

Diversity and dynamics of riparian vegetation

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Summary

- ~ Riparian plant habitats are temporally and spatially heterogeneous as a result of fluvial disturbance and comprise numerous different habitat types including; channel, channel bank, floodplain and wetland habitats.
- ~ Plant diversity in Australian habitats comprises a range of taxonomic groups, life forms and functional groups and includes plants only found in riparian areas, as well as those that can move between environments.
- ~ Riparian plant species exhibit a diversity of morphological, physiological and life history adaptations which enable them to persist in these variable and dynamic habitats.
- ~ Vegetation communities in riparian habitats are temporally and spatially dynamic as a result of fluvial disturbance.
- ~ Threats to riparian vegetation in Australia include hydrological change, weeds and inappropriately managed grazing.

2.1 Riparian plant habitats

Riparian zones are amongst the world's most diverse and dynamic plant habitats (Malanson 1993, Naiman & Décamps 1997). As a result of complex interactions between hydrology and geomorphology, riparian zones are characterised by a high degree of temporal and spatial heterogeneity and can be perceived as mosaics of habitat patches within which soil moisture, sediment and nutrient properties vary (Stromberg 2001). In general, surface water hydrology is considered to be the principal determinant of riparian vegetation diversity, and water dynamics such as flooding exert an overriding influence on riparian habitat characteristics both temporally and spatially (Gregory et al. 1991, Blom et al. 1994, Naiman & Décamps 1997, Stromberg 2001).

Riparian zones typically have higher soil moisture and nutrient content than neighbouring upland systems and this may favour plant biomass production (Megonigal et al. 1997). During inundation, however, soils become anoxic and toxic ions, e.g. of manganese and iron, accumulate in bio-available forms as a result of soil microbial processes (Blom & Voesenek 1996). In addition to changes in temperature and light that occur during submergence, such alterations to the soil can restrict normal plant metabolic processes, including respiration, photosynthesis and nutrient uptake (Hook 1984). Soil compaction may also result from flooding, increasing resistance to the growth of plant roots (Blom & Voesenek 1996). Additionally, flooding can cause mechanical damage to plants via hydraulic influence on stems (Menges 1986, Young et al. 2001) or through erosion and abrasion of sediments (Naiman & Décamps 1997). Deposition of sediments associated with flooding may bury seedlings or impede germination of propagules (Sluis & Tandarich 2004) but can also create areas of bare substrate suitable for plant colonisation (Stromberg 2001). Furthermore, flooding can provide an additional vector for propagule dispersal called 'hydrochory' as many riparian plant species possess buoyant seeds (Nilsson et al. 1991). Over longer time periods, flooding may influence riparian plant habitats by altering the geomorphic template through changes to channel morphology such as the formation of meanders or abandoned channels (Stromberg 2001).

Hydrochory: dissemination of seeds through water.



Top: Lawn Hill Creek, a stream with permanent flow, and the riparian vegetation dominated by *Melaleuca leucadendra* and *Livistona rigida*. Middle left: Permanent lagoon in the Suttor River system with moderate seasonal rise, in which riparian vegetation, with *Eucalyptus camaldulensis* and *Eucalyptus microtheca*, is seasonally inundated. Middle right: Logan Creek has a riparian zone that is inundated by slow moving floodwaters, here with the base of the dominant trees *Eucalyptus microtheca* and *Acacia cambagei* seasonally submerged. Above left: Barratta Creek, a system with permanent swift flowing water and seasonally inundated, here with *Melaleuca leucadendra*, *Nauclea orientalis* and *Livistona decora*. Above right: A section of the Burdekin River with permanent flow and seasonal dynamic floods, dominated by *Melaleuca leucadendra*. All photos John Dowe.

The effects of flooding on riparian plant habitats depend upon hydrological attributes of flood events such as timing, depth and duration, and frequency. Plant responses to flooding can be influenced by the seasonal timing of flood events, for example if flooding coincides with seed dispersal or germination cues related to temperature (Baskin & Baskin 1998). Flooding depth can control the light environment of submerged plants, and the duration of inundation is significant as many of the stresses to plants associated with flooding, for example, soil anoxia, are cumulative over time (Blom & Voesenek 1996). The rates of floodwater rise and recession may also be influential as, for instance, faster rates of change might be more likely to result in mechanical damage to stems. Finally, flood frequency is an important hydrological attribute as the time elapsed since a prior event will affect which plants are present in a habitat as well as their life history stages and hence, their responses to flooding.

Flood frequency can also determine the influence of other factors in riparian plant habitats as regional characteristics, such as soil properties, rainfall or drought, are more likely to be important when flood frequency is low (Capon 2005). In riparian habitats with a high flood frequency, for example, salinity and fire can have a reduced impact as frequent flooding can wash away salts and fuel, e.g. plant litter and debris (Stromberg 2001). Frequent flooding can also replenish groundwater supplies on which some riparian plants may be partially or totally dependent (Lamontagne et al. 2005). Other characteristics of riparian habitats which are likely to influence vegetation include light, which is often greatest at the edge of riparian habitats and decreases along a gradient perpendicular to the waterbody, intra-specific and inter-specific plant competition and herbivory. Flooding, however, is generally considered to be the primary factor structuring vegetation in riparian habitats (Naiman & Décamps 1997).



