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Effects of Edaphic Factors and Flood Frequency on the Abundance of Lignum (*Muehlenbeckia florulenta* Meissner) (Polygonaceae) on the River Murray Floodplain, South Australia

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Abstract

Lignum is a native woody perennial which forms extensive thickets in low-lying areas of the floodplain of the lower River Murray, although its range and abundance have been affected by land clearance, salinisation, flow regulation and possibly grazing on seedlings. Comparisons between lignum cover and edaphic data for three sites (Chowilla, Morgan and Overland Corner) showed a negative correlation with soil hardness. Cover was also correlated positively with soil moisture and negatively with time since last flooded, but not correlated with flood recurrence interval. Principal Components Analysis revealed a complex component, loaded by moisture, salinity, pH and organic content, that explained most of the variation in lignum cover. A greenhouse experiment indicated that the salinity and volume of water supplied to plants have significant effects on stem growth. Stands of lignum may be best maintained by flooding low-lying areas every 3–10 years or areas with saline soils more frequently.

Introduction

The dynamics of floodplain vegetation communities are governed by the flood regime of the parent river (e.g. flood frequency, period of inundation and flood-related physical damage) and by edaphic and biological factors (e.g. soil texture, drainage and aeration, nutrients, depth to groundwater and seedling flood tolerance) (e.g. Junk and Welcomme 1990). These effects are ultimately related to the distance from the river channel, although the relationship may be complicated by minor variations in relief (Buchholz 1981). There are often distinct zones of vegetation that reflect the flood regime, and the gradient may be intensified for floodplain rivers in semi-arid regions where the plants are prone to severe water stress (cf. Breen *et al.* 1988). This is probably true for the floodplain of the River Murray in south-eastern Australia, although the work undertaken so far has been descriptive rather than analytical (cf. Margules and Partners *et al.* 1990). Extensive studies have been made of the Murray's river red gum forests (*Eucalyptus camaldulensis* Dehnh.), mainly with regard to the effects of river regulation (e.g. Bren 1988), but little is known of the other species.

Lignum (*Muehlenbeckia florulenta* Meissner, formerly *M. cunninghamii* (Meissn.) F. Muell.: see Harden 1990) is a member of the family Polygonaceae. It is a multi-stemmed, woody, perennial shrub with rigid, tangled, intertwining branchlets sometimes ending in a spine (Sainty and Jacobs 1981; Chorney 1986). The common name, lignum, is a contraction of *Polygonum*, a genus to which the species was formerly assigned (Specht 1972; Cunningham *et al.* 1981). Lignum is widespread in south-eastern Australia, and particularly common in flood-prone areas of the Murray–Darling Basin. It occurs as an understorey in eucalypt woodlands or in riverflat shrublands, and may form dense thickets 2–3 m high. The plants often appear to be in poor condition, with dry, brown stems and no leaves, but are notable for their ability to produce green shoots rapidly

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following rain or flood (Campbell 1973). Lignum thickets are an important habitat for terrestrial animals and, during times of flood, provide a sanctuary for waterfowl, fish and aquatic invertebrates (Cunningham *et al.* 1981; Briggs and Maher 1983; Boulton and Lloyd 1991; Lloyd *et al.* 1991). The species therefore is significant for floodplain management, and it is remarkable that it has not previously attracted ecological studies.

On the floodplain of the lower River Murray, lignum is most abundant in low-lying areas subject to flooding every 2–8 years (National Environmental Consultancy 1988). Its distribution appears to be influenced also by the depth and salinity of the groundwater, although it tolerates a salinity of at least 10 000 mgL^{-1} (Van der Sommen 1980; National Environmental Consultancy 1988). It is more salt-tolerant than the common eucalypts of the Murray floodplain (river red gum and black box, *E. largiflorens* F. Muell.) but less so than samphires (Chenopodiaceae: *Halosarcia* spp.) found on the most saline soils (Margules and Partners *et al.* 1990). Lignum grows vigorously beside the upper pools of the weirs where river levels are comparatively stable, perhaps because the local groundwater levels are also stable (cf. Barnett 1989; Margules and Partners *et al.* 1990; Walker *et al.* 1992). Flow regulation, salinisation, land clearance, grazing and other factors probably have affected the regional distribution and abundance of the species over the past century, but there are no supporting historical data.

In this paper we examine the effects of edaphic and flood-related factors on the distribution and abundance of lignum at three sites on the Murray floodplain in South Australia. Field work involved measurements of abiotic variables potentially determining lignum cover. This was complemented by a greenhouse experiment to elucidate the effects of flooding and salinity on stem growth. The results enable us to make some recommendations regarding the maintenance of lignum shrublands along the lower Murray.

Materials and Methods

Study Areas

In the Riverland, South Australia (Fig. 1), the Murray flows across a broad (4–10 km) floodplain from the state border to near Overland Corner, where it enters a limestone gorge (1–2 km). The regional

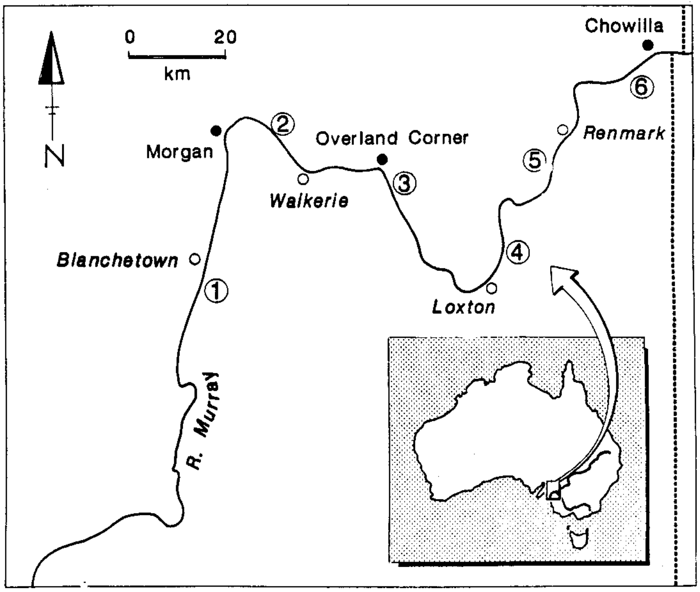

Fig. 1. The lower River Murray, showing the three study areas (●). Numbers refer to weirs.

