Ecol Res
DOI 10.1007/s11284-014-1198-2

ORIGINAL ARTICLE

Olusegun O. Osunkoya · Sadiq Ali · Thi Nguyen
Christine Perrett · Asad Shabbir · Sheldon Navie
Amalia Belgeri · K. Dhileepan · Steve Adkins

Soil seed bank dynamics in response to an extreme flood event in a riparian habitat

Received: 23 December 2013 / Accepted: 21 August 2014

Abstract A significantly increased water regime can lead to inundation of rivers, creeks and surrounding floodplains- and thus impact on the temporal dynamics of both the extant vegetation and the dormant, but viable soil-seed bank of riparian corridors. The study documented changes in the soil seed-bank along riparian corridors before and after a major flood event in January 2011 in southeast Queensland, Australia. The study site was a major river (the Mooleyember creek) near Roma, Central Queensland impacted by the extreme flood event and where baseline ecological data on riparian seed-bank populations have previously been collected in 2007, 2008 and 2009. After the major flood event, we collected further soil samples from the same locations in spring/summer (November–December 2011) and in early autumn (March 2012). Thereafter, the soils were exposed to adequate warmth and moisture under glasshouse conditions, and emerged seedlings identified taxonomically. Flooding increased seed-bank abundance but decreased its species richness and diversity. However, flood impact was less than that of yearly effect but greater than that of seasonal variation. Seeds of trees and shrubs were few in the soil, and were negatively affected by the flood; those of herbaceous and graminoids were numerous and proliferate after the flood. Seed-banks of weedy and/or exotic species were no more affected by the flood than those of native and/or non-invasive species. Overall, the studied riparian zone showed evidence of a quick recovery of its seed-bank over time, and can be considered to be resilient to an extreme flood event.

Keywords Disturbance · Ecosystem resiliency · Extreme events · Inundation · Riparian-zone · Seed-bank · Vegetation dynamics · Weeds

Electronic supplementary material The online version of this article (doi:10.1007/s11284-014-1198-2) contains supplementary material, which is available to authorized users.

O. O. Osunkoya (✉) · C. Perrett · K. Dhileepan
Invasive Plant and Animal Science Unit, Biosecurity Queensland, Department of Agriculture, Fisheries and Forestry, Ecosciences Precinct, Dutton Park, Brisbane, QLD 4102, Australia
E-mail: olusegun.osunkoya@daff.qld.gov.au; Segun.Osunkoya@jcu.edu.au
Tel.: +61-7-4232-1242

S. Ali · T. Nguyen · A. Shabbir · S. Navie · A. Belgeri · S. Adkins
Tropical and Subtropical Weed Research Unit, School of Agriculture and Food Sciences, University of Queensland, St Lucia, Brisbane, QLD 4072, Australia

S. Ali
Department of Weed Science, University of Agriculture, Peshawar, KPK, Pakistan

T. Nguyen
Department of Ecology and Evolutionary Biology, Faculty of Biology, University of Science, 227 Nguyen Van Cu Street, District 5, Ho Chi Minh City, Vietnam

A. Shabbir
Institute of Agricultural Sciences, University of the Punjab, Quaid-e-Azam Campus, Lahore 54590, Pakistan

Present address:
O. O. Osunkoya
College of Marine and Environmental Sciences, James Cook University, Cairns Campus, Qld 4870, Australia

Introduction

Riparian corridors in human dominated landscape are extremely fragile due to their linear, often narrow width (mostly < 30 m) of vegetation and influx or exchange of propagules, nutrients, water and sediment loads with the surrounding matrix of varying land-use types (Naiman and Decamps 1997; Goodson et al. 2001; Stromberg et al. 2008). Many studies have documented the dynamics of riparian zone above-ground vegetation in relation to various anthropogenic and natural disturbances, such as flooding and drying regimes (e.g., Bagstad et al. 2005; Ilg et al. 2008; Stromberg et al. 2008). In contrast, except in the last decade, little is known concerning the spatio-temporal dynamics of the below ground flora and fauna, including that of the viable soil seed bank, insect and microbial communities of riparian corridors (but see

Ward et al. 1998; Goodson et al. 2001; Capon and Brock 2006; Ilg et al. 2008; Williams et al. 2008; Osunkoya et al. 2011). Yet, knowledge of the above- and below-ground processes of riparian corridors is essential for better conservation and management of this fragile ecosystem. Viable soil seed banks facilitate plant community dynamics by providing species persistence in a dormant state until suitable conditions for their germination and establishment occur (Roberts 1981; Baskin and Seeds 2001; Martinez-Duro et al. 2011).

A significantly changed water regime, such as that brought about by a sudden increase in precipitation, can lead to inundation (of varying magnitude and duration) of rivers, creeks and surrounding floodplains, impacting on the temporal dynamics of both the extant vegetation and the dormant, but viable soil seed bank (Siebentritt et al. 2004; Kehr et al. 2014). Such an extreme event can be considered as a form of disturbance, and through its influence on sediment reworking, plays an important role in re-shaping of wetland communities and ecosystems (Naiman and Decamps 1997; Nilsson et al. 2010; Greet et al. 2012). One such an extreme event happened in the later months of 2010 and continued into mid January 2011 in eastern Australia (Fig. 1). It resulted in several days of inundation and affected more than 80,000 km^2 of Queensland south-east coastal and inland floodplains, rivers and riparian corridors (Honert and McAneney 2011; Queensland Government 2011). This rare catastrophic event provided a unique opportunity to study the effect of climate variability at a specific location upon ecosystem dynamics and resilience; the phenomenon allowed us to document pre- and post-flood abundance and composition of the soil seed banks along a Queensland riparian corridor-the Mooleyember Creek, near Injune, 100 km north-east of the township of Roma, central Queensland. We chose this site due to the availability of data that had been collected on temporal dynamics of its seed banks spanning back several years prior to the flood event (Adkins and McFadyen 1996; Navie et al. 2004; Nguyen 2011). Our collections and analyses of post-flood data and the comparison with the previously collected pre-flood data set allow us to explore several testable hypotheses.

1) Irrespective of the underlying process operating during the flood, we hypothesized a significant change in seed bank signature both in terms of quantity (abundance) and quality (species richness and diversity), and that the change caused by the extreme event will be greater than that due to regular temporal (yearly and seasonal) factors. Some past studies have suggested that flooding induce eutrophication (due to large input of dissolved and particulate nutrients) and hence promote rapid vegetation growth of specific taxa, leading to a decrease in species richness (Smith et al. 1998; Bagstad et al. 2005). Others argued that flooding may reduce competition intensity, favoring weak competitors, leading to a higher diversity in the standing vegetation (Stromberg et al. 1993; Gerard et al. 2008).
2) The magnitude and direction of flooding effect upon the viable seed bank will vary, depending on the plant functional group and/or their life history traits. For example, theory predicts that the trajectory pathways of invasive exotics are significantly different from those of native or non-invasive species (e.g., Hölzel and Otte 2004; Catford et al. 2011; Greet et al. 2012). Flooding, being a form of disturbance that can creates new niches, should favour exotic invasive species over native species because of their higher competitive ability in these modified environments (Greet et al. 2012). Wetland and aquatic plant species are better adapted to moisture, and hence their seeds, following flooding can float and survive better than those of species that are less adapted to such condition (especially terrestrial specialists). Similarly it can be expected that the response of opportunist species (annual/biennials, herbaceous and graminoids) that complete their life cycles in short periods of time will be different from the response of long-lived perennials, trees and shrubs. Thus it is predicted that in the post-flood environment, annuals, short-lived perennials, hygrophilous, and invasives will make-up the majority of plant species found in the seed bank (Bagstad et al. 2005; Catford et al. 2011; Greet et al. 2012).
3) The riparian zone seed-bank will show resiliency to the flood disturbance, recovering from its impact within a short time. In ecological terms, resilience refers to (i) the capacity of an ecosystem to undergo disturbance but maintain core functions and controls and (ii) the capacity of the ecosystem to resist disturbance and return to equilibrium afterward (Collof and Baldwin 2010). The more rapidly it returns and with the least fluctuations, the more stable it is considered to be. Wetzel et al. (2004) and Bilkovic et al. (2012) have suggested that changes associated with drought and floods tend to be temporary, with aquatic community (marsh and riparian corridors) returning to their previous compositions within 2 years (see also Capon and Brock 2006; Ilg et al. 2008). If this is true, we hypothesized that the magnitude of the flood impact, irrespective of its direction, will decrease over time. Thus, in the process of searching for resilience of riparian ecosystem to rare, extreme disturbance event, we quantify (1) the impact of the major flood in Queensland, Australia of 2011 on soil seed bank composition and functional group assemblage, and (2) the effect of the flood disturbance relative to yearly, seasonal and micro-topographic factors. Seasonal observations are important because riparian vegetation often displays dramatic seasonal changes (Reid and Quinn 2004), and thus vegetation and seed-bank changes associated with flooding are hypothesised to be more apparent at different seasons of the year (Hölzel and Otte 2004; Greet et al. 2012).

