

The responses of floodplain primary production to flood frequency and timing

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Summary

1. River regulation and abstraction have dramatically altered the natural flow regime of many rivers world-wide, but experimental investigations of the biological effects are infrequent. In the mid-region of the Murray River, Australia, river regulation has reduced the frequency and duration of spring floods and increased the frequency of summer floods. We used controlled floods (treatments: no floods, spring floods, summer floods and spring + summer floods) to determine how the growth of river red gum *Eucalyptus camaldulensis* trees, aquatic macrophytes and biofilms varied with the seasonal timing and frequency of flooding.

2. After 6 years of controlled flooding, above-ground net production of wood by river red gum trees was equal and greatest in plots receiving spring + summer floods and summer floods (mean 496 g m⁻² year⁻¹). Production was significantly lower in plots receiving spring floods or no controlled floods, which had similar rates of production (mean 330 g m⁻² year⁻¹).

3. During 2 years of measurement in wetlands created by flooding, production and species richness of aquatic macrophyte were both greater in spring than in summer floods. The history of flood frequency at any experimental site did not affect macrophyte production or species richness. The aquatic macrophyte community in shallow regions of wetlands differed significantly with the seasonal timing of floods, but not flood frequency.

4. The accumulation of chlorophyll *a* and total mass of biofilm on wood surfaces in wetlands created by flooding were greater in spring (mean chlorophyll *a*, 0.88 µg cm⁻²; mean mass, 0.066 mg cm⁻²) than in summer floods (mean chlorophyll *a*, 0.09 µg cm⁻²; mean mass, 0.034 mg cm⁻²). The history of flood frequency at any experimental site did not affect accumulation of either the autotrophic or heterotrophic components of biofilms.

5. Spring flooding, while not as beneficial for tree growth, is critical for the growth of wetland macrophytes, the maintenance of macrophyte species richness, and favours better development of autotrophic biofilms. Maintenance of both the timber harvest and wetland conservation values of these floodplains will require the return of more natural flood flows in the spring period. Restoration of floodplain rivers requires a thorough understanding of the relationships between ecological functions and the natural flow regime.

Key-words: conservation, floodplain, flood regime, wetland primary production, wood production.

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Introduction

Floods provide the physical linkages between floodplain habitats and adjacent river channels that control

biogeochemical cycles and the structure of biotic communities of floodplain river systems (Welcomme 1979; Junk, Bayley & Sparks 1989; Ward 1998; Tockner *et al.* 1999). Alterations to the flow regime following damming and extraction of water from rivers have resulted in serious deterioration of floodplain river ecosystems world-wide (Dynesius & Nilsson 1994; Sparks 1995; Poff *et al.* 1997; Molles *et al.* 1998).

For floodplain habitats, primary production is closely related to the hydrological regime, and changes to flood frequency, seasonal timing and duration have marked impacts on patterns of production (Brinson 1990). In the Murray River in south-eastern Australia the impact of river regulation and extraction of water for agriculture varies along the length of the river (Maheshwari, Walker & McMahon 1995). In the floodplain regions below the main storage dams and until 300 km downstream, the highest flows now occur in summer rather than in spring, and there has been a significant reduction in the frequency of small and medium-sized floods in the spring. Flooding now occurs more frequently in summer than it did prior to river regulation (Bren 1988).

The vegetation of the floodplains in this region is dominated by the river red gum *Eucalyptus camaldulensis* Denhn., which occurs in almost pure stands in areas subject to frequent flooding (Smith & Smith 1990). The largest natural red gum forest in the world, the 60 000-ha Barmah–Millewa forest complex, occurs on the upper Murray River floodplain. The forest has been subject to forest management for timber production since late last century (Donovan 1997). The Barmah Forest is listed as a wetland of international significance (Frazier 1999), and the Barmah–Millewa forest complex has national and regional significance for the conservation of biota and river function (Mackay & Eastburn 1990; Sharley & Huggan 1994; Robertson *et al.* 1999).

Litter and wood from red gum trees contribute significant dissolved and particulate organic matter to riverine food chains, and provide important habitat structure for a variety of biota (Briggs & Maher 1983; O'Connor 1992; Briggs, Maher & Tongway 1994; Lake 1995; Crook & Robertson 1999; Glazebrook & Robertson 1999; Robertson *et al.* 1999; O'Connell *et al.* 2000; Robinson & Robertson, in press). In low-lying areas of these floodplains numerous wetlands support abundant aquatic macrophytes and autotrophic biofilms that provide habitat and food for biota and exert significant influences on riverine material cycles (Briggs & Maher 1985; Sorrell & Boon 1992; Scholz & Boon 1993; Briggs, Thornton & Lawler 1997; Healey, Thompson & Robertson 1997; Robertson *et al.* 1999).

Alterations to the flow regime and other factors, such as grazing by livestock and the feeding activities of exotic fish, have contributed to shifts in the distribution patterns of vegetation among habitats (Dexter, Rose & Davis 1986; Bren 1988, 1992). There have also been within-habitat shifts in the composition of macrophytes and biofilm communities in floodplain wetlands and riparian areas (Leslie 1995; Roberts *et al.* 1997; Robertson 1997; Robertson, Healey & King 1997; Thoms, Ogden & Reid 1999; Burns & Walker 2000).

