in the spring-inundation treatment overall, with these taxa flowering mostly in spring and summer, i.e. prior to inundation (Figure 3c; Table 4).

Emergent macrophytes and native amphibious forbs that flowered most frequently contributed most to the dissimilarity between the two treatments, but both of these groups flowered frequently in both treatments (Table 5). In contrast, there were a number of native annuals that flowered only in the spring-inundation treatment (following emersion): *Isolepis marginata*, *Centipeda minima*, *Alternanthera denticulata*, and *Euchiton involucratu*s. Conversely, the cool-season exotic grasses *Bromus diandrus** and *Ehrharta erecta** flowered only in the summer-inundation treatment (prior to inundation) (Table 5).

Discussion

Our study highlights the importance of taking into consideration plant life-histories when considering vegetation responses to changes in seasonal flow timing. In our experiments, delaying inundation of riverbank sods until summer allowed several cool-season exotic grasses to flourish and flower. Conversely, inundation in early spring promoted the growth of native amphibious forbs and the subsequent recruitment and flowering of a number of native annual taxa, while inundation in summer did not. Our results provide evidence that natural seasonal timing of flow peaks is important for the maintenance of native riverbank vegetation and reducing the extent of terrestrial exotic species within the riparian zone. While our research was undertaken in south-east Australia, we believe that the results are relevant for the many regulated river systems in which the seasonality of flow regimes has been affected.

Effects of timing of inundation

Terrestrial taxa, which included most of the exotic taxa, typically senesced in response to six weeks of inundation in either early spring or summer. Terrestrial species have been reported to be most sensitive to summer flooding due to their greater sensitivity to anoxia at this time (Glenz et al. 2006; van Eck et al. 2006), and there was a tendency for the cover of terrestrial taxa to be reduced more by summer inundation than by spring inundation. However, our results are confounded by the fact that plants were larger (i.e. their cover was greater) by summer. Regardless, inundation in either spring or summer had the effect of reducing the competition within the sods from terrestrial exotic taxa (however, these taxa did gradually re-establish following emersion).

In contrast, many native taxa were flood-tolerant and overall, the cover of native taxa was promoted by inundation in early spring. Flood-tolerant taxa possess physiological adaptations that enable them to tolerate or respond to inundation such as through aerenchyma formation or shoot elongation (Blom and Voesenek 1996; Voesenek et al. 2006). Shoot elongation was an evident response of the native forbs *Persicaria decipiens*, *P. praetermissa* and *Crassula helmsii*, with shoots of these species often reaching the water's surface during submergence. These native amphibious forbs were particularly favoured by inundation in early spring, compared to inundation in summer. This is likely to be because the period of spring-early summer (following early spring inundation) is more favourable for their growth. Following emergence from inundation in summer, new plant growth of these species appeared susceptible to desiccation due to hot temperatures at this time.

Early spring inundation was particularly important for native annual forbs. For example, *Persicaria hydropiper* germinated and grew prolifically following inundation in early spring, but senesced following inundation in summer. Similarly, the native annual forbs *Alternanthera denticulata*, *Persicaria lapathifolia* and *Centripeda minima* commonly germinated following inundation in spring, but not following inundation in summer. In temperate regions, non-flooded conditions during the growing season are considered especially important for the recruitment of summer-annuals associated with aquatic environments (Baldwin et al. 2001; Baskin and Baskin 1998; Greet et al. 2012b). Furthermore, early spring floods serve to create bare ground for colonisation by summer-annuals (Osawa and Mitsuhashi 2010).