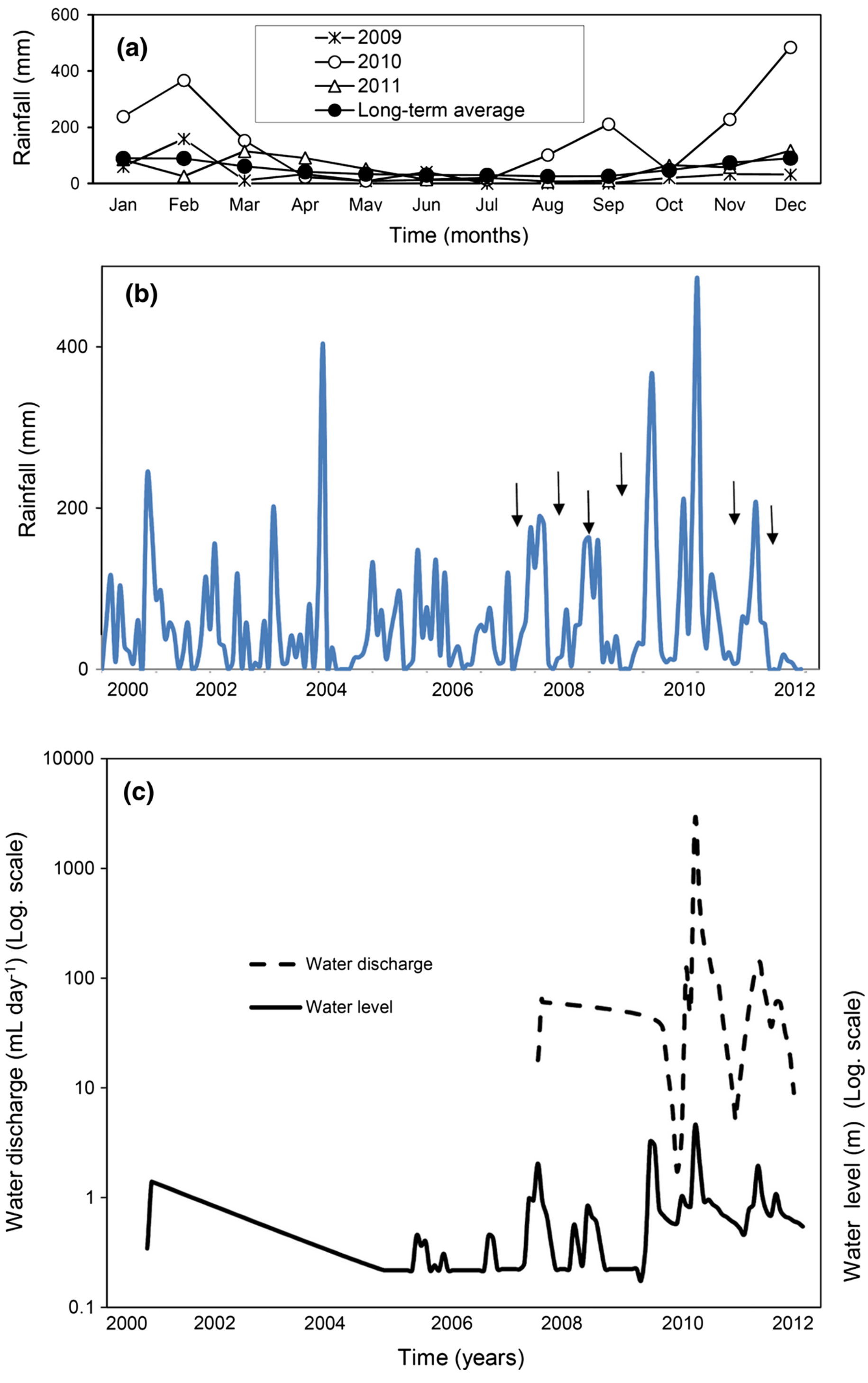

Fig. 1 Long-term rainfall (**a**, **b**) and water level fluctuations (**c** *lower graph* is water level, and *upper graph* is water discharge) in the study area based on gauges on Brown River into which the study Mooloyember creek, central Queensland, Australia flows into (source: Australian Bureau of Meteorology). **a** shows the monthly rainfall patterns around the survey periods compared to long-term monthly average values. *Arrows* in **b** indicate soil-sampling periods

Methods

Study region and site

The site selected for this study was the Moolayember Creek, 90 km south of Rolleston (latitude 25°S, longitude 149°E), near Roma, central Queensland, Australia. The 32 km-long Creek is at an elevation of 262–350 m above sea level and flows into the Brown River. The study area has a humid subtropical climate, with an average rainfall ca. 630 mm per year, the majority of which falls in summer months of December–February (Fig. 1a). The catchment, which is part of Fitzroy basin, is warm with maximum daytime temperatures in spring-summer (September–February) of 28.5–34.3 °C and 20.2–25 °C in the autumn–winter (March–August) months. There are no flow gauges on Moolayember Creek, and hence the flow data from the downstream Brown River into which the creek flows into are the best available for the study site. The long term data indicate that surface water discharge and river levels are extremely variable with periods of average, low, and occasionally above average values during the last decade (Fig. 1b, c). In November 2010 to mid January 2011, due to four strongest La Niña events since 1900 (see http://www.bom.gov.au/climate/current/soihtm1.shtml) more than 80,000 km^2 of south-east and central Queensland lands were inundated, resulting in a relatively rare, large flood pulse with a peak discharge of $\sim$60,000 $ML.day^{-1}$ (compared with normal value of 585 $ML.day^{-1}$) and a peak height of 9.95 m of the Brown River (QLD Dept of NRWM 2011). By early January 2011, anecdotal evidence suggested that a record height of 3–4 m of water above the Moolayember Creek bench was recorded and these lasted for several days, and resulted in the inundation of creek channel areas and the surrounding floodplains.

The vegetation along the creek and surrounding floodplain is mainly of short-medium height grasses (including *Imperata cylindrical*, *Paspalum dilatatum*) and associated sedges (e.g. *Carex inverse*) punctuated with variable abundance of open succulent herbs/shrubs such as *Chenopodium* and *Wahlenbergia* species and many exotic and invasive species (e.g., *Argemone sp., Xanthium pungens, Asclepias physocarpa*). Scattered trees of *Angophora floribunda* (rough-barked apple), *Eucalyptus tereticornis* (the pale smooth flooded gum) and *E. camaldulensis* (river red gum) are dominant along the banks of the creek, while *Casuarina cunninghamiana* (she oak) and *Corymbia citriodora* (lemon scented gum) can be found further in the floodplain areas. The soil is predominantly a sandy loam.

Sampling protocols

Pre-flood collection of soil samples were made in December 2007, April 2008, December 2008, May 2009 (see Fig. 1) from three locations, each being at least 2 km apart, along the Moolayember Creek (Nguyen 2011), with the sole aim of monitoring the long-term seed bank size and the extent of dispersal of the invasive arable weed, *Parthenium hysterophorus* in the region (Adkins et al. 1996). Thirty composite soil samples (ten from each location) were collected per survey period for the pre-flood samples (see collection details below). After the flood event, further collections were made in November 2011 and March 2012 at the same three locations along the creek. These sampling periods coincided with early summer (November- December) and early autumn (March–May), which are the main growing seasons in the region (Navie et al. 2004; Dhileepan 2012).

Post-flood sampling protocol was the same as that of pre-flood, except that additional effect of distance from the creek-line on seed bank was incorporated and hence necessitated doubling the sample size. At each location, two transects, each 100 m in length and running parallel to the creek bank were set up. One transect was close (ca. 2–3 m) to the creek bank while the second one was 10 m away towards the floodplains. Along each transect, a total of 10, 1 × 1 m quadrats were established at 10 m intervals. Five soil cores were removed from each quadrat, one from each of the four corners and one from the centre, using a brass ring soil corer (7.2 cm diameter and 10 cm deep). The soil samples of each quadrat were pooled to make a single (composite) sample. The 10 (pre-flood) and 20 (post-flood) samples collected per location were placed individually into zip-lock plastic bags sealed and stored at ca. 25 ± 5 °C for 2–3 days while being transferred from the field to the glasshouse facility at the University of Queensland, Brisbane, Australia for immediate seed germination trials. The soil samples were spread thinly over a 2 cm layer of sterilised compost contained within shallow seedling trays (20 × 25 × 6 cm; w/l/h) that were distributed randomly on benches in the glasshouse. The temperature in the glasshouse over each of the germination periods ranged between 20–38 °C (spring/summer time) and 10–31 °C in the autumn/winter months, while the photosynthetic light intensity was in the order 300–990 $\mu mol.m^2.sec$. Trays were watered daily through overhead sprinklers to maintain soil moisture content close to field capacity. The trays were observed regularly (at least once a week) for newly emerging seedlings. Once seedlings were fully formed, they were taxonomically identified and removed, or in the case of where identification was not possible, representative individuals were planted into small pots and grown on to maturity, to allow later identification. After 4 months, when seedling emergence had almost ceased, the soil in the trays was allowed to dry for 2 weeks, then stirred, rewetted and inspected for any further seedling emergence over another 3 month period. This enabled the detection of species that required moisture and temperature fluctuations to stimulate their germination, and hence were present but dormant during the initial 4 months of the trial. The final record of seedling emergence was taken when no further germination occurred for a period of 2 weeks.