A key to achieving a balance between production and conservation uses of river red gum forests is an understanding of the relationships between aspects of the flood regime and the productivity of forests and wetland communities. Here we report the results of experiments in which primary production by river red

gum trees, macrophytes and biofilms was measured in areas subjected to controlled floods of different frequency (one flood per year and two floods per year) and seasonal timing (spring and summer floods). We asked the following specific questions. (i) What combination of flood timing and frequency results in the greatest wood production by river red gum trees? (ii) Do the floods which result in the greatest growth of trees also maximize the growth of the major wetland primary producers (macrophytes and biofilms) and the composition of the macrophyte community?

Methods

The study site was located in Gulpa Island State Forest, which forms part of the Barmah–Millewa red gum forest on the Murray River (Fig. 1). The open forest is dominated by *E. camaldulensis* with a grassy understorey of *Vulpia/Bromus* spp. on higher portions of the floodplain, and with the aquatic macrophytes *Eleocharis acuta* R.Br. and *Triglochin procerum* R.Br. common in more flood-prone areas (Bacon *et al.* 1993a).

The climate is semi-arid, with a predominantly winter rainfall (mean annual rainfall 460 mm, mean annual evaporation 1530 mm). Forest growth in such a climate is dependent on regular flooding from the Murray River and its tributary streams, the Edwards River and Gulpa Creek. The forest is dissected by a series of shallow, ephemeral, natural floodways from which floodwaters spread. These floodways are locally called flood runners. The forest in this region was selectively logged in the early 1970s, but has not had trees removed since that time (Bacon *et al.* 1993a).

EXPERIMENTAL DESIGN

Earth banks equipped with pipes and moveable metal doors were established in 12 natural flood runners at the study site in such a way that water could be gravity-fed or pumped to provide different flood treatments for experimental purposes (Fig. 1). Wetlands produced by experimental flooding were contained within the flood runners and ranged in surface area from 0.5 to c. 2 ha.

The natural flood regime for these forests was flooding in spring (August–November) of most years. Since river regulation, small and medium floods are less frequent in spring and small floods are more frequent in summer (Bren 1988; see above). In order to determine how such shifts in the flood regime influence the growth of trees and wetland macrophyte and biofilms, we established four experimental flood treatments: no experimental floods (no flood), an annual late winter flood with spring recession (spring flood), an annual summer flood (summer flood), and two floods per year in spring and summer (spring + summer flood). There were three replicate flood runners for each of these flood treatments.

The duration of each flood varied from 4 to 8 weeks, reflecting annual variation in water availability in the nearby creek and lagoons used as the source of water

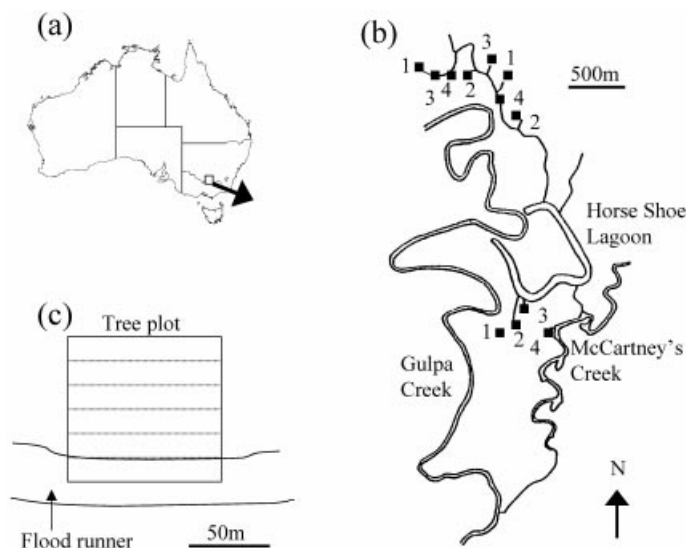


Fig. 1. (a) Location of the study area on the Murray River floodplain in south-eastern Australia and (b) the position of flood treatment sites on flood runners in Gulpa Island State Forest. Permanent lagoons and waterways are shown and black lines are the distributary floodways, or flood runners. 1 = no experimental floods, 2 = spring floods, 3 = summer floods, 4 = spring + summer floods. (c) Position of tree plots and rows within plots relative to flood runners.

for the experimental floods. Between 1990 and 1995 most floods were of approximately 4-week duration. All floods in 1995 and later were of 8-week duration.

TREES

To investigate the response of wood production to flood treatments, in 1990 one plot of approximately 1 ha in area was established in and adjacent to each of the 12 flood runners (Fig. 1). The idealized plot dimension was 100×100 m. However, the actual size was determined by variation in tree density and microtopography of the floodplain, and ranged from 0.60 to 1.14 ha (mean 0.83 ha). One side of each plot ran along the centre of a flood runner (Fig. 1). Two boundary lines marked with posts extended perpendicular to the flood runner to the top of the highest surrounding ground (< 1.5 m above the middle of the flood runner). Each plot was divided into six rows using pegs, with each row running parallel to the flood runner. The first row was in the flood runner and the experimental flood typically flooded the first row of trees and part of the second row of trees. The width of rows varied slightly between plots, but was typically 15 m. Partitioning the plot into rows allowed us to investigate how tree growth responded to increasing distance from the floodwaters.

All plots were flooded in July and August 1990 to establish a baseline soil moisture availability, and then plots were randomly assigned to one of the four flood treatments that were employed for the next 6 years. During the 6-year experimental period over which we determined tree growth, one large natural flood (December 1993) inundated all plots. No attempt was made to pump water from plots following the flood.

