Integrating hydrology and land use to understand the ecology of floodplain wetlands in the Condamine Catchment, southern Queensland, Australia

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Abstract

Floodplain ecosystems support an abundant and diverse range of species. However, in many agricultural landscapes, hydrological and land use changes have caused a decline in the extent and condition of wetlands. There are numerous hydrological based concepts which have helped provide a basis for understanding, predicting and managing the ecological impacts of hydrological changes on floodplain systems. However, while hydrology focused concepts have proved highly informative, they have also lead to much research being exclusively focused on the independent effects of hydrological factors (e.g. reductions in stream flow and flood events). This may limit the ecological understanding and management in three important ways. Firstly, as most studies are carried out in floodplains of large perennial rivers, many current concepts neglect smaller non-flowing habitats, such as floodplain wetlands. Secondly, as research is often exclusively focused on hydrological factors it may not adequately consider the additional impacts of other drivers, such as land use factors. Thirdly, current research gives little consideration to the nature of interactions between different hydrological and land use factors and how they may exacerbate and mitigate effects.

To help test these potential limitations, two alternate hypothesis were developed for the ecology of floodplain wetlands. The “hydrology hypothesis” views these systems as being driven exclusively by hydrological factors. In contrast, the “interactive hydrology-land use hypothesis” considers hydrological and land use factors and their interactions as drivers of ecological patterns in floodplain wetlands. These competing hypotheses are not designed to test which factors are of most relative importance, but to ask whether hydrology focused research is limited by not considering land use and interactions. These hypotheses were tested using data from surveys on the dominant tree species, *Eucalyptus camaldulensis* Dehnh., of floodplain wetlands in the Condamine Catchment, south east Queensland, Australia. The catchment has undergone extensive hydrological and land use alteration to support agricultural production and therefore offers an ideal setting to test these competing hypotheses.

The hydrological characteristics (inundation frequency, river connectivity, groundwater depth and rain volume) of 102 modified and 149 ‘natural’ unmodified wetlands across the Condamine Catchment were determined using data derived from satellite imagery and digital elevation models and compared. The hydrology of unmodified and modified wetlands differed significantly (ANOVAs; $p<0.001$), with unmodified wetlands on average, less connected to the river and characterised by significantly lower rain volume.

The condition of the dominant riparian species, *E. camaldulensis* (as measured by crown vigour), and stag abundance (all trees) in three broad size classes (small trees: <20cm; medium trees: 20-50cm; and large trees: >50cm cbh) at 37 unmodified wetlands were surveyed and modelled against hydrological metrics and land use factors (grazing, agricultural land cover and remnant vegetation cover) using generalized linear models (GLMs). Specifically, this study tested whether exclusively hydrological models were better than a hydrological plus land use models for understanding variation in crown vigour of *E. camaldulensis*) and stag abundance. Crown vigour and stag abundance was consistently best explained by hydrological factor only models (GLMs; $p<0.05$). Consequently, a hydrological-focused perspective (hydrology hypothesis) may not necessarily be limited when studying aspects of tree condition, such as crown vigour, in floodplain wetlands.

The distribution (occurrence) of *E. camaldulensis* in five size classes (<10, 10-20, 20-50, 50-75 and >75cm cbh) across 37 unmodified wetlands was also modelled against hydrology and land use factors using GLMs. Contrasting, with models on crown vigour and stag abundance, *E. camaldulensis* occurrence was significantly related to both hydrological and land use factors (GLMs; $p<0.05$). Models which included both hydrological (distance from weir, river connectivity and groundwater depth) and land use factors (agricultural land cover and grazing intensity) performed better (R^2 0.04 to 0.24 and AUC 0.06 to 0.16 greater) than those developed using only hydrological factors. It was concluded that hydrology focused research that does not consider land use may not be suitable for understanding impacts on the distribution of *E. camaldulensis.*

A Bayesian network modelling approach was used to integrate the results from the individual studies to develop a broad model of the drivers of *E. camaldulensis* occurrence and condition and overall wetland condition and to explore possible interactions between these drivers. *E. camaldulensis* response to hydrology and land use factors was better characterised by their combined interactive effects than their independent effects. Interactions identified were classified as synergistic, antagonistic and qualitative. Of these, qualitative interactions (an interaction between two factors that causes a change in both the magnitude and direction of response) have not been described in previous ecological research and as such, may be important for broader thinking about interactions in ecosystems. It was concluded that the failure to consider interactions, and how they vary (e.g. synergistic, antagonistic and qualitative), may lead to an over or under estimation of how species relate to their environment and potentially counterproductive management actions.

The conflicting responses of the variables tested suggest that neither the hydrology hypothesis nor interactive hydrology – land use hypothesis was universally applicable for understanding all aspects of *E. camaldulensis* in the floodplain wetlands examined. The two hypothesises are therefore not mutually exclusive; both are applicable depending on the aspect examined (i.e. crown vigour or occurrence). As a consequence, neither can be rejected until more research is carried out on a wider range of hydrological and land use factors. Nonetheless, the results did show that it is not valid to assume that only hydrological factors are important drivers of all

ecological aspects in these systems. Consequently, the additional consideration of land use factors is needed to give a more complete understanding of how this species relates to its environment. Without this broader examination, then other factors (e.g. land use) limiting the occurrence of *E. camaldulensis*, as well as how it responds to interactions between these factors, may be overlooked and as such ecological understanding and management may be missing important information and thus could be ineffectual (or even detrimental) for wetlands.

The results of this research suggest that management of floodplain systems, particularly the vegetation of floodplain wetlands, which focuses exclusively on hydrological factors and does not consider land use and different types of interactions, may be significantly limited. Accepting the hydrology hypothesis and a hydrological focus for wetlands in the Condamine Catchment would mean that negative land use impacts from grazing and agricultural may be overlooked and as such, ecological conservation measures limited. Additionally, it would mean that the response of *E. camaldulensis* to multiple hydrological (e.g. groundwater, river connectivity, inundation frequency) and land use (e.g. grazing) factors could be over or under estimated if they interact synergistically, antagonistically and / or qualitatively. The results of this thesis therefore highlight some potentially significant limitations of hydrology focused research and management which currently predominates in floodplain systems. Future research should (1) more broadly test the limitations of the hydrology and interactive hydrology-land use hypotheses in floodplain systems; (2) test the importance of considering different types of interactions, especially qualitative interactions, for a range of different biota in different settings to examine whether they apply more broadly to other species and ecosystems.

CERTIFICATION OF DISSERTATION

I certify that the ideas, experimental work, results, analyses, discussions and conclusions reported in this dissertation are entirely my own work, except where otherwise acknowledged. I also certify that the work is original and has not previously been submitted for any other award.

____ Date: ……/……/……
Signature of Candidate

ENDORSEMENT

____ Date: ……/……/……

Signature of Supervisor (1)

____ Date: ……/……/……

Signature of Supervisor (2)

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Chapter 1. General Introduction

1.1 Overview

Globally, anthropogenic activities use around half of all available freshwater runoff (Postel et al. 1996; Jackson et al. 2001; Brauman et al. 2007). In addition, hydrological regulation currently impacts rivers in almost every part of the world, with approximately 40,000 large (> 15m height) and 800,000 small dams, altering flows for two-thirds of all freshwater rivers flowing to the ocean (Nilsson and Berggren 2000; Rosenberg et al. 2000; Nilsson et al. 2005). Furthermore, in parts of the world where surface water may be limited, groundwater extraction often occurs at rates greater than recharge, causing the lowering of water tables across large areas (Jackson et al. 2001; Llamas and MartÃ-nez-Santos 2005; Panda et al. 2007; Brikowski 2008). These high levels of water extraction, in combination with widespread river regulation, have caused significant changes in floodplain and river hydrology (Nilsson and Berggren 2000).

In many places, hydrological alterations, caused by water extraction and regulation, have also coincided with extensive changes to land use patterns from agricultural and urban development (Miller et al. 1995; Thompson and Polet 2000; Nilsson et al. 2005). In large river systems throughout the world, catchments affected by dams are associated with approximately twenty-five times more economic activity per unit of water (Nilsson et al. 2005). These broad scale changes to land use patterns have re-shaped entire landscapes, causing wide spread ecological degradation and species loss (Chase et al. 1999; Sala et al. 2000; Lambin et al. 2001; Foley et al. 2005; Batlle-Aguilar et al. 2011). In many places, including floodplains, these hydrological and land use changes have been ecologically, socially and economically catastrophic (Poff et al. 1997; Postel 1999; Kingsford 1999; Sala et al. 2000, Lambin et al. 2001; Jackson et al. 2001; Zedler 2003; Vorosmarty et al. 2010).

As a consequence of hydrological and land use changes, the last few decades have seen the widespread loss of wetlands (Finlayson and Rea 1999; Lemly and Kingsford 2000). To date, 9000 km^2 of wetlands have disappeared from Mesopotamian (Iraq) floodplains along the Tigris and Euphrates Rivers (UNEP 2001). In northern Nigeria, almost 60% of the Hadejia-Nguru floodplain has been lost as a result of altered hydrology (Barbier and Thompson 1998). Similarly, in Europe, as a result of dykes along the Danube River, there has been a 20,000 km^2 reduction in natural floodplain area over the last 50 years (Nachtnebel 2000). In addition, as a consequence of hydrological changes, many European wetlands no longer perform their natural functions (Tockner and Stanford 2002). In Australia, an estimated 50% of wetlands have also been destroyed since European colonisation (Jensen 1998), with losses in agricultural regions ranging from 70 to 98% (Streever 1997; Jensen 2002).

The impacts hydrological and land use changes may be particularly important for wetlands and especially, smaller floodplain wetlands, for which ecological knowledge is particularly poor (Kingsford 2000). However, to date much research on the ecology and conservation of river-floodplain systems has focused on the impacts of impoundments on large perennial rivers (O'Connor 2001). Rarely are non-flowing smaller water bodies, such as floodplain wetlands, explicitly considered (Kingsford 2000; Davies et al. 2008).

This bias is also evident for ecological management, which is often targeted at larger more permanently inundated wetlands, such as lakes (Hayashi and Rosenberry 2002). For example, in Australia, the focus of literature and management of environmental flows has been predominately restricted to in-channel biota and ecological processes (Kingsford 2000). Furthermore, in many instances the methodology applied to estimate environmental flows for the restoration of ecologically degraded floodplains, is often focused on species that inhabit river channels (Poff et al. 1997). Arguably, this 'river-centric' perspective has also meant that the allocation of environmental flows has been insufficient for providing overbank flooding important for the biota of floodplain wetlands (Coops et al. 2006). As a result, research and management aimed at addressing declines in the ecological communities of river-floodplains has largely neglected floodplain wetlands (Kingsford 2000).