The species identified were assigned into functional groups, including plant longevity (perennial or annual/biennial), life form (tree, shrub, herb or graminoid), habitat/moisture requirement (wetland or terrestrial), weed status (invasive or non-invasive) and origin (native or exotic to Australia), using the literature (Stanley and Ross 1983–1995; Hussey et al. 1997) and electronic databases (Plantnet—National Herbarium of New South Wales- http://www.rbgsyd.nsw.gov.au and Weeds Australia- http://www.weeds.org.au). The 'unidentified species' term was used for several seedlings that had died before they could be identified; the proportion of 'unidentified species or individuals' ranged between

5–15 % of total count for the pre-flood data and 1 % for the post-flood data (see Table S1).

Data analyses

Data were subjected to a series of univariate and multivariate analyses. At the univariate level, we used repeated-measure ANOVA, χ^2 or *t* tests to compare seed bank abundance, richness, diversity and assemblages in relation to season (summer or autumn), inundation condition (pre- or post-flood years), and landscape/topographic effect (near and far from the creek bank). In the ANOVA, time (the five sampling years) was the repeated factor. The assumption of sphericity was tested (using Mauchly criterion) and was found not violated in all analyses. In many instances, the repeated-measure ANOVA was restricted to main effects and 2-way interactions of these main effects because sampling design was not completely balanced as data for the three locations at each pre-flood survey period were not separated during initial stage of data compilation; also spring and autumn (i.e., complete seasonal) data were often not collected for each sampling year. Functional composition was examined by assigning species to functional groups (as explained earlier) and assessing the significance of the differences in the patterns between pre- and post-flood conditions using χ^2 analysis. The abundance and richness data were log +1 transformed due to low or zero species counts in some samples and to meet the assumption of normality.

For a measure of habitat resilience, we estimated proportional change in seed bank species abundance and richness in response to the flood using the expression: [(postflood-preflood)/preflood] × 100 and significance of the change tested using a critical limit of 10 % difference (see Welleck 2003).

At the multivariate level, patterns of seed bank species assemblage were investigated using non-metric multidimensional scaling (MDS) in two–three dimensions with inundation, season, year and topographic distance as main factors. PRIMER ver. 6.0 statistical software (Clarke and Gorley 2006) was used. Species abundance or presence/absence data were used; both gave comparable trends and hence only that of abundance are presented. MDS was based on a Bray-Curtis dissimilarity matrix following log (x + 1) transformation of the data. The extents of clustering of species seed bank in response to the extreme flood event and/or above-mentioned temporal and topographic factors were then assessed by analyses of similarity (ANOSIM) and similarity percentage (SIMPER), again using the Primer software. Analogous to ANOVA, ANOSIM compares the mean difference of ranks within and between groups, generating the Global statistic R (Clarke and Warwick 2001). Values of R range from −1 to +1, with negative values and values near 0 indicating similarity among groups and values approaching $R = 1$ indicating a strong dissimilarity among groups. SIMPER identifies species that contributed most to the average dissimilarity between groups that have been selected a priori (in our case, between pre- and post-flood condition or between seasons or amongst sampling years) and those that contributed most to the average similarity within group. This procedure computes the average contribution of each species to the overall dissimilarity between two groups. Discriminating species are those characterised by a high ratio between their average contribution to the dissimilarity between groups and its standard deviation (Clarke and Warwick 2001). The overall percentage similarity between groups ranges between 0 and 100, with 100 expressing maximum similarity.

Results

Overall trends

In the 5 years of survey, a total of 132 species were found in the soil seed bank at the Moolayember Creek site, consisting of Poaceae (30), Asteraceae (21), Chenopodiaceae (8), Cyperaceae (7), Malvaceae (6), Verbenaceae (5), Solanaceae, Amaranthaceae, Brassicaceae (four each), Campanulaceae, Onagraceae (three each) and 37 other species distributed across 15 families (Electronic Supplementary Material Table S1). The density of all species in the seed bank ranged from 3,145 to 61,090 (mean: 171,020) seeds per m^2. An average of 26.0 ± 0.5 species emerged per m^2 of soil sample collected (Fig. 2). For the post-flood data set, we found only minimal difference in the soil seed bank composition (abundance) and species richness across the three locations along the creek or between the two vertical (bar and bench) distances from the creek line. Hence the post-flood data across the three locations and between the two creek distances were pooled during further statistical analyses carried out. Abundance and species number per unit area, as well as species richness and diversity fluctuated from year to year and in response to season and flooding condition (Table 1).

Seasonal effect

Two-way ANOVA suggested that with the exception of species count per sample and species richness, all other species and taxonomic indices showed significant flood condition x season interaction effects. This result implied that after the flood, the magnitude and/or direction of seed bank response varied significantly, depending upon the season (Table 1; Fig. 2). Subsequently, seasonal variation was taken into consideration when exploring the effect of the extreme flood event on seed bank assemblages.

After accounting for yearly variation, most indices of seed bank species diversity, including taxonomic distinctness indices were affected by season (Table 1).

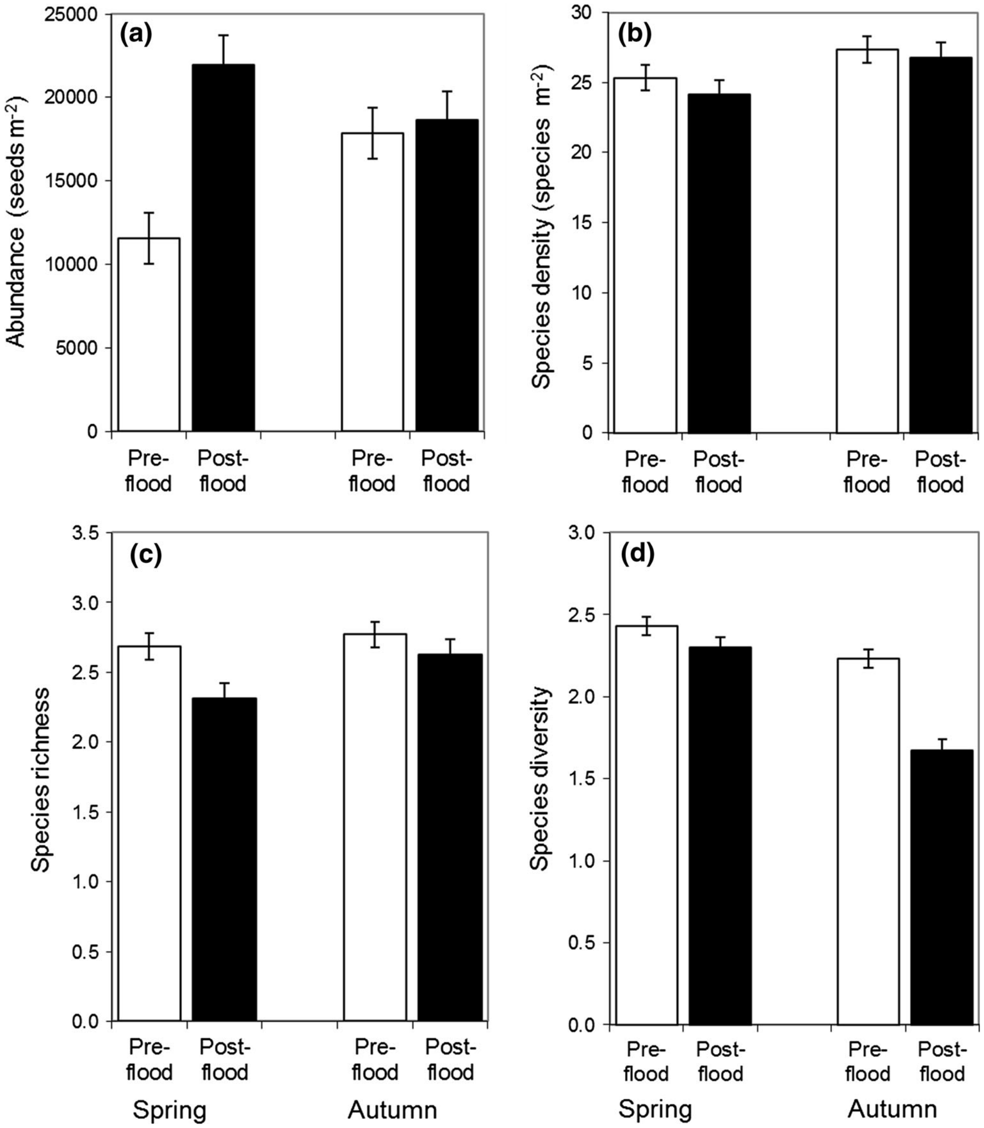

Fig. 2 Indices (mean ± SE) of species assemblage of seed bank from Mooleyember creek, Central Queensland in response to inundation and seasonality of spring/summer (October–February) and autumn/winter (March–July)

Table 1 Summary ANOVA of effects of flooding, season and year on various aspects of soil seed bank composition of Mooloyember creek, Central Queensland, Australia

Factor	Abundance	Species indices			Taxonomic indices			
	Individuals m^{-2}	No. of species	Species richness[a]	Species diversity[b]	Δ	$\Delta+$	Phi	Phi+
Flooding	***	NS	**	***	*	NS	NS	NS
Season	NS	*	*	***	***	NS	*	*
Flooding x season	**	NS	NS	***	*	**	**	NS
Year	***	**	***	***	***	***	***	***

Δ taxonomic diversity, $\Delta+$ average taxonomic distinctness using presence/absence, *Phi* average taxonomic diversity using presence/absence, *Phi*+ total phylogenetic diversity

*** $P < 0.001$; ** $P < 0.02$; * $P < 0.05$; *NS* not significant (i.e., $P > 0.05$)

[a] Species richness referes to Margalef index

[b] Species diversity refers to Shannon index

Abundance per m^2 was higher in autumn (18,250 ± 1,165) but the differences did not differ statistically from values obtained for the spring months (16,753 ± 765; Table 1; Fig. 2a). Equally, species count and richness values were significantly higher in autumn than in the spring months (Table 1; Fig. 2b, c); however, the opposite pattern was observed with species diversity and most indices of taxonomic distinctness, which were of higher values in spring compared to the autumn periods (Table 1; Fig. 2d).