climate is semi-arid, with mean annual rainfall and evaporation of 278 and 2250 mm respectively at Loxton (Kernich 1984). The floodplain soils are poorly drained, saline grey clays which increase in sand content from the lower to higher terraces (Cole 1978; Walker *et al.* 1992). The groundwater has a salinity near seawater, and is 1–2 m below the low terraces and 3–4·5 m below the high terraces (Barnett 1989). There are major saline inflows to the Murray throughout the region and groundwater interception schemes are either proposed or are already commissioned (e.g. National Environmental Consultancy 1988; O'Malley and Sheldon 1990).

Fieldwork was carried out in three areas below, near and above the river's entry to the gorge, where lignum occurs as part of the understorey to red gums on the river flats and to black box in more elevated areas. The choice of study areas was influenced by the availability of supporting hydrological data from boreholes maintained by the S.A. Department of Mines and Energy.

(1) The *Morgan* study area (M) was on Crown Land at Pelican Point, 11 km south of Morgan on the western bank of the Murray, where lignum occurs among eucalypts and patches of river cooba (*Acacia stenophylla* A. Cunn. ex Benth.). The floodplain is 900 m wide and confined by cliffs, and the area is not grazed by stock.

(2) The *Overland Corner* study area (OC) was in a National Trust reserve on the northern river bank at Overland Corner. Lignum is the dominant woody species, with a grass understorey. Red gums did occur formerly, but were logged to fuel riverboats during the 19th century. The floodplain is 700 m wide, confined by cliffs and not grazed.

(3) The *Chowilla* study area (C) was on Chowilla Station, on the northern bank near Monoman Island, where lignum occurs as an understorey in eucalypt woodlands or as dense thickets with a grass understorey. The floodplain is 3 km wide and dissected by two anabranches, Chowilla and Monoman Creeks. Sheep and feral goats are present.

Sampling Methods

Sampling was in May 1988 at Chowilla and in July 1988 at Morgan and Overland Corner. Sites were at 100-m intervals along transects perpendicular to the river. There were six sites at Morgan and Overland Corner and 16 sites at Chowilla.

The percentage cover of lignum was estimated by the line-intercept method (Canfield 1941). Parallel 5-m lines were located randomly along a 10-m baseline perpendicular to each transect and the proportion of each line intercepted by lignum was recorded. For accuracy, more short lines were used rather than fewer long ones (Greig-Smith 1983). Between 5 and 20 samples were necessary to obtain a standard deviation smaller than or equal to the mean. Three random points at each site were chosen to provide environmental data. An auger was used to obtain 500-g soil samples from 25 cm depth; these were sealed in plastic bags, transported in an insulated box to minimise water loss and later analysed for moisture, organic content, pH and conductivity (see below). Soil hardness was determined as the mean of five measurements at each point using a hand-held penetrometer. The number of trees (river red gum, black box and river cooba) over 2 m in height within a 20-m radius of the mid-baseline at each site was recorded, and the elevation of this point measured with a Schokitsh automatic level. Reference elevations for the river end of each transect were obtained from the Engineering and Water Supply Department, Adelaide (EWS).

Laboratory Analysis

Soil moisture was determined by drying 100-g subsamples to constant weight at 105° C (British Standards Institute 1975). Organic content was measured as the weight loss of oven-dried soil after 2 h in a muffle furnace at 550° C. Values of pH and conductivity were determined in 1 : 2·5 soil–water suspensions made by shaking 20 g of 2 mm sieved, air-dried soil and 50 mL distilled water in a 225-mL flask for 1 h and allowing the contents to settle for 30 min. Measurements of pH were made with a direct-reading portable meter. Conductivity was determined by a Radiometer meter and corrected to 25° C (Williams 1986).

Flood Frequency

Flood frequencies at each site were represented by the average recurrence interval, years since last flooded and days inundated between 1973 and 1982. This information was estimated from elevation measurements at each site and topographic data, historical river stage records and backwater curves

Table 1. Summary environmental data (means and standard errors) for sites at the three study areas
(M, Morgan; OC, Overland Corner; C, Chowilla)

