PLANT COMMUNITY RESPONSES TO WETTING AND DRYING IN A LARGE ARID FLOODPLAIN

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ABSTRACT

The flow regimes of large arid river catchments are amongst the most variable in the world. Plant communities which inhabit arid floodplains typically exhibit high spatial heterogeneity and are temporally dynamic in response to changing flow conditions. It has been suggested that arid floodplain ecosystems, adapted as they are to variability, will be relatively resilient to anthropogenic alterations to flow. This paper argues that floodplain plant communities in arid catchments, as in temperate and tropical regions, are primarily structured by flow regimes despite their inherent unpredictability. Consequently, changes to flood pulses through water extraction can be expected to result in changes in vegetation composition and structure which in turn may have a dramatic effect on wider ecosystem functioning. Results are presented from an ongoing study of the Cooper Creek floodplain in central Australia which illustrate the relationships between plant community dynamics and variable flood pulses. These results indicate that alterations to flow may result in a shift in community structure and an eventual loss of biodiversity. It is essential, therefore, that water resource managers in arid regions consider the requirements of floodplain plant communities when allocating environmental flows. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: arid floodplains; plant ecology; flood pulses

INTRODUCTION

Environmental flow requirements of large floodplain river catchments include those which sustain processes and biota of what are traditionally considered to be terrestrial systems. Floodplains can more appropriately be conceived of as riparian systems or aquatic–terrestrial ecotones (Gregory et al., 1991). Plant communities of temperate and tropical floodplains are structured primarily by flow (Conner et al., 1981; Hupp and Osterkamp, 1985; Menges, 1986; Walker et al., 1986; Blom et al., 1990; Pautou and Arens, 1994; Trebino et al., 1996; Ferreira, 1997; Hughes and Cass, 1997; Ferreira and Stohlgren, 1999). Alterations to flow, through river regulation and water extraction, therefore can result in widespread changes in vegetation (Conner et al., 1981; Bren, 1992; Friedel et al., 1993; Davies et al., 1995; Kingsford and Thomas, 1995).

Such observations concur with the predictions of the flood pulse concept (Junk et al., 1989) whereby organisms are adapted to hydrological attributes, e.g. flood pulse timing, duration, size, etc., which are, in temperate and tropical catchments, reasonably regular and to some extent predictable. In these catchments, the flow requirements of healthy riparian plant communities may include, for instance, a particular seasonality in flooding or a slow drawdown of the flood pulse (Blanch et al., 1996).

Relatively few studies, however, have investigated the occurrence of similar linkages in large arid floodplain catchments which have amongst the most variable hydrological characteristics in the world (Puckridge et al., 1998). The original presentation of the flood pulse concept suggests that floodplain biota in arid catchments are unlikely to exhibit adaptations to flood pulse attributes due to this inherent variability (Junk et al., 1989). What, therefore, are the potential impacts of anthropogenic alterations to such variable flow regimes in large arid floodplain catchments?

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This paper aims to explore the flow-related responses of plant communities in a large arid floodplain, compare these to patterns observed in temperate and tropical catchments and finally to make suggestions concerning the likely impacts, if any, of alterations to flow. These aims have been approached using a conceptual framework adapted from existing models of floodplain vegetation dynamics described below.

Plant communities and floodplain gradients

The models of vegetation dynamics which have been developed through studies of temperate and tropical floodplains can be summarized as ‘gradient models’. Flooding frequency and duration create complex hydrological gradients across the floodplain, along which plant communities can be found in predictable locations (Hughes, 1988). Common features of these gradients include dominance by a few flood-tolerant species in near-channel or frequently flooded zones, versus communities structured predominantly by competition at the edge of the floodplain or least frequently flooded zones (Pautou and Arens, 1994; Blom and Voesnek, 1996; Trebino et al., 1996). Similarly, annual and perennial species have been found to dominate the wetter and drier areas respectively (Menges, 1986; Trebino et al., 1996).