Despite a lack of research and management on smaller non-flowing wetlands, their ecological importance is still recognised in many parts of the world (Williams et al. 2003; Nicolet et al. 2004; Pott and Pott 2004). In Britain and Northern Europe, smaller non-flowing wetlands (referred to as ponds in Europe) were a common feature of the landscape in the past and today, remaining ponds play an important role for biodiversity (Williams et al. 2003; Nicolet et al. 2004). At regional scales, smaller non-flowing water bodies, such as ponds, are some of the most species-rich aquatic habitats for wetland plants and macro invertebrates (Williams et al. 2003; Davies et al. 2008). In tropical environments, these smaller wetland systems are also prevalent and important features for biodiversity in the landscape (Pott and Pott 2004). Likewise in Australia, floodplain wetlands are characterised by extraordinary biodiversity, providing habitat for diverse populations of avifauna, fish, vegetation and invertebrates (Kingsford 2000). However, while smaller non-flowing wetlands support unique ecological communities, they have received relatively little attention and are also often the first to be lost as a result of agricultural development and river regulation (Buijse et al. 2002; Jensen 2002; Coops et al. 2006).

In addition to the dearth of knowledge on floodplain wetlands, current research is often almost singularly focused on how hydrological factors affect floodplain river and wetland ecology (e.g. Taylor et al. 1996; Benger 1997; Horton et al. 2001; Stromberg 2001; Rood et al. 2003a; Rood et al. 2003b; Rood et al. 2005; van der Valk 2005; Renofalt et al. 2007; Raulings et al. 2010). This focus on hydrology is not surprising, given that alterations to hydrological regimes are believed to be the key threat to the future ecological persistence of river-floodplain systems (Sparks 1995; Ward et al. 1999; Bunn and Arthington 2002). Nevertheless, while the importance of hydrology is widely accepted, this does not mean that other factors should not be also considered. For example, non-hydrological factors, such as surrounding land use impacts, may be important additional determinants of floodplain wetland ecology (Robertson 1997). Furthermore, in some instances, interactions between land use and hydrological factors may change how species respond to certain environmental changes (e.g. reductions in stream flow Matthaei et al. 2010). However, whether a hydrological focus limits ecological understanding about floodplain systems and wetlands specifically, is largely untested.

1.2 Scope of review

To help address these potential knowledge gaps, this review examines how hydrology and land use context influence the ecology of floodplain systems in agricultural landscapes. It will focus on floodplain wetlands (here defined as any non-flowing water body not directly part of the riverine stream network, including billabongs, oxbow lakes, backwaters, etc.). However, as literature on floodplain wetlands is lacking, studies on the broader floodplain-river system (here defined as the bedded alluvial landform neighbouring the river channel)(after Nanson and Croke 1992) will also be drawn upon.

Initially, current concepts about how hydrology shapes the ecological functioning of floodplains, rivers and wetlands will be outlined. In addition, examples of how these concepts have been applied to help understand the impacts of hydrological changes from river regulation, groundwater extraction and other similar impacts on floodplain ecosystems will be discussed. Throughout, special regard will be placed on trees and vegetation communities of floodplain systems, not only because of the extensive literature on this biota, but also because they represent structurally and functionally integral components of wetland ecosystems (Kansiime et al. 2007). Subsequently, two potential limitations of current concepts and hydrology focused research will be outlined, namely little consideration of land use factors and interactions. Finally, hypotheses representing a hydrology focused perspective and a contrasting interactive hydrology – land use perspective will be proposed. A summary of the studies carried out to test these two alternate hypotheses will then be outlined. The review will be limited to topics and concepts directly relevant to the hypotheses being tested. Other topics, such as floodplains as pulsed systems, complex response of floodplain ecosystems; regime shifts in floodplains; adaptive cycles and floodplains; the hierarchical natural of floodplain systems, will not be directly addressed. These concepts, while important for understanding floodplain systems, while important are not being tested in this thesis and as such will not be covered.

1.3 Hydrology and wetland ecology - Current hydrological concepts

Hydrology is widely recognised as a major driver of the ecology of river-floodplain landscapes (Tockner and Stanford 2002). Water availability, spatially and temporally shapes the physical, chemical and biological factors driving the functioning of wetlands (Boulton 1999; Mitsch and Gosselink 2000; Brooks 2005). For example, the timing, frequency and duration of hydrologic inputs and outputs to and from wetlands triggers the release of nutrients from soils, grasses and accumulated tree debris (Junk et al. 1989; Reid and Brooks 2000; Gabriel et al. 2008). These nutrient pulses in turn support the growth and reproduction of vegetation, which helps to maintain soil structure and provides organic material and food sources for aquatic invertebrates as well as habitat for birds (Boulton and Lloyd 1991; Briggs et al. 1997; Brauman et al. 2007). In floodplains and wetlands, the spatial and temporal variability in water availability that drives ecological processes creates a diverse and heterogeneous landscape of habitats, important for supporting biodiversity (Tockner and Stanford 2002; Leigh et al. 2010; Raulings et al. 2010).

To assist in understanding about how hydrological dynamics influence the ecology of floodplain systems, various concepts have been developed. These include the flood pulse concept (Junk et al. 1989) and extensions of the flood pulse concept, which incorporate flow pulses, describing how hydrological processes facilitate the transportation of matter throughout floodplains (Tockner et al. 2000). There are also concepts which highlight various aspects of hydrological connectivity (Vannote et al. 1980; Ward 1997; Ward and Stanford 1989; Pringle 2001; Amoros and Bornette 2002; Pringle 2003), defined as the water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle (*sensu* Pringle 2001). There are also concepts focusing on temporal hydrological dynamics (e.g. variability, timing, duration of flows), which may also be broadly referred to as the hydrologic regime (flow regime in river or water regime in wetlands) (Poff et al. 1997; Mitsch and Gosselink 2000). Collectively, these concepts and their multiple derivations have formed the basis of much research in floodplain system ecology.

However, although the aforementioned concepts are varied and highlight different hydrological processes in floodplains, in a broad and simplified way, a consistent theme throughout is that the major driving force of floodplain landscapes is the variability of hydrological flows, which facilitates the temporal and spatial exchange of matter and species throughout floodplains (Junk et al. 1989; Tockner et al. 2000). Indeed, hydrology has been described as a 'master variable' which structures the ecology of floodplains (e.g. Walker et al. 1995; Bunn and Arthington 2002; Lytle and Merritt 2004; Leigh et al. 2010). However, while these concepts have proven integral for understanding floodplain systems, two concepts that may be particularly important for floodplain wetlands and their vegetation are those related to hydrological connectivity and wetland water regime.

1.3.1 Hydrological connectivity

In a spatial sense, hydrological connectivity can occur longitudinally along rivers, such as the river-continuum concept (Vannote et al. 1980; Minshall et al. 1985; Ward and Stanford 1989), laterally between floodplains, rivers and wetlands (Amoros and Bornette 2002; Pringle 2003), as well as vertically between surface and groundwater layers (Pringle 2001). Spatial hydrological connectivity, lateral and vertical connectivity are also likely of greatest significance for floodplain wetlands and their resident biota.

Vertical connectivity

The maintenance of vertical connectivity between surface and ground waters is a fundamental aspect of the ecological functioning of floodplain habitats, especially in water limited environs, where vegetation may require groundwater to persist (Zencich et al. 2002; Eamus et al. 2006; Chen et al. 2008; Costelloe et al. 2008). In the southwest of the United States of America, reduced vertical hydrological connectivity, from groundwater decline has been linked with the degradation of riparian habitats (Stromberg et al. 1992; Busch and Smith 1995; Stromberg et al. 1996). In other instances, where groundwater levels have risen, causing increased vertical connectivity, changes in vegetation composition and condition have also been noted (Xu et al. 2007; Chen et al. 2008). For example, diversion of water to the lower reaches of Tarim River in the Xinjiang Uygur region of western China caused groundwater levels to rise from 9.87m to 3.16m, which in turn triggered changes in vegetation composition and increases in the condition of perennial vegetation (e.g. *Populus euphratica*) (Chen et al. 2008). Consequently, changes in vertical hydrological connectivity through the raising and lowering of groundwater levels is likely to have significant ecological consequences for the ecology of floodplain rivers and wetlands.

Lateral connectivity

Lateral hydrological connectivity, between different components of floodplain landscapes is another critical aspect of ecological functioning in floodplain systems (Grubaugh and Anderson 1988; Jenkins and Boulton 2003; Thoms 2003; Cook and Hauer 2007; Vercoutere et al. 2007). Lateral hydrological connectivity facilitates the exchange of water between different components of floodplains and plays a critical role in various ecological processes, by distributing plant propagates, organic matter, nutrients and sediments important for productivity and general ecological functioning (Tockner et al. 1999; Thoms 2003; Leyer 2006; Gurnell et al. 2008). Throughout the Middle Elbe River floodplain, Germany, areas with the highest river-floodplain connectivity had the greatest number of seedlings and vegetation species richness (Leyer 2006). Similarly, amongst floodplain wetlands, in the Middle Ebro River channel, Spain, as river connectivity increased so did macro-invertebrate species richness and total abundance (Gallardo et al. 2008). Consequently, reductions in connectivity between rivers and floodplains that often result from extraction and stabilisation of flows through river regulation structures (e.g. dykes, weirs, damns etc.) are likely to have significant ecological effects for the ecology of floodplains and their wetlands (Kingsford 2000; Leyer 2006).

1.3.2 Wetland water regime

The timing, frequency, duration, variability and extent and depth of hydrological outputs and inputs shape the water regime of wetlands (Bunn et al. 1997; Mitsch and Gosselink 2000). Collectively and individually, these aspects of the water regime play a significant role in shaping the ecology of wetlands (e.g. Toner and Keddy 1997; Leck and Brock 2000; Pettit and Froend 2001; Warwick and Brock 2003; Siebentritt et al. 2004; Capon and Brock 2006; Barrett et al. 2010). In the New England Tablelands, eastern Australia, Brock et al. (1999) argued that many wetland species are reliant on dynamic and fluctuating water regimes to maintain diversity of habitats. Similarly, in the Great Lakes, Michigan, Wilcox and Nichols (2008) found that differences in the frequency of inundation, which altered wet and dry periods, were an important condition for generating diversity in the plant community. Warwick and Brock (2003) also found that the duration of flooding had strong influence on plant species composition for wetlands of New England, New South Wales. Consequently, alterations in the timing, duration, frequency, extent and variability of hydrological inputs (i.e. the water regime) may have significant impacts on wetland ecology (Brock 2003). Today, various anthropogenic activities, from river regulation, water extraction and direct physical modifications to wetlands all alter the water regimes of wetlands (Walker and Thoms 1993; Reid and Brooks 2000; Frazier et al. 2003; Lloyd et al. 2004), often to the detriment of native biota (Kingsford 2000).

1.3.3 Competing hypotheses regarding wetland ecology

The usefulness of hydrological connectivity and water regime concepts in understanding and predicting how floodplain species relate to their environment have highlighted the critical role that hydrological processes play in floodplain systems (e.g. Toner and Keddy 1997; Leck and Brock 2000; Leyer 2006). The success of these concepts has also arguably led to much research being exclusively focused on the role that hydrology plays in shaping floodplain, river and wetland ecology (e.g. Hughes 1990; Toner and Keddy 1997; Vervuren et al. 2003; Lite et al. 2005). However, other studies on riparian and wetland vegetation have suggested that land use context (the spatial configuration of elements in the broader landscape) may also be important for understanding floodplain (Turner et al. 2004), riparian (Meeson et al. 2002) and wetland ecosystems (Ogden 2000), potentially challenging the proposition that a hydrology focused perspective is the only driver of processes within floodplain wetland ecosystems. Thus, despite the utility of current hydrological concepts for understanding and predicting losses and degradation of river-floodplains and their dependent species, it has been argued that current concepts would benefit from a more holistic and interdisciplinary approach, which takes better account of amongst other things; geomorphology, land use and interactions across different scales (Minshall et al. 1985; Robertson 1997; Thoms and Sheldon 2002; Thoms 2003). Of these limitations, one which may be particularly pertinent for understanding floodplain wetlands in an agricultural context is the failure to explicitly consider surrounding land use.