Flooding effect on abundance, species richness, and functional types

Flooding affected the species indices more than it did on the taxonomic indices. It decreased species diversity and richness, but increased abundance per unit area while having marginal or no effect on the taxonomic indices (Table 1; Fig. 2). A summary of the abundance and species richness of plant functional types detected in the seed bank is given in Table 2.

Seed bank abundance showed significant changes following the flood, though the directions (either increasing or decreasing) were often not consistent across functional types (Table 2; Fig. 3). In the first post-flood survey, abundance of the herbs and graminoids showed a major increase (90-110 %) while those of shrubs and trees were largely reduced (up to 80 % reduction) (Fig. 3a). By the second post-flood survey, all life form groups showed reduced seed bank abundance except those for herbs, which showed a marginal positive gain. It must be pointed out that the abundance of trees and vines in the seed bank was low with mean value of 4.4 ± 2.4 seeds per m^2 (Table 2). The seed bank abundance of both wetland and terrestrial plant species responded positively to the flood, but the effect was much more dramatic for terrestrial (ca. 100 % increase) com-

Table 2 Summary of abundance and richness of plant functional groups in the seed bank of Moolayember creek, central Queensland, Australia during pre-and post-flood periods

Functional type	Spring		Autumn	
	Pre-flood	Post-flood	Pre-flood	Post-flood
(a) Abundance (mean ± SE individuals m^{-2})				
Life history group				
Forb (herb)	116.4 ± 31.72	240.10 ± 67.82	205.40 ± 56.63	220.18 ± 87.38
Graminoid	45.87 ± 42.67	87.07 ± 91.22	48.82 ± 76.17	43.36 ± 117.54
Shrub	9.82 ± 104.52	8.99 ± 223.45	22.99 ± 186.59	7.59 ± 287.91
Tree	4.10 ± 159.66	0.25 ± 34.33	3.69 ± 285.02	5.05 ± 439.79
Vine	0.61 ± 195.54	0.76 ± 418.04	20.27 ± 349.07	0.57 ± 538.63
Habitat				
Terrestrial	79.88 ± 26.52	162.22 ± 56.84	136.35 ± 47.20	143.85 ± 72.37
Wetland	128.73 ± 120.73	194.89 ± 125.93	137.23 ± 105.06	133.87 ± 161.08
Plant longevity				
Annual/biennial	121.23 ± 33.41	267.12 ± 71.09	216.67 ± 59.58	240.64 ± 91.83
Perennial	43.37 ± 34.51	64.64 ± 73.32	52.83 ± 61.44	39.71 ± 94.69
Invasiveness				
Non-invasive	41.95 ± 38.92	79.62 ± 83.22	48.63 ± 69.47	41.54 ± 107.3
Invasive	110.77 ± 30.96	227.73 ± 66.21	194.88 ± 55.27	209.33 ± 85.15
Origin				
Native	78.34 ± 32.55	118.48 ± 69.32	85.28 ± 57.28	106.32 ± 88.31
Exotic	75.16 ± 36.26	229.66 ± 77.24	200.87 ± 64.26	187.33 ± 99.07
(b) Number of species (mean ± SE m^{-2})				
Life history group				
Forb (herb)	62.25 ± 2.83	44.00 ± 3.51	63.25 ± 14.14	38.29 ± 2.52
Graminoid	35.00 ± 3.54	23.45 ± 3.22	28.89 ± 6.36	16.45 ± 2.00
Shrub	5.99 ± 0.71	3.07 ± 0.57	7.99 ± 2.12	3.00 ± 0.00
Tree	4.21 ± 0.71	3.11 ± 1.15	2.98 ± 0.71	1.12 ± 0.05
Vine	1.11 ± 0.59	1.09 ± 0.29	1.12 ± 0.70	0.92 ± 0.58
Habitat				
Terrestrial	86.45 ± 5.67	61.25 ± 6.25	86.02 ± 19.09	50.00 ± 1.53
Wetland	22.22 ± 5.78	11.98 ± 1.73	17.05 ± 3.05	8.27 ± 1.01
Plant longevity				
Annual/biennial	57.98 ± 11.31	41.23 ± 4.58	52.01 ± 12.01	26.25 ± 2.52
Perennial	49.01 ± 4.24	32.21 ± 3.46	49.99 ± 10.61	22.22 ± 1.53
Invasiveness				
Non-invasive	38.25 ± 2.12	26.45 ± 4.58	37.08 ± 14.14	16.97 ± 1.00
Invasive/weed	69.24 ± 2.56	47.01 ± 3.46	65.23 ± 8.48	41.11 ± 0.58
Origin				
Native	60.79 ± 6.36	35.00 ± 5.19	58.22 ± 3.56	23.00 ± 5.77
Exotic	46.98 ± 6.95	38.25 ± 3.00	45.40 ± 19.09	35.21 ± 4.77

Data are back-transformed values from a log (x + 1) transformation in a repeated-measure ANOVA

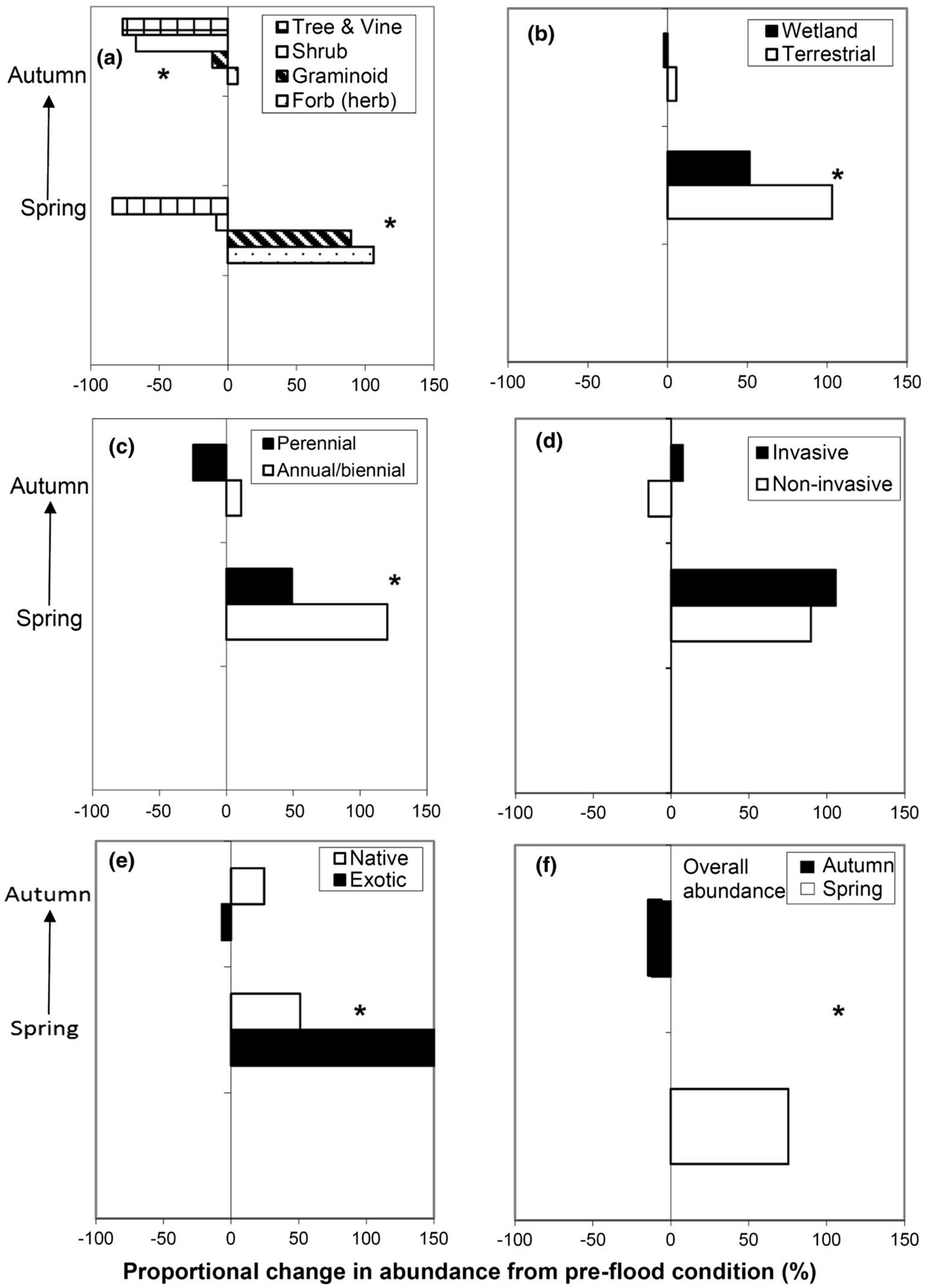

Fig. 3 Changes in seed bank abundance of plant species function types at 10 months (spring) and 15 months (autumn) after the extreme flood event in Mooleyember creek, Central Queensland: **a** plant life form; **b** plant habitat; **c** plant longevity; **d** plant weedy status; **e** plant origin; and **f** overall performance at each season. *Asterisks* (*) refer to significant difference ($P < 0.05$) between functional types in their responses to the flood in a given season, except the last graph **f** that depicts differences between seasons. *Arrow* indicates increasing time since the flood