Left: The Belyando River in flood, with slow moving flood waters, and submerged riparian vegetation of *Eucalyptus camaldulensis*, *Eucalyptus microtheca* and *Melaleuca bracteata*. Right: Flood debris on the banks of Lolworth Creek, a system that has dynamic seasonal floods. Photos John Dowe.



Left: The Murrumbidgee River in flood with *Eucalyptus camaldulensis*. Photo Lu Hogan. Right: *Eucalyptus coolabah* in the Coongie Lake. Photo Roger Charlton.

Habitat types

Given its broad definition, a diverse array of habitats can be considered 'riparian'. From a vegetation perspective, however, these can be classified into four major groups on the basis of their geomorphologic and hydrological characteristics (Brock et al. in press):

- ~ channel habitats,
- ~ channel bank habitats,
- ~ floodplains, and
- ~ wetlands.

Factors exerting a significant influence on vegetation, and particularly the frequency and magnitude of flooding, vary with some degree of predictability between these. It is important to note, however, that these habitat types do not necessarily occur all together and their distribution depends on position within the landscape. Riparian habitats in constrained upstream reaches, for example, are likely to be restricted to channel and channel bank habitats, while floodplains and their wetlands occur more commonly in alluvial downstream reaches.

Channel habitats

Depending on the permanency of surface water flows, significant areas of active river or stream channels can be exposed for varying periods of time, providing habitat for colonisation by riparian plants. Such habitats experience extreme fluvial disturbance, including high frequency and magnitudes of flooding, as well as erosion and deposition of bed sediments, crucial in determining the composition and structure of within-channel vegetation. When surface water is present, hydraulics can play a significant role, as some macrophyte species may

be restricted to areas of slow-flowing water (Mackay et al. 2003). Canopy cover and, therefore, light reaching channel habitats is another important factor (Mackay et al. 2003, Fritz et al. 2004). Channel habitats also include geomorphic features such as depositional bars and islands which are typically composed of coarse substrate materials but are flooded less frequently than channel beds, therefore providing a slightly more stable habitat for riparian plants (Hupp & Osterkamp 1985).