Land use change and intensification in agricultural landscapes- impacts on floodplain ecosystems

The impacts of land use, especially through agricultural intensification, defined as an increase in the amount of inputs and outputs of cultivated and reared products per unit of area and time, are well known in ecology (Matson et al. 1997; Lambin et al. 2001). Land use changes, like the alteration of hydrological flows are a global phenomenon, which have significantly altered ecological functioning across the Earth (Lambin et al. 2001). Globally, changing land use patterns have been linked with amongst other things, declines in biodiversity, climate change and soil degradation (Chase et al. 1999; Sala et al. 2000; Lambin et al. 2001; Batlle-Aguilar et al. 2011).

The impacts of land use on floodplain ecosystems are well recognised (Knox 2006). Land use changes have been linked to increases in nonpoint pollution, sedimentation, and nutrient inputs, which may cause changes in species composition, reduction in species richness and abundance and even local extinctions in freshwater ecosystems (e.g. Allan 2004). In Australian aquatic ecosystems, Lake and Bond (2007) have also argued that land use changes, both directly and indirectly impact biota, through land clearing, vegetation depletion, soil loss and physical disturbance. In eastern Ontario Canada, Houlahan et al. (2006) found that the intensity of adjacent land use was negatively related to wetland plant species richness. (Houlahan et al. 2006) argued that forest cover correlations with soil and nutrient levels may have contributed to this relationship. Consequently, understanding the impacts of different land use practices is likely important for understanding the ecology of wetlands in agricultural landscapes.

At local scales, land use practices such as grazing, are also known to have significant effects on the riparian vegetation communities of freshwater systems (e.g. Meeson et al. 2002). In wetlands, grazing can reduce plant biomass, growth and reproduction (Brock 2003). Along the Murrumbidgee River, southern New South Wales, Robertson and Rowling (2000) demonstrated that livestock grazing reduced the abundance of seedlings and saplings of the dominant riparian *Eucalyptus* species, compared to when grazing was absent. The impacts of different land use practices at both local (e.g. grazing intensity) and sub-catchment and catchment scales (e.g. land cover change) may be important influences on the ecology of wetlands that are not accounted for by a hydrology focused hypothesis.

However, despite research illustrating the impacts of land use in floodplain systems, there has been little concerted effort to understand what this means for hydrology focused research. This raises a general question of: is hydrologically-focused research, derived from current concepts (e.g. connectivity, flood pulse, hydrological variability; water regime), sufficient for understanding the drivers of loss and decline of wetland species or would it be improved by the additional consideration of coinciding land use practices? To date, relatively few studies have simultaneously compared hydrological and land use factors and thus, this has rarely been explicitly tested (but see Meeson et al. 2002; Northcott et al. 2007).

Furthermore, while some studies may have investigated both hydrological and land use factors, none have explicitly assessed the merit of an exclusively hydrological approach relative to one where various land use factors are also considered. For example, while Meeson et al. (2002) examined land use impacts, such as grazing and hydrological factors related to stream flow, they did not examine other factors which may be important (e.g. groundwater). Northcott et al. (2007) study did not consider groundwater either. Additional to this these studies were restricted to riverine habitats. Studies examining a wide range of hydrological and land use factors on floodplain wetlands are lacking.

This knowledge gap could have significant implications for ecological management. Research that has addressed land use practices, such as grazing, has argued that management based solely on hydrological factors may be sub-optimal if it does not consider the impacts of coinciding land use (e.g. Meeson et al. 2002). Furthermore, others have argued that even if significant hydrological changes are addressed, for example, through the use environmental flows, then various negative impacts from agriculture are still likely to persist (Ogden 2000). Nias et al. (2003) has even questioned whether in some agricultural lands it is even possible to recover habitat values just by re-instating hydrological flows. Houlahan et al. (2006) further argued that failure to incorporate adjacent land use practices which impact on wetlands makes some current management practices inadequate. However, knowledge regarding the importance of additional consideration of land use for understanding floodplain wetlands is limited in many landscapes.

1.3.4 Interactions and multiple stressors

Another potential limitation of current hydrology-focused research is a lack of explicit consideration about the nature of interactions between different environmental factors (or stressors). A stressor is here defined as any factor that has a negative influence on an ecological response. Across many ecological studies, the focus has been commonly on the effects of individual factors, with studies on the nature of interactions, that is whether multiple factors act synergistically or antagonistically together, much rarer (Crain 2008; Crain et al. 2008). Breitburg et al. (1998) argue that anthropogenic factors usually interact with environmental factors to produce novel effects. As such, investigations on the effects of environmental factors may be limited if interactions between factors are not considered. Currently, research into the importance of interactions between different environmental changes and their consequences for floodplains and ecosystems more broadly is generally lacking (Tylianakis et al. 2008; Poff and Zimmerman 2010).

The limited studies that have examined interactions have suggested that synergistic and antagonistic responses to multiple factors are common and likely have significant ecological consequences (Crain et al. 2008). For example, Brook et al.

(2008) argued that synergies among stressors may act as self-reinforcing mechanisms that accelerate extinction. Folt et al. (1999) examined the effects of multiple stressors on the reproduction and survival of two species of cladoceran zooplankton and observed both synergistic and antagonistic interactions. Crain et al. (2008) reviewed studies on the cumulative effects of multiple stressors in marine and coastal environments for various key ecological variables (i.e. species richness, biomass, abundance, disease severity) by classifying effects as additive, synergistic or antagonistic. They found that relationships could be classified as additive (26%), synergistic (36%) and antagonistic (38%). Crain et al. (2008) argue that collectively, these studies in marine communities provide robust evidence that multiple stressors generally interact in marine ecosystems.

Floodplains which are highly altered by anthropogenic hydrological and land use changes, may provide an ideal system for studying the impact of multiple stressors on ecological systems (Tockner et al. 2010). To date, there has been relatively little research on the nature of interactions in floodplain systems (but see Leyer 2005 and Matthaei et al. 2010). However, as with research in marine systems, research in floodplains and freshwater streams has noted that species may respond to antagonistic and synergistic interactions between factors (e.g. Townsend et al. 2008; Matthaei et al. 2010). For example, along the Elbe River, Germany, Leyer (2005) observed that in recent (hydrological active) and older (hydrological inactive) floodplains, interactions with average groundwater levels influenced the distribution of herbaceous plant species (e.g. *Poa palustris* and *Deschampsia cespitosa*). Older floodplain areas acted synergistically with average groundwater levels, suggesting that in these areas plants had an increased susceptibility to groundwater declines (Leyer 2005). The failure to consider interactions may lead to the over and under estimation of the effects of certain environmental changes (Crain et al. 2008; Matthaei et al. 2010). Hydrology focused research may therefore be significantly limited by not considering that interactions among hydrological factors and potentially land use factors, may lead to synergistic and antagonistic responses (e.g. Matthaei et al. 2010). To date, there is no research which has examined how different types of interactions between hydrology and land use factors influence the biota of floodplain wetlands.

1.4 Thesis rationale & guiding question

Wetlands ecosystems support an abundant and diverse range of species; however, in many agricultural landscapes, hydrological and land use changes have caused a decline in the extent and condition of wetlands (Kingsford 2000; Zedler et al. 2003). Many current concepts and much research have helped to link changes in hydrology to the ecological degradation and loss of floodplain systems (e.g. Junk et al. 1989; Poff et al. 1997; Toner and Keddy 1997; Mitsch and Gosselink 2000; Leyer 2006). However, despite this current research in floodplain systems may be limited in three important regards. Firstly, there is a dearth of research on wetlands, relative to larger perennial flowing rivers (Kingsford 2000). Secondly, there is often an exclusively hydrological focus, which may not adequately consider the additional impacts of land use and other factors (Robertson 1997; Meeson et al. 2002). Finally, current research gives little consideration to the nature of interactions between different hydrological and land use factors and specifically, how they may exacerbate and mitigate effects.

Taking these knowledge gaps into consideration, two hypotheses regarding the influence of hydrology and land use factors on a dominant tree species, *Eucalyptus camaldulensis,* in floodplain wetlands of an Australian agricultural landscape were developed. The first, in line with hydrology focused research (hereafter referred to as the “hydrology hypothesis”), views these systems as being driven exclusively by hydrological factors (see below). In contrast, the second hypothesis presents a perspective where both hydrological and land use factors and potential interactions are considered, “hereafter the interactive hydrology-land use hypothesis”. These competing hypotheses are not designed to test which factors are of most relative importance. It is clear that hydrology is the most important factor in many floodplain-riverine systems (Tockner and Stanford 2002). Instead, the above hypotheses are designed to ask whether hydrology focused research is limited by not considering land use and interactions.

1.4.1 Alternate hypotheses

Hydrology hypothesis: Hydrological processes are of overriding significance. The hydrology and vegetation of floodplain wetlands is best understood by exclusively focusing on processes related to hydrology (here defined as factors directly related to stream flow, groundwater and rainfall and / or their regulation). Variation in other factors throughout the landscape (i.e. land use practices, such grazing and land use cover) are of little consequence and do not need to be considered to understand wetland ecosystems. This concept would support a perspective where river hydrology is a 'master variable' that controls the ecological processes of floodplains (e.g. Walker et al. 1995; Bunn and Arthington 2002; Lytle and Merritt 2004; Leigh et al. 2010).

Interactive hydrology-land use hypothesis: Both land use and hydrology are important. Understanding the ecology of floodplain wetlands requires an examination of the impacts of both hydrological and land use factors. Management and research based solely on hydrological processes may not account for all factors causing degradation and therefore be sub-optimal (e.g. Robertson 1997; Ogden 2000; Messon et al. 2002). Furthermore, interactions between hydrological and land use factors are important, with the two interacting in ways which may both mitigate and exacerbate their impacts on species in floodplain wetlands.

The following section outlines the thesis chapters and the four specific studies which examine how hydrology and land use impacts floodplain wetlands in an agricultural landscape. Each is designed to test the two above hypotheses.

1.5 Chapter summaries

Chapter 2 provides an overview of the study area, the Condamine Catchment of south east Queensland, Australia, detailing key information about historical and current land use practices, climate, hydrology, soil and geology.

Chapter 3 examines the hydrology of floodplain wetlands in the catchment and develops various metrics relating to wetland hydrology, likely to be important for the ecology of these systems (e.g. inundation frequency, river connectivity, groundwater depth and catchment area). These metrics are also used to examine if agriculturally modified and unmodified wetlands differ in hydrology.

Chapter 4 utilises the hydrological metrics developed in Chapter 3, as well as selected land use factors (grazing intensity, agricultural land cover and remnant vegetation cover), to test whether an exclusively hydrological perspective ('hydrology hypothesis') is better than a hydrological plus land use perspective ('interactive hydrology-land use hypothesis') for understanding variation in the tree crown vigour of the dominant riparian species (*E. camaldulensis*) and stag abundance (all trees) of floodplain wetlands.