These models imply a kind of successional development in floodplain plant communities, early successional species appearing in response to flooding and successional processes continuing during periods of drying (Junk et al., 1989; Walker et al., 1986). Consequently, a large flood could be expected to ‘reset’ these processes and homogenize plant associations across the floodplain. Subsequent floods of a smaller size and duration would therefore maintain early successional communities in near-channel zones and allow communities in the middle and edges of the floodplain to diverge.

The gradient of flooding intensity employed by floodplain vegetation models could alternatively be perceived as two opposing gradients of wetting and drying intensity. Plant communities in wetter zones are therefore structured by processes associated with flooding, e.g. germination of flood-tolerant species and mortality of flood-intolerant species, whilst drying-related processes, e.g. competition, mortality of drought-intolerant species etc., structure plant associations at the other extreme. This model could provide a useful conceptual framework for predicting the outcomes of alterations to flow. Given that water extraction will, in most cases, result in a reduction of flows reaching the floodplain environment, the dominance of drying processes over those associated with wetting could be expected. Subsequently, shifts in vegetation composition and structure would follow.

The study presented in this paper explores plant community responses to several wetting and drying phases in a large arid floodplain in central Australia and suggests how alterations to the flow regime could potentially affect spatial patterns in the vegetation.

METHODS

Study area

The Cooper Creek catchment is located in arid inland Australia (Figure 1). With an area of 296 000 km², the majority of the catchment receives less than 400 mm average annual rainfall (Queensland Department of Natural Resources, 1998). Hydrologically, Cooper Creek is thought to be one of the world’s most variable rivers (Puckridge et al., 1998). Flows fluctuate unpredictably between long periods of drought, including 21 months of zero flows from 1951 to 1952, and huge floods (Figure 2). The mean annual discharge at the Curraheva gauging station is approximately 3 320 000 Ml (Queensland Department of Natural Resources, 1998), but annual discharges as high as 23 \times 10^8 Ml, in 1974, have also been recorded. During large floods the anastomosing distributary channels facilitate the inundation of vast areas, often for considerable lengths of time. The flood event of 1990, for example, inundated a total area of 25 900 km² (Queensland Department of Natural Resources, 1998). Floodplain soils of cracking grey and brown clays occupy almost one-third of the catchment (Graetz, 1980) and the floodplain spans approximately 60 km at its widest point.

Woody vegetation in the Cooper Creek floodplain is mostly restricted to the margins of more permanently watered channels. The majority of the floodplain is composed of short grass and forb associations with scattered
Figure 1. Map of the study area. The inset illustrates the location of the catchment in central Australia. The approximate locations of field survey sites are indicated.

Figure 2. Annual discharges recorded at the Windorah gauging station, Cooper Creek (source: figure obtained from Queensland Department of Natural Resources).

communities of *Muehlenbeckia florulenta* (lignum) and *Chenopodium auricomum* (Queensland bluebush). During favourable times, the floodplain provides some of the world’s best cattle fattening pasture and cattle grazing is the predominant land-use throughout the catchment. The Cooper Creek catchment provides an ideal location for studying processes associated with a natural flow regime in a large arid floodplain, as little water extraction currently occurs.

**Field surveys**

Twelve sites, each comprising a $50 \text{ m} \times 50 \text{ m}$ quadrat, were selected for the field surveys across a spatial gradient with four sites at each of three broad locations: (1) Near Channel, (2) Mid Floodplain and (3) Far Floodplain (Figure 1). Except for sparsely scattered *Eucalyptus coolibah* (Coolibah) across the floodplain, woody vegetation was absent from all sites.

At each site, the field survey consisted of recording percentage cover of every species within ten $1 \text{ m} \times 1 \text{ m}$ random quadrats. These smaller quadrats were positioned away from any trees. The survey was repeated five times over a 19 month period in February, May and October 2000 and May and October 2001. A large flood event, inundating all sites, preceded the May 2000 survey (Figure 3a). The smaller flood event, prior to the May 2001 survey, inundated the Near Channel and Mid Floodplain sites only. The magnitude of this event gave significantly shorter duration of inundation. Very little rainfall or flow occurred during the winter months of either 2000 or 2001 and at the time of the October surveys in both years, the catchment was considered to be in a state of drought (Figure 3b). Conditions preceding the first survey were reasonably wet as a small flood was received in late 1999 (Figure 3a). All sites were subjected to cattle grazing throughout the survey period.