In winter 1990 the stem diameter at breast height (d.b.h.) (1.3 m) over bark was determined for all trees

> 10 cm d.b.h. in all plots, and trees were tagged. Initially 1941 trees were measured and marked in all plots. During the 6 years of the experiment a further 317 trees > 10 cm d.b.h. were recruited into all plots. These recruits were marked in the year in which they attained 10 cm d.b.h. The trees in each plot were measured and checked each winter between 1990 and 1996, but in this paper we deal only with girth increments over the total 6-year period.

To determine the relationship between d.b.h. and tree mass, 11 red gum trees were harvested from the forest surrounding the experimental plots at the study site in winter 1997. The trees ranged in size from 11.1 to 96.5 cm d.b.h. All trees were measured (d.b.h.) and felled by cutting as close to ground level as possible. All leaves and twigs (< 1 cm diameter) were bagged and weighed in the field. All branches and trunks were separated and weighed in the field. In the case of smaller trees this was accomplished using a set of large scales, but for the largest trees, trunks and branches were loaded separately on a truck and weighed at a commercial weighbridge. Subsamples of trunk, branch and canopy material were weighed fresh in the field and returned to the laboratory. Subsamples were dried (4 weeks at 70°C for wood, 2 weeks at 70°C for canopy material; Robinson & Robertson, in press) and weighed to obtain conversion factors for expressing mass in dry weight terms. The regression equation describing the relationship between d.b.h. and the dry mass of total wood (trunk + branches > 1 cm diameter) was $\log_{10}\text{MASS} = 2.3075\log_{10}\text{DBH} - 0.7769$, $r^2 = 0.99$.

The mean wood biomass of trees across all rows and treatments at the start of the experiment in 1990 ranged from 0.91 to 3.21 kg m^{-2} , with an overall mean of 1.76 kg m^{-2} (Fig. 2). At the beginning of the flood experiment in 1990 there was no significant difference

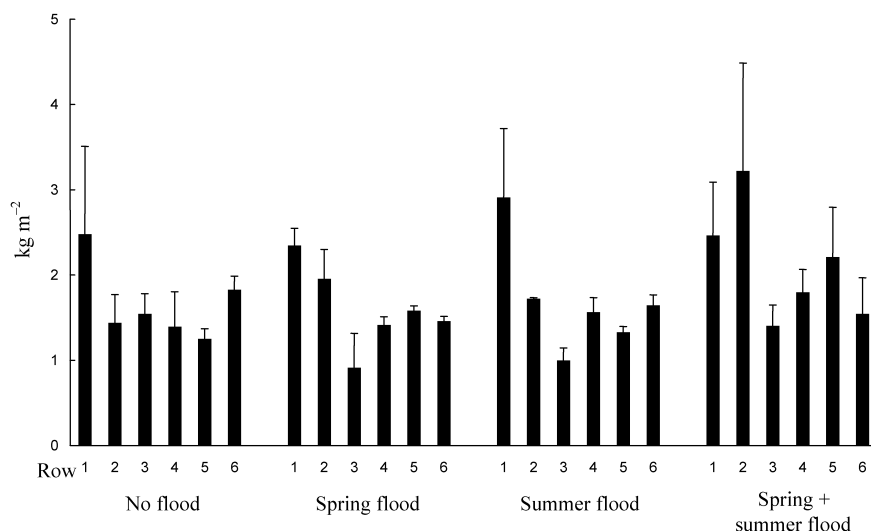


Fig. 2. Mean (+1 SE) biomass of *Eucalyptus camaldulensis* wood in different rows of flood treatment plots in 1990. Increasing row numbers implies increasing distance from and height above flood runners.

Table 1. Analysis of variance for tree biomass in all flood treatment plots and rows in 1990. All data were $\log_{10}x$ -transformed prior to analysis. *** $P < 0.001$, NS = not significant

Source of variance	d.f.	Mean square	F
Plots (P)	3	0.039	1.41 NS
Rows (R)	5	0.148	5.31***
P × R	15	0.025	0.89 NS
Within	48	0.028	

in wood biomass between flood treatment plots (Table 1 and Fig. 2). However, within plots mean tree biomass was significantly greater in rows close to flood runners (Fig. 2 and Table 1).

Net annual above-ground production of trunks and branches by river red gums (wood production, P_w) during the 6-year experimental period was estimated as: $P_w = (\Sigma\Delta M + M_d + M_r)/6$, where $\Sigma\Delta M$ is the sum of the net total increase in the mass of marked trees during the 6-year period, M_d the mass lost by death of individual trees, and M_r the mass gained as new individuals (> 10 cm d.b.h.) entered the population of trees (Attwill & Leeper 1987). Such estimates were obtained for each row in each tree plot using the following analytical procedures. For trees that died during the experiment, their d.b.h. at time of death was converted to dry mass, which was summed over all trees within rows to obtain M_d . For trees that were recruits during the experimental period, their d.b.h. at year 6 was converted to dry mass, which was summed over all trees within rows to obtain M_r . All trees ($n = 14$) > 100 cm d.b.h. were excluded from the database. This was because the allometric relationship between wood mass and d.b.h. was based on trees < 100 cm d.b.h. and small d.b.h. increments in a few large trees can bias estimates of mass increase

at the plot level. At the end of the experiment in 1996, the number of trees (size range > 10–100 cm d.b.h.) per plot ranged from 178 to 308 (mean 187).