Sample site	Lignum cover (%)		Trees in 20-m radius	Soil hardness (kg cm^{-2})		Soil pH		Soil conductivity (mS cm^{-1})		Soil organic content (%)		Soil moisture (%)		Distance from river (m)	Elevation (m AHD)	Flood recurrence interval (y)	Years since inundated	Days inundated
	Mean	s.e.		Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.	Mean	s.e.					
M-0	10	(1·9)	6	1·5	(0·054)	6·4	(0·533)	0·7	(0·225)	4·4	(0·132)	19·1	(1·069)	180	5·62	5·5	6·58	410
M-1	0	(0)	4	1·5	(0·150)	6·8	(0·233)	1·0	(0·276)	4·5	(0·074)	20·0	(0·413)	270	5·39	5	6·58	417
M-2	22	(6·7)	12	1·5	(0·091)	5·4	(0·780)	1·1	(0·185)	5·3	(0·284)	17·3	(2·122)	365	5·28	4·5	6·58	439
M-3	30	(3·8)	6	1·5	(0·107)	4·8	(0·088)	0·8	(0·050	5·0	(0·124)	17·3	(0·824)	455	5·52	5	6·58	412
M-4	41	(7·8)	5	1·25	(0·056)	4·7	(0·208)	1·1	(0·100)	5·2	(0·321)	16·7	(2·080)	550	6·31	10	6·58	296
M-5	3	(0·8)	0	2·25	(0·250)	5·3	(0·318)	2·0	(0·301)	5·8	(0·291)	20·3	(1·086)	640	5·71	6	6·58	401
OC-0	37	(11·03)	0	2·0	(0·150)	5·6	(0·117)	3·6	(0·257)	3·1	( )	16·6	(2·07)	75	8·43	3	3·50	803
OC-1	61	(5·85)	0	1·25	(0·079)	5·2	(0·017)	1·2	(0·173)	4·0	( )	15·9	(0·69)	170	8·39	3	3·50	803
OC-2	2	(0·44)	1	2·25	(0·133)	5·4	(0·192)	4·0	(0·551)	3·5	( )	14·7	(2·16)	235	8·47	3	3·50	803
OC-3	5	(2·01)	2	2·0	(0·094)	5·9	(0·120)	3·5	(0·560)	3·1	( )	14·8	(1·88)	320	8·34	3	3·50	803
OC-4	38	(7·56)	0	1·5	(0·148)	8·4	(0·033)	0·2	(0·007)	2·5	( )	9·8	(1·59)	455	9·17	4	3·58	685
OC-5	0	(0)	10	2·75	(0·276)	8·4	(0·088)	0·3	(0·060)	2·8	( )	4·2	(1·30)	515	9·89	5	6·58	451
C-0	13	(4·04)	23	1·5	(0·201)	5·3	(0·076)	0·9	(0·062)	6·9	(0·173)	17·2	(1·08)	500	19·97	4·5	6·50	466
C-1	63	(8·24)	10	1·5	(0·153)	5·1	(0·115)	1·3	(0·064)	5·8	(0·139)	17·8	(1·59)	430	19·57	4·5	6·50	466
C-2	47	(7·82)	19	1·25	(0·111)	5·5	(0·117)	1·5	(0·174	6·6	(0·236)	20·1	(0·12)	300	20·43	5·5	6·50	426
C-3	7	(2·94)	42	2·25	(0·225)	5·4	(0·120)	1·5	(0·152)	6·4	(0·299)	17·3	(0·37)	200	20·60	6	6·50	377
C-4	0	(0)	32	3·5	(0·181)	4·9	(0·130)	0·9	(0·132)	4·9	(0·363)	10·9	(0·44)	170	21·13	16	12·25	143
C-5	0	(0)	6	4·25	(0·177)	5·3	(0·017)	2·3	(0·225)	3·1	(0·225)	11·3	(0·82)	160	18·65	4·5	6·50	466
C-6	3	(1·75)	14	3·0	(0·237)	4·9	(0·176)	1·1	(0·180)	4·1	(0·425)	12·9	(1·52)	65	20·32	4·5	6·50	447
C-7	0	(0)	35	1·75	(0·126)	7·8	(0·346)	1·7	(0·405)	5·6	(0·192)	15·0	(0·99)	12	21·35	33	12·33	48
C-8	0	(0)	63	2·75	(0·333)	5·1	(0·173)	2·1	(0·178)	6·5	(0·512)	11·0	(0·51)	110	21·04	20	12·25	143
C-9	0	(0)	0	4·75	(0·115)	6·3	(0·088)	0·8	(0·026)	5·2	(0·362)	11·1	(0·15)	470	18·84	4·5	6·50	466
C-10	1	(0·50)	5	4·5	(0·151)	5·8	(0·174)	0·3	(0·056)	5·1	(0·109)	10·0	(0·85)	530	19·80	4·5	6·50	466
C-11	35	(6·26)	10	1·75	(0·226)	5·5	(0·050)	0·6	(0·193)	6·1	(0·091)	15·5	(0·98)	70	19·09	4·5	6·50	466
C-12	1	(0·59)	0	3·25	(0·293)	6·2	(0·219)	0·6	(0·104)	5·3	(0·077)	10·9	(0·66)	240	19·10	3·5	6·50	466
C-13	10	(2·07)	3	3·5	(0·311)	6·4	(0·153)	0·7	(0·019)	5·1	(0·035)	12·8	(3·01)	340	19·15	3·5	6·50	466
C-14	38	(5·28)	1	2·25	(0·402)	5·3	(0·033)	0·2	(0·032)	6·2	(0·126)	17·5	(1·96)	440	18·96	3·5	6·50	466
C-15	6	(2·14)	0	4·75	(0·077)	6·6	(0·088)	2·0	(0·153)	4·2	(0·063)	9·8	(0·75)	540	19·44	4·5	6·50	466

for given flow rates (EWS records), and from average flood-recurrence intervals at Morgan (Lange *et al.* 1987).

Experimental Design

Eighty lignum plants (60–100 cm height, 2–6 branches, without leaves) were collected near the Morgan study area in July 1988. Each plant was transferred intact to a 6-L plastic pot containing 3·6 kg of well mixed native surface soil (a mixture of silt, sand and clay) and acclimatised for 10 days in a glasshouse. Sixty-four plants were selected and assigned randomly to orthogonal treatments comprising four levels of weekly watering (10, 225, 450, 900 mL) and four salinities (0, 250, 10 000, 40 000 mg L^{-1}), with each combination replicated four times. These levels mimic the seasonal range of natural conditions (e.g. 225 mL of 10 000 mg L^{-1} water weekly approximates average March rainfall and groundwater salinity). Saline water was prepared by adding NaCl to distilled water. The plants were positioned randomly in the glasshouse and rotated through all positions over a 10-week period (July–September). Average daily temperature extremes were 13·0 and 27·1°C. Stem growth was measured relative to a mark near the base of the stem (repeated measurements on several plants indicated an error of 0·10%). The data were analysed by using a two-way non-parametric ANOVA (Scheirer *et al.* 1976; see Zar 1984: 219).