![Figure 3. Discharge and rainfall received in the upper Cooper Creek preceding and during the field surveys. (a) Total monthly discharge recorded at Longreach on the Thomson River (source: data obtained from Queensland Department of Natural Resources. Note that the Windorah gauging station ceased to operate after 1988, consequently these are the best figures available). (b) Total monthly rainfall recorded at Windorah](image-url)
Data analysis

Patterns in plant community data from across the floodplain were explored using multivariate statistics in the PATN software package (Belbin, 1995). The presence/absence of a species at a site for all survey times was used as the database with the Bray–Curtis coefficient used as the measure of dissimilarity between sites. Semi-strong hybrid multidimensional scaling (SSH) ordinations were computed from the Bray–Curtis similarity matrix. Solutions were calculated in three dimensions. The two-dimensional solution presented here had a stress of 0.168. The stress measure gives an indication of the ‘goodness of fit’ for the ordination. Mean Bray–Curtis distances between sites for each of the five survey times were also calculated. One-way analysis of variance (ANOVA) was then used to determine if sites were significantly closer in the ordination space at any of the survey times.

Presence/absence data provide no information on the extent of cover and do not distinguish between more complex attributes at each site. To allow a more thorough comparison of the plant community at each site the total dataset was split into plant groups: shrubs, hydrophytes, annual grasses, perennial grasses, legumes and non-leguminous forbs. Species were assigned to these plant types using major lifeform classifications described in Cunningham et al. (1992); aquatic species including Cyperus spp. and Marsilea drummondii, or nardoo, were grouped as hydrophytes. At each site, an index of cover for each plant group was calculated by summing the total cover percentages of all species within each group across all ten 1 m × 1 m quadrats. This was necessary due to vertically overlapping plant layers and to avoid working with percentages greater than 100. An index of total cover was calculated similarly from the cumulative total of all covers recorded within the site. Cover indices were then transformed \( \log_{10}(x + 1) \) in order to reduce the heteroscedasticity of the data required under the assumptions of ANOVA (Zar, 1999). Two-way ANOVAs were performed on each cover index with location (i.e. Near Channel, Mid Floodplain and Far Floodplain) and survey time as factors. The statistics package SPSS was used (SPSS, 1999). Due to highly significant interaction terms in half of the cases, the data file was split and one-way ANOVAs were subsequently conducted for each location with survey time as the factor. The Student–Newman–Keuls post-hoc test was used to determine which means differed significantly. Similar analyses were conducted for species richness.

RESULTS

Floristics

Eighty-two species belonging to 31 families were recorded throughout the survey period. At all survey times, grasses were by far the most common pasture component. Dominant grass species included the annuals Echinochloa turnerana (channel millet) and Iseilema spp. (Flinders grasses), and the perennials Eragrostis spp. and Sporobolus spp. The aquatic fern, Marsilea drummondii (nardoo) was widespread across all sites at each survey time. Other frequently occurring hydrophytic species included members of Cyperaceae. A scattered shrub layer, mostly consisting of Muehlenbeckia flordentia (lignum), Chenopodium auriculum (Queensland bluebush) and other chenopods was recorded, predominantly in the Mid Floodplain sites. Leguminous forb species included Trigonella suavissima (Cooper clover), Aeschynomene indica (budda pea) and Cullen cinerea. Non-leguminous forb species belonging to Euphorbiaceae, Goodeniaceae, and Asteraceae, particularly during the winter surveys, were also prevalent.

Trends in community composition in relation to wetting and drying

Ordination of the species’ presence/absence data highlighted the community response to flooding (Figure 4). The trajectories suggest that sites from all floodplain locations responded similarly to wetting and drying. The Near Channel and Mid Floodplain sites, which both received two floods during the survey time, mimic each other in their movement through the ordination space. The Far Floodplain sites, which were not inundated in the second year, follow this pattern until the fourth survey time where they diverge from the remaining sites. Sample points within the ordination space have also separated with relation to wet and dry survey times. The lower right diagonal portion of the ordination contains sites from all locations which were surveyed after the two drought periods as well as the Far Floodplain sites at the fourth survey time (Figure 4). This ordination suggests that sites become more similar to each other after receiving equivalent wetting and drying treatments. This similarity is statistically

significant \( (p < 0.05) \) as shown in Table I. This analysis indicates that sites across the floodplain were most divergent from each other at the fourth survey time when only some locations had been inundated.