pared to wetland species (ca. 52 % increase) in the first post-flood survey. Likewise in terms of plant longevity, across the two post-flood survey periods, the positive effect of inundation was greater on the seed bank density of the annuals/biennials (ca. 75 % net increase) compared to the perennials (ca. 12 % net-increase). The flood event also increased the abundance of the seed bank of the invasive and exotic species over that of non-invasive and native species (Table 2; Fig. 3d, e), especially by the first survey period. Nonetheless, post-flood seed bank abundance of native species increased almost linearly with increasing number of exotics (r^2 = 0.96, n = 6; P = 0.001; Fig. 4a); the same trend occurred, irrespective of origin, between non-invasive and invasive species (r^2 = 0.59, n = 6; P = 0.02; Fig. 4b). Overall, the flood effect diminished with time from ca.75 % net-increase in seed bank abundance at 11 months (first post-flood survey) to a much lower value (ca.12 % net decrease) at 15 months (second post-flood survey) (Fig. 3f).

The direction of the flood effects was more consistent on species richness as compared to abundance; in most cases and irrespective of plant functional group or survey season, a negative effect was the observed trend (Fig. 5; Table 2). Compared to those of shrubs, graminoids and herbs, the negative effect of the flood on species richness of trees and vines in the soil seed bank was much reduced - from 67 % decrease in the first survey to 25 % by the second survey after the flood (Fig. 6a); note however that like the abundance data, number of species that are trees and vines in the seed bank are low (mean: 1–4 per m^2; see Table 2). It appeared that seed bank species richness of wetland plants were more affected by the flood compared to that of the terrestrial plants (Fig. 5b). The seed bank of both perennial and annual/biennial plants were also negatively affected by the flood, but the adverse effect was more pronounced in the perennial group (Fig. 5c). The flood negatively affected both invasive and non-invasive groups, but we could not detect any significant difference between the two sub-groups by the second post-flood survey (Fig. 5d). Likewise, the negative effect of the flood was more pronounced on seed bank richness of natives compared to those of the exotics (Fig. 5e). Again like the abundance data, the richness data suggested that the negative influence of the flood was more pronounced in the first post-flood survey (overall decrease across function types: 45 %) compared to the second survey period (autumn) (ca. 31 % decrease) (Fig. 5f).

Overall and relative effects of temporal and environmental factors on seed bank

Multivariate analyses confirmed many of the trends observed with the univariate ANOVA that seed bank abundance varied yearly, seasonally and in response to the flood. The ordination (MDS) and ANOSIM showed that the magnitude of differences in seed bank assemblage in relation to the factors examined was in the order: year effect > inundation effect > seasonal effect (Fig. 6), with Global R values of 0.653, 0.478, and 0.253, respectively. These effects were all significant (P < 0.001). Of the 32 families represented in the soil seed bank, only five families were major drivers of the differences observed due to the flood effect as indicated by ANOSIM (pre- vs. post-flood): Chenopodiaceae (Global R = 0.389); Asteraceae (Global R = 0.271); Solanaceae (Global R = 0.143); Poaceae (Globa R = 0.12); and Cyperaceae (Globa R = 0.108) (P < 0.02 in all cases).

SIMPER analyses showed a high average dissimilarity (64.0 %) between pre- and post-flood conditions (Table 3; Fig. 6b), both in spring and autumn seasons (data not presented). Notable weedy species driving this dynamics are: *Parthenium hysterophorus, Conyza, Argemone* and *Gamochaeta*; for native species these are *Crassula, Chenopodium, Wahlenbergia, Cyperus, Juncus, Pseudognaphalium* and *Oxalis*. A full list of species for which the differences in abundance between pre-flood and post flood conditions were highest is presented in Table 3. It should be noted that no particular species or functional group overwhelmingly drives the dichotomy, as contribution of each of the top 20 species was low, ranging between 1.6 and 2.5 %.F

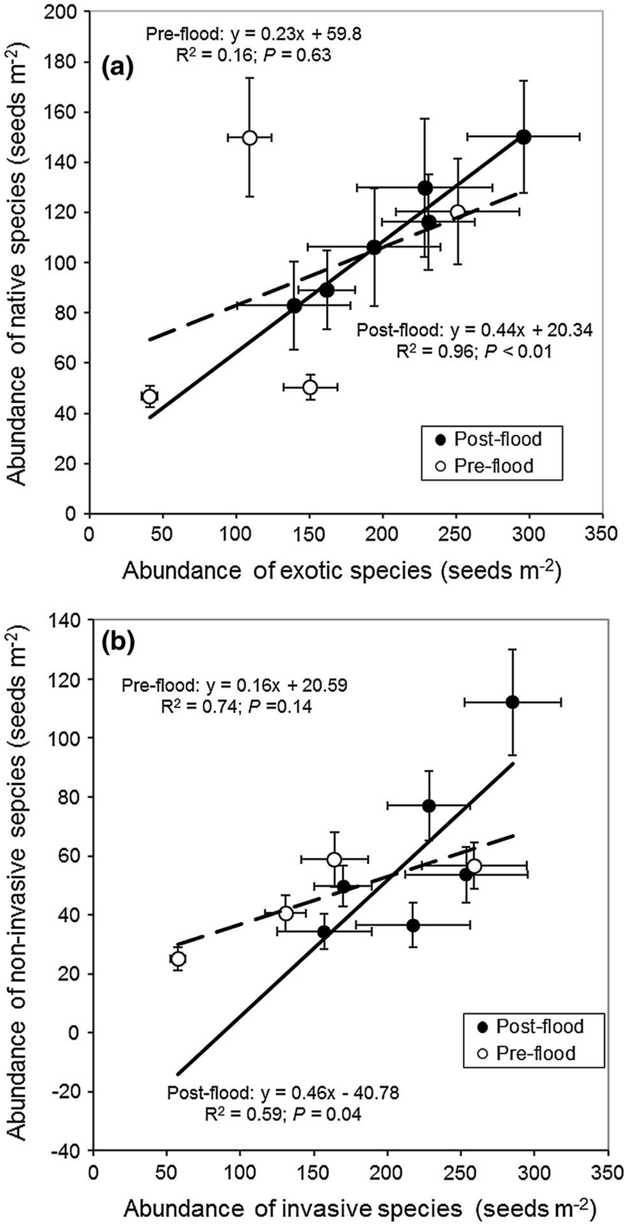

Fig. 4 Relationship between seed bank abundance of **a** native vs. exotic species, and **b** invasive vs. non-invasive species. Each point is the mean (±SE) data for a survey year (pre-flood), or location (post-flood). Significant trends (P < 0.05) are in *continuous lines*