Chapter 5 focuses on the long term persistence of *E. camaldulensis* by developing logistic regression models based on presence and absence. Similar to Chapter 4,this study tests whether a hydrology hypothesis is better than an interactive hydrology-land use hypothesis for understanding variation in the tree (*E. camaldulensis*) presence/absence across floodplain wetlands in southern Queensland.

To assess whether the hydrology hypothesis is limited by not considering interactions, Chapter 6 examines the different ways in which environmental factors interact and the consequences for *E. camaldulensis*. It synthesises the results from Chapters 4 and 5 and develops a Bayesian Network model to test the independent and combined interactive effects of hydrology and land use factors. It also determines the types of interactive responses that best characterise *E. camaldulensis* response. This approach provides a framework to help tackle the interdisciplinary nature of eco-hydrological studies which consider multiple factors.

Chapter 7 synthesises the main findings from the preceding chapters and discusses the relevance of the findings for the research and management of floodplain wetlands in agricultural landscapes. Limitations of the research are discussed and potential for future research is highlighted.

Chapter 2. Physical characteristics, hydrology and vegetation of the agriculturally dominated Condamine Catchment, south east Queensland, Australia

2.1 Introduction

Much of Australia is characterised by a semi-arid and arid climate with poor infertile soils (Martin 2006); however, throughout parts of eastern and south-western Australia, fertile soils and sufficient water resources have allowed the extensive development of agriculture. In eastern Australia, the Murray-Darling Basin (MDB), covering over 1 million km^2 (Figure 2.1), is the most agriculturally utilised region in the country (Walker and Thoms 1993). The Condamine Catchment, covering approximately 24,434 km^2, is at the headwaters of the MDB in south east Queensland (Biggs and Carey 2006; Figure 2.1). As with many other regions throughout the MDB, the Condamine Catchment is heavily utilised for agriculture. Since European colonisation, changes to land use caused by extensive tree clearing and alteration of hydrological flows have resulted in significant eco-hydrological changes throughout the MDB (e.g. Pierce et al. 1993; Walker and Thoms 1993). Similarly, in the Condamine Catchment, the past two centuries have also seen dramatic hydrological and land use changes as a result of agricultural development (Biggs and Carey 2006).

Since the mid-1800s, the Condamine Catchment has been subject to extensive clearing of native vegetation and has undergone major hydrologic alterations to support agricultural development (Fensham and Fairfax 1997; Thoms and Parsons 2003). As a result, less than 30% of the historically occurring vegetation remains in the catchment (Accad et al. 2008) (Figure 2.1). Land use, and coinciding hydrological changes, were initiated by grazing in the 1840s and then more significantly by cropping in the early 1900s (Biggs and Carey 2006). During the 1960s, the construction of public water storages allowed the further development and expansion of irrigated agriculture throughout the region, which has further altered hydrologic processes (Thoms and Parsons 2003).

Today, the Condamine Catchment is well known for its agricultural productivity, supporting a wide range of economically important summer and winter crops (Biggs and Carey 2006). In 2006-07, irrigated agriculture generated $3,869 per hectare, while dry land agriculture generated $666 per hectare (ABARES, 2009). However, while agriculture has been highly productive, it has been most intensive on the fertile alluvial soils of the floodplain and as such, has caused some of the most extensive vegetation loss and hydrological alterations in these areas (Biggs and Carey 2006; Figure 2.1).

This chapter outlines the physical, hydrological and land use characteristics of the Condamine catchment. The general characteristics of wetlands in the catchments floodplains will also discussed. Finally, the dominant tree species of these wetlands, *Eucalyptus camaldulensis,* which will be used in the following chapters to examine the importance of hydrological and land use factors, will be described.

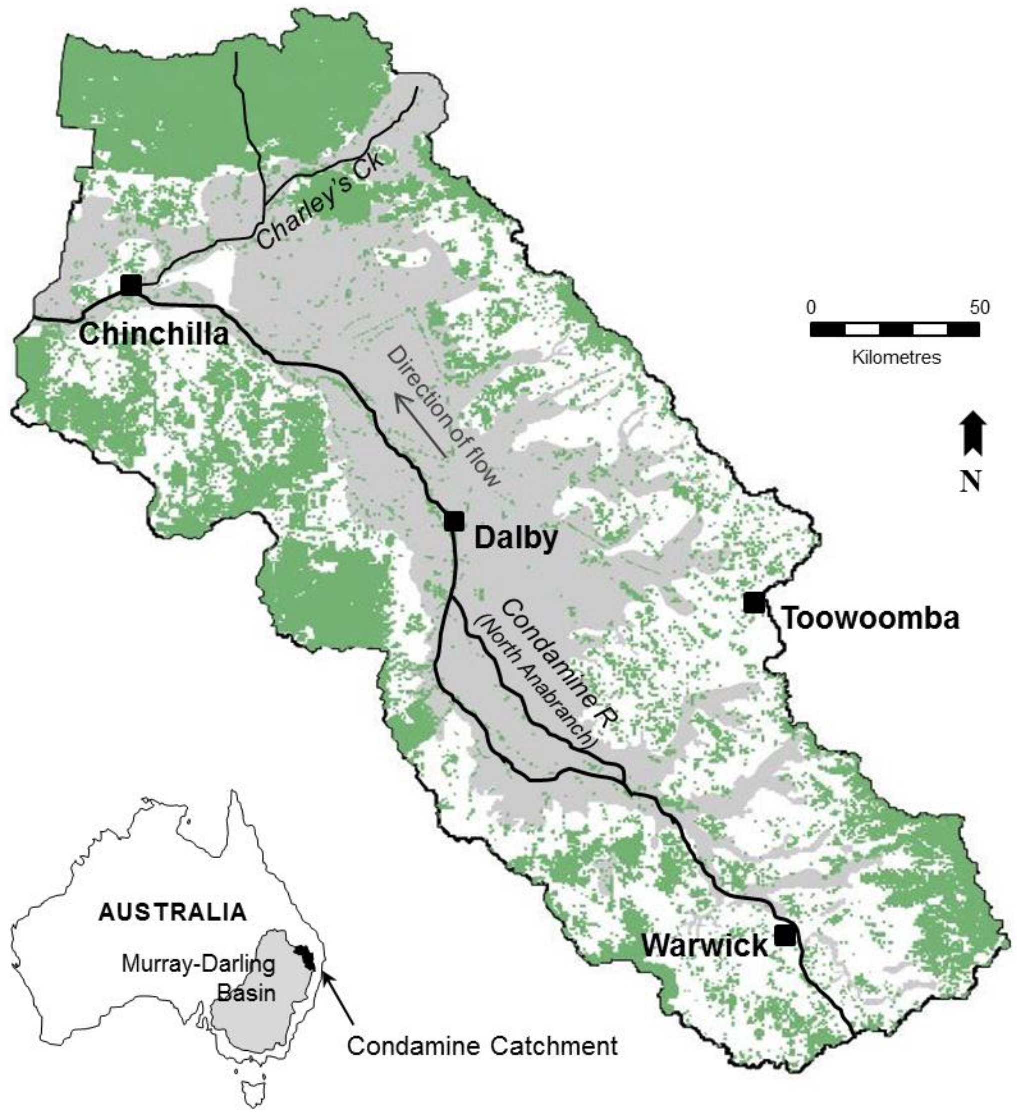


Figure 2.1 Map of the Condamine catchment showing major towns, the Condamine River and floodplain (light grey) (data source: Queensland Environmental Protection Agency 2008) remaining remnant vegetation (dark grey) throughout the catchment (data source: Queensland Department of Environment and Resource Management 2005)

2.2 Physical characteristics

2.2.1 Climate

The Condamine Catchment is characterized by a variable sub-tropical to semi-arid climate and is influenced by weather systems in the northern tropics and southern temperate regions of Australia (Vandersee 1975; Searle 2007). The Catchment is also influenced by the El Ni*ñ*o Southern Oscillation (ENSO), which has strong relationships with stream flow and precipitation that are enhanced during the La Niña phase of ENSO (Verdon et al. 2004). Inter-annual rainfall variability is therefore high, ranging from approximately 1200 mm per annum in the ‘wet’ La Niña phase to 250 mm per annum in the ‘dry’ El Niño phase of ENSO (Figure 2.2).

Rainfall in the catchment typically occurs in the summer months as a result of tropical monsoonal activity (Thoms and Parsons 2003); however, droughts and floods may still occur at any time of the year (Porter 2002; Clewett 2003; Thoms and Parsons 2003). On average, the catchment receives almost two thirds of its annual rainfall during the summer months, from November to March (Figure 2.3) (Harris et al. 1999). Over the long term (1890-2010), mean annual precipitation for the area varies from between 673 mm at Chinchilla, in the west, to 691mm at Warwick in the south-east (Australian Bureau of Meteorology 2010). Temperatures range from a mean minimum of -1.3°C in July, to a mean maximum of 33.2°C in December (Australian Bureau of Meteorology 2009).

2.2.2 Recent and future climate

In the Condamine Catchment, the last few decades and especially 1990-95 and 2000-05, have seen moderate drought (5-10% of driest years on record) and severe droughts (<5% of driest years on record), respectively (Clewett 2003). Since 1990, there has also been an overall trend of declining rainfall (Australian Bureau of Meteorology 2009). Furthermore, in the catchment and surrounding areas, there are predictions of rainfall declines of between 2-6% for the periods 2031-2050 (Cottrill 2009). Under scenarios of climate change, the best estimate is that by 2030 there will also be a 9% decrease in mean annual run-off (CSIRO 2008). Consequently, while rainfall variability is high in the Condamine Catchment, there will likely be overall declines in rainfall and water availability in the future.