AQUATIC MACROPHYTES

We used the experimental flood treatments to investigate the influence of flood timing and frequency on species richness, community composition and primary production of aquatic macrophytes in the wetlands created in flood runners. Because, by definition, aquatic macrophytes occur in wetlands, the no flood treatment was eliminated from this section of our research. With this exception, the experimental design was the same as that used for wood production. Sampling of macrophytes occurred in the spring and summer flood periods of 1997 and 1998.

In each replicate experimental flood site we sampled all aquatic macrophytes in four, 0.25-m², randomly placed quadrats at up to four water depths (> 40 cm, 30 cm, 15 cm, < 10 cm). In several of the experimental flood sites, water depth never exceeded 20 cm, and macrophytes were sampled at only the two shallowest depths (see below). Sampling occurred at the beginning and end of each 8-week flood period.

In each quadrat we clipped all plants at the sediment surface, placed all material in a labelled plastic bag, and returned them to the laboratory for sorting. In the laboratory all plants were sorted to species, placed in labelled paper bags, dried at 60 °C for at least 1 week and weighed to the nearest 0.01 g.

For each flood treatment in each season and year the species richness (S) of macrophytes at the end of the 8-week flood period was calculated separately for shallow (< 30 cm) and deep (≥ 30 cm) regions of each experimental flood site. Species richness was the total number of species of plants recorded in eight quadrats in each depth region of a flood site.

For each flood treatment in each season and year, net production by macrophytes (P_m) was estimated for shallow (< 30 cm) and deep (\geq 30 cm) regions of each experimental flood site using a harvest method (Wetzel & Likens 1991). Using this approach, $P_m = B_{max} - B_{min}$, where B_{max} is the mean maximum total biomass of all macrophyte species in each experimental flood site, and B_{min} is the mean minimum total biomass of all macrophytes (both means based on $n = 8$ quadrats). Using a harvest method to estimate production assumes there is no loss of leaves from plants during the measurement period (Wetzel & Likens 1991). During our 8-week experimental floods there was no loss of leaves from the two dominant macrophytes, *T. procerum* and *E. acuta* (A. Robertson, personal observation). However, the oldest leaves of *T. procerum* were often senescent after 8 weeks and had lost up to 50% of their mass prior to sampling. The harvest method thus provided a conservative estimate of net production.

All experimental flood sites had shallow regions, and thus there were three replicate estimates of macrophyte community composition, species richness (S) and production (P_m) for shallow waters for each flood treatment. However, owing to variation in topography of flood runners, for two of the experimental flood sites that received one flood per year in spring and one that received one flood per year in summer there were no deep regions, and thus there were less than three replicate estimates of community composition, S and P_m for deep waters in some experimental treatments.

BIOFILMS

In order to assess the impact of different flood timing and frequency on biofilm growth, we measured the mass of biofilm (auto- and heterotrophic components) that accumulated on preconditioned red gum blocks during each 8-week experimental flood period (Scholz & Boon 1993). Blocks of red gum wood ($4 \times 4 \times 2$ cm) were cut from a red gum log that had lain in the forest for 2 years. All blocks were then left submerged in the field for 10 weeks in order to leach soluble compounds. Blocks were then scrubbed clean and air-dried prior to use in the experiments. At the commencement of each 8-week experimental flood, three wood blocks were suspended from floats in each flood site, using velcro attachments, so that they were 10 cm below the water surface. At the end of the 8-week flood period, each block was carefully removed from its float so as not to disturb algal growth and attached particles, placed in a labelled plastic bag, and frozen for later analysis. In the laboratory, with the exception of the surface with the velcro attachment, each block was scrubbed carefully with a toothbrush so that all macroscopic material adhering to the block was captured in 400 ml of distilled water. The sample was homogenized by swirling in a beaker and split so that both chlorophyll *a* concentration and the total dry mass of the biofilm could be estimated for each block. Two-hundred millilitres of each homogenized sample

were filtered through a pre-dried and weighed GF/F filter, which was then dried for 1 week at 40 °C and weighed to the nearest 0.00001 g. The total dry mass of biofilm was then expressed as g cm^{-2} . The remaining sample was filtered onto a glass fibre filter (GF75 Advantec MFS, Inc. California), placed into a test tube containing 90% ethanol for the extraction of pigments, and processed for the determination of chlorophyll *a* concentration using a spectrophotometric method (King, Robertson & Healey 1997). Chlorophyll *a* concentrations were then expressed as $\mu\text{g cm}^{-2}$. For each flood runner site used in each flood treatment in each season we calculated the mean mass of chlorophyll *a* and total mass of biofilm (based on $n = 3$). These mean values were used in the statistical analyses (below).

DATA ANALYSES

We used analysis of variance (ANOVA) models to determine the significant sources of variation in tree biomass at the beginning of the experiments (flood treatment and row as fixed factors), wood production (flood treatment and row as fixed factors), macrophyte species richness and macrophyte primary production in shallow regions of flood runners (year, season and flood treatment as fixed factors), and biofilm accumulation (season and flood treatment as fixed factors). For deep regions of flood runners we had only one replicate of macrophyte species richness and primary production for flood runners that received one flood per year in spring and two replicates for flood runners that received one flood per year in summer (see above). It was clear from the graphical analysis that the history of flooding frequency did not have a significant effect on species richness or production in deep waters (see the Results). Thus to compare means, data were pooled over flood frequency. We used a two-factor ANOVA (with year and season as fixed factors) with unequal but proportional subclass numbers (Sokal & Rohlf 1981) to compare means. For all ANOVAs, raw data were tested for homogeneity of variances (Levene's test) and data were transformed to achieve equal variances where required.