Some exotic taxa, such as the semi-aquatic rhizomatous grass *Paspalum distichum**, responded positively to inundation in summer. *P. distichum** has previously been reported to thrive when inundated during high temperatures (e.g. 30-40°C, Rogers and Ralph 2011). Similarly, the semi-aquatic rhizomatous grasses *Phalaris arundinacea** and *Spartina pectinata** are susceptible to desiccation, and grow at higher rates when flooded than when not flooded during hot weather (Bonilla-Warford and Zedler 2002; Klimesova 1994). Timing of inundation, however, did not appear to affect native and exotic emergent macrophytes such as *Isolepis inundata*, *Juncus* spp., and *Cyperus eragrostis**. Regardless of timing of inundation, such plants tolerated submergence then grew following emersion. New individuals of such taxa also often germinated from the seed bank contained within the sods; these taxa maintain large persistent seed banks (Greet et al. 2012b). Emergent macrophytes are morphologically adapted to tolerate inundation and may respond well to inundation anytime during the growing season (spring or summer) (Rogers and Ralph 2011).

The divergent growth patterns of plants in the spring- and summer-inundation treatments had significant implications for plant reproduction. Delaying inundation until summer meant that greater numbers of cool-season exotic grasses were able to flower; this reflects their behaviour in the field, where many agricultural grass weeds typically flower in spring (Wilding et al. 1986). In contrast, inundation in early spring promoted the recruitment and subsequent flowering of a number of native annuals that did not flower in the summer-inundation treatment. Other studies on the effects of timing of inundation on plant reproduction have similarly reported reduced flowering of short-lived plants that germinated following inundation later in the growing season (Van der Sman et al. 1992; Warwick and Brock 2003). Nonetheless, for a number of perennial flood-tolerant taxa, timing of inundation did not affect their sexual reproduction. Many emergent macrophytes and amphibious forbs flowered commonly in both treatments. Similarly, Warwick and Brock (2003) found amphibious species able to respond morphologically to water presence or absence and flower under a wider range of conditions. Also, several exotic and native summer-growing terrestrial weeds (e.g. *Solanum nigrum** and *Helichrysum luteoalbum*) were able to flower in both treatments following periods without inundation. This is likely to be because the warm temperatures of much of the period of the experiment (i.e. late spring-autumn) were amenable to their growth and reproduction.

Implications for riparian vegetation composition

The results of this study have shown that regulation-induced changes to the timing of flow peaks have implications for the growth and reproduction of riparian plants. Undoubtedly, absence of inundation is likely to cause a terrestrialisation of riparian vegetation, which in temperate environments, is likely to favour exotic species (Catford et al. 2011; Chaneton et al. 1988; Stokes et al. 2010). While inundation is therefore important for reducing the extent of terrestrial weeds (which tend to be exotic grasses and annual and biennial forbs), our research shows that the timing of such inundation events is also important. If inundation occurs later in the growing season, cool-season grasses and forbs may have already flourished, flowered and set seed. Inundation events may then disseminate these seeds, encouraging the spread of such weeds (Greet et al. in press). We suspect that these processes are at least partly responsible for the predominance of exotic annuals/biennial forbs and grasses along rivers in south-eastern Australia subject to seasonally-inverted flow patterns (i.e. low winter-spring flows, high

summer-autumn flows) (Greet et al. 2012a). We therefore contend that high flows preceding the growing season (i.e. in winter-early spring) serve to reduce the extent of exotic taxa within the riparian zone. However, we recognise that such flows would be unlikely to reduce the extent of exotic macrophytes. We also conclude that high water levels during warmer times of year (typical of summer irrigation releases) are likely to promote the growth of flood-tolerant rhizomatous grasses.

In temperate environments, inundation in early spring and subsequent water recession is likely to be important for the growth and reproduction of many riparian plants. In our experiments, native amphibious forbs were able to flourish following inundation in early spring and the dieback of terrestrial taxa (mostly exotic species). Seasonally non-flooded habitats are likely to promote the growth of ephemeral forbs that resprout and grow from dormant rootstock (e.g. *Persicaria* spp., *Gratiola peruviana*) and the recruitment of riparian annuals. Furthermore, an absence of flooding during the growing season is likely to be particularly important for enabling annuals to complete their life-cycle and produce seeds necessary for subsequent generations (Baldwin et al. 2001). Recurrent summer flooding could prevent such plants from replenishing seed banks, and thus threaten the viability of local populations. Indeed, within the study area, native ephemeral and annual forbs are much less abundant at sites experiencing high summer flows than at sites with natural seasonal flow patterns (i.e. low flows in summer) (Greet et al. 2012a). Seasonal timing of inundation is likely to be less important for emergent macrophytes as these often reproduce clonally and have reproductive phenologies adaptable to variable water regimes (Froend and McComb 1994; Rogers and Ralph 2011). For such plants, the magnitude and frequency of inundation, rather than its timing, are likely to determine their extent (Lytle and Poff 2004).