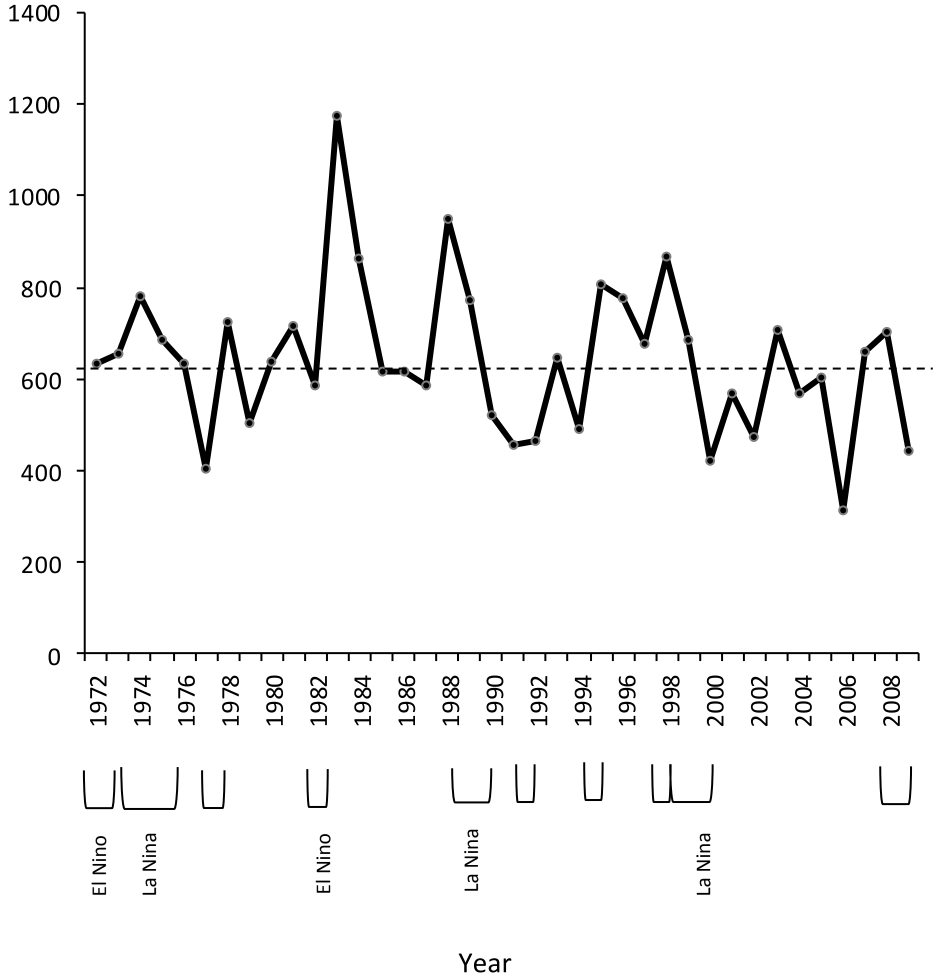
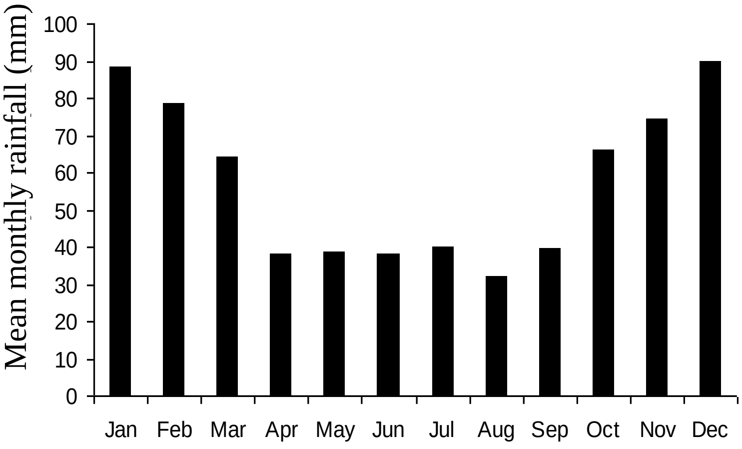
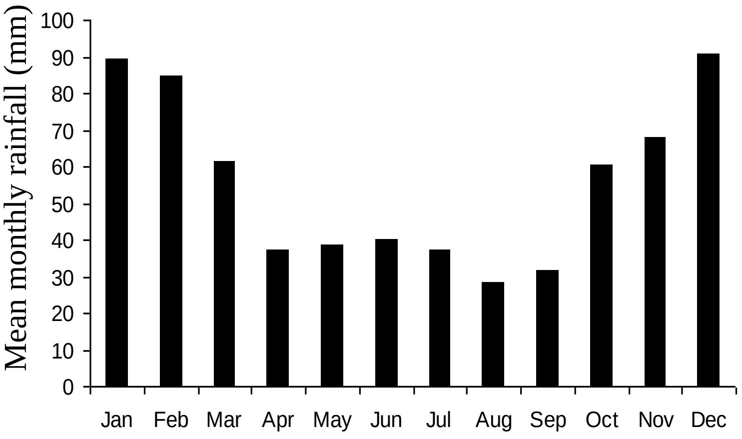


Figure 2.2 Annual rainfall for Macalister (25 km north of Dalby) from 1972 to 2009 Dashed line represents median rainfall, El Nino and La Nina phases are also indicated (data source: Australian Bureau of Meteorology 2011)

(a) Warwick



(b) Dalby



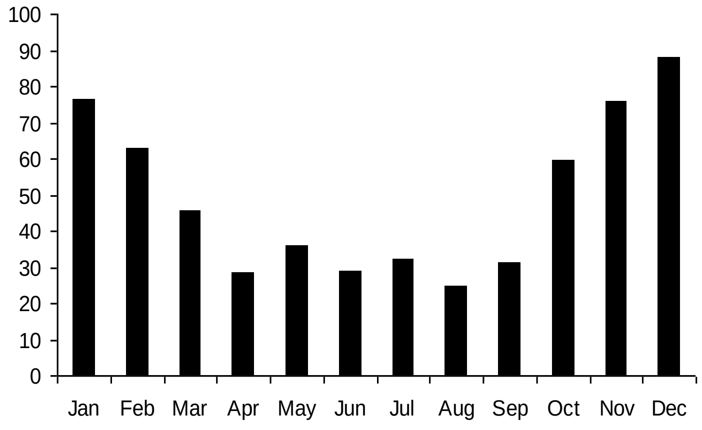


Figure 2.3 Mean monthly rainfall at (a) Canning Downs (3.6km from Warwick) (1879-2009) at (b) Tingha (5.6km from Dalby) (1959-2009) and (c) Chinchilla (1989-2009) (data source: Australian Bureau of Meteorology 2009).

2.2.3 Hydrology

The headwaters of the Condamine River are sourced from the Great Dividing Range, east of the catchment. The Condamine River flows in a north to north westerly direction from its headwaters, being feed by numerous tributaries along its course (Vandersee 1975). As the river flows north-westerly along the catchment, it becomes multi-channelled across the gently sloping alluvial plains (Vandersee 1975). The river flows north to north westerly until it reaches Surat where it flows west and forms the Balonne River, eventually joining with the Darling River and the Murray River to form the longest river system in Australia.

The hydrology of the Condamine River reflects the region's variable subtropical and semi-arid climate, with flooding occurring irregularly. The river has had major floods (> 1250 $m^3 s^{-1}$) in February 1942, January 1956, May 1983, April 1988 and 1990 and January 1996 and January, 2011 (Australian Bureau of Meteorology 2011; Figure 2.4). Mean annual stream flow for the river varies from 90.8 GL (1.91 $m^3 s^{-1}$) in the south-east at Warwick (1920-2006), to 340.6 GL (2.29 $m^3 s^{-1}$) at Dalby (1968-2007) and 476.1 GL (2.4 $m^3 s^{-1}$) in the west at Chinchilla (1920-2007) (Queensland Department Environment and Resource Management 2009a; Figure 2.4). Coinciding with flow magnitude, variability also increases as the river flows north west, being highest at Chinchilla with a co-efficient of variation (C_v) of 1.38 and lowest in the south at Warwick with a C_v of 1.05 (Queensland Department Environment and Resource Management 2009a).

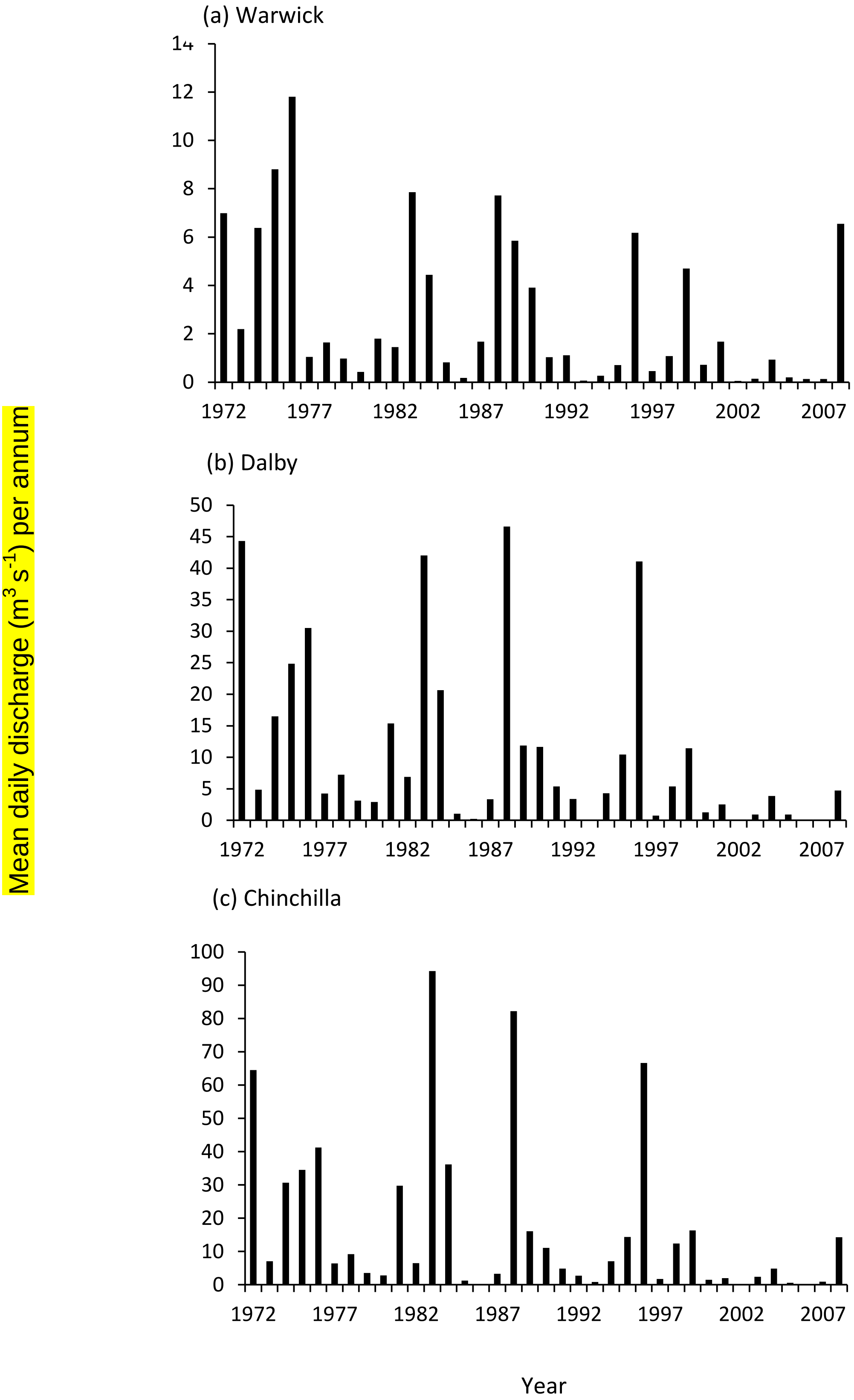


Figure 2.4 Mean daily discharge ($m^3 s^{-1}$) per annum at (a) Warwick gauging station (b) Loudoun gauging station near Dalby and (c) at Chinchilla weir gauging station (data source: Queensland Department of Natural Resources 2009a).

The Condamine River's high variability has led to significant anthropogenic modifications in an attempt to make flows more reliable for agricultural production (Harris et al. 1999). As a result, the hydrology of the Condamine River and floodplain has been modified by water extraction and physical alterations (Harris et al. 1999; Thoms and Parsons 2003). The Condamine River is now a highly modified river, with its flows regulated by numerous weirs and in-stream storage structures along its length (Thrupp and Moffatt 2001). Today, some 31 weirs are present along the Condamine River and its associated tributaries within the catchment (Australian Natural Resources Atlas 2009). The largest public water storages in the area, servicing irrigation and domestic supply are Leslie Dam (106250 Ml capacity) near Warwick and the Chinchilla weir (9800 Ml capacity) in the north. As a consequence of river regulation and water-resource development, Thoms and Parsons (2003) argue that the Condamine River has been homogenised so that temporal hydrological diversity has declined.