Field Data Analysis

A correlation matrix was computed from the environmental variables and lignum cover data for each site. Spearman rank correlations were employed because some variables were unlikely to be normally distributed. A Principal Components Analysis (PCA) was performed to identify the components that accounted for most covariance among the environmental data. The procedure was a sampling unit ordination, as described by Ludwig and Reynolds (1988: program PCA) except that Spearman correlations were substituted for Pearson correlations. Values of percentage lignum cover were superimposed on plots of components with eigenvalues exceeding 1·0 (Chatfield and Collins 1980) to identify variables associated with high lignum cover. These relationships were further explored using direct plots of key environmental factors and lignum cover.

Results

Table 1 shows a synopsis of the data obtained at each site. The most favourable conditions for lignum appear to be on open riverflats with few trees, where flooding occurs about once in 3–10 years. The approximate soil characteristics associated with maximal lignum cover are: moisture >15%, hardness 2 kg cm^{-2}, conductivity <1·5 mS cm^{-1}, organic content about 5% and pH about 5.

Correlations

The percentage lignum cover was negatively correlated with soil hardness (r_s = –0·67, P <0·001) and time since last flooded (r_s = –0·42, P <0·05) and positively correlated with soil moisture (r_s = 0·46, <0·01) (data for all study areas combined: n = 28). Soil moisture was negatively correlated with hardness (r_s = –0·64, P <0·05). Soil pH and organic content were correlated with lignum cover only for some combinations of study areas, indicating that there were site-specific differences. Soil conductivity, tree density (per 125 m^2) and distance from river showed no significant correlations with lignum cover. Surprisingly, lignum cover did not vary with flood frequency (Fig. 2), although the sites where lignum was present fall within a 3–10-year flood recurrence interval.

Principal Components Analysis

The first component of the PCA explains 37% of the total variance (Table 2) and separates the sites at Overland Corner from the others (Fig. 3*a*). This reflects their greater flooding frequency and the lack of trees (the two variables contributing most

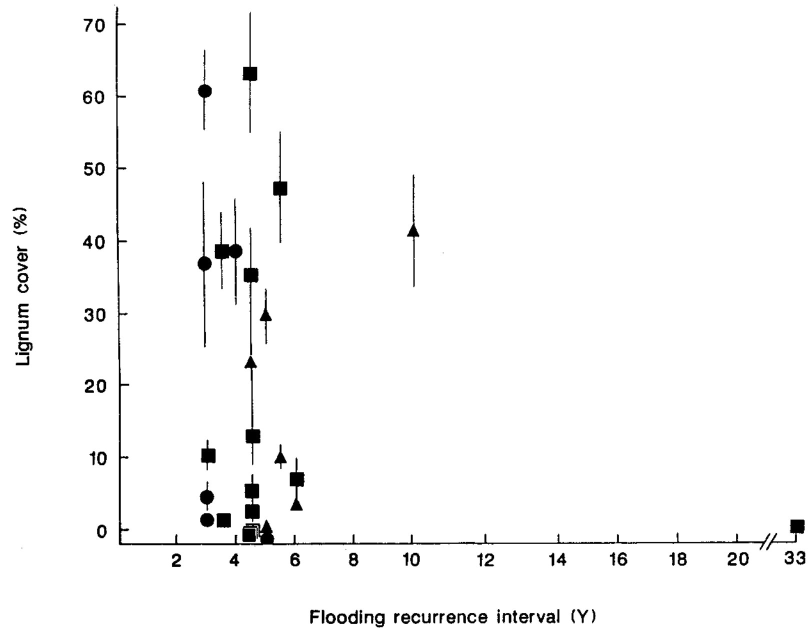

Fig. 2. The relationship between percentage lignum cover and flood recurrence interval at Chowilla (squares), Morgan (triangles) and Overland Corner (circles).

variation). Increasing scores on the second and third components indicate a gradient of increasing lignum cover, excepting sites OC–4 (unusual in having sandy soil) and OC–0 (see below) (Fig. 3*b*). This suggests interactions between soil hardness and moisture, which together contribute most to the variation on component II (Table 2), and between

Table 2. Results of the Principal Components Analysis, showing the variance associated with components I–IV and the correlations with each environmental variable

Only variables which account for more than 10% are shown. Underlines indicate a negative correlation between the respective component and variable

Variable	Component			
	I	II	III	IV
Percentage of explained variation	37·0	20·6	13·7	10·2
Distance from river (m)			44·9	$\underline{14{\cdot}8}$
Number of trees	19·3			
Flooding				
Recurrence interval	19·4			
Years since flooded	24·5			
Days flooded, 1973–82	$\underline{23{\cdot}4}$			
Soil				
Hardness		$\underline{27{\cdot}4}$		$\underline{19{\cdot}5}$
pH		$\underline{10{\cdot}2}$		44·0
Conductivity			$\underline{30{\cdot}6}$	$\underline{10{\cdot}3}$
Organic content	10·5	10·2		
Moisture		39·0		