Our study focussed on small or young plants, as large plants were not collected within our sods. Effects of timing of inundation are likely to vary between the life-history stages of perennial species (e.g. seedlings compared with tussocks or saplings), with more developed plants less sensitive to inundation (Denton and Ganf 1994; Klimesova 1994). This suggests that timing of inundation is also important in allowing seedlings that recruit following inundation events to develop sufficiently to survive subsequent inundation (Weisner and Ekstam 1993). For example, although seedlings of native woody taxa did not survive inundation in either spring or summer, those that germinated following inundation in early spring would be more likely to survive subsequent inundation events than those that germinated following inundation in summer because of their greater level of development (Streng et al. 1989).

In conclusion, timing of inundation can affect plant growth and reproduction with plant responses dependent on their life-history strategy. In temperate environments, inundation preceding the growing season followed by non-flooded conditions will promote native riparian plants with life-history strategies adapted to natural flow regimes. Seasonally-inverted flows (i.e. low flows in winter-spring and high summer-autumn flows) are likely to promote exotic species, particularly tufted cool-season grasses, and reduce the abundance of amphibious forbs and riparian annuals. We contend that for temperate rivers, natural flow peaks (i.e. in winter-early spring) are important for the maintenance of native riverine plant communities and reducing the extent of exotic species within the riparian zone.

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References

- Baldwin AH, Egnatovich MS, Clarke E (2001) Hydrologic change and vegetation of tidal freshwater marshes: field, greenhouse, and seed-bank experiments. *Wetlands* 21 (4):519-531
- Baskin CC, Baskin JM (1998) Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, CA, USA
- Blom C, Voesenek L (1996) Flooding: the survival strategies of plants. *Trends in Ecology & Evolution* 11 (7):290-295
- Bonilla-Warford CM, Zedler JB (2002) Potential for using native plant species in stormwater wetlands. *Environmental Management* 29 (3):385-394
- Bunn SE, Arthington AH (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* 30 (4):492-507
- Casanova MT, Brock MA (2000) How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology* 147 (2):237-250
- Catford JA, Downes BJ, Gippel CJ, Vesk PA (2011) Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. *Journal of Applied Ecology* 48 (2):432-442
- Chaneton EJ, Facelli JM, Leon RJC (1988) Floristic changes induced by flooding on grazed and ungrazed lowland grasslands in Argentina. *Journal of Range Management* 41 (6):495-499
- Clarke K, Gorley R (2001) PRIMER v5: user manual/tutorial. PRIMER-E Ltd, Plymouth, UK
- Crossle K, Brock MA (2002) How do water regime and clipping influence wetland plant establishment from seed banks and subsequent reproduction? *Aquatic Botany* 74 (1):43-56
- Denton M, Ganf GG (1994) Response of juvenile *Melaleuca halmaturorum* to flooding: management implications for a seasonal wetland, Bool Lagoon, South Australia. *Australian Journal of Marine and Freshwater Research* 45 (8):1395-1408
- Dixon MD (2003) Effects of flow pattern on riparian seedling recruitment on sandbars in the Wisconsin River, Wisconsin, USA. *Wetlands* 23 (1):125-139
- Froend RH, McComb AJ (1994) Distribution, productivity, production and reproductive phenology of emergent macrophytes in relation to water regimes at wetland of south-western Australia. *Australian Journal of Marine and Freshwater Research* 45 (8):1491-1508
- Gerritsen J, Greening HS (1989) Marsh seed banks of the Okefenokee swamp - effect of hydrologic regime and nutrients. *Ecology* 70 (3):750-763
- Glenz C, Schlaepfer R, Iorgulescu I, Kienast F (2006) Flooding tolerance of Central European tree and shrub species. *Forest Ecology and Management* 235 (1-3):1-13
- Greet J, Cousens RD, Webb JA (2012a) More exotic and fewer native plant species: riverine vegetation patterns associated with altered seasonal flow patterns. *River Research and Applications*:doi: 10.1002/rra.2571
- Greet J, Cousens RD, Webb JA (2012b) Flow regulation associated with riverine soil seed bank composition: potential implications for restoration *Journal of Vegetation Science*:doi: 10.1111/j.1654-1103.2012.01445.x
- Greet J, Cousens RD, Webb JA (in press) Flow regulation affects temporal patterns of riverine plant seed dispersal: potential implications for plant recruitment. *Freshwater Biology*