The significance of differences between macrophyte community composition due to season or frequency of flooding was determined using a two-way crossed analysis of Bray-Curtis similarities (ANOSIM; Clarke & Warwick 1994). Bray-Curtis similarities were based on biomass data for each macrophyte species using pooled data for 2 years of sampling. We removed macrophyte species from the data set if they represented less than 0.1% of the total mass of macrophytes sampled in the 2 years.

Results

WOOD PRODUCTION

Mean annual wood production across rows and treatments ranged from 169 to 722 $\text{g m}^{-2} \text{year}^{-1}$ (Fig. 3), with an overall mean of 413 $\text{g m}^{-2} \text{year}^{-1}$. Wood production

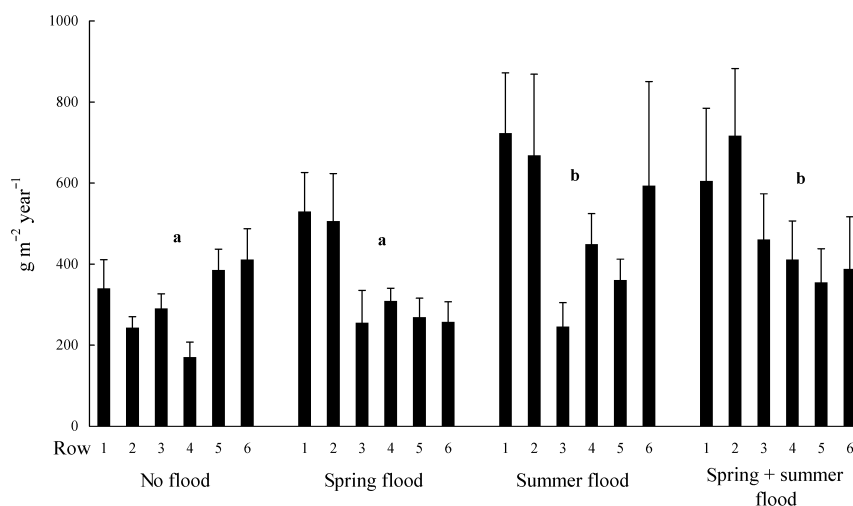


Fig. 3. Mean (+1 SE) annual wood production by *Eucalyptus camaldulensis* in different rows in all flood treatment plots. Increasing row numbers implies increasing distance from and height above flood runners. Bold letters indicate which mean plot-level production estimates differed significantly between flood treatments based on Tukey's honest significant difference test.

Table 2. Analysis of variance for wood production by river red gum trees in experimental plots. ** $P < 0.01$, NS = not significant

Source of variance	d.f.	Mean square	F
Flood treatment (F)	3	175811.2	4.64**
Rows (R)	5	130000.4	3.43**
F × R	15	36000.1	0.99 NS
Within	48	37868.0	

varied with flood treatment and distance from flood runners (= row number in plots) (Fig. 3 and Table 2). Production was greatest in plots receiving summer floods, and spring + summer floods. Significantly lower rates of production occurred in plots that received spring floods or no experimental floods (Fig. 3). A large natural flood inundated all experimental plots in December 1993, in the middle of the experimental period. This large flood effectively turned our no-flood control plots into plots that received a flood every 3 years.

In plots receiving spring floods and those receiving spring + summer floods, rates of production generally decreased with distance from the flood runner. However, in plots receiving summer flooding and those that received no experimental floods, this pattern was less clear and lowest values were recorded in middle rows (Fig. 3).

AQUATIC MACROPHYTE COMMUNITY COMPOSITION

Season of flooding, but not frequency of flooding or year of sampling, had a significant influence on the species richness of macrophytes in shallow and deep regions of flood runners (Table 3). More species grew in wetlands in spring floods than in summer floods (Fig. 4). For shallow water regions of wetlands created by floods the composition of the macrophyte community also differed significantly between seasons (ANOSIM, $R = 0.37$, $P = 0.02$) but not with differences in flood frequency (ANOSIM, $R = -0.43$, $P = 0.93$). For deep regions of wetlands there was no significant difference in macrophyte

Table 3. Summary of analyses of variance for the species richness and production of aquatic macrophytes in shallow (< 30 cm) and deep (> 30 cm) regions of wetlands. Note that for deep regions of wetlands, data were pooled over flood frequencies (see the Methods) and thus flood frequency was not included as a factor contributing to variation. Significant F -ratio values are marked, all others are not significant at $P = 0.05$. ** $P < 0.01$; *** $P < 0.001$

Source of variation	Species richness		Production	
	Shallow ($F_{1,16}$ -ratios)	Deep ($F_{1,14}$ -ratios)	Shallow ($F_{1,16}$ -ratios)	Deep ($F_{1,14}$ -ratios)
Year (Y)	2.5	0.0	0.6	0.3
Flood frequency (F)	1.5	–	0.0	–
Season (S)	22.8***	10.6**	9.0**	17.3***
Y × F	0.3	–	0.2	–
Y × S	0.0	1.9	0.1	0.1
F × S	0.8	–	0.1	–
Y × F × S	2.5	–	0.2	–