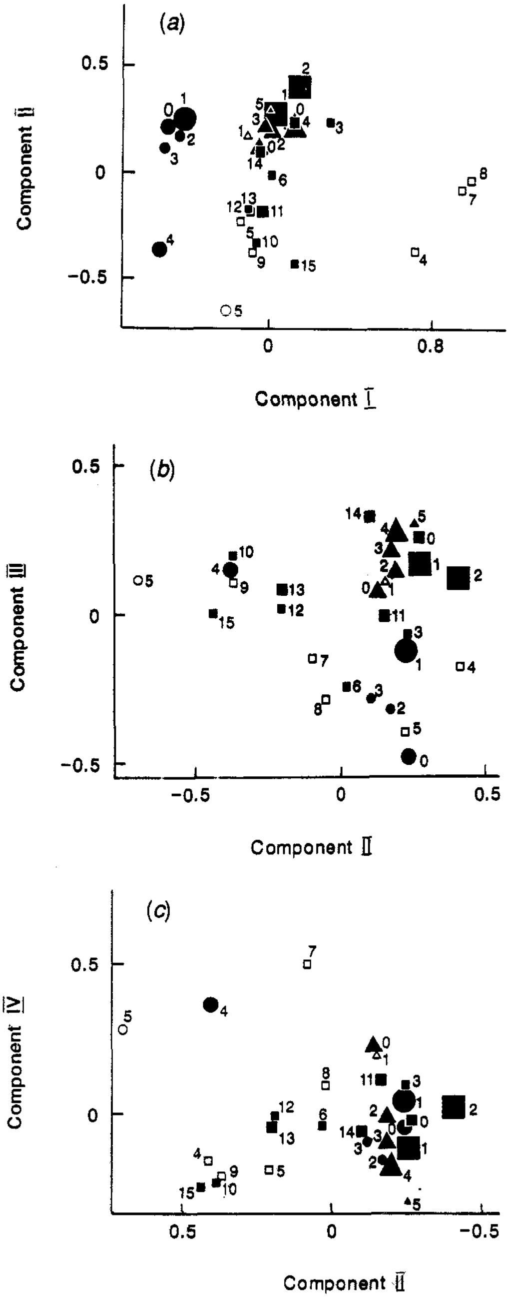

Fig. 3*a*, *b*, *c*. Principal Components Analysis for the three study areas. Percentage lignum cover at sampling sites is indicated by the diameter of the symbols: >40% (large solid symbols), 10·0–39·9% (medium solid), 0·1–9·9% (small solid), no lignum (open symbols). Sites referred to in the text are Chowilla (squares), Morgan (triangles) and Overland Corner (circles), 0, 1, 2, 3... = increasing distance from the river).

conductivity and distance from the river, which load heavily on component III. The close alignment of the gradient with component II suggests that lignum cover is more strongly associated with soil hardness and moisture than with soil conductivity (cf. Table 1). A cluster of sites with >10% lignum cover lies over a small range of values of component IV (Fig. 3*c*; again, OC–4 is exceptional). This suggests that soil pH, which explains 44% of the variation on component IV (Table 2), may also interact with soil moisture and hardness.

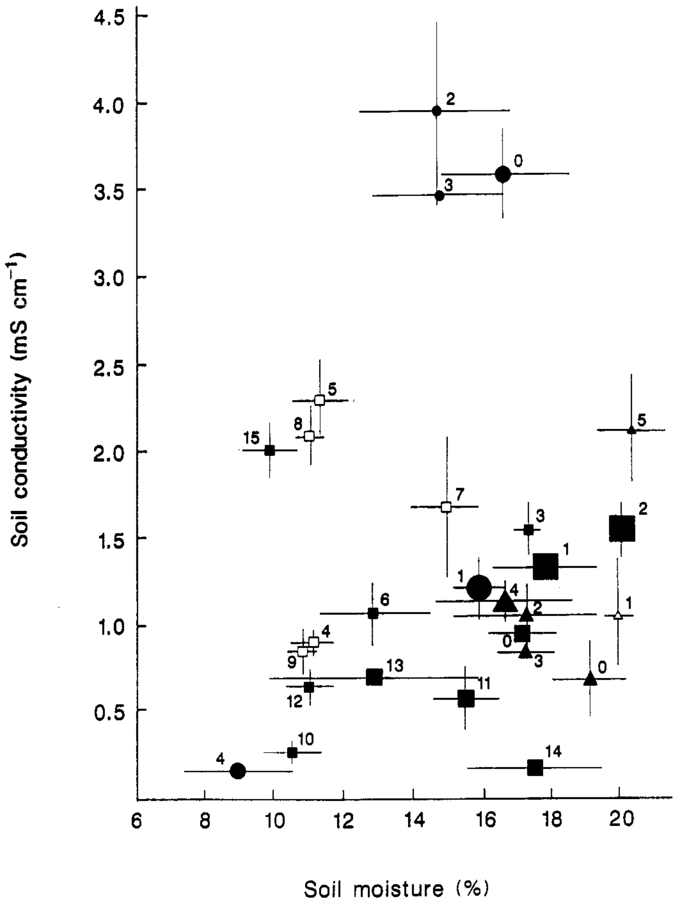

Fig. 4. Lignum cover *v.* soil moisture and conductivity. Symbols as in Fig. 3. Site OC-5 (no lignum) is omitted due to its low soil moisture (4·2 ± 1·3%).

Direct Plots

Most sites with >10% lignum cover had high soil moisture (>15%) and low soil conductivity (<1·5 mS cm^{-1}) (Fig. 4; Table 1). Two sites are anomalous: site 1 at Morgan had high soil moisture and no lignum despite low soil conductivity; and site 0 at Overland Corner had high soil moisture and abundant lignum, despite high conductivity. There is clearly an interaction between soil moisture and conductivity, as moist sites with low lignum cover had high conductivities whereas drier sites with dense lignum cover had relatively low conductivities.

Similarly, most sites with >10% lignum cover had high soil moisture and low soil pH (Fig. 5). The two exceptions to the trend shown in Fig. 4 (M–1, OC–0) conform to the correlations between lignum cover and soil moisture and pH. Four sites (M–5, OC–2, OC–3, C–3), all with low lignum cover, fall within the range of soil moisture and pH of sites with high lignum cover (Fig. 5), but all had high conductivities (Fig. 4). Two sites (M–0, C–13) with high lignum cover fall outside the ranges of soil moisture and pH at other sites with high lignum cover, but had low conductivities.

Fig. 6 shows a cluster of sites with >10% lignum cover, characterised by high soil moisture and relatively high organic content (4·4–6·9%). Three of the sites that do not conform are at Overland Corner (OC–0, OC–1, OC–4), where the organic content is low (there are no nearby trees) and there are too few data to indicate variability.