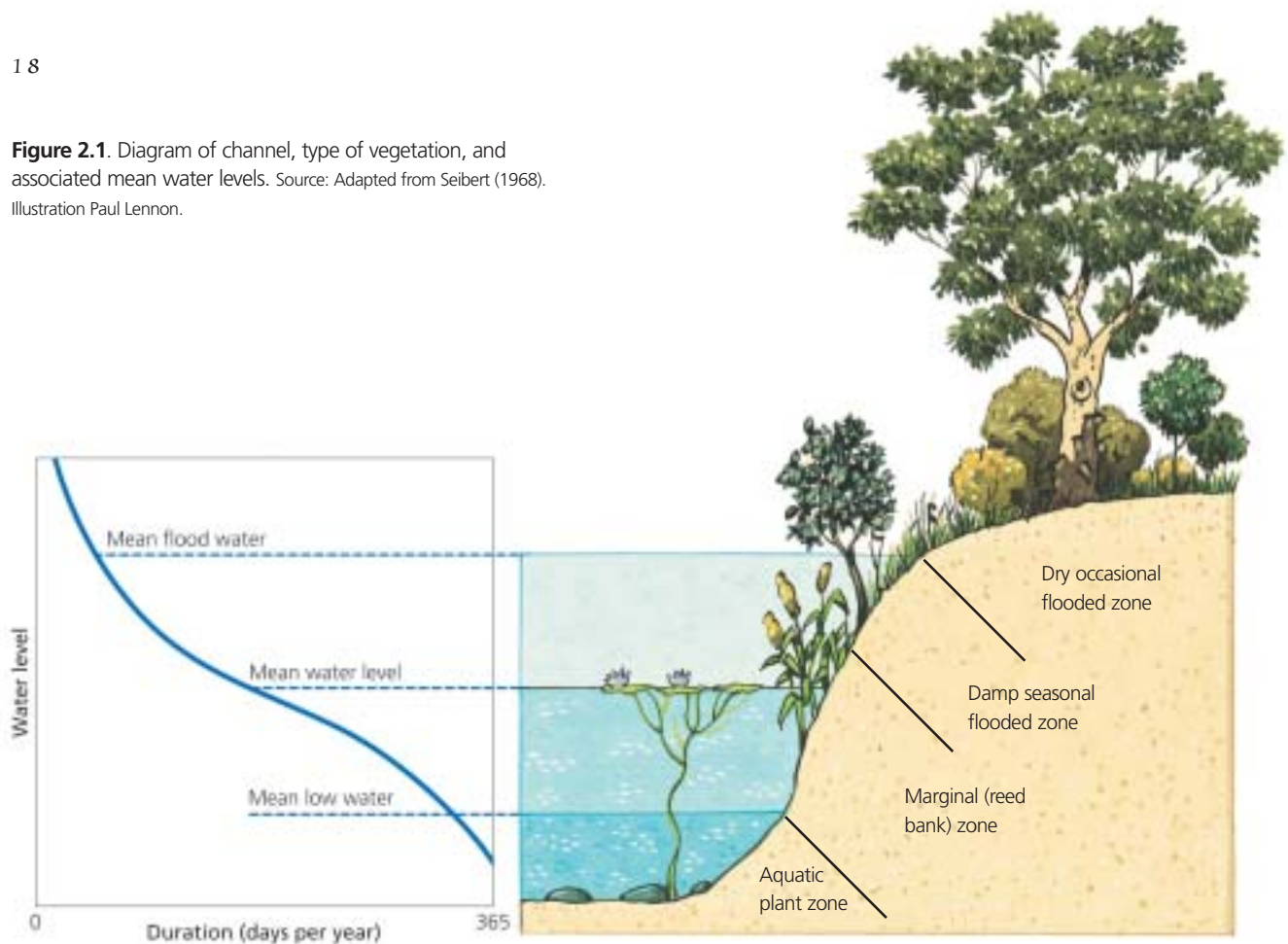
Channel bank habitats

Channel bank habitats comprise those areas immediately adjacent to channels and include levee banks. Flood frequency is lower in channel bank habitats than channel habitats and generally decreases along lateral gradients of elevation or distance away from the channel. The capacity of soils to hold water following inundation is an important determinant of vegetation dynamics in these riparian habitats, and reflects sediment depth and composition as well as height above the stream water level. Levee banks, for example, often flood frequently but may dry out faster than lower lying channel bank areas resulting in differences between vegetation communities (Naiman & Décamps 1997). In channel bank habitats, plants, and particularly deeply rooted trees, are also likely to have access to more permanent surface water within the adjacent channel, as well as to groundwater where this is hydrologically connected to the stream. Other significant physical factors influencing vegetation in channel bank habitats include light, which is likely to be higher at the channel edge, and erosion and deposition of sediments, particularly at the immediate interface with the active channel.

Thick wet season growth in a section of the Burdekin River with sloping banks. Photo John Dowe.



Figure 2.1. Diagram of channel, type of vegetation, and associated mean water levels. Source: Adapted from Seibert (1968). Illustration Paul Lennon.



This photo shows some of the characteristics of an intact riparian zone as illustrated in the above diagram. Photo CSIRO Sustainable Ecosystems.



Narran Lakes in flood. Photo Narran Lakes Ecosystem Project.

Floodplains

Floodplains can be defined as ‘areas of low lying land that are subject to inundation by lateral overflow water from rivers with which they are associated’ (Junk & Welcomme 1990). Typically, these occur beyond immediate channel bank habitats and may extend for several kilometres away from channels. In the large floodplains of the channel country, however, floodplains can be up to 60 kilometres in width. Vegetation composition and structure in floodplain habitats is determined primarily by flood frequency, depth and duration, which, as in channel bank habitats, usually decline along complex lateral gradients of increasing elevation or distance from channels (Capon 2003, 2005).

Wetlands

A wide variety of wetland habitats can be considered to be riparian based on the definition used here, including freshwater and saline lakes, oxbow lakes, abandoned channels, back swamps, claypans and springs. Within each of these habitat types, further differentiation may also exist between open water or ‘bed’ habitats and fringing habitats that may be comparable to channel banks. Hydrological properties of wetlands, e.g. permanence of surface water, will have a significant influence on their plant communities and these will depend on a wetland’s proximity to the channel as well as local drainage characteristics. Other important factors may include sediment composition, groundwater connectivity and salinity.

One of the Falkiner Memorial Field Station wetlands on the Murray River following flooding to promote growth of black box, nardoo, spikesedge and flowering lignum. Photo NSW Murray Wetlands Working Group.



2.2 Riparian plant diversity

Riparian floristics

Riparian vegetation throughout much of Australia is dominated by a relatively small number of plant species (Cole 1986) and can be characterised as having low species diversity but with locally high individual species abundance (Fielding & Alexander 1996). A wide range of life forms are represented, including trees, shrubs, monocots (i.e. grasses and sedges) and forbs, the latter two groups of which include perennial, annual and ephemeral species. Of the non-vascular plants, many Bryophytes (mosses, liverworts, and hornworts) are restricted to the riparian zone and submerged charophytes (green macro-algae) are also frequently encountered in channel and wetland habitats. Amongst vascular plants, ferns and fern allies have a limited occurrence in riparian zones, e.g. *Marsilea* spp. (nardoo) (Capon 2003), with angiosperms generally comprising the dominant component of riparian flora.

Monocots: an abbreviation of *monocotyledon* (*mono*, single; *cotyledon*, leaf), which is one of the two major classes of plants, and typified by seedlings with a single leaf; an absence of cambium (i.e. wood); stems with thickened basal portions forming corms, rhizomes, and bulbs; linear leaves with parallel venation; and flowers parts usually in multiples of threes (i.e. commonly six sepals, six petals, etc.).