Groundwater

There are substantial groundwater reserves throughout the Condamine Catchment associated with both basaltic uplands and alluvia (Searle 2007). The Condamine River alluvium provides the largest store of groundwater in the catchment and supports various agricultural and urban areas (Harris et al. 1999). Groundwater quality is generally high, with low salinity levels throughout (Searle 2007). Groundwater extraction commenced in the 1960's and is now most intensive throughout the catchments floodplain (Porter 2002; Kelly and Merrick 2007). In the Upper Condamine (Dalby and Warwick) extraction rates exceed recharge by 38% and based on historical rainfall would exceed recharge in over 90% of years (CSIRO 2008).

The extraction of water has caused substantial declines in groundwater levels throughout much of the catchment's floodplain (Figure 2.5 & 2.6). Over the longer term, from 1967-2007, reductions of up to 15 to 25 m in groundwater levels have occurred in some areas (Kelly and Merrick 2007). In most other areas, groundwater levels have also been declining steadily for many years (Porter 2002). Consequently, aside from localised areas where recharge occurs directly to shallow aquifers directly from the River and some of its smaller tributaries, monitored ground water levels have been falling steadily in recent decades (Porter 2002) (Figure 2.6).

The Condamine River has also suffered reductions in flow as a result of groundwater extraction activities that have increased leakage of river water to groundwater (Barnett and Muller 2008). Barnett and Muller (2008) estimate that in some areas, if current groundwater extraction continues at 30 GL $year^{-1}$, then stream flow will be reduced by 12 GL $year^{-1}$. Currently, the Condamine River from Tummaville to Chinchilla Weir is already losing between 0.37 and 1.3 ML/day/km (Barnett and Muller 2008; CSIRO 2008). As a consequence, the majority of the Condamine River is under ‘maximum losing’ conditions and no longer receives water from underlying aquifers (Barnett and Muller 2008).

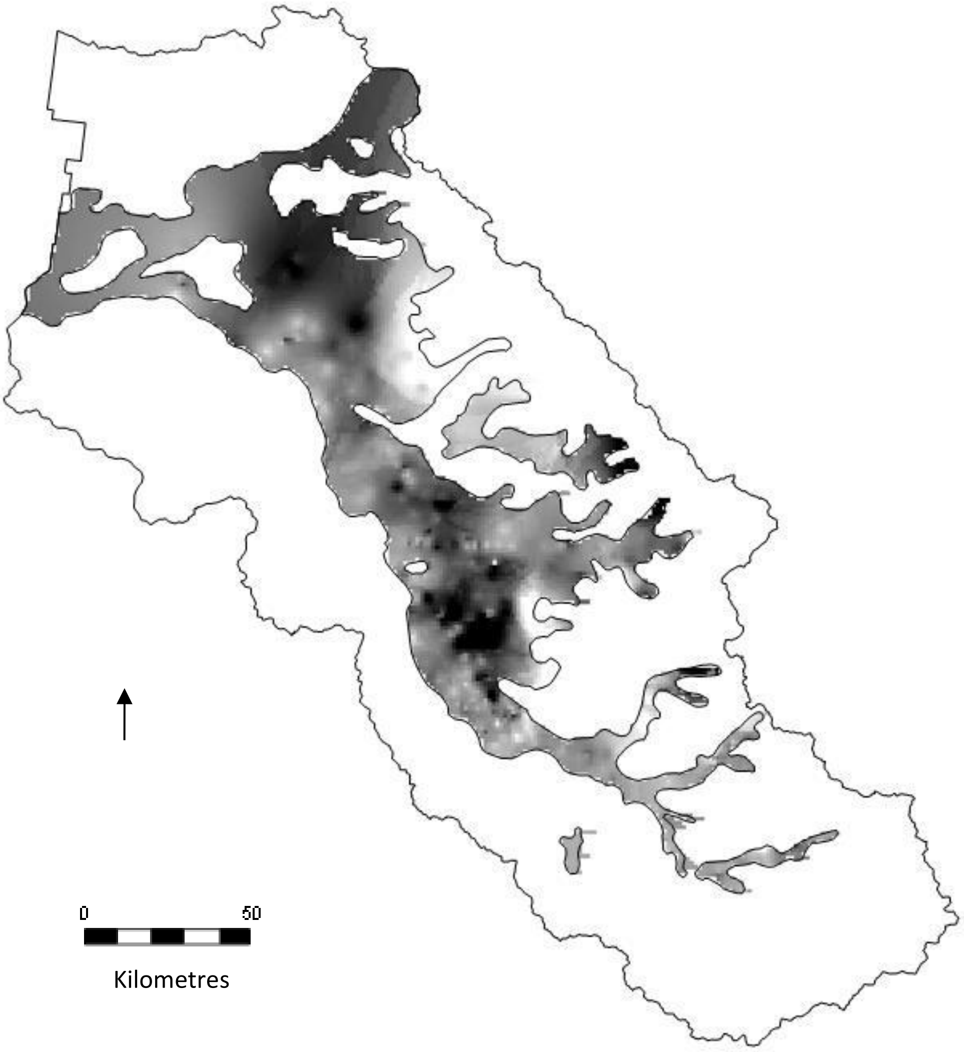
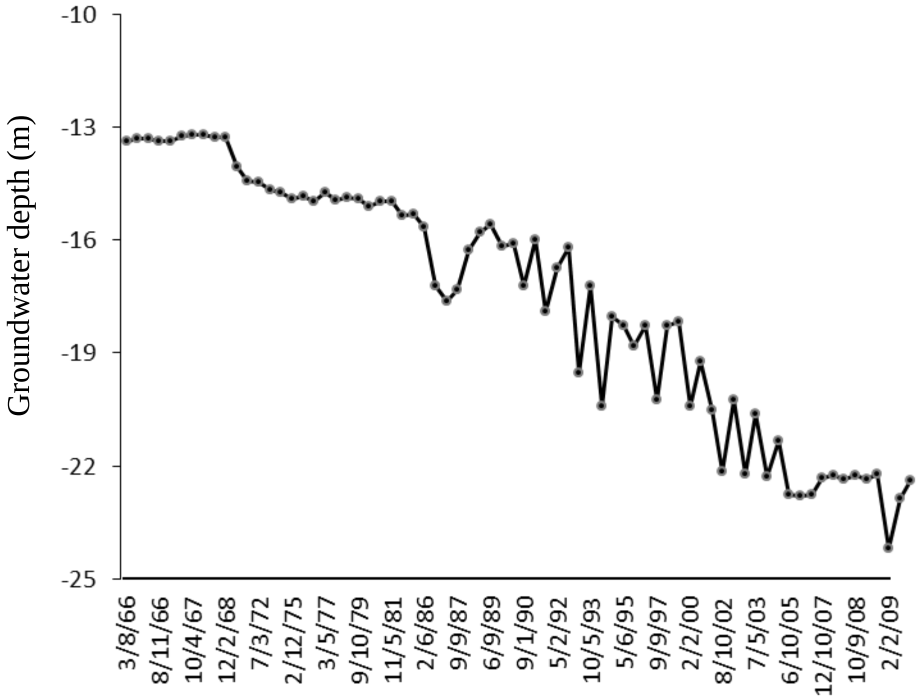


Figure 2.5 Groundwater decline throughout the Condamine floodplain (bounded by the black line) from 1987 to 2009. □ Small (>5m); ■ Moderate (5-20m); ■ Large (20-30m) declines (data source: Queensland Department of Environment and Resource Management 2009b).

(a) Dalby region



(b) Warwick region

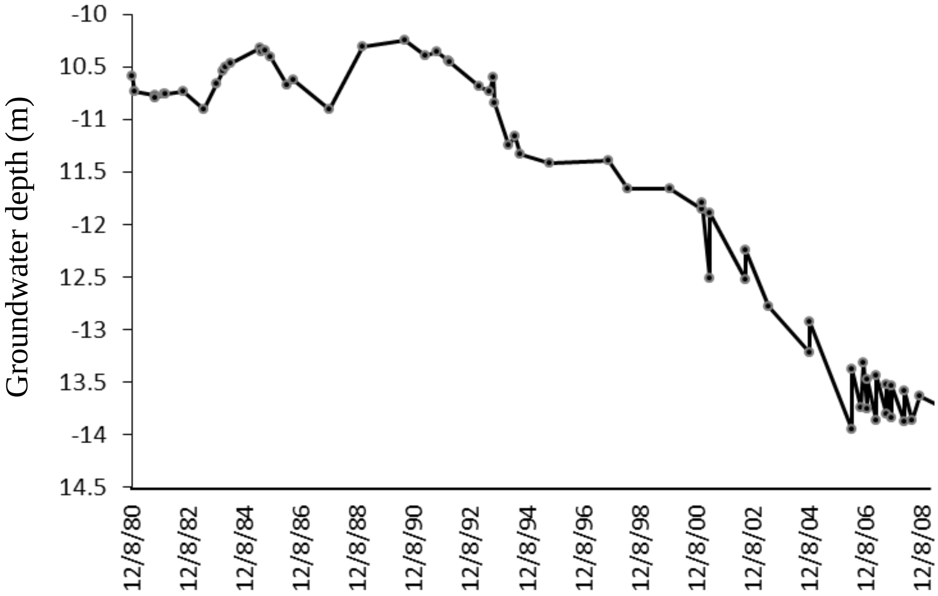


Figure 2.6 Examples of declining groundwater levels at bores in the study area. Bore number (a) 42230156 (Dalby region) and (b) 42231243 (Warwick region) (data source: Queensland Department of Environment and Resource Management 2009b).

2.2.4 Geology and Land form

The geology of the catchment is characterised by Tertiary olivine basalts from volcanics erupted onto Jurassic sediments (Searle 2007). In the south east, Tertiary basalt substrates dominate, while in the north-east Triassic-Jurassic sediments are prevalent (Sattler and Williams 1999). In the east, the catchment is bounded by the Great Dividing Range, where maximum elevation is 1367 m (Clayton et al. 2006; McDougall et al. 2008). On the lower floodplain areas, minimum elevation is 278 m (McDougall et al. 2008).

Throughout the central areas of the catchment, alluvia floodplains dominate the geological landscape (Sattler and Williams 1999), covering approximately 8,500 km^2 (Vandersee 1975; Knowles-Jackson and McLatchey 2002). Over time, the erosion of basaltic and sedimentary surfaces has formed the extensive alluvial surfaces of the floodplain (Harris et al. 1999). Locally, regions of the floodplain are also influenced by sandstone, basalt and traprock (Harris et al. 1999).

Nanson and Croke (1992) recognise three classes of floodplain systems (1) high energy non-cohesive, (2) medium energy non-cohesive and (3) low-energy cohesive floodplains. The geomorphology of the Condamine River floodplain areas can be characterised by two different zones. In the south, there is an armoured zone with relatively immobile sediment and small adjacent floodplains and in the north, a mobile zone, with highly active river sediments and channel morphology (Thoms and Parsons 2003).