**Trends in total cover and species richness with relation to wetting and drying**

Species richness and total cover were both found to change significantly with survey time although this was dependent on the floodplain location (Table II). Changes in species richness (Figure 5a), were not found to relate clearly to wetting or drying during the survey period. However, there was a trend for higher species richness in the first two survey times which was significant in the Near Channel sites (Table III). This may be due to the generally wetter conditions experienced during and preceding these surveys.

There was a significant difference \( (p < 0.05) \) in total cover over time (Table III), with increases and decreases in cover uniformly corresponding to wetting and drying respectively (Figure 5b). The exception was the Far Floodplain sites where, interestingly, total cover increased with the extended period of drying between the third and last surveys. However, this response was not significant.

**Trends in cover of plant types with relation to wetting and drying**

Cover in most plant types displayed significant changes over the survey time (Tables II and III). Annual grass cover increased with wetting and decreased with drying at all locations (Figure 6a). This response was significant.

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**Table I.** Mean (± standard error) Bray–Curtis distances between sites at each survey time

<table>
<thead>
<tr>
<th>Survey time</th>
<th>Mean Bray–Curtis distance</th>
<th>Homogenous subset*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Feb 2000</td>
<td>0.475202 ± 0.018231</td>
<td>b</td>
</tr>
<tr>
<td>2. May 2000</td>
<td>0.348648 ± 0.014613</td>
<td>a</td>
</tr>
<tr>
<td>3. Oct 2000</td>
<td>0.391385 ± 0.014469</td>
<td>a</td>
</tr>
<tr>
<td>4. May 2001</td>
<td>0.605942 ± 0.023233</td>
<td>c</td>
</tr>
<tr>
<td>5. Oct 2001</td>
<td>0.458450 ± 0.018543</td>
<td>b</td>
</tr>
</tbody>
</table>

* Determined by Student–Newman–Keuls post-hoc test \( (p < 0.05) \).
in Far Floodplain sites where annual grass cover decreased dramatically over the last three surveys (Table III). Annual grass cover was also highest in the Near Channel sites and lowest in the Far Floodplain sites throughout the survey (Figure 6a). Comparatively, perennial grass cover was highest in the Far Floodplain sites (Figure 6b). With the exception of generally lower cover during the third survey time, perennial grass cover did not vary significantly with wetting or drying (Table III).

Hydrophyte cover behaved in a similar manner to that of annual grasses, with increases and decreases in cover corresponding to wetting and drying respectively (Figure 6c). This was significant ($p < 0.05$) in the Near Channel and Mid Floodplain sites (Table III). Cover of hydrophytic species was also highest in the Near Channel sites and lowest in the Far Floodplain sites.

Shrubs occurred mostly in the Mid Floodplain sites and these were significantly reduced in cover ($p < 0.05$; Table III) after the major flood at the second survey time (Figure 6d). The second smaller flood, however, did not affect shrub abundance (Figure 6d).

### Table II. F-statistics obtained from two-way ANOVAs of species richness and transformed total cover and plant group covers with survey time and location as factors