- Greet J, Webb JA, Cousens RD (2011) The importance of seasonal flow timing for riparian vegetation dynamics: a systematic review using causal criteria analysis. *Freshwater Biology* 56 (7):1231-1247
- Johansson ME, Nilsson C (2002) Responses of riparian plants to flooding in free-flowing and regulated boreal rivers: an experimental study. *Journal of Applied Ecology* 39 (6):971-986
- Johnson WC (2000) Tree recruitment and survival in rivers: influence of hydrological processes. *Hydrological Processes* 14 (16-17):3051-3076
- Klimesova J (1994) The effects of timing and duration of floods on growth of young plants of *Phalaris arundinacea* L. and *Urtica dioica* L.: an experimental study. *Aquatic Botany* 48 (1):21-29
- Lenssen JPM, ten Dolle GE, Blom C (1998) The effect of flooding on the recruitment of reed marsh and tall forb plant species. *Plant Ecology* 139 (1):13-23
- Lytle DA, Poff NL (2004) Adaptation to natural flow regimes. *Trends in Ecology & Evolution* 19 (2):94-100
- Merritt DM, Cooper DJ (2000) Riparian vegetation and channel change in response to river regulation: a comparative study of regulated and unregulated streams in the Green River Basin, USA. *Regulated Rivers-Research & Management* 16 (6):543-564
- Naiman RJ, Décamps H (1997) The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics* 28:621-658
- Nilsson C, Svedmark M (2002) Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Environmental Management* 30 (4):468-480
- Osawa T, Mitsuhashi H (2010) River confluences enhance riparian plant species diversity. *Plant Ecology* 209:95-108
- Poff NL, Allan JD, Bain MB, Karr JR, Prestegard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime. *Bioscience* 47 (11):769-784
- Poff NL, Zimmerman JKH (2010) Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* 55 (1):194-205
- Reily PW, Johnson WC (1982) The effects of altered hydrologic regime on tree growth along the Missouri River in North-Dakota. *Canadian Journal of Botany-Revue Canadienne De Botanique* 60 (11):2410-2423
- Richardson DM, Holmes PM, Esler KJ, Galatowitsch SM, Stromberg JC, Kirkman SP, Pysek P, Hobbs RJ (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Diversity and Distributions* 13 (1):126-139
- Roberts J (2002) Species-level knowledge of riverine and riparian plants: a constraint for determining flow requirements in the future. *Australian Journal of Water Resources* 5 (1):21-31
- Robertson AI, Bacon P, Heagney G (2001) The responses of floodplain primary production to flood frequency and timing. *Journal of Applied Ecology* 38 (1):126-136
- Rogers K, Ralph TJ (2011) Floodplain wetland biota in the Murray-Darling basin: water and habitat requirements CSIRO Publishing, Collingwood, VIC. Australia
- Stokes K, Ward K, Colloff M (2010) Alterations in flood frequency increase exotic and native species richness of understorey vegetation in a temperate floodplain eucalypt forest. *Plant Ecology* 211 (2):219-233
- Streng DR, Glitzenstein JS, Harcombe PA (1989) Woody seedling dynamics in an East Texas floodplain forest. *Ecological Monographs* 59 (2):177-204
- Ström L, Jansson R, Nilsson C (2012) Projected changes in plant species richness and extent of riparian vegetation belts as a result of climate-driven hydrological changes along the Vindel River in Sweden. *Freshwater Biology* 57:49-60
- Stromberg JC, Patten DT (1990) Riparian vegetation instream flow requirements - a case-study from a diverted stream in the eastern Sierra-Nevada, California, USA. *Environmental Management* 14 (2):185-194