Prominent riparian tree species in semi-arid and monsoonal northern Australia include *Eucalyptus camaldulensis* (river red gum), broad and narrow leaved *Melaleuca* species (*M. argentea*, *M. fluviatilis*, *M. leucadendra*, *M. trichostachya*, *M. viridiflora*), *Casuarina cunninghamiana* (she oak), *Terminalia* spp., and *Lophostemon grandiflorus*, among others. In south-east continental Australia, dominant riparian species include *Callistemon viminalis*, *Casuarina cunninghamiana*, *Eucalyptus camaldulensis*, *Eucalyptus largiflorens*, *Potamophila parviflora*, *Tristania neriifolia* and *Waterhousea floribunda*; in Tasmania *Acacia axillaris*, *Callitris oblonga*, *Micrantheum hexandrum*; and in south-western Australia *Eucalyptus rudis* and *Melaleuca raphiophylla* are common. Riparian trees in the arid inland catchments of Australia are often restricted to channel bank habitats and typically include *Eucalyptus camaldulensis*, *Eucalyptus coolabah* and *Acacia stenophylla*. In the very wet rainforest areas of north-east Queensland, it is difficult to identify specifically riparian tree species



Melaleuca leucadendra, Burdekin River. Photos this page John Dowe.



Melaleuca fluviatilis, *Casuarina cunninghamiana* and *Corymbia tessellaris* on Lolworth Creek.

as most that occur in channel bank habitats are also present in adjacent habitats. Understorey species throughout Australian riparian habitats often include many monocot species with emergent sedges typically dominating fringing vegetation in frequently flooded habitats. Annual and ephemeral forbs can also be frequently encountered in channel bank and floodplain habitats though their appearance in the extant vegetation is often highly dependent on seasonal conditions. Submerged, free-floating and floating-attached aquatic plants are common in channel and wetland habitats but often have patchy distributions.

Plant diversity at the family level in the riparian zone more or less follows the general diversity found across much of Australia. Species in the family Myrtaceae (Australia's most diverse family), in the genera *Eucalyptus*, *Callistemon*, *Leptospermum*, and *Melaleuca*, account for many riparian species. Families well represented in riparian habitats also include Cyperaceae (*Baumea*, *Cyperus*, *Schoenoplectus*), Poaceae (*Brachiaria*,

Chrysopogon, *Megathrysus*, *Phragmites*), Proteaceae (*Banksia*, *Grevillea*, *Lomatia*), Mimosaceae (*Acacia*, *Carthormion*), Fabaceae (*Aeschynomene*, *Sesbania*), Arecaceae (*Archontophoenix*, *Livistona*), and Euphorbiaceae (*Calycopeplus*, *Cleistanthus*, *Flueggea*). The riparian species in these families can be regarded as evolutionarily specialised members that have been able to adapt to, and successfully exploit, a unique habitat, i.e. the riparian zone. Other families that are represented in riparian vegetation with specialised species, but otherwise have the majority of other genera in non-riparian habitats, include Polygonaceae (*Muehlenbeckia*, *Persicaria*, *Polygonum*) and Onagraceae (*Ludwigia*). Although there are a few grass species that are riparian specialists, most grass species that occur in riparian zones also occur in other habitats, reflecting the ability of grass species to adapt to a diversity of habitats. Additionally, the palm family Arecaceae, has a relatively high proportion of riparian species in northern Australia, particularly in *Archontophoenix* and *Livistona*.



Livistona rigida, Gregory River. Photos this page John Dowe.



Schoenoplectus mucronataus (foreground) and *Pandanus spiralis* (background) Beames Brook.



Melaleuca trichostachya, Douglas River, with typical leaning response to seasonal flooding. Photo John Dowe.

In an investigation of riparian species, van Steenis (1981) listed 12 Australian species as obligate rheophytes, which he defined as ‘*plant species which are in nature confined to the beds of swift-running streams and rivers and grow there up to flood-level, but not beyond the reach of regularly occurring flash floods*’. Additionally, a small number were discussed as facultative rheophytes or riparian trees. These included *E. camaldulensis*, described as a riparian species with seedlings able to develop in swift-flowing water; *Melaleuca argentea* which was described as a rheophyte of sandy and gravelly stream banks and beds; and *Melaleuca bracteata* (to include *M. trichostachya* and *M. linariifolia*) as a riverine species and not a rheophyte.

Evolution of riparian vegetation

Floristic diversity in the riparian zone cannot be separated from processes of evolution and historical biogeography. From the point of view of evolution of riparian vegetation in northern Australia, Bowman and Woinarski (1994) and Bowman (2000) speculated that once diversification of myrtaceous elements commenced following the contraction of rainforest due to continental drying during the Eocene, now extinct diverse gallery forests were eventually replaced by the simpler *Melaleuca/Eucalyptus* associations that are dominant in Australian tropical river systems today. They highlighted the differences between Australian riparian vegetation, being very simple and dominated by only a few species, and that which occurs in South America, which is relatively diverse and not usually dominated by single or

Obligate: limited to a particular ecological mode, i.e. confined to a particular habitat.

Facultative: able to adapt from one ecological mode to another, and not strictly bound to one environment.