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Survey time (d.f. = 4, 45$^1$)</th>
<th>Location (d.f. = 2, 45$^1$)</th>
<th>Survey time × location (d.f. = 8, 45)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness$^1$</td>
<td>12.445*</td>
<td>0.307*</td>
<td>2.330*</td>
</tr>
<tr>
<td>Total cover$^2$</td>
<td>12.723*</td>
<td>2.812</td>
<td>3.945*</td>
</tr>
<tr>
<td>Annual grass cover$^2$</td>
<td>3.919*</td>
<td>13.948*</td>
<td>2.373*</td>
</tr>
<tr>
<td>Perennial grass cover$^2$</td>
<td>3.640</td>
<td>10.272*</td>
<td>1.986</td>
</tr>
<tr>
<td>Hydrophyte cover$^2$</td>
<td>82.808</td>
<td>10.030*</td>
<td>1.475</td>
</tr>
<tr>
<td>Shrub cover$^2$</td>
<td>5.174*</td>
<td>13.974*</td>
<td>0.720</td>
</tr>
<tr>
<td>Leguminous forb cover$^2$</td>
<td>1.310*</td>
<td>0.633*</td>
<td>4.149*</td>
</tr>
<tr>
<td>Non-leguminous forb cover$^2$</td>
<td>14.629*</td>
<td>0.830</td>
<td>1.237</td>
</tr>
</tbody>
</table>

*Significant at $p < 0.05$.

Figure 5. Changes in mean species richness (a) and total cover (b) at each location during the survey period (transformed total cover index is shown in (b)).

Table II. F-statistics obtained from two-way ANOVAs of species richness and transformed total cover and plant group covers with survey time and location as factors

not appear to affect shrub cover, perhaps due to a shorter duration of inundation. Forb cover, both leguminous (Figure 6e) and non-leguminous (Figure 6f), did not display any significant patterns related to wetting or drying, although a trend for increased legume cover in Near Channel and Mid Floodplain sites was evident during the wetter survey times (Table III).

**DISCUSSION**

*Plant community processes associated with wetting and drying*

The plant communities surveyed in this study exhibited significant responses to both the wetting and drying phases which occurred during the survey period. Flooding was found to have similar effects on plant communities at all sites regardless of their location on the floodplain, as was drying. This is demonstrated most clearly by the species presence/absence data (see Figure 4). Sites follow parallel paths within the ordination space after inundation and again with drying. Consequently, the temporal trajectories of the Near Channel and Mid Floodplain sites...
are comparable as both these locations received equivalent wetting and drying treatments during the study. The Far Floodplain sites diverge from a similar path only when further drying rather than inundation was received at the fourth survey time. These changes in plant community composition in response to wetting and drying can be attributed, in part, to patterns identified in the univariate analyses.

Plant community processes which can be uniformly associated with wetting, as indicated by this study’s results, include an increase in total cover. Cover of annual grasses and hydrophytes also increased with wetting. This concurs with observations of previous studies of floodplain grasslands where flooding has been found to induce increased productivity levels and, particularly, an increased abundance of graminoids (e.g. Insausti et al., 1999). These increases in cover would result from both germination from the soil seed bank and growth promoted by wetting. Many floodplain species are known to maintain large, persistent seed banks (Brock and Rogers, 1998; Blom et al., 1990) which may germinate in response to inundation. Colonizing vegetation appearing after inundation has previously been observed to regenerate primarily from the soil seed bank (Poiani and Johnson, 1989). In the Cooper Creek floodplain, therefore, it appears that wetting processes include the germination of large numbers of annual grasses and hydrophytes from the soil seed bank and probably high levels of productivity amongst these groups.

Mortality of shrubs also occurred in response to the large flood event in 2000. This is likely to be due to anoxia and the accumulation of toxic substances in the soil which results from prolonged flooding (Kozlowski, 1984). The shrub layer recovered during the remainder of the survey period and was not similarly affected by the second,
smaller inundation event. This indicates the importance and varying roles of flood pulses with different magnitudes. For instance, the removal of the shrub layer may have facilitated higher productivity in annual grasses and hydrophytes at this time than would otherwise have occurred.

Drying phases during this survey period corresponded with decreases in total cover (Figure 5b) and cover of annual grasses (Figure 6a) and hydrophytes (Figure 6c). This would be expected if these plant groups germinate and grow in response to wetting. Other plant types did not increase in cover with drying although total cover did appear to increase with extended drying, albeit not significantly, in the Far Floodplain sites. The ordination (Figure 4), however, demonstrates that species composition of the Far Floodplain sites diverged substantially from the other locations with continued drying. It is likely that a greater species pool adapted to drying conditions is present in these locations, including species which may invade from neighbouring dune communities (personal observation). These results infer that processes which respond to drying include the germination, colonization and growth of species adapted to such conditions in addition to reduced germination and growth of annual grasses and hydrophytes.