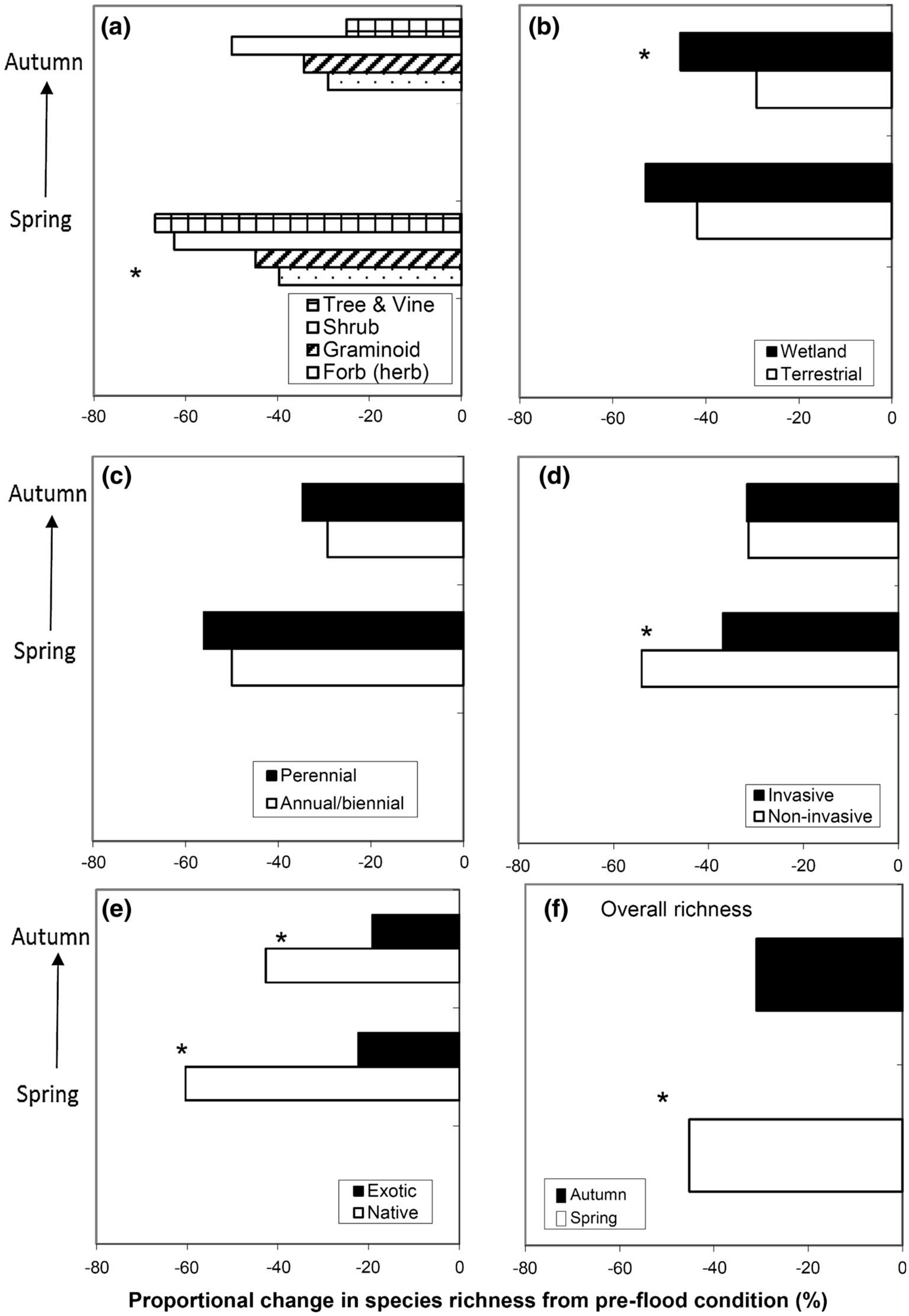

Fig. 5 Changes in seed bank richness of plant species function types at 10 months (spring) and 15 months (autumn) after the extreme flood event in Mooleyember creek, Central Queensland: **a** plant life form; **b** plant habitat; **c** plant longevity; **d** plant weedy status; **e** plant origin; and **f** overall performance at each season. *Asterisks* (*) refer to significant difference ($P < 0.05$) between functional types in their responses to the flood in a given season, except the last graph **f** that depicts differences between seasons. Arrow indicates increasing time since the flood

Discussion

Our seed bank density estimate is large ($>10{,}000$ seeds m^{-2}) but is similar to values reported in the literature both for riparian corridors and wetland habitats in general (e.g., Goodson et al. 2001; Siebentritt et al. 2004; Gerard et al. 2008). Soil seed bank homogeneity detected across the three disparate locations along the creek is not unusual despite heterogeneity in observed above ground vegetation (Osunkoya OO, unpublished data). Similar

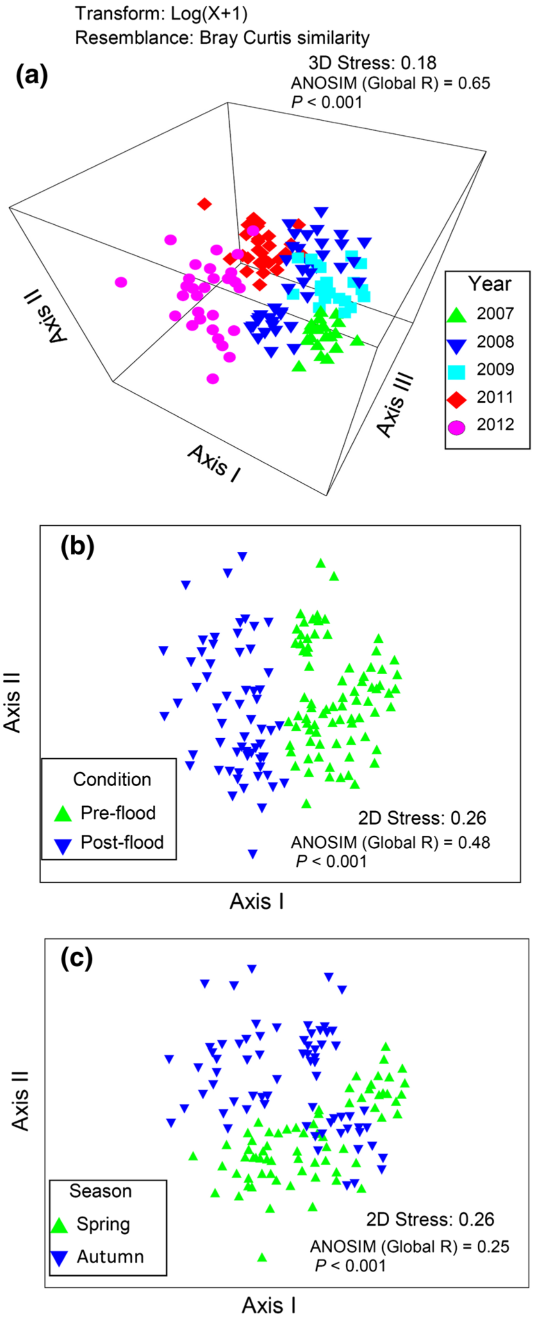

Fig. 6 Multidimensional scaling (MDS) ordination and analyses of similarity (ANOSIM) results of seed bank data for Mooleyember creek, Central Queensland based on **a** survey year, **b** flood condition, and **c** survey season. Flood condition and season representations are in two axes, but a 3D graph is presented for the year effect to show that an additional axis could portray the trend much better as stress is reduced from 0.26 to 0.18

trend has been observed in many wetland and other aquatic ecosystems (e.g., Haukos and Smith 1994; Capon and Brock 2006; Williams et al. 2008). This could be attributable to the widespread dispersal of propagules across the landscape by the floodwater, though we could not be completely certain of this assertion because of lack of similar data for the pre-flood periods.

The strong influence of season on our data set demonstrates the transient condition of many seeds in the soil. Many previous works have shown that both above and below ground plant communities of river and wetland systems can change sharply between seasons and years (Britton and Brock 1994; Navie et al. 2004; Capon 2005; Stromberg 2007). In general, in line with our hypothesis and trend reported elsewhere, seed bank appeared seasonally patterned with higher abundance and species richness occurring in late autumn/summer (when most plant species are reproductive and dispersing their seeds) and became depleted over winter-spring periods (Britton and Brock 1994; Goodson et al. 2001; Dhileepan 2012).

The ordination results indicate that flooding can influence seed bank dynamics, but its effect was much lower compared to that due to year-to-year variation. In the pre-flood years, there were periods of moisture stress (year 2007 and year 2009) and periods when moisture though not excessive was above the long-term average (year 2008) (Fig. 1). Such intermittent dry and wet spells are typical of most creeks and wetlands of inland central and western Queensland (Colloff and Baldwin 2010), and it is conceivable that the local flora over evolutionary time have adapted to such dynamics. Thus the excessive rainfall of late 2010, though created a major flood event in early January 2011, was not exceptional; consequently such a lack of uniqueness, coupled with long-term adaptation of riparian local flora to the stochasticity of water availability and hence disturbance, could account for the observed lower influence of flooding compared to yearly effect (see also Capon 2005; Capon and Brock 2006).

We sampled 10 months after the flood (spring/summer time), during which seed bank density was higher compared to the pre-flood period. This is often due to establishment and initiation of massive reproductive activity of new recruits from the seed bank (especially annuals; see Fig. 3), and/or from resprouting of vegetative remnants some of which could have re-stocked the soil following the initial post-flood germination flush (see Jutila 2001); it could also have resulted from transported seeds brought by drift with the creek inflow/flooding.

In contrast to abundance, we detected across functional groups, a significant reduction in species richness and diversity in response to the flood. Some studies of wetland, riverine and riparian vegetation (and seed bank) have also reported reduced richness after large magnitude floods perhaps due to large shearing stresses, scouring of vegetation and propagule sources (Smith et al. 1998; Hölzel and Otte 2004; Bagstad et al. 2005). The reduction in richness could also be due to seed mortality of certain functional/taxonomic group incapable of withstanding long period of anaerobic condition (Bilkovic et al. 2012).