Myrtaceous: belonging to the family Myrtaceae, which includes genera such as *Callistemon*, (bottlebrushes), *Eucalyptus* (gums and bloodwoods) and *Melaleuca* (paperbarks).

Aerenchyma: a form of plant tissue with large spaces between cells in which gases are stored and diffused.

Adventitious roots: with reference to roots emerging from an unusual place on a plant, and which function in a secondary manner to those roots which are produced in the normal places on the plant.



small numbers of species. On a reduced time-frame, Fielding and Alexander (2001) provided an examination of river-bed fossils in eastern Australia that indicated that trees structurally similar to present-day *Melaleuca* species were present in past ages, and may be evidence of the previous occurrence of variable discharge and periodically flooded watercourses associated with a strongly seasonal climate.

Plant adaptations

Plants persisting in riparian habitats usually exhibit adaptations that allow them to survive through periodic episodes of fluvial disturbance. These can be either physiological or morphological adaptations, through which plants tolerate flooding as mature individuals, or life history adaptations that enable plants to tolerate the stresses associated with flooding in time or space.

Common morphological adaptations amongst flood tolerant plants include the ability to rapidly elongate stems and petioles upon submergence, allowing plants to emerge from the low light conditions of floodwaters (Blom & Voesenek 1996). The development of aerenchyma in stems and roots, facilitating better gas exchange, is another widespread response to flooding amongst tolerant plants (Blom & Voesenek 1996). Many riparian plant species also develop adventitious roots or initiate increased branching of lateral roots when flooding occurs (Blom et al. 1990). Physiological adaptations may include the ability to switch to alternative metabolic pathways during flooding so respiration can continue under anoxic conditions (Hook 1984).



Melaleuca fluvialis, Lolworth Creek, with root masses conserving stream bank stability. Photo John Dowe.

Riparian plant species may also display a variety of life history adaptations to flooding, including, for instance, timing significant reproductive events to coincide with regular flood pulses. Some species may delay flowering and seed production until seasonal floodwaters have receded (Blom et al. 1990) while others might flower prior to seasonal floods but have dormant seeds which germinate in response to conditions occurring during floodwater recession (Pautou & Arens 1994). Plants that release seeds before or during a flood may be dispersed widely by floodwaters through hydrochory (Nilsson et al. 1991). Many annual and ephemeral riparian monocots and forbs are likely to maintain large persistent soil seed banks that enable plants to persist within a habitat as dormant propagules until conditions suitable for their germination and establishment occur (Leck & Brock 2000). Germination cues (e.g. temperature, light and oxygen availability) in wetland plant species are often related to flooding (Leck 1989). Furthermore, annual plant species, and some perennial monocots and forbs, frequently exhibit extremely rapid life cycles maximising opportunities for replenishment of the soil seed bank prior to further flooding or the onset of drought (Blom & Voeselek 1996). The ability of riparian trees to regenerate depends on a set of conditions that allows seed dispersal, germination and establishment.

Riparian plants can exhibit adaptations to other stresses and disturbances depending on their occurrence within a particular region. In arid and semi-arid regions, for instance, some riparian plant species are tolerant of

both flooding and drought. The widely distributed riparian shrub, *Muehlenbeckia florulenta* (lignum), for example, persists as dormant stems during dry periods, initiating leaf and flower production in response to rainfall or inundation. Investigation of the rheophytic characteristics of *E. camaldulensis*, provided by Sena Gomes and Kozlowski (1980), has also demonstrated that this species is, apart from flood resistant and able to produce active growth whilst water-logged, correspondingly drought-resistant because of a unique arrangement of stomata in the leaves. Some riparian tree species are able to vary their water sources over time in response to climatic conditions (Snyder & Williams 2000, Drake & Franks 2003). Many Australian plants, including members of the Myrtaceae, Proteaceae and Fabaceae families that can occur in riparian habitats,

Rheophytic: a plant adapted to fast flowing water, most often inhabiting stream banks or stream beds, and may have certain morphological or reproductive characteristics.

Stomata: microscopic perforations consisting of a unique arrangement of cells on a leaf surface through which exchange of gases and transpiration of water vapour occurs between a plant and the environment.



Melaleuca fluviatilis, on seasonally flooded Keelbottom Creek. Photo John Dove.

possess mechanisms that enable regeneration following fire such as the ability to resprout. In naturally saline riparian habitats such as saline wetlands, mudflats or estuarine areas of channels, plants may also display specialised adaptations for salt tolerance, e.g. the ability to excrete salt through leaves. Adaptations to minimise the impact of herbivory and grazing, such as morphological and chemical defences, can also be present in some riparian plant species.

Plant functional groups

A useful approach for considering relationships between plant species and their habitats, and how these contribute to temporal and spatial vegetation dynamics, is to classify plants into functional groups. Naiman and Décamps (1997) describe four broad functional groups of riparian plants based on their adaptations and response to fluvial disturbance:

- ~ **invaders** that colonise alluvial sediments via large quantities of wind- and water-dispersed seeds,
- ~ **endurers** that can resprout from stems or roots following damage by flooding, fire or grazing,
- ~ **resisters** that are tolerant to disturbances such as flooding or fire, and
- ~ **avoiders** that lack specific adaptations to disturbance and do not survive in unfavourable habitats.