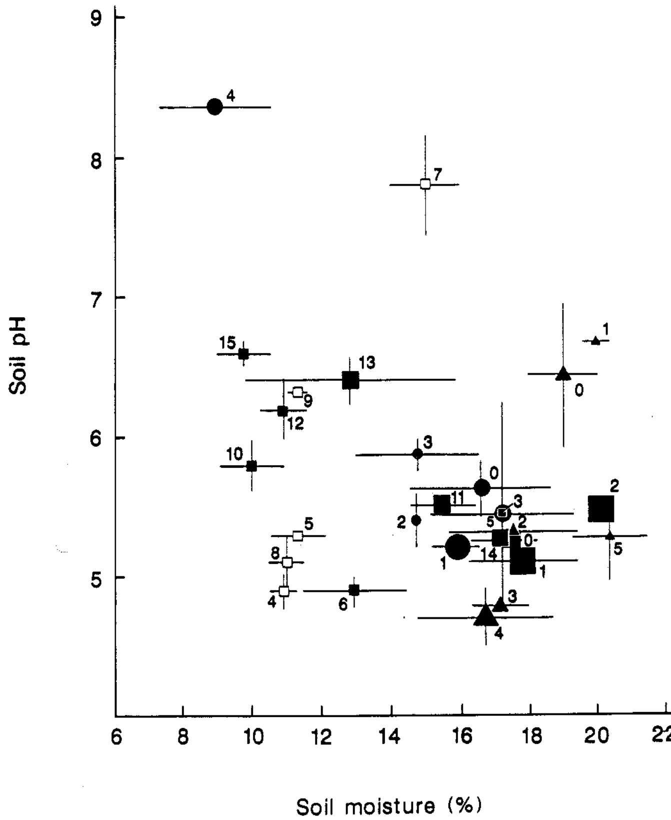

Fig. 5. Lignum cover *v.* soil moisture and pH. Symbols as in Fig. 3. Site OC–5 (no lignum) is omitted due to its low soil moisture (4·2 ± 1·3%).

Experimental Results

The non-parametric ANOVA (Table 3) revealed significant effects on stem length associated with the volume and salinity of irrigation water, but no significant interaction. The greatest increases in stem length occurred for plants irrigated with comparatively large volumes (450–900 mL) of slightly saline water (250 mg L^{-1}). There was little difference between the soil conductivities of treatments given distilled (0 mg L^{-1}) and slightly saline water (250 mg L^{-1}), indicating that the effects of the saline treatments on soil conductivities were not consistent.

Table 3. Non-parametric ANOVA showing the effects of the salinity and volume of irrigation water on the stem growth of potted specimens of lignum

The Kruskal-Wallis statistic *H* is the ratio between the computed s.s. and the total mean square (346·67); critical values are approximated by the distribution of Chi-squared for the given degrees of freedom (d.f.).

Source	s.s.	d.f.	*H*	
Volume	6570·88	3	18·95	$P<0·001$
Salinity	5568·09	3	16·06	$P<0·01$
Interaction	3924·66	9	11·32	$P>0·05$
Total	16063·63	15		

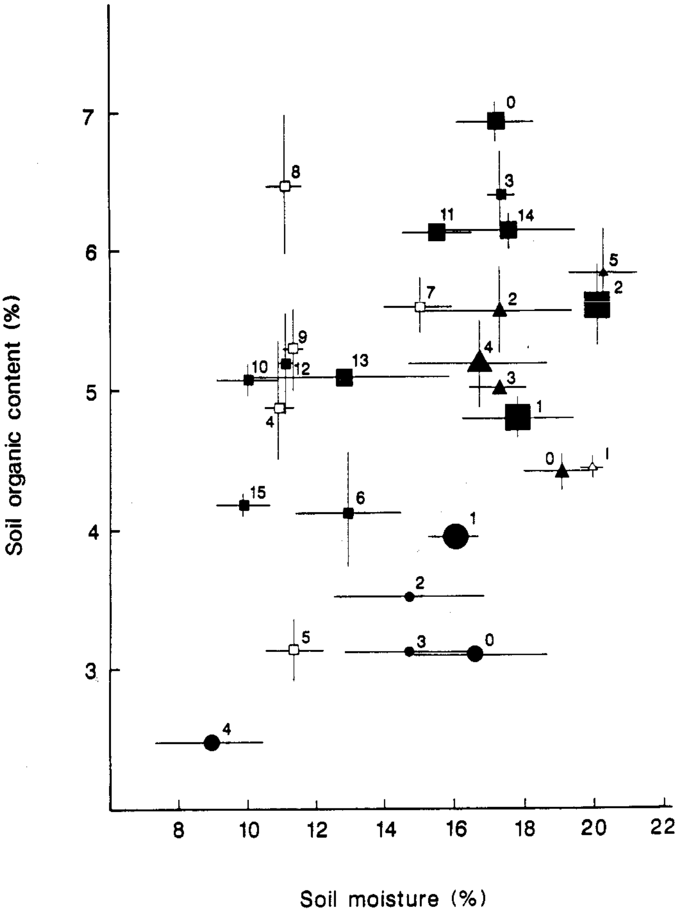

Fig. 6. Lignum cover *v.* soil moisture and organic content. Symbols as in Fig. 3. Site OC-5 (no lignum) is omitted due to its low soil moisture (4·2 ± 1·3%). Note that error bars could not be computed for sites at Overland Corner.

Discussion

The frequency and extent of flooding across the Murray floodplain have changed markedly since the advent of flow regulation after about 1920 (Walker 1992), and have undoubtedly contributed to the apparent general decline of the riparian vegetation (Margules and Partners *et al.* 1990). Other factors include salinisation, land clearance for agriculture and the impact of stock and feral grazing animals (e.g. rabbits). The floodplain is over-run by weed species (Margules and Partners *et al.* 1990), reflecting a high degree of disturbance (cf. Fox and Fox 1986; Breen *et al.* 1988), although the vegetation of intermittent wetlands is apparently resistant to invasion (McIntyre *et al.* 1988). So little research has been carried out that the nature of these changes and the mechanisms of their effects remain largely matters for speculation.