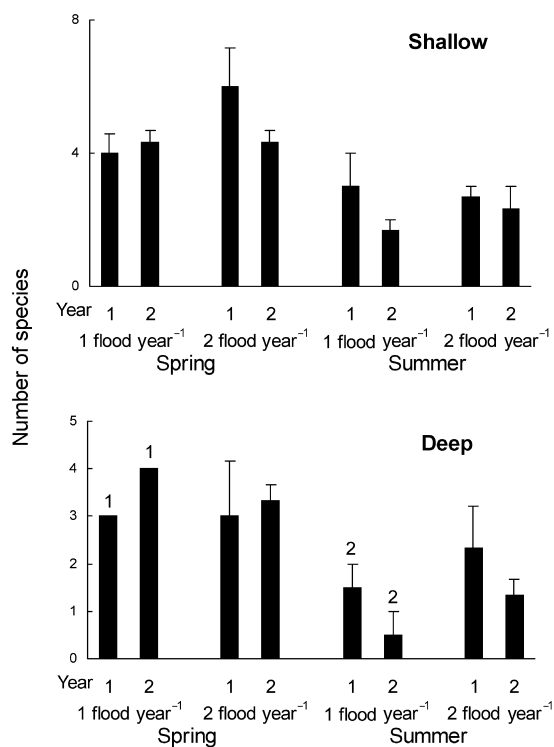


Fig. 4. Mean (+1 SE) species richness of aquatic macrophytes in shallow and deep regions of wetlands created by experimental flood treatments. Data are for 2 years and for samples taken at the end of the spring (October) and summer (March) flood periods. Numbers above bar graphs give the number of replicates, where $n < 3$.

community composition with season (ANOSIM, $R = 0.19$, $P = 0.267$) or flood frequency (ANOSIM, $R = -0.19$, $P = 0.880$).

AQUATIC MACROPHYTE PRODUCTION

Mean macrophyte production in flood runners ranged from 0.01 to 0.75 $\text{g m}^{-2} \text{day}^{-1}$ across flood treatments and years (Fig. 5). For shallow regions of flood runners macrophyte production was significantly higher during spring floods than summer floods, but there was no significant effect of the number of times per year a site had been flooded in the past, nor were there differences between years (Fig. 5 and Table 3). For deep regions of flood runners it was clear that season was the factor that contributed most to differences in macrophyte production, with production significantly greater in spring than in summer floods (Fig. 5 and Table 3).

BIOFILM ACCUMULATION

The mean mass of chlorophyll *a* and total biofilm mass accumulated on wood blocks after 8 weeks of inundation ranged from 0.09 $\mu\text{g cm}^{-2}$ and 0.034 mg cm^{-2} in summer to 0.88 $\mu\text{g cm}^{-2}$ and 0.066 mg cm^{-2} in spring (Fig. 6). The accumulation of chlorophyll *a* and the total mass of biofilm during 8-week flood periods were

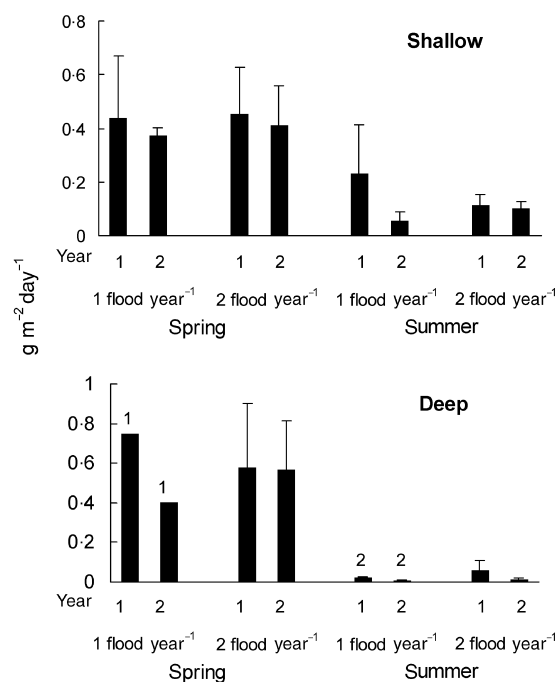


Fig. 5. Mean (+1 SE) production by aquatic macrophytes in 2 years in shallow and deep regions of wetlands created by experimental flood treatments. Numbers above bar graphs give the number of replicates, where $n < 3$.

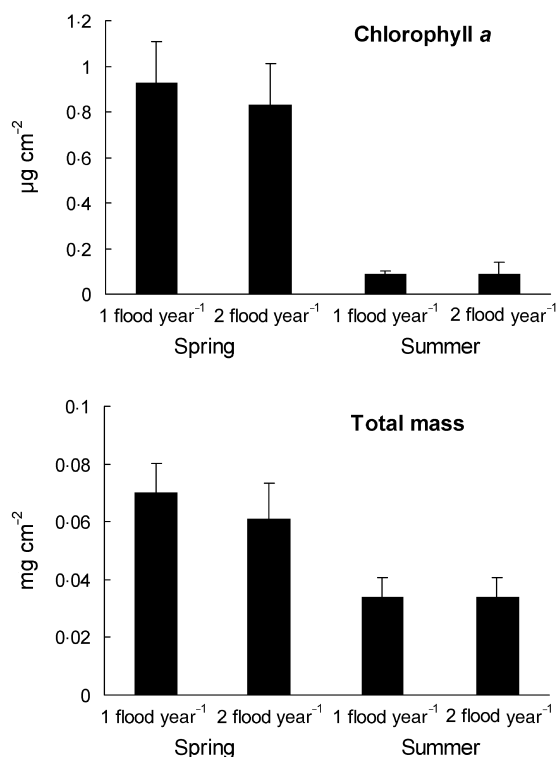


Fig. 6. Mean (+1 SE) chlorophyll *a* and total dry mass accumulation of biofilm on red gum wood blocks under different flood treatments. Note that biofilm data were collected for only 1 year.

significantly greater during spring floods than during summer floods but did not differ between flood runners with different histories of flood frequency (Fig. 6 and Table 4).