Herbaceous and graminoid plants dominated the seed banks while propagule presence of structurally larger plants (i.e., trees and shrub) was low. Lower seed bank richness and abundance of trees and shrubs are not uncommon partly due to low diversity and abundance of

Table 3 SIMPLER analysis of Mooloyember creek, central Queensland, Australia seed bank data for pre- vs. post-flood periods

Species	Groups: pre-flood and post-flood Average dissimilarity = 64.03 %					
	Average abundance					
	Pre-flood	Post-flood	Av.Diss	Diss/SD	Contrib %	*P*
Crassula sieberiana	5.22	6.19	1.55	1.30	2.42	***
Chenopodium carinatum	3.98	0.00	1.50	1.56	2.34	***
Argemone mexicana$^{\text{inv-ex}}$	3.71	4.22	1.47	1.27	2.30	†
Wahlenbergia gracilis	1.50	4.07	1.40	1.22	2.18	***
Argemone ochroleuca$^{\text{inv-ex}}$	5.09	4.55	1.39	1.29	2.18	†
Parthenium hysterophorus$^{\text{inv-ex}}$	5.85	7.43	1.35	1.25	2.10	***
Cyperus gracilis	3.66	3.94	1.32	1.38	2.06	†
Juncus usitatus	6.17	4.46	1.27	1.24	1.99	†
Pseudognaphalium luteoalbum	4.42	3.71	1.25	1.26	1.95	**
Gamochaeta pensylvanica$^{\text{inv-ex}}$	6.85	5.26	1.23	1.10	1.92	**
Oxalis corniculata	5.06	2.68	1.23	1.39	1.91	***
Conyza sumatrensis$^{\text{inv-ex}}$	5.23	4.38	1.19	1.29	1.85	NS
Einadia trigonos	3.52	3.08	1.17	1.27	1.83	NS
Dysphania carinata	0.13	3.15	1.16	1.03	1.82	***
Hydrocotyle acutiloba	3.44	3.06	1.16	1.28	1.81	NS
Cyclospermum leptophyllum$^{\text{inv-ex}}$	1.54	2.84	1.07	1.08	1.67	NS
Cyperus difformis	2.85	0.79	1.05	1.06	1.65	***
Verbena litoralis$^{\text{inv-ex}}$	1.65	2.50	1.04	1.01	1.62	NS
Lepidium bonariense$^{\text{inv-ex}}$	1.14	2.71	1.02	1.05	1.59	**
Echinochloa colona$^{\text{inv-ex}}$	1.60	2.13	0.97	0.96	1.51	NS
Verbesina encelioides$^{\text{inv-ex}}$	2.47	1.27	0.96	1.08	1.51	NS
Conyza bonariensis$^{\text{inv-ex}}$	2.25	2.44	0.94	1.36	1.47	†
Austrostipa verticillata	2.35	1.35	0.93	1.01	1.45	NS
Wahlenbergia tenuifolia	2.44	0.00	0.92	0.79	1.44	***
Eragrostis cilianensis$^{\text{inv-ex}}$	2.39	1.01	0.91	1.08	1.42	*
Xanthium pungens$^{\text{inv-ex}}$	0.94	2.44	0.90	1.16	1.40	***
Cynodon dactylon$^{\text{inv-ex}}$	1.82	1.75	0.90	0.99	1.40	NS
Sida rhombifolia$^{\text{inv-ex}}$	1.60	2.24	0.88	1.09	1.37	*
Centipeda minima	2.15	1.56	0.84	1.21	1.32	NS
Wahlenbergia tumidifructa$^{\text{inv-ex}}$	1.74	1.33	0.82	0.98	1.28	NS
Nicotiana velutina	2.11	0.49	0.80	0.94	1.25	NS
Urochloa panicoides$^{\text{inv-ex}}$	0.26	2.04	0.78	0.76	1.22	NS
Sporobolus elongatus	1.51	1.08	0.74	0.81	1.16	NS
Chloris divaricata	0.20	1.85	0.71	0.81	1.11	***
Glandularia aristigera$^{\text{inv-ex}}$	1.65	1.00	0.71	0.93	1.10	NS
Malvastrum coromandelianum$^{\text{inv-ex}}$	1.00	1.55	0.69	1.06	1.07	**
Bidens pilosa$^{\text{inv-ex}}$	0.17	1.82	0.68	1.16	1.07	***
Schenkia spicata	1.75	0.54	0.67	0.89	1.05	NS
Portulaca pilosa$^{\text{inv-ex}}$	1.18	1.25	0.67	0.85	1.05	NS
Digitaria ciliaris$^{\text{inv-ex}}$	1.16	1.12	0.62	0.90	0.96	NS
Heliotropium amplexicaule$^{\text{inv-ex}}$	0.28	1.58	0.61	0.72	0.95	***
Eragrostis parviflora	1.25	0.67	0.57	0.74	0.89	NS
Portulaca oleracea$^{\text{inv-ex}}$	0.58	1.30	0.56	0.69	0.88	†
Malvastrum americanum$^{\text{inv-ex}}$	1.42	0.13	0.56	0.70	0.87	***
Cyperus sesquiflorus$^{\text{inv-ex}}$	1.41	0.28	0.55	0.74	0.87	**
Digitaria didactyla$^{\text{inv-ex}}$	0.12	1.44	0.55	0.57	0.86	***
Sporobolus creber	1.22	0.44	0.53	0.70	0.83	*
Einadia nutans	0.59	1.17	0.53	0.83	0.83	**
Dysphania pumilio	0.54	1.16	0.53	0.80	0.82	NS
Verbena gaudichaudii	0.47	1.19	0.52	0.71	0.81	**
Cenchrus ciliaris$^{\text{inv-ex}}$	0.36	1.20	0.50	0.71	0.78	NS
Eragrostis elongata$^{\text{inv-ex}}$	0.73	0.84	0.47	0.65	0.74	NS
Eriochloa procera	0.68	0.88	0.47	0.76	0.73	NS
Cyperus polystachyos	1.30	0.00	0.46	0.64	0.72	***
Solanum nodiflorum$^{\text{inv-ex}}$	0.00	1.24	0.45	0.64	0.71	***
Wahlenbergia stricta	1.13	0.12	0.45	0.59	0.71	**
Verbena bonariensis	1.20	0.00	0.45	0.50	0.69	***
Rumex brownii	0.40	0.86	0.42	0.56	0.66	†
Paspalum distichum	0.60	0.65	0.41	0.54	0.64	NS
Senecio pinnatifolius	1.07	0.10	0.40	0.59	0.63	***
Solanum nigrum$^{\text{inv-ex}}$	0.21	0.96	0.40	0.64	0.62	***
Fimbristylis dichotoma	0.83	0.27	0.38	0.56	0.59	NS

Table 3 continued

Species	Groups: pre-flood and post-flood Average dissimilarity = 64.03 %					
	Average abundance					
	Pre-flood	Post-flood	Av.Diss	Diss/SD	Contrib %	*P*
Verbena rigida^{inv-ex}	0.16	0.93	0.38	0.56	0.59	**
Physalis lanceifolia^{inv-ex}	0.06	0.98	0.37	0.53	0.57	***
Gomphrena celosioides^{inv-ex}	0.35	0.71	0.36	0.60	0.56	NS
Cotula australis	0.40	0.72	0.35	0.64	0.55	†
Typha domingensis	0.79	0.19	0.34	0.54	0.52	†
Melaleuca sp.	0.42	0.55	0.32	0.54	0.50	NS
Scoparia dulcis^{inv-ex}	0.74	0.05	0.30	0.42	0.46	*

Values are average abundance ranking (rare-1; common-2; very common-3; >4 dominant) and the contribution (%) to the dissimilarity between the two survey periods. Invasive and/or exotic species are indicated by superscript (inv-ex) next to their names.

Diss dissimlarity, *SD* standard deviation. *P* refers to probability of a significant difference between pre-flood and post-flood using non-parametric independent *t* test, *NS* not significant

* $P < 0.05$; ** $P < 0.02$; *** $P < 0.001$;

†$P < 0.10$

large above ground plants in riparian corridors (Capon and Brock 2006).

Though seed bank abundance was higher for exotic and invasive species compared to native and non-invasive species, but a near linear positive relationship was detected between the two groups, especially for the post-flood dataset (Fig. 4)—suggesting that seeds of both groups of plants responded in a similar manner to the flood disturbance. Both groups also contributed to the pre-vs. post-flood dichotomy observed in the ordination space (Table 3). Hence it could be argued that the exotic species are not necessarily major drivers of the riparian zone in this landscape (MacDougall et al. 2005). This finding buttressed Catford's et al. (2011) assertion that while exotic/invasive species will no doubt establish between floods, inundation (through its scouring effect) will ensure that the group does not dominate the wetlands (including riparian corridors) for decades at a time and might even provide opportunity for native riparian plants to regenerate and disperse (see also Siebentritt et al. 2004; Lunt et al. 2012). However, the resiliencies of the invasive/exotic species as ecological groups were much higher than that of the non-invasive/native species (see Figs. 3, 5), which over a longer time might translate to their increasing dominance in the riparian landscape.

Synthesis, management applications, caveats and conclusions

We lack replication of site (i.e., creek) for this study. Thus future work on flood impact on riparian ecosystems will need to examine more sites and locations to increase robustness of the findings. Nonetheless, as we sampled same locations over several years and seasons, we can retain some confidence that findings can be generalise to other creek systems. We analysed seed bank by the seedling emergence method (Roberts 1981)—a technique considered appropriate by many for determining germinable soil seed bank (e.g., Capon and Brock 2006). However it is quite possible that we failed to account for total viable soil seed bank (see Ter-Heerdt et al. 1996; Bernhardt et al. 2008), due to inability of our germination method (a moist watering method) to break dormancy of certain group of seeds, e.g., species that require complete submergence for germination.