Effects of the flow regime on vegetation patterns across the floodplain

The composition of plant communities structured by wetting processes during the course of this survey was found to be reasonably distinct from the composition of those structured by drying processes. This is evident in the separation of sites on the basis of species presence/absence (Figure 4). Over time, the varying intensities of wetting and drying processes across the floodplain could be expected to create a spatial gradient along which plant community composition differs. As previously described, such patterns have been found in floodplains of numerous temperate and tropical floodplain catchments. In these floodplains, frequently flooded near-channel sites are often dominated by annual species and species which are flood-tolerant (Blom et al., 1990; Bren, 1992; Pautou and Arens, 1994; Blom and Voesnek, 1996; Lenssen et al., 1999; Trebino et al., 1996). Less frequently inundated zones are usually dominated by perennial species and are thought to be structured more by biotic processes such as competition (Blom and Voesnek, 1996; Trebino et al., 1996). The results of this study indicate that comparable patterns may also be present in variable arid floodplains and that these can be explained partly by the processes associated with wetting and drying described above. Although not tested for, annual grass cover and hydrophyte cover, shown to be associated with wetting processes, were found to be greatest in the Near Channel sites and lowest in Far Floodplain sites (Figure 6). Conversely, perennial grass cover was highest in the Far Floodplain sites. These results suggest that a spatial gradient amongst plant communities on an arid floodplain may well be created by the flow regime, despite its variability.

Differentiation of plant community composition across the floodplain gradient was found to be promoted by the variable wetting and drying regimes which were received by sites at the various locations. Sites were most similar to each other after the major flood event and most divergent when inundation was received by only some sites (see Table 1). If equivalent wetting and drying phases were experienced across the floodplain it is possible that plant community composition could converge. Variable flood pulses of arid floodplain catchments therefore maintain a heterogeneous mosaic of plant communities which are dynamic both temporally and spatially.

Potential impacts of water extraction

It is apparent from this study that both wetting and drying induce substantial responses amongst the Cooper Creek’s floodplain plant communities and that these have probably contributed to spatial patterns in the vegetation over time. Anthropogenic alterations to flow are therefore likely to have some impact on vegetation. Rather than following a successional gradient model, this study suggests that spatial patterns in floodplain vegetation can be perceived more simply as being determined by the prevalence of wetting versus drying processes. Water extraction would most often result in an increase in drying processes and a decrease in wetting processes. In the case of Cooper Creek, the effects of this could include a reduction in cover of annual grasses and hydrophytes in Near Channel and Mid Floodplain sites. Species adapted to drier conditions could be expected to colonize these zones from the Far Floodplain sites. Replacement of hydrophytic species by more mesic species has previously been recorded in studies of floodplains subjected to flow regulation (e.g. Kingsford and Thomas, 1995; Bren, 1992).
The predominance of drying processes in the Cooper Creek catchment, could lead to the convergence of community composition in Mid Floodplain sites with Far Floodplain sites. Hughes and Cass (1997) also predict that flow regulation would result in a narrowing and streamward migration of vegetation zones. Homogenization of floodplain plant communities could additionally occur through a reduction in the distribution of potential floras (Hughes and Cass, 1997). A decline in wetting processes occurring in Far Floodplain sites, for instance, may reduce the potential of these sites to respond to future inundation events, as soil seed banks of flood-tolerant species would not be maintained. The overall effects of water extraction would therefore include the loss of spatial and temporal heterogeneity amongst plant communities and eventually, local extinctions of hydrophytic species.

This study has found that both wetting and drying processes contribute to the structure of plant communities in this arid floodplain. Furthermore, spatial patterns in vegetation composition appear to reflect the intensities of these processes and such patterns are comparable to those observed in temperate and tropical catchments. Despite the inherent variability of arid zone flow regimes, water extraction could potentially have a dramatic impact on floodplain plant communities, and consequently, the wide range of ecological and economic values which these provide.

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