Table 4. Analysis of variance for the mass of chlorophyll *a* and total mass of biofilms that accumulated on wood blocks during 8-week flood periods. * $P < 0.05$, *** $P < 0.001$, NS = not significant

Source of variance	Chlorophyll <i>a</i> ($F_{1,8}$ -ratios)	Total mass ($F_{1,8}$ -ratios)
Season (S)	35.5***	11.1*
Flood frequency (F)	0.1 NS	0.3 NS
S × F	0.1 NS	0.3 NS

Discussion

In the Murray River, regulation and water extraction have shifted the seasonal pattern of flooding in the Barmah–Millewa forest so that the frequency of small to medium-sized floods has been reduced, there is less spring flooding than in the period prior to regulation, and there is an increased frequency of short summer floods (Bren 1988). These changes to the flow regime have had significant impacts on floodplain vegetation and hence on fauna and biogeochemical cycles (Chesterfield 1986; Smith & Smith 1990; Briggs, Thornton & Lawler 1997; Robertson *et al.* 1999).

It is clear from our study that there are significant differences in the response of components of floodplain vegetation to the seasonal timing of flooding. Highest production and greatest expression of macrophyte communities occurred during spring floods, and the accumulation of biofilms was also greatest in spring. In contrast, wood production by river red gum forests was greatest in plots receiving summer flooding. For all components of the vegetation, differences in the frequency of flooding employed in our experiments had little influence on variation in primary production.

For trees, it is not so surprising that plots receiving summer floods had the highest rates of wood production, despite spring flooding being the natural flood pattern (Bren 1988). *Eucalyptus camaldulensis* normally drops most of its leaf litter in summer in response to drought conditions (Lake 1995). Previous work in the region has shown that lateral movement of water through floodplain soils may influence the growth of red gum trees up to 70 m from the surface floodwaters (Bacon *et al.* 1993b). Short summer floods, even when confined to flood runners, can thus provide water to large sections of the forest at a time when trees would be naturally drought-stressed under the prevailing conditions of high summer temperatures and high rates of evaporation and evapotranspiration (Bacon *et al.* 1993a). Flooding also results in larger leaves and reduced rates of herbivory by insects on red gum tree crowns (Stone & Bacon 1994). Prior to river regulation, it is possible that floods that occurred naturally in early summer may have accounted for substantial proportions of wood growth (D. Leslie, Ecologist, State Forests of New South Wales, personal communication).

Our experiments also showed that plots that received only spring floods had similar rates of wood production to plots that received no experimental floods. It is likely that this is explained by the effect of the large natural flood that inundated all plots in December 1993. This flood effectively changed our no-flood control treatment to one equivalent to a treatment of one flood every 3 years. The conclusion from this is that one large inundation every 3 years appears to have an effect on wood production similar to that resulting from regular, short, spring flooding over a number of years.

Wood production varied with distance from surface floodwaters in our experiments, but the pattern was inconsistent across flood treatments. In most cases, production was greatest in the rows closest to floodwaters; however, similarly high rates of production were measured at up to 75 m from floodwaters in some treatments. Much of the variation between plots and treatments may reflect small-scale differences in sediment types across the floodplain, and hence variation in groundwater availability to trees (Bacon *et al.* 1993a,b).

Most previous work on the effects of changed flood regimes on forest production has been done in more humid forests where drought stress is not such a major problem (Brinson 1990). In Louisiana, forest production increased in the order permanent flooded sites < natural flooded sites < less frequently flooded sites (Conner, Gosselink & Parrondo 1981). In contrast, increases in basal area growth rate of trees on a floodplain in Illinois increased as a function of average river discharge, but growth slowed when water levels were raised permanently by beaver dams (Mitsch, Dorge & Wiemhoff 1979).

The measured mean production by river red gums in our study (grand mean for plots 413, range 169–722 g m⁻² year⁻¹) was at the lower end of the scale for forested floodplains globally. Brinson (1990) reported a range of 177–1888 g m⁻² year⁻¹, with a mean for 16 studies of 694 g m⁻² year⁻¹. Most of the studies reviewed by Brinson were from relatively humid regions of the United States and Europe. The relatively low production rates for river red gum may be explained by the more arid climate of the Murray floodplain (Bacon *et al.* 1993b) and the greater variation in discharge of the Murray River relative to rivers elsewhere in the world (Walker, Sheldon & Puckridge 1995). However, variation in production (P) by floodplain forests is also a function of forest biomass (B). After excluding data for young forests recovering from disturbance, the mean P/B ratio for eight floodplain forests world-wide is 0.032 year⁻¹ (from data in Brinson 1990). In comparison, P/B ratios for river red gum in our study ranged from 0.025 to 0.036 year⁻¹ across plots and rows. Thus the site we studied was near the average for other floodplain forests in terms of annual wood biomass turnover.

Clearly, summer flooding, while promoting the highest rates of wood production by red gum trees, is detrimental to macrophyte communities and biofilm accumulation. Macrophyte communities that developed during summer

floods in our study differed in species composition from those that developed during spring floods, were relatively depauperate in the number of species and had significantly lower rates of production.