In conclusion, the low presence of seeds of long-lived plants (i.e., shrubs and trees) in the soil germination trials reported, suggests, as in many studies of riparian zones (e.g. Capon et al. 2006; Greet et al. 2012) that species of these life-form groups cannot rely on buried seeds for recruitment. Rather the riparian corridors will benefit from influx of tree and shrub propagules from the surrounding landscape and/or from assisted regeneration for desired biodiversity. Though we have shown that extreme flood will impact seed bank signature of riparian corridors, it does not necessarily promote the proliferation of exotic invasive over native species, perhaps in part due to scouring effect of the rare event, and perhaps in part due to isolation of the focal riparian vegetation from human habitation. The proportional change due to the flood was in opposite direction for abundance and species richness, (Figs. 3, 5), but in both indices the magnitude of the differences in pre- and post-flood data had decreased with time from 45 to 70 % at 11 months to ca. 20 % at 14 months after the disturbance. Though it is difficult to disentangle seasonal effect as a co-contributing factor to this reduced effect with time, our finding is in line with the suggestion by Wetzel et al. 2004 and Bilkovic et al. 2012 that changes associated with drought and floods tend to be temporary. Ward et al. (1998) note that the generally high resilience of lotic ecosystems to disturbance is attributable, in part, to high spatio-temporal heterogeneity; and also because habitat patches less affected by a particular perturbation may serve as refugia from which survivors may recolonize more severely affected areas. Thus it is safe to infer that seed bank assemblage at the Mooleyember creek show resilience to the extreme flood event. No doubt to justify this assertion, additional longer-time data beyond two years after the flood may be required.

Acknowledgments Initial operational fund for this research was provided by the Vietnamese Government (Project 322), the Queensland Murray Darling Committee and the University of Queensland. We thank Queensland Government for providing travel and research fund for the post-flood survey and monitoring work.

References

Adkins SW, Navie SC, McFadyen RE (1996) Control of Parthenium weed (*Parthenium hysterophorus* L.): a centre for tropical pest management team effort. In: Shepherd RCH (ed). Proceedings, 11th Australia Weeds Conference, Weed Science Society, Victoria, Australia pp 573–578

Bagstad KJ, Stromberg JC, Lite SJ (2005) Response of herbaceous riparian plants to rain and flooding on the San Pedro River, Arizona, USA. Wetlands 25:210–223

Baskin CC, Seeds Baskin JM (2001) Ecology, biogeography, and evolution of dormancy and germination. Academic Press, London

Bernhardt KG, Koch M, Kropf M, Ulbel E, Webhofer J (2008) Comparison of two methods characterising the seed bank of amphibious plants in submerged sediments. Aquat Bot 88:171–177

Bilkovic DM, Mitchell MR, Hershner CH, Havens KJ (2012) Transitional wetland faunal community characterization and response to precipitation-driven salinity fluctuations. Wetlands 32:425–437

Britton DL, Brock MA (1994) Seasonal germination from wetland seed banks. Aust J Mar Fresh Res 45:1445–1458

Capon SJ (2005) Flood variability and spatial variation in plant community composition and structure on a large arid floodplain. J Arid Environ 60:283–302

Capon SJ, Brock MA (2006) Flooding, soil seed bank dynamics and vegetation resilience of a hydrologically variable desert floodplain. Freshw Biol 51:206–223

Catford JA, Downes BJ, Gippel CJ, Vesk PA (2011) Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. J Appl Ecol 48:432–442

Clarke KR, Gorley RN (2006) Primer v 6:User manual/ Tutorial. PRIMER-E, Plymouth

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analyses and interpretation, 2nd edn. PRIMER-E, Plymouth

Colloff MJ, Baldwin DS (2010) Resilience of floodplain ecosystems in a semi-arid environment. Rangeland J 32:305–314

Dhileepan K (2012) Reproductive variation in naturally occurring populations of the weed *Parthenium hysterophorus* (Asteraceae) in Australia. Weed Sci 60:571–576

Gerard M, El-Kahloun M, Mertens W, Verhagen B, Meire P (2008) Impact of flooding on potential and realised grassland species richness. Plant Ecol 194:85–98

Goodson JM, Gurnell AM, Angold PG, Morrissey IP (2001) Riparian seed banks: structure, process and implications for riparian management. Prog Phys Geog 25:301–325

Greet J, Cousens RD, Webb JA (2012) More exotic and fewer native plant species: riverine vegetation patterns associated with altered seasonal flow patterns. River Res Appl 29:686–706

Haukos DA, Smith LM (1994) Composition of seed banks along an elevational gradient in playa wetlands. Wetlands 14:301–307

Hölzel N, Otte A (2004) Inter-annual variation in the soil seed bank of flood-meadows over two years with different flooding patterns. Plant Ecol 174:279–291

Hussey BMJ, Keighery GJ, Cousens RD, Dodd J, Lloyd SG (1997) Western weeds: A guide to the weeds of western Australia. Plant Protection Council of Western Australia Inc., Perth

Ilg C, Dziock F, Foeckler F, Follner K, Gerisch M, Glaeser J, Rink A, Schanowski A, Scholz M, Deichner O, Henle K (2008) Long-term reactions of plants and macro-invertebrates to extreme floods in floodplain grasslands. Ecology 89:2392–2398

Jutila HM (2001) Effect of flooding and draw-down disturbance on germination from a seashore meadow seed bank. J Vege Sci 12:729–738

Kehr JM, Merritt DM, Stromberg JC (2014) Linkages between primary seed dispersal, hydrochory and flood timing in a semi-arid region river. J Vege Sci 25:287–300

Lunt ID, Jansen A, Binns DL (2012) Effects of flood timing and livestock grazing on exotic annual plants in riverine floodplains. J App Ecol 49:1131–1139

MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86:42–55

Martinez-Duro E, Luzuriaga AL, Ferrandis P, Escudero A, Herranz JM (2011) Does aboveground vegetation composition resemble soil seed bank during succession in specialized vegetation on gypsum soil? Ecol Res 27:43–51

Naiman RJ, Decamps H (1997) The ecology of interfaces: riparian zones. Ann Rev Ecol Syst 28:621–658

Navie SC, Panetta FD, McFadyen RE, Adkins SW (2004) Germinable soil seed banks of central Queensland rangelands invaded by the exotic weed *Parthenium hysterophorus* L. Weed Biol Manag 4:154–167

Nguyen TLT (2011) The invasive potential of Parthenium weed (*Parthenium hysterophorus* L.) in Australia. PHD Thesis, University of Queensland, Australia

Nilsson C, Brown RL, Jansson R, Merritt DM (2010) The role of hydrochory in structuring riparian and wetland vegetation. Biol Rev 85:837–858

Osunkoya OO, Polo C, Andersen AN (2011) Invasion impacts on biodiversity: responses of ant communities to infestation by cat's claw creeper vine, *Macfadyena unguis-cati* (Bignoniaceae) in subtropical Australia. Biol Invasions 13:2289–2302

QLD Dept of NRWM (2011) Queensland government, Australia water monitoring program Available at http://www.watermonitoring.derm.gov.au. Accessed Dec 2013

Queensland Government (2011) Queensland Floods Commission of Inquiry: Interim report, Brisbane, Queensland, Australia Available at http://www.floodcommission.qld.gov.au. Accessed 22 Nov 2013

Reid MA, Quinn GP (2004) Hydrologic regime and macrophyte assemblages in temporary floodplain wetlands, implications for detecting responses to environmental water allocations. Wetlands 2:586–599

Roberts HA (1981) Seed banks in the soil. Adv Appl Biol 6:1–55

Siebentritt MA, Ganf GG, Walker KF (2004) Effects of an enhanced flood on riparian plants of the River Murray, South Australia. River Res Appl 20:765–774

Smith MP, Keevin P, Mettler-McClure P, Barkau R (1998) Effect of the flood of 1993 on *Boltonia decurrens*, a rare floodplain plant. Regul Rivers Res Manag 141:91–202

Stanley TD, Ross EM (1983–1995) Plants of South-east Queensland, vol 1–3. Queensland Government, Brisbane, Australia

Stromberg JC (2007) Seasonal reversals of upland-riparian diversity gradients in the Sonoran Desert. Divers Distrib 13:70–83

Stromberg JC, Richter BD, Patten DT, Wolden LG (1993) Response of a Sonoran riparian forest to a 10-year return flood. Great Basin Nat 53:118–130

Stromberg JC, Boudell JF, Hazelton AF (2008) Differences in seed mass between hydric and xeric plants influence seed bank dynamics in a dryland riparian ecosystem. Funct Ecol 22:205–212

Ter-Heerdt GNJ, Verweij GL, Bekker RM, Bakker JP (1996) An improved method for seed bank analysis: seedling-emergence after removing the soil by sieving. Funct Ecol 10:144–151 van den Honert RC, McAneney J (2011) The 2011 Brisbane floods: causes, impacts and implications. Water 3:1149–1173

Ward JV, Bretschko G, Brunke M, Danielopol D, Gibert J, Gonser T, Hildrew AG (1998) The boundaries of river systems: the metazoan perspective. Freshw Biol 40:531–569

Welleck S (2003) Testing statistical hypotheses of equivalence. Chapman Hall, London

Wetzel PR, Kitchens WM, Brush JM, Dusek ML (2004) Use of a reciprocal transplant study to measure the rate of plant community change in a tidal marsh along a salinity gradient. Wetlands 24:879–890

Williams L, Reich P, Capon SJ, Raulings E (2008) Soil seed banks of degraded riparian zones in southeastern Australia and their potential contribution to the restoration of understorey vegetation. River Res Appl 24:1002–1017