An alternative approach has been provided by Brock and Casanova (1997) who classify wetland plants into three major groups; 1) submerged, 2) amphibious

and 3) terrestrial, on the basis of where and when germination, establishment and reproduction occur in relation to the presence of surface water. Aquatic plants are also often divided into groups on the basis of their form, i.e. submerged, free floating, floating-attached and emergent (Sainty & Jacobs 1994). Other means of classifying riparian plants into functional groups use traits such as life form (i.e. tree, shrub, sub-shrub, monocot or forb) and life span (i.e. annual or perennial) (Capon 2005). Such groups can help to explain temporal and spatial dynamics in riparian vegetation composition and structure with regard to both natural and human disturbances.

2.3 Riparian vegetation dynamics

Temporal patterns

Riparian habitats are temporally dynamic and their characteristics change dramatically over time in relation to flooding. Vegetation tends to reflect these changes with shifts in composition and structure occurring at both short and longer time scales.

Depending on their functional attributes and life history stage, riparian plants can respond to flooding in the short term in a variety of different ways. The hydrological attributes of a flood event, e.g. timing and duration, will also influence vegetation response at this scale. Terrestrial or avoider species may be unable to survive extended periods of inundation and can become locally extinct from the extant vegetation in a riparian



Naturally regenerating river red gums along the Talbragar River. Photo John Powell.

habitat following inundation. In Australian riparian habitats, woody shrubs such as *Acacia* spp. or sub-shrubs including members of the Chenopodiaceae family are often terrestrial species and intolerant of waterlogged soils, dying following long periods of flooding (Pettit et al. 2001, Capon 2003). In contrast, growth may be favoured by flooding amongst many amphibious or submerged plants and invader species can colonise bare sediments following floodwater recession (Hudon 2004). Other species will germinate in response to flooding although very few plant species are capable of germinating in completely anoxic conditions, with the exception of most submerged and some emergent species, e.g. grasses belonging to the *Echinochloa* genus (Baskin & Baskin, 1998).

Most riparian and wetland plant species with persistent soil seed banks tend to germinate during waterlogged conditions following floodwater recession (van der Valk 1981, Baskin & Baskin 1998, Boedeltje et al. 2002, Crossle & Brock 2002). The timing and duration of flood events can be influential in determining germination responses from riparian soil seed banks (Casanova & Brock 2000). In floodplains and temporary wetlands of semi-arid and arid Australia, for example, summer flooding generally promotes the germination of grasses while forbs tend to germinate following winter flooding.

Recruitment of tree and shrub species is also frequently related to patterns of flooding in riparian habitats. Common riparian tree species such as *E. camaldulensis*, *E. largiflorens*, *E. coolabah* and *Casuarina*

cunninghamiana often germinate in dense patches following inundation (Dexter 1967, Capon 2002, Woolfrey & Ladd 2001). Longer-term survival of seedlings, however, depends on future climatic conditions and further flooding (Dexter 1967), as well as competition and herbivory. Consequently, seedling and canopy composition in riparian zones can differ substantially indicating that riparian canopy composition can fluctuate over time (Jones et al. 1994).

Large flood events tend to homogenise riparian vegetation composition and particularly that of the understorey. Common monocot and forb species are generally widely distributed within floodplain and wetland soil seed banks and, as a result, germination responses to flooding can be comparable between riparian habitats in close proximity to channels as well as areas at the far edges of floodplains (Capon 2003). With drying, however, vegetation composition exhibits further shifts as species adapted to moist conditions can no longer survive and are replaced by those more tolerant of mesic and xeric conditions.

Mesic: found in areas with regular availability of water.
Xeric: adapted to arid conditions.

Spatial patterns

Due to differences in flooding patterns, riparian zones are extremely heterogeneous spatially, both between and within habitat types. Typically, riparian habitats comprise complex gradients of flood frequency, depth or duration along which vegetation communities can often be found in predictable locations. In frequently flooded areas, vegetation is influenced primarily by abiotic variables and flood tolerant species and evaders, avoiders, submerged and amphibious plants, tend to dominate. Annual and ephemeral species may also be more common in frequently flooded areas as they can quickly complete their life cycles between inundation events (Menges 1986, Trebino et al. 1996, Capon 2003, 2005). In rarely flooded areas, biotic factors such as competition and herbivory are likely to be more important in determining vegetation composition (Blom et al. 1990, Lenssen et al. 1999). Population structures of tree species may also be determined spatially in relation to flood frequency with younger stands commonly occurring in more frequently flooded areas where higher levels of fluvial disturbance can prevent stands from reaching maturity (Gregory et al. 1991, Pettit et al. 2001).

Spatial patterns in riparian vegetation composition and structure also occur along longitudinal gradients within river catchments (Ward et al. 2002). In general, maximum species diversity tends to occur in riparian habitats of the middle reaches or a river catchment. Riparian plant species richness is also often higher along the main channel of a drainage basin than on its tributaries (Nilsson et al. 1994).