The mechanisms underlying such differences are not clear, but several factors may be involved. Summer flooding of flood runners triggers more rapid decomposition of red gum litter in flood runners than spring floods (Glazebrook & Robertson 1999). The result is that in summer the concentration of dissolved organic carbon (DOC) derived from leaf litter in flooded areas may be up to 60 mg l^{-1} (A. Robertson, unpublished data) and the black-water conditions that prevail reduce the light available for macrophytes in deeper regions ($> 30 \text{ cm}$ depth) of flood runners. Such high concentrations of DOC can also have a direct allelopathic affect on macrophytes (Pflugmacher, Spangenberg & Steinberg 1999). In addition, cattle, which are stocked at low densities on the floodplain to reduce potential fire fuel loads, concentrate around water during summer and reduce the biomass of emergent macrophytes such as *Eleocharis* spp. (Robertson 1997).

For several reasons we expected that more frequent flooding might affect macrophyte community composition and macrophyte production. First, frequent relatively short-duration floods may not allow sufficient time for plants to produce viable seed. A history of short floods may thus reduce the seed reserves in wetlands. In addition, leaf growth in many wetland plants following flooding depends upon carbohydrate stored in rhizomes (Rea & Ganf 1994). Frequent short-duration floods may not allow sufficient time to maintain sufficient reserves. The results of our experiments in the period 1996–98 indicate that there was no difference in the growth and community composition of macrophytes in sites that had received floods once or twice a year since controlled flooding began in 1990 (Bacon *et al.* 1993a).

Briggs & Maher (1985) estimated total submerged macrophyte production to be *c.* $1.9 \text{ g m}^{-2} \text{ day}^{-1}$ in a shallow wetland on the Lachlan River floodplain *c.* 200 km north of our study site, and, globally, wetland macrophyte production often exceeds $2 \text{ g m}^{-2} \text{ day}^{-1}$ (Mitsch & Gosselink 1993). The relatively low macrophyte production at our study site may reflect low light conditions under the well-developed river red gum canopy within flood runners and competition for nutrients with dense stands of trees.

The accumulation of chlorophyll *a* in biofilms and the total mass of biofilms were significantly greater in spring floods than in summer floods. In permanent wetlands on the floodplains of the Murray River and nearby Murrumbidgee River, time of exposure of surfaces, depth, turbidity and, to a minor extent, season all influence the rate of accumulation of biofilm chlorophyll *a* and mass on wooden blocks (Scholz & Boon 1993; Robertson, Healey & King 1997). Nutrient availability, grazing and allelopathic substances also play important roles in controlling biofilm growth in wetlands (Goldsborough & Robinson 1996).

Identifying the controlling factors on biofilm accumulation is a difficult task in any situation (Wetzel 1983) and our experiments did not target the causes of seasonal differences in biofilm accumulation. A number of mechanisms may have been responsible for the difference in accumulation rates between spring and summer floods. We did not measure biofilm production, because no estimates were made of the loss of chlorophyll *a* through grazing, sloughing or leaching. However, very high concentrations of DOC and very low subsequent oxygen concentrations $< 1 \text{ mg l}^{-1}$ in wetlands created by summer floods (A. Robertson, unpublished data) means that it is unlikely that grazing pressure by invertebrates causes the low chlorophyll and total biofilm mass in summer. It is also unlikely that light or nutrient availability were responsible for seasonal differences. Wood blocks were positioned only 10 cm from the water surface, and despite black-water conditions caused by high DOC concentrations in summer, sufficient light would have reached blocks to support primary production. Dissolved phosphorus and inorganic nitrogen concentrations in wetlands also did not differ significantly between seasons (A. Robertson, unpublished data).

The DOM derived from live and decomposing vegetation can influence algal growth (Planas *et al.* 1981; Wium-Anderson *et al.* 1982; Weak 1988) and terrestrial leaf litter is often added to wetlands and lakes to control algal growth (Pillinger, Cooper & Ridge 1994; Ridge, Walters & Street 1999). Thus a possible mechanism explaining the low biofilm development in summer floods in our study may be the allelopathic influence of the very high concentrations of DOM derived from river red gum litter.

MANAGEMENT IMPLICATIONS

River red gum forests on the Murray River floodplain support a significant timber industry (Bacon *et al.* 1994; Donovan 1997). At the same time, river red gum trees, macrophytes and biofilms are important contributors to river–floodplain organic matter budgets (Lake 1995; Robertson *et al.* 1999) and floodplains provide essential habitat for birds and other biota (Chesterfield 1986; Smith & Smith 1990; Briggs, Thornton & Lawler 1997; Healey, Thompson & Robertson 1997).

Short summer flooding is clearly advantageous for wood production. However, the agencies responsible for the sustainable management of river red gum forests along the Murray River have international, national and regional obligations to conserve the biota of floodplain habitats of the Barmah–Millewa forest complex (Forestry Commission of New South Wales 1985; Sharley & Huggan 1994; Frazier 1999). Our data make it clear that the seasonal timing of floods is an important issue in determining the structure and function of plant communities in the many ephemeral wetlands in low-lying areas of red gum forests. Spring flooding, while not as beneficial for tree growth, is critical for the growth of wetland macrophytes, the maintenance of

macrophyte species richness, and favours better development of biofilms. Thus maintaining the conservation values of wetlands within river red gum forests will require a focus on the return of small and medium flood flows in the spring period.

The restoration of floodplain rivers that have been degraded by flow regulation and water diversion depends on the return of more natural flow regimes (Sparks 1995; Poff *et al.* 1997; Molles *et al.* 1998; Tockner *et al.* 1999). Decisions regarding flow management need to be based on the best possible knowledge of the ecological responses to altered flows.

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