- 432 Van der Sman AJM, Blom CWPM, Van de Steeg HM (1992) Phenology and seed production in
433 *Chenopodium rubrum*, *Rumex maritimus*, and *Rumex palustris* as related to photoperiod in river
434 forelands. Canadian Journal of Botany-Revue Canadienne De Botanique 70 (2):392-400
- 435 van Eck W, Lenssen JPM, van de Steeg HM, Blom C, de Kroon H (2006) Seasonal dependent effects of
436 flooding on plant species survival and zonation: a comparative study of 10 terrestrial grassland
437 species. Hydrobiologia 565:59-69
- 438 van Eck WHJM, van de Steeg HM, Blom CWPM, de Kroon H (2004) Is tolerance to summer flooding
439 correlated with distribution patterns in river floodplains? A comparative study of 20 terrestrial
440 grassland species. Oikos 107:393-405
- 441 Voesenek L, Colmer TD, Pierik R, Millenaar FF, Peeters AJM (2006) How plants cope with complete
442 submergence. New Phytologist 170 (2):213-226
- 443 Walsh N, Stajsic V (2007) A Census of the Vascular Plants of Victoria Eighth Edition edn. Royal Botanic
444 Gardens, Melbourne, Australia
- 445 Warwick NWM, Brock MA (2003) Plant reproduction in temporary wetlands: the effects of seasonal
446 timing, depth, and duration of flooding. Aquatic Botany 77 (2):153-167
- 447 Weisner SEB, Ekstam B (1993) Influence of germination time on juvenile performance of *Phragmites*
448 *australis* on temporarily exposed bottoms - implications for the colonization of lake beds.
449 Aquatic Botany 45 (2-3):107-118
- 450 Wilding JL, Barnett AG, Amor RL (1986) Crop Weeds. Inkata Press, Melbourne, Australia
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455 **Table 1. Summary of taxa observed across all sods. For full list of taxa see Appendix 1.**

Plant type	native	Exotic
rush	6	2
sedge	7	2
grass	4	14
forb	29	40
tree/shrub	5	3
terrestrial	24	50
annual/biennial	10	32
ALL	54	62

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459 **Table 2. ANOVA for the test of the effect of timing of inundation on plant growth: results for tests of fixed effects (timing of**
 460 **inundation, season of survey and their interaction) for the various response variables. Significant results ($p < 0.05$) in bold.**

Response variable	Timing of inundation			Season of survey			Timing x Season		
	<i>F</i>	df	<i>p</i>	<i>F</i>	df	<i>p</i>	<i>F</i>	df	<i>p</i>
cover of native taxa	1.73	1	0.190	209.67	3	<0.001	3.42	3	0.017
cover of exotic taxa	0.08	1	0.784	54.57	3	<0.001	29.05	3	<0.001
cover of native amphibious forb taxa	4.89	1	0.028	45.98	3	<0.001	8.45	3	<0.001
cover of exotic grass taxa	3.95	1	0.049	6.23	3	<0.001	19.29	3	<0.001

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464 **Table 3. Responses (change in cover between surveys) to inundation in spring, inundation in summer and overall (sum of**
 465 **responses to both inundation events) of various taxa. Taxa presented are those that contributed to a cumulative 90% of the**
 466 **dissimilarity between the pre- and post-inundation surveys for either the spring- or summer-inundation, and for which a**
 467 **response ≥ 0.05 was observed for either inundation treatment or overall. Exotic taxa indicated by an asterisk.**