Thompson and Beckman (1959, cited in Vandersee 1975) argue that the floodplains developed from two major deposition periods, with the most recent deposition being derived almost exclusively from basalt. These more recent alluvial deposits are characterised by a range of features, including levees, terraces, ox-bows and prior streams (Harris et al. 1999). In contrast, the older deposition event resulted in a floodplain of mixed basaltic and sedimentary origin (Harris et al. 1999). This ‘older alluvia floodplain’ is characterised by a flat and geologically featureless form. Due to its higher elevation and current water regulation activities, this older section of the floodplain is minimally affected by over-bank flows, so that today erosion occurs mainly as a result of catchment derived overland flows (Harris et al. 1999).

2.2.5 Land use

Agricultural is present throughout the entire Condamine Catchment; but dominates on fertile floodplain soils where vegetation clearing has been the greatest (Figure 2.1 & 2.7). Land use on the floodplains can be broadly classified into five different types (Figure 2.7):

- intensive agriculture - characterised by intensive animal production, such as dairy and cattle and pig feedlots;

- irrigated agriculture - involves the irrigated production of various crops, such as cereals and cotton;

- dryland agriculture - including forestry, cropping and grazing on cleared and modified pastures, without the use of irrigation;

- production from relatively natural environments, which most commonly involves grazing of natural vegetation; and,

- remnant vegetation, which is not used for any agricultural production.

The distribution of land use is not uniform throughout the catchment, with remnant vegetation and grazing in natural environments most prevalent in the north, while irrigated and intensive agriculture more common in the central and southern areas of the Catchment (Figure 2.7). However, collectively, dryland agriculture and grazing in natural environments dominate land use in the catchment, covering over twice the area taken up by irrigated and intensive agriculture (Figure 2.8).

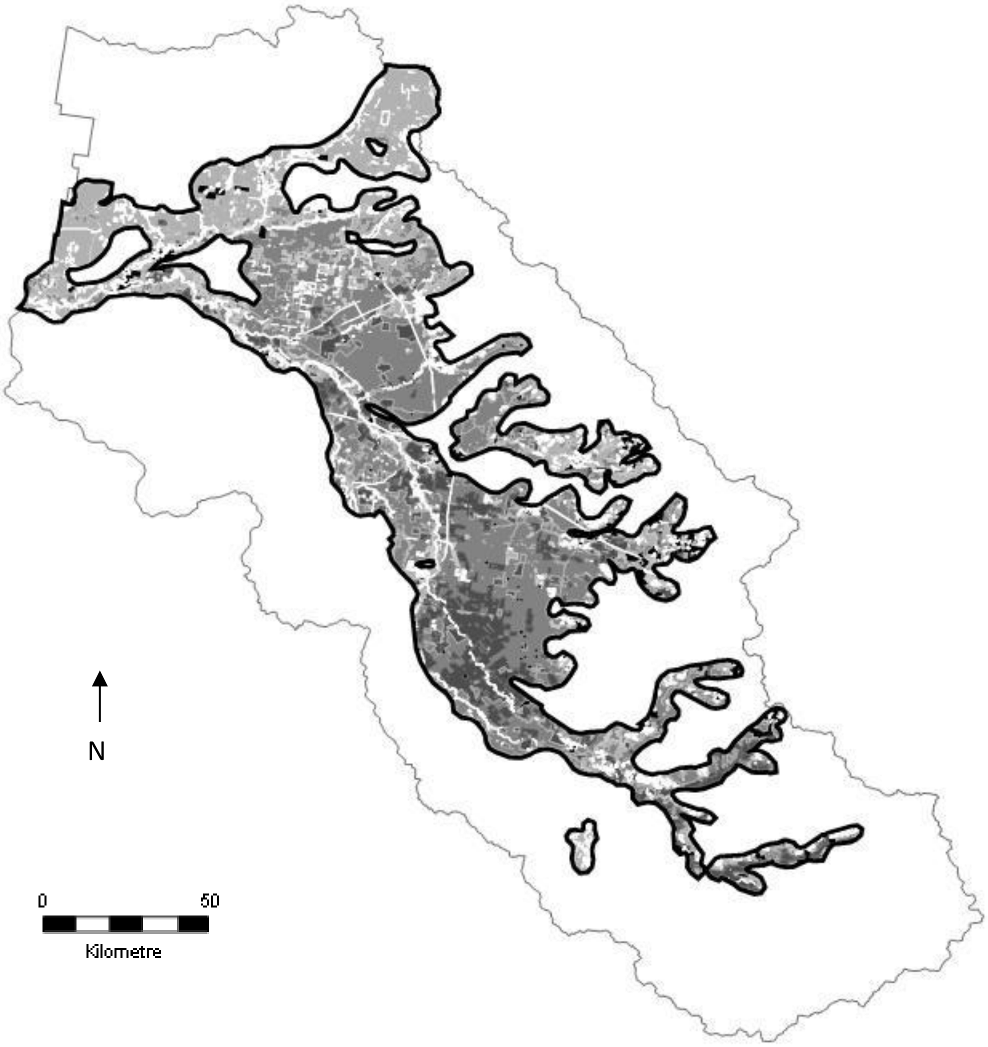


Figure 2.7 Distribution of agricultural land use types throughout the floodplain areas (bounded by the black line) of the Condamine catchment. ■ Intensive; ■ Irrigated; ■ Dryland; ■ Production from natural areas / Grazing; and □ Remnant vegetation (no agricultural production) (data source: Queensland Department of Environment and Resource Management 1999)

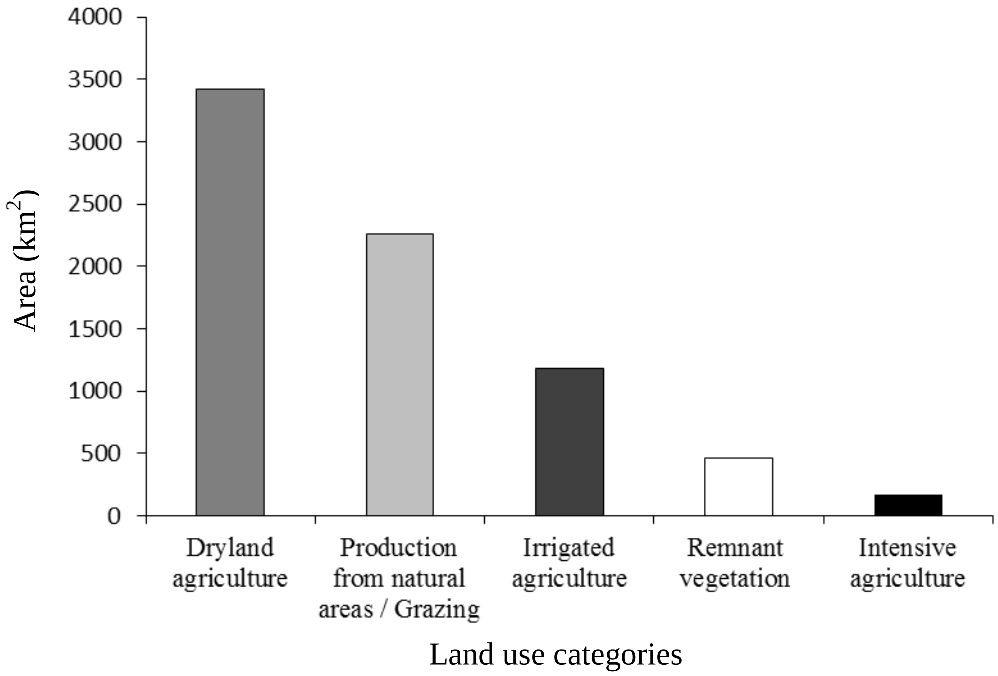


Figure 2.8 Area of different land use types within the Condamine catchment floodplain (data source: Queensland Department of Environment and Resource Management 1999).

Other land uses, such as mining and urban areas, also occur in the catchment, but are not as wide spread as agricultural. The major population centres in the catchment are Toowoomba (population ~90,000), Dalby and Warwick (~12,000 each) and Chinchilla (~7,000). Coal mines exist in the centre of the Catchment, near Dalby and in the south near Millmerran (Biggs and Carey 2006). Natural gas and coal seam gas production is also becoming prevalent in the north of the Catchment, near Chinchilla (Queensland Department of Environment and Resources 2010). Currently, mining is causing small scale changes to land use patterns, but in the future these may cover larger areas, and as such have larger scale impacts (Queensland Department of Environment and Resources 2010).

2.3 Wetlands in the Condamine Catchment

Throughout the catchment, wetlands cover 32,000 to 35,400 ha (Queensland Environmental Protection Agency 2008). Of the 2000 mapped wetlands in the catchment, including rivers and streams, 430 of these are classified as non-flowing (lentic) (Clayton et al. 2006; Queensland Environmental Protection Agency 2008; Figure 2.9). These non-flowing wetlands collectively support up to 35 amphibian, 19 fish, 90 water bird (including 22 migratory) and 79 plant species (Clayton et al. 2008). Various water-dependent turtles, lizards and invertebrates are also known to be present (Clayton et al. 2008). In addition, the wetlands also provide critical habitat for various rare and threatened fauna (e.g. *Adelotus brevis, Littoria revelata, Lechriodus fletcheri*) and flora (e.g. *Aponogeton queenslandicus*, *Fibristylis vagans*) (Clayton et al. 2008).

Vegetation in the Condamine Catchment has been characterised into four broad groups by Fensham (1998):

- *Eucalyptus camaldulensis* and *E. tereticornis* woodlands;
- grasslands (*Dicanthium sericeum*) on fertile floodplain soils;
- *Eucalyptus populnea* woodlands on clay loam terraces; and,
- woodlands of *E. albens*, *E. crebra*, *E. melliodora* and *E. orgadophila* on the higher elevation clay loam soils characterised by relatively rocky and hilly terrain.

The fringing vegetation of remaining wetlands are typically dominated by *E. camaldulensis* (River red gum) woodland, with co-dominate riparian species of *E. coolabah* (Coolabah) and *Acacia Stenophylla* (River Cooba) present in some instances. In the northern areas of the catchment, *E. coolabah* are also present on the periodically flooded alluvium floodplains and often coincide with *E. camaldulensis* woodlands (Beadle 1981; Sattler and Williams 1999). Depending on local environmental conditions, a variety of understorey vegetation including shrubs (e.g. *Acacia*), sedges and herbs (e.g. *Cyperu*s sp. *Marsilea* sp.), as well as grasses, may also be present within these floodplain wetland vegetation communities.

Figure 2.9 Non-flowing wetlands in the Condamine catchment (data source: Queensland Environmental Protection Agency 2008).

These vegetation communities may also vary structurally depending on environmental conditions, such as hydrology. According to Specht and Specht (1999), the structure of *E. camaldulensis* communities is related to hydrological conditions, such as groundwater level and the timing and frequency of flooding. Throughout the Condamine Catchment there have been no specific assessments of the structural characteristics of *E. camaldulensis* woodlands or of wetland woody fringing vegetation, but a diversity of structural types reflecting local hydrological and potentially land use conditions are likely to be present.