Compared with other Murray floodplain species, lignum is extremely tolerant of waterlogging and moderately tolerant of salinity, but vulnerable to drought (Caldwell Connell Engineers 1981). It has little or no value as fodder for stock (e.g. Leigh and Mulham 1977), although seedlings may be browsed by kangaroos and possibly rabbits (D. C. Cheal, personal communication, 1982) and insects. In some parts of its range it may be threatened by irrigation (Murray-Darling Basin Ministerial Council 1987), but this covers a variety of indirect effects including vegetation clearance and salinisation. Clearly, there is great scope for ecological and physiological studies.

Our preliminary data show that lignum grows best in areas flooded every 3–10 years, although percentage cover is not correlated with flood frequency *per se*. The data also demonstrate correlations between lignum cover and edaphic conditions including high moisture, high organic content, low conductivity and low pH.

The correlation between lignum cover and soil moisture may be due to the shade provided by dense lignum, preventing evaporation. It may also reflect indirect relationships with microtopography and soil texture, which affect available soil moisture (cf. National Environmental Consultancy 1988). Texture may govern the correlation between soil hardness and lignum cover. Microtopography may affect soil moisture indirectly, through concentration and dispersal of runoff. The correlation between lignum cover and soil organic content undoubtedly reflects accumulations of fallen leaves, dead twigs and root material near the bases of the plants. In addition, dense lignum thickets often have abundant faecal pellets from rabbits and other animals. The apparent association with soil pH is consistent with Van der Sommen's (1980) observation that lignum is highly tolerant of acid soils. Further, the possible interaction between pH and other soil factors is consistent with the known effects of pH on plants. The direct effects of pH in the range 4·0–8·0 on plant growth are negligible, other environmental features being equal (Jeffrey 1987), but there may be many indirect effects. For example, pH affects the solubility of certain elements, including toxins and nutrients (Salisbury and Ross 1978). The association with pH may also reflect competition with other plants (Salisbury and Ross 1978). Given appropriate soil conditions, lignum may be most abundant because it out-competes other species. It may also grow well under other soil conditions, but be out-competed by other species. It would be instructive to test the hypothesis that lignum grows equally well over a range of soil moisture, pH and conductivity conditions.

Soil nutrients were not measured in this study, for logistic reasons, and there are no published data for lignum that might be used to speculate about their role in germination, establishment and growth. In the absence of these data, organic content might be taken as a rough indication of soil fertility. Logistic problems also precluded direct observations of groundwater or the soil profile. Although the depth to groundwater was known to be 1–2 m and its salinity was near that of seawater, minor variations in these factors may have influenced the local abundance of lignum. Soil samples were taken only near the surface (25 cm depth), although the salinity of floodplain soils increases with depth (Van der Sommen 1980). As sampling was in winter, the salinities reported here probably are lower than those experienced by the plants at greater depth. The pH of regional floodplain soils also increases with depth: the surface generally is neutral to acidic, but below 30 cm the soil is alkaline (F. Van der Sommen, personal communication). Moisture would increase with depth, and organic content would decrease. Surface soil conditions would influence the growth (and germination) of lignum, as most plant roots occur in the upper half of the rooting zone (Jeffrey 1987; cf. Cunningham *et al.* 1981). The plants are relatively deep-rooted, however, and are likely to be influenced by conditions at depths greater than 25 cm. Roots of 2·2 m were observed along eroding banks at Overland Corner in 1989, and the maximum length is likely to be >3 m depending on soil type.

Correlations between the abundance of adult plants and environmental factors are unlikely to reveal completely the factors controlling species abundance because of differences in scale relative to factors affecting germination and seedling growth (Harper 1977). The requirements for germination and seedling growth, especially tolerance to anaerobic conditions, must play a role in determining the range and abundance of the species. Lignum is known to germinate in wet mud (Cunningham *et al.* 1981), but it is also capable of vegetative reproduction and this may overcome problems of seedling tolerance or survival.

Our working hypothesis is that, under the conditions on the lower Murray floodplain, lignum grows most vigorously when soil moisture is high, pH relatively low and conductivity relatively low. The interaction between soil moisture and conductivity, evident from the field study, suggests that higher soil moisture compensates for relatively high conductivities. Within the ranges of moisture and conductivity where sites with high lignum cover occur, sites with higher moisture tend to have higher conductivities and *vice versa* (Fig. 5). This is consistent with an interaction between these variables, as the effect of salt is to lower soil water potential, impeding water absorption by plant roots (Salisbury and Ross 1978). The effect of more soil moisture, however, is to raise soil water potential. Thus, high moisture may compensate for higher conductivity. This may explain why C-13 (Fig. 5) had over 10% lignum cover despite a relatively low soil moisture content; it also had a low conductivity (0·7 mS cm^{-1}).

Management strategies for maintaining lignum growth should include flooding every 3–10 years. The apparent interaction between soil moisture and conductivity suggests that saline soils would require more frequent flooding to enable lignum to grow vigorously.

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References

Barnett, S. (1989). The hydrogeology of the Murray Basin in South Australia, with special reference to the alluvium of the River Murray floodplain. M.Sc. Thesis, Flinders University of South Australia.

Boulton, A. J. and Lloyd, L. N. (1991). Macroinvertebrate assemblages in floodplain habitats of the lower River Murray, South Australia. *Regulated Rivers: Research and Management* **6**. (In press.)

Breen, C. W., Rogers, K. H., and Ashton, P. J. (1988). Vegetation processes in swamps and flooded plains. In 'Vegetation of Inland Waters'. (Ed. J. J. Symoens), pp. 223–47. (Kluwer Academic: Dordrecht.)

Bren, L. J. (1988). Effects of river regulation on flooding of a riparian red gum forest on the River Murray, Australia. *Regulated Rivers: Research and Management* **2**, 65–77.

Briggs, S. V., and Maher, M. T. (1983). Litter fall and leaf decomposition in a river red gum (*Eucalyptus camaldulensis*) swamp. *Australian Journal of Botany* **31**, 307–16.