2.4 Threats to riparian vegetation

Hydrological change

Changes to natural flooding regimes through flow regulation and water extraction, pose one of the greatest threats to vegetation communities in riparian zones throughout the world (Nilsson & Svedmark 2002, Tockner & Stanford 2002). Riparian vegetation is particularly sensitive to flow alterations and changes in vegetation diversity and dynamics can occur even if mean annual flows are preserved (Auble et al. 1994). In Australia, river regulation commonly involves the reduction of mean annual flows and simultaneous increases in median annual flows (Walker et al. 1995, Puckridge et al. 1998) resulting in reduced frequency and magnitude of flooding. Consequently, riparian habitats are inundated less often and for shorter durations, with reductions in areas wetted also occurring. Additionally,

the seasonal timing of annual flood pulses has been reversed through river regulation in some catchments, e.g. the Murray Darling Basin (Thoms & Sheldon 2000).

Hydrological changes affect the character of riparian habitats and have significant implications for the diversity and dynamics of riparian vegetation. Recruitment amongst riparian tree species, for example, is likely to be adversely affected by reductions in overbank flooding (Zamora-Arroyo et al. 2001, Stave et al. 2003). Other species which require flooding to complete important life history stages such as germination, e.g. obligate submerged species, may also decline in riparian habitats if flood volume or frequency are reduced, often to be replaced by more mesic (or xeric) species that are favoured by new habitat conditions (Alvarez-Cobelas et al. 2001). Consequently, spatial patterns in riparian vegetation, such as zonation along flood frequency gradients, might shift in response to altered flooding regimes. In the Macquarie Marshes, for example, reduced frequency of flooding has led to the invasion of grass plains by river red gum (Bren 1992). In general, the overall affect of flow regulation on riparian vegetation is a reduction in vegetation heterogeneity which often results in an eventual loss of biodiversity.



Above: Macquarie Marshes. Photo Bill Johnson. Below: Red gum on a dry creek bed on the Paroo River where it depends on irregular floods for its survival, growth and reproduction. Photo Alison Curtin.



Weeds

Weeds are also serious threats to the ecological integrity and productivity of many Australian vegetation communities (Grice & Brown 1999) and riparian zones are highly susceptible to weed infestation (Grice 2004). Weed infestations are often the result of disturbance or the build-up of nutrient levels caused by fertilisers or grazing animals. Primary disturbances include vegetation clearance, fire, and stock grazing. Altered flooding regimes may also enable the establishment of weed species in riparian zones (Stromberg 2001). Some weeds are able to infest undisturbed and intact riparian vegetation, in which case the weeds are able to outcompete the native species with regards to light, space,

nutrients and moisture. Throughout Australia, many weeds now dominate riparian areas, their dominance perpetuated by grazing activities, associated impacts, and ineffective land management practices. The cost of weed eradication and/or control is high, and if weeds are neglected and become dominant, the productivity and diversity of native riparian vegetation can seriously decline. Although the riparian zone occupies only a small proportion of the landscape, it exerts an influence that affects most of the adjacent landscape, and the presence of weeds limits critical catchment processes and reduces productivity. The study of weed biology is now receiving more attention, and significant funds are being devoted to weed control and eradication.



Top left: Rubber vine, *Cryptostegia grandiflora*, Lolworth Creek. Photo John Dowe. Top right: Willows (probably *Salix babylonica*) growing into the stream of the Lachlan River. Photo Phil Price. Middle right: Castor oil plant, *Ricinus communis*, Keelbottom Creek. Photo John Dowe. Below left: Riparian zone with Para grass, *Brachiaria mutica*, and the aquatic weed Water hyacinth, *Eichhornia crassipes*, Healeys Lagoon. Photo John Dowe. Bottom right: Artichokes are a significant weed problem in the arid parts of South Australia and elsewhere. Photo Phil Price.



Grazing

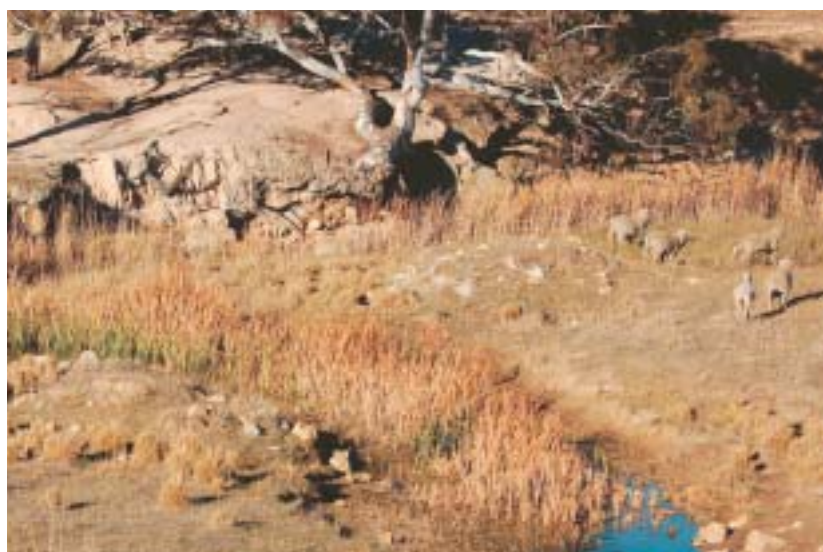
Grazing is the dominant land-use in Australia (Stewart 1996), and the riparian zone is often severely impacted upon by the activities of domestic stock (Jansen & Robertson 2001), especially when their access to riparian zones is not controlled. Grazing by feral and native animals can also affect the diversity and condition of riparian vegetation. Riparian zones offer a number of attractions for stock, including shelter, relatively higher quality of forage, and access to water. The primary impacts that stock have on riparian vegetation include overgrazing and trampling, both of which may lead to erosion, soil compaction and weed infestation (Clary 1999, Shaw & Kernot 2004), which in turn causes loss of biodiversity, degradation of the natural conditions and loss of water quality (Burrows 2001, 2004). Some secondary effects on riparian vegetation, that are associated with grazing, include the establishment of ponded pastures and burning, both of which significantly affect the structure and composition of vegetation (Douglas & Pouliet 1997).