Taxa	Response to inundation		
	spring	summer	overall
<i>Holcus lanatus</i> *	-0.29	-0.26	-0.55
<i>Bromus diandrus</i> *	-0.20	-0.22	-0.42
<i>Conyza</i> spp.*	-0.18	-0.18	-0.36
<i>Verbena bonariensis</i> *	-0.12	-0.14	-0.26
<i>Lotus</i> spp.*	-0.04	-0.22	-0.26
<i>Cirsium vulgare</i> *	-0.11	-0.13	-0.24
<i>Sonchus oleraceus</i> *	-0.07	-0.11	-0.18
<i>Solanum nigrum</i> *	-0.05	-0.13	-0.18
<i>Cynodon dactylon</i> *	-0.07	-0.10	-0.17
<i>Hypochaeris radicata</i> *	-0.05	-0.12	-0.17
<i>Senecio glomeratus</i>	-0.05	-0.11	-0.16
<i>Acacia dealbata</i>	-0.01	-0.15	-0.16
<i>Ranunculus repens</i> *	-0.05	-0.06	-0.11
<i>Plantago lanceolata</i> *	-0.04	-0.06	-0.10
<i>Paspalum dilatatum</i> *	-0.05	-0.05	-0.10
<i>Epilobium hirtigerum</i>	-0.06	-0.03	-0.09
<i>Ehrharta erecta</i> *	-0.05	-0.04	-0.09
<i>Agrostis</i> spp.*	-0.08	0	-0.08
<i>Centaurium erythraea</i> *	0	-0.07	-0.07
<i>Mimulus moschatus</i> *	0	-0.07	-0.07
<i>Eucalyptus camaldulensis</i>	-0.06	-0.01	-0.07
<i>Lachnagrostis filiformis</i>	-0.02	-0.03	-0.05
<i>Calystegia sepium</i>	0.02	-0.07	-0.05
↑ increasingly flood sensitive	↓ increasingly flood tolerant		
<i>Persicaria hydropiper</i>	0.21	-0.16	0.05
<i>Juncus prismatocarpus</i>	0	0.05	0.05
<i>Rumex</i> spp.*	0.02	0.03	0.05
<i>Euchiton</i> spp.	0	0.06	0.06
<i>Paspalum distichum</i> *	0.01	0.06	0.07
<i>Ludwigia palustris</i> *	0.01	0.07	0.08
<i>Juncus articulatus</i> *	0.05	0.05	0.10
<i>Crassula helmsii</i>	0.14	0	0.14
<i>Callitriche stagnalis</i> *	0.10	0.08	0.18
<i>Helichrysum luteoalbum</i>	0	0.19	0.19
<i>Juncus</i> spp. subgenus <i>genuini</i>	0.09	0.10	0.19
<i>Isolepis inundata</i>	0.07	0.14	0.21
<i>Persicaria praetermissa</i>	0.14	0.07	0.21
<i>Cyperus eragrostis</i> *	0.18	0.10	0.28

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<i>Persicaria decipiens</i>	0.21	0.14	0.35
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Table 4. ANOVA results for tests of fixed effects (timing of inundation, season of survey and their interaction) on plant reproduction for the various response variables. Significant results ($p < 0.05$) in bold.

Response variable	Timing of inundation			Season of survey			Timing x Season		
	<i>F</i>	df	<i>p</i>	<i>F</i>	df	<i>p</i>	<i>F</i>	df	<i>p</i>
no. of native taxa flowering	0.83	1	0.365	150.15	3	<0.001	1.51	3	0.210
no. of exotic taxa flowering	1.42	1	0.236	62.00	3	<0.001	8.54	3	<0.001
no. of exotic grass taxa flowering	12.25	1	<0.001	9.26	3	<0.001	7.51	3	<0.001

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476 Table 5. Results of the SIMPER analysis comparing the mean number of flowering plants per sod between the spring- and
 477 summer-inundation treatments (pooling all surveys). Taxa contributing to a cumulative 90% of dissimilarity between the two
 478 treatments presented. Exotic taxa indicated by asterisks. Exotic grass taxa are underlined and native annual/biennial taxa
 479 bolded, the former taxa flowered only in the summer-inundation treatment and the latter taxa flowered mostly in the
 480 spring-inundation treatment.