British Standards Institute (1975). 'Methods of Test for Soils for Civil Engineering Purposes.' (British Standards Institute: London.)

Buchholz, K. (1981). Effects of minor drainages on woody species distributions in a successional floodplain forest. *Canadian Journal of Forest Research* **11**, 671–6.

Caldwell Connell Engineers Pty Ltd (1981). 'Katarapko Island Evaporation Basin Environmental Study.' (Engineering and Water Supply Department: Adelaide.)

Campbell, D. A. (1973). Living with lignum. *Agricultural Gazette, NSW* **84**, 290–2.

Canfield, R. (1941). Application of the line interception method in sampling range vegetation. *Journal of Forestry* **39**, 388–94.

Chatfield, C., and Collins, A. J. (1980). 'Introduction to Multivariate Analysis.' (Chapman and Hall: London.)

Chorney, K. (1986). Polygonaceae. In 'Flora of South Australia, Part 1' (Eds J. P. Jessop and H. R. Toelken.), pp. 173–84. (Government Printer: Adelaide.)

Cole, P. J. (1978). Soils and land use of the River Murray Valley in South Australia. *Proceedings of the Royal Society of Victoria* **90**, 167–74.

Cunningham, G. M., Mulham, W. E., Milthorpe, P. L., and Leigh, J. H. (1981). 'Plants of Western New South Wales.' (Government Printer: Sydney.)

Fox, M. D., and Fox, B. J. (1986). The susceptibility of natural communities to invasion. In 'Ecology of Biological Invasions: An Australian Perspective' (Eds R. H. Groves and J. J. Burdon.), pp. 57–66. (Australian Academy of Science: Canberra.)

Greig-Smith, P. (1983). 'Quantitative Plant Ecology.' (Blackwell: Oxford.)

Harden, G. J. (Ed.) (1990). 'Flora of New South Wales. Vol. 1.' (New South Wales University Press: Kensington.)

Harper, J. L. (1977). 'Population Biology of Plants.' (Academic Press: London.)

Jeffrey, D. W. (1987). 'Soil–Plant Relationships: An Ecological Approach.' (Croom-Helm: Kent, UK.)

Junk, W. J., and Welcomme, R. L. (1990). Floodplains. In 'Wetlands and Shallow Continental Water Bodies'. Vol. 1. (Ed. B. C. Patten.), pp. 491–524. (SPB Academic Publishing: The Hague.)

Kernich, A. M. (1984). The climate of the River Murray and environs, South Australia. River Murray Irrigation and Salinity Program Technical Paper 11. (Dept of Agriculture: Adelaide.)

Lange, Dames and Campbell (Australia) Pty Ltd (1987). 'River Murray at Morgan: Flood Frequency Study.' (Engineering and Water Supply Dept: Adelaide.)

Leigh, J. H., and Mulham, W. E. (1977). Vascular plants of the Riverine Plain of New South Wales with notes on distribution and pastoral use. *Telopea* **1**, 225–93.

Lloyd, L. N., Puckridge, J. T., and Walker, K. F. (1991). Fish populations of the Murray–Darling river system: their significance and requirements for survival. In 'Management of the River Murray System — Making Conservation Count'. (Eds T. Dendy and M. Coombe.) pp. 86–99. (Dept of Environment and Planning: Adelaide.)

Ludwig, J. A., and Reynolds, J. F. (1988). 'Statistical Ecology: A Primer on Methods and Computing.' (Wiley: New York.)

Margules and Partners, Smith, P. and J., and Department of Conservation, Forests and Lands, Victoria (1990). 'Riparian Vegetation of the River Murray.' (Murray–Darling Basin Commission: Canberra.)

McIntyre, S., Ladiges, P. Y., and Adams, G. (1988). Plant species-richness and invasion by exotics in relation to disturbance of wetland communities on the Riverine Plain, NSW. *Australian Journal of Ecology* **13**, 361–73.

Murray-Darling Basin Ministerial Council (1987). 'Murray–Darling Basin Environmental Resources Study.' (State Pollution Control Commission: Sydney.)

National Environmental Consultancy (1988). 'Chowilla Salinity Mitigation Scheme: Draft Environmental Impact Statement.' (Engineering and Water Supply Dept: Adelaide.)

O'Malley, C., and Sheldon, F. (Eds) (1990). 'Chowilla Floodplain Biological Study.' (Nature Conservation Society of South Australia: Adelaide.)

Sainty, G. R., and Jacobs, S. W. L. (1981). 'Waterplants of New South Wales.' (Water Resources Commission: Sydney.)

Salisbury, F. B., and Ross, C. W. (1978). 'Plant Physiology.' (Wadsworth: California.)

Scheirer, C. J., Ray, W. S., and Hare, N. (1976). The analysis of ranked data derived from completely randomized factorial designs. *Biometrics* **32**, 429–34.

Specht, R. L. (1972). 'The Vegetation of South Australia.' 2nd Edn. (Government Printer: Adelaide.)

Van Der Sommen, F. (1980). Ecology of floodplain plant communities. *Riverlander* (Murray Valley League), March 1980, 22–3.

Walker, K. F. (1992). A semi-arid lowland river: the River Murray, Australia. In 'The Rivers Handbook'. Vol. 1. (Eds P. Calow and G. E. Petts.). (Blackwell: Oxford.) (In press.)

Walker, K. F., Thoms, M. C., and Sheldon, F. (1992). Effects of weirs on the littoral environmental of the River Murray, South Australia. In 'River Conservation and Management'. (Eds P. J. Boon, P. Calow and G. E. Petts.), pp. 271–92. (Wiley: Chichester.)

Williams, W. D. (1986). Conductivity and salinity of Australian salt lakes. *Australian Journal of Marine and Freshwater Research* **37**, 177–82.

Zar, J. H. (1984). 'Biostatistical Analysis'. 2nd Edn. (Prentice-Hall International: New Jersey.)

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