The presence and grazing of stock have a direct influence on species composition in most habitat types. Low intensity grazed areas have a relatively greater abundance and dominance of native shrubs, twiners and geophytes than high intensity grazed areas in temperate Australia (Clarke 2003). In north eastern Australia, riparian sites that are naturally protected by basalt flows from stock, but with the sites grazed by macropods, had higher species richness, however, there was a higher diversity and abundance of annual grasses in the cattle grazed areas (Fensham & Skull 1999). Following the cessation of grazing, there is evidence suggesting that the natural species composition will be restored, in time, if nearby seed sources are present and able to disperse into the stock exclusion area (Pettit & Froend 2001). With regards to palatable pasture weeds in riparian zones, stock may be used to control some weeds such as para grass (*Brachiaria mutica*) and hymenachne (*Hymenachne acutigluma*) and restore ecological functioning to areas dominated by such weeds (Burrows 2001).



This page. Uncontrolled stock access is the single greatest cause of riparian zone degradation across Australia. Photos: (above) Jenny O'Sullivan, (top right) Roger Charlton, (right) Ian Bell.

Opposite page. Top: This riparian area has been fenced off to exclude stock. Photo Mike Wagg. Below: Fencing used to protect remnant strip of riparian vegetation. Photo John Dowe.



Fencing is the most effective method of controlling access to the riparian zone by stock (Burrows 2001), and is the current recommended management practice in areas where high to moderate intensity grazing occurs (Productivity Commission 2003, Roth et al. 2004). Fencing facilitates the construction of water points away from the source of the water and, as a result, stock can be concentrated away from the riparian zone. However, this may lead to situations where pasture is depleted or reduced to poor quality in the vicinity of water points. Controlled seasonal access to the riparian zone alleviates pressure on riparian vegetation when it is most vulnerable, for example when the seedling establishment phase is active, or during flowering and fruit development phases. A number of methods of rehabilitation of the riparian vegetation following stock exclusion or even when stock are still present have been proposed, including re-establishment of indigenous riparian vegetation with selection of species based on remnant vegetation surveys, historical records, pollen surveys and field trials (Webb & Erskine 2003).



2.5 Management principles

The following are a list management principles for protecting, maintaining and rehabilitating riparian vegetation.

- ~ First, identify and protect areas of existing riparian vegetation assessed to be in good condition. Areas can be compared with local undisturbed or reference sites, and/or assessed for their capacity to provide crucial riparian zone functions and to self-regenerate. Identify threats and act to remove or mitigate them.
- ~ The next priority is to promote natural regeneration or recolonisation where this is possible. This may require checking for availability of seed in the soil or on plants, removal of threats such as grazing animals or weeds, and sometimes deliberate action to promote regeneration (e.g. use of fire).
- ~ Replanting, whether by tubestock or direct seeding, is more expensive and requires careful attention to site preparation, especially for weed management and removal of other threats. Species selection, based on reference to undisturbed sites and local knowledge, is required for different parts of the riparian zone, and for different stages of revegetation succession (e.g. early colonisers versus slow-growing climax spp). If early support (e.g. artificial watering) is needed to ensure success, it may be best to replant small areas sequentially.
- ~ Revegetation activities need to be timed according to season and growth periods, as well as for the likelihood of floods and other disturbances. Plan for follow-up work after the planting, especially to maintain stock exclusion and weed control until the 'new' vegetation is fully established. Make use of the detailed guides to revegetation that are now available for most parts of Australia (e.g. through Greening Australia, government agencies, and catchment and community groups).

Conclusion

This chapter has discussed the diversity and dynamics of vegetation in riparian habitats in Australia. In addition to reviewing significant characteristics of riparian plant habitats, this chapter has provided an overview of floristic diversity in Australian riparian zones. It has focused in particular on the importance of flooding and associated fluvial disturbances in maintaining patterns of temporal and spatial heterogeneity and has discussed the major factors currently threatening riparian vegetation in Australia today.

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