Taxa	Spring-inundation treatment – mean no. of flowering plants per sod	Summer-inundation treatment – mean no. of flowering plants per sod	Contribution (%) to dissimilarity
<i>Isolepis inundata</i>	0.6	0.63	32.97
<i>Persicaria hydropiper</i>	0.19	0.15	10.17
<i>Cyperus eragrostis</i> *	0.14	0.05	7.57
<i>Juncus articulatus</i> *	0.15	0.09	4.91
<i>Persicaria praetermissa</i>	0.07	0.1	4.57
<i>Persicaria decipiens</i>	0.03	0.08	3.68
<u><i>Bromus diandrus</i></u> *	<u>0</u>	<u>0.03</u>	3.5
<i>Juncus bufonius</i>	0.03	0.02	2.54
<i>Solanum nigrum</i> *	0.02	0.02	2.07
<i>Ludwigia palustris</i> *	0.03	0.04	2.04
<i>Fumaria</i> sp.*	0.01	0.01	1.8
<i>Helichrysum luteoalbum</i>	0.02	0.01	1.38
<i>Lachnagrostis filiformis</i>	0.03	0.03	1.38
<i>Isolepis marginata</i>	0.03	0	1.35
<i>Centipeda minima</i>	0.03	0	1.27
<u><i>Ehrharta erecta</i></u> *	<u>0</u>	<u>0.04</u>	1.21
<i>Verbena bonariensis</i> *	0.01	0.02	1.19
<u><i>Paspalum dilatatum</i></u> *	<u>0</u>	<u>0.01</u>	1.11
<i>Crassula helmsii</i>	0.01	0	0.92
<i>Isolepis levynsiana</i> *	0	0.01	0.87
<i>Alternanthera denticulata</i>	0.04	0	0.84
<i>Cyperus ihotskyanus</i>	0.01	0.02	0.84
<i>Plantago lanceolata</i> *	0	0.01	0.75
<i>Euchiton involucratus</i>	0.02	0	0.75
<i>Aster subulatus</i> *	0.01	0	0.72

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484 Figure 1. Study sites (filled circles) from which sods were collected.

485 Figure 2. Fitted mean ($\pm$ standard error) cover per sod of a) native taxa, b) exotic taxa, c) native amphibious forb taxa and d)
 486 exotic grass taxa for the spring- and summer-inundation treatments (solid and dashed lines respectively) by season of survey
 487 (winter – autumn); N.B. spring inundation occurred prior the spring survey (beginning of six-weeks inundation period
 488 indicated by solid arrow), while the summer inundation occurred after the summer survey (dashed arrow). Timing of
 489 inundation events were intended to reflect typical peak flow periods of the natural and regulated flow regimes, respectively,
 490 of the study area (Greet et al. 2012a).

491 Figure 3. Fitted mean ($\pm$ standard error) number of a) native taxa, b) exotic taxa and c) exotic grass taxa per sod flowering for
 492 the spring- and summer-inundation treatments (solid and dashed lines respectively) by season of survey (winter – autumn);
 493 N.B. spring inundation occurred prior the spring survey (beginning of six-weeks inundation period indicated by solid arrow),
 494 while the summer inundation occurred after the summer survey (dashed arrow). Timing of inundation events were intended
 495 to reflect typical peak flow periods of the natural and regulated flow regimes, respectively, of the study area (Greet et al.
 496 2012a).

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Author/s:

Greet, J;Cousens, RD;Webb, JA

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