As a result of agricultural development, most wetlands of the Condamine Catchment have been exposed to various hydrological alterations at the local scale. In a survey throughout the Upper Condamine Catchment Thrupp and Moffatt (2001) found that 10% of wetland sites have had their hydrology altered by ring tanks, 27% by levees, 20% by channels and 14% by water pumps. Furthermore, Thrupp and Moffatt (2001) observed that 96% of sites were impacted by grazing, 73% by compaction and that all had been subject to some vegetation clearing.

2.3.1 **Eucalyptus camaldulensis** ***and its importance for floodplain wetlands***

Within the study area, *E. camaldulensis* is one species which may be particularly useful for understanding the impacts of hydrological and land use change on floodplain wetlands in agricultural landscapes. *E. camaldulensis* is the most widely distributed eucalypt species in Australia, often being present on alluvial soils and dominating major drainage areas, watercourses and frequently inundated areas of floodplains (Beadle 1981; Di Stefano 2001). As such, *E. camaldulensis* often dominate the vegetation of remaining wetlands in agricultural landscapes of the Murray Darling Basin (Reid and Brooks 2000; Wen et al. 2009). The prevalence of *E. camaldulensis* in wetlands of agricultural landscapes makes it an ideal species for examining the coinciding impacts of hydrological and land use changes.

The wide range and dominant nature of *E. camaldulensis* in floodplain environments also means that the species is of critical ecological importance (Bond et al. 2008). Roberts and Marston (2000) have associated *E. camaldulensis* vegetation with healthy functioning of lowland rivers, arguing that it plays an important functional role through litter fall, carbon form and flux. In floodplain habitats, *E. camaldulensis* also provides organic material and food sources for aquatic invertebrates, habitat for birds, maintains soil structure and helps facilitate nutrient cycling between floodplains and rivers (Boulton and Lloyd 1991; Briggs et al. 1997; Law and Anderson 1999; Mac Nally et al. 2001; Francis and Sheldon 2002; Wen et al. 2009). *E. camaldulensis* is therefore a functionally dominant species that play a key ecological role in floodplain wetlands. Consequently, how *E. camaldulensis* is impacted by hydrological and land use changes likely has implications for the biota of floodplain wetlands in agricultural landscapes more generally.

2.4 Conclusion

The Condamine Catchment of southern Queensland resides at the headwaters of the Murray- Darling Basin, Australia. It is characterised by a variable climate and is prone to both floods and droughts. Large areas of the catchment are also covered by an extensive alluvial floodplain, which supports a range of biota. However, the floodplain of the Condamine Catchment, as in many other agriculturally productive areas, has been subject to extensive clearing of native vegetation and undergone major hydrologic alterations. These changes may be particularly important for the ecology of floodplain wetlands and the biota residing within them, such as *E. camaldulensis*.

Chapter 3. Hydrological differences between modified and unmodified wetlands

3.1 Introduction

Much research has documented the impacts of flow regulation and extraction on floodplain wetlands (Quinn et al. 2000; Reid and Brooks 2000; Nias et al. 2003; Jenkins et al. 2005; Page et al. 2005; Frazier and Page 2006; Colloff and Baldwin 2010). In many landscapes, flow regulation and extraction has altered connectivity between floodplain wetlands and rivers and have caused changes to the timing, duration and frequency of inundation events (Walker and Thoms 1993; Reid and Brooks 2000; Frazier et al. 2003; Lloyd et al. 2004). In addition to the diversion and extraction of overland flows from the floodplain (e.g. Porter 2002), regulation may also alter connectivity to wetlands, by reducing overbank flows and ultimately reduce the frequency and volume of flows to wetlands (Kingsford 2000). For example, the construction of levees and channelization to regulate flows has narrowed and straightened rivers, often severing river connectivity with the surrounding landscape, reducing the frequency of overbank flows and consequently, the number of inundation events for floodplains and their wetlands (Poff et al. 1997).

However, in addition to the effects of river regulation and extraction, local scale modifications to wetlands may also alter their hydrology. Modified wetlands are becoming increasingly common in many agricultural landscapes and represent a novel and distinct wetland type (Brock et al. 1999; Austin et al. 2003). Modified wetlands are broadly defined here as those subject to identifiable and direct local hydrological modifications as a result of agriculture; this includes weirs, dams, levees and pumps for water extraction (after Clayton et al. 2006). However, despite the increasing prevalence of modified wetlands in agricultural landscapes, there is relatively little knowledge about how they differ hydrologically from remaining ‘natural’ or unmodified wetlands. This chapter asks the question, are modified and unmodified wetlands in the Condamine Catchment, southern Queensland, hydrologically different

3.1.1 Scale-dependent effects of agriculturally modifying wetlands

Inundation frequency

Similar to the effects of flow regulation and extraction, local agricultural modification may alter the hydrology of individual wetlands by making them more continuously dry or wet (Brock et al. 1999; Neilsen and Brock 2009). These modifications to wetlands may occur through both changes to morphology (i.e. levees and deepening) (Lutton et al. 2010) or from the direct storage and extraction of water (Kingsford 2000). Accordingly, agricultural modification may make wetlands either more continuously dry (if water is extracted) or wet (if water is stored) (Brock et al. 1999). In contrast, un-modified wetlands, which have not undergone morphological changes and are less utilised for water storage and extraction, may therefore have different inundation frequencies.

The spatial and temporal variability of water drives the physical, chemical and biological functioning of wetlands (Boulton and Brock 1999; Mitsch and Gosselink 2000; Brooks 2005), which help facilitates the reproduction, growth and colonisation for a range of flora and fauna species (Brock et al. 2000). As such, differences in the inundation frequency of wetlands may have significant ecological implications for biota. For example, in Australia, it has been argued that the modification of wetlands to water storages for agriculture has resulted in the loss of native species adapted to dynamic hydrological conditions (Kingsford 2000). Understanding the extent to which modified and unmodified wetlands differ hydrologically, is therefore an essential first step in understanding the consequences of future modifications and of potentially mitigating the ecological consequences of current ones.

River connectivity

Modified and unmodified wetlands may also differ in terms of river connectivity. Hydrological connectivity between floodplains and the river is fundamental for ecological functioning, helping facilitate the dispersion of species and the transfer of organic matter and influencing water chemistry and soils (Chapter 1; Tockner et al. 1999; Pringle 2001; Leyer 2006; Cook and Hauer 2007). Connectivity between the river and wetland facilitates the exchange of water between these different components of the floodplains and plays a critical role in various ecological processes, by distributing plant propagates, organic matter, nutrients and sediments important for productivity and general ecological functioning (Tockner et al. 1999; Thoms 2003; Leyer 2006; Gurnell et al. 2008). In areas where river connectivity is lower, there may be significant ecological effects for wetlands (Kingsford 2000). For example, in the Middle Ebro River channel, Spain, as river connectivity to floodplain wetlands decreased, so did macro invertebrate species richness and total abundance (Gallardo et al. 2008). Consequently, if there are differences in river connectivity between modified and unmodified wetlands this is likely to have significant ecological implications.

Despite the importance of river connectivity, few studies have examined how it differs between modified and unmodified wetlands (Austin et al. 2003; but see Daniels and Cumming 2008 and Lutton et al. 2010). Studies that have investigated differences in the distribution of modified and unmodified wetlands have shown that modified wetlands may be both more (Daniels and Cumming 2008) and less (Lutton et al. 2010) connected to the riverine network. If differences in river connectivity and other hydrological aspects (e.g. inundation frequency) are common between modified and unmodified wetlands in agricultural landscapes, then these wetlands may differ in the species and ecological functions they support. Consequently, in agriculturally altered landscapes understanding how modified and unmodified wetlands differ in aspects, such as river connectivity, is an important issue for the ecological conservation of floodplain wetlands and their biota (Lutton et al. 2010).

3.1.2 Quantifying landscape hydrological metrics

Detailed information on wetland hydrology is lacking in many landscapes (Hulsmans et al. 2008) and as such, quantifying local and landscape differences in hydrology between modified and unmodified is difficult. The integration of remotely sensed satellite data with long term hydrological records is one way of overcoming these challenges (e.g. Frazier et al. 2003; Overton 2005; Powell et al. 2008). Lichvar et al. (2002) examined 21 years of Landsat imagery of dry lake beds (playas) in the western Mojave Desert, California, USA and combined them with 50 years of precipitation records to develop a threshold rainfall bracket of average minimum precipitation needed to inundate the playas.

Remotely sensed satellite imagery and stream flow data have also been utilised to help understand the water regime of floodplain wetlands along reaches of the Murray and Darling Rivers in Australia (e.g. Frazier et al. 2003; Overton 2005; Powell et al. 2008). Frazier et al. (2003) utilised daily discharge data from river gauges as well as before and after flood sequences of Landsat Thematic Mapper (TM) imagery to relate floodplain wetland inundation to stream flow. Thus, while such approaches may utilise coarse resolution metrics and lack sufficient data on some parameters, such as evaporation (Lichvar et al. 2002), they still provide important insights into wetland hydrology over broad spatial (e.g. catchment) and temporal scales (10-20 years).

The development of hydrological metrics relating to wetland hydrology also offers the opportunity to study the eco-hydrology of numerous individual wetlands over large areas. Hydrological factors have been referred to as a 'master variable' controlling the ecological processes of river-floodplain landscapes and their wetlands (Chapter 1; Walker et al. 1995; Lytle and Merritt 2004). As such, the development of hydrological metrics related to groundwater, stream flow and rainfall, are likely to be an important first step in understanding wetland ecosystems. Various studies have developed metrics relating to each of these factors, especially rainfall and stream flow, for hydrological (e.g. Lichvar et al. 2002; Frazier et al. 2003; Overton 2005; Powell et al. 2008) and ecological (e.g. Turner et al. 2004) models, but this approach has yet to be utilised to study the eco-hydrology of small hydrologically dynamic wetlands in agricultural landscapes.

This study utilised data derived from annual satellite imagery on wetland hydrology from the Queensland Dams and Water body dataset (Queensland Department Environment and Natural Resouces and Water 2005) and integrated it with datasets on the agricultural modification of wetlands (Clayton et al. 2006; Queensland Environmental Protection Agency 2008) in the Condamine Catchment of southern Queensland, Australia. Previous research in the study area has shown water resource development has homogenised the Condamine River so that temporal hydrological diversity has declined (Thoms and Parsons 2003). However, there is no research on the hydrological nature of floodplain wetlands in the catchment, or the impacts of wetland modification through regulation and extraction. To help address this knowledge gap, this study seeks quantify the hydrological nature of wetlands in the Condamine Catchment, southern Queensland, and test whether unmodified and agriculturally modified wetlands differ significantly in hydrological characteristics (i.e. inundation frequency, river connectivity, groundwater depth and rain volume).

3.2 Methods

3.2.1 Site selection

Queensland Environmental Protection Agency Wetland Mapping version 1.2 (2008) and Department of Natural Resource and Water (2005), Queensland Dams and Water Body (QDWB 2005), datasets were used to select wetlands and derive data on hydrology.

From these datasets, 251 wetlands were classified as non-riverine (non-flowing water bodies, <50ha) within three sub-regions of the Condamine catchment (Figure 3.1). Wetland selection was limited to those wetlands for which hydrological data from the QDWB (2005) dataset was available, which was approximately 50% (251/509) of all mapped non-riverine (floodplain wetlands) being within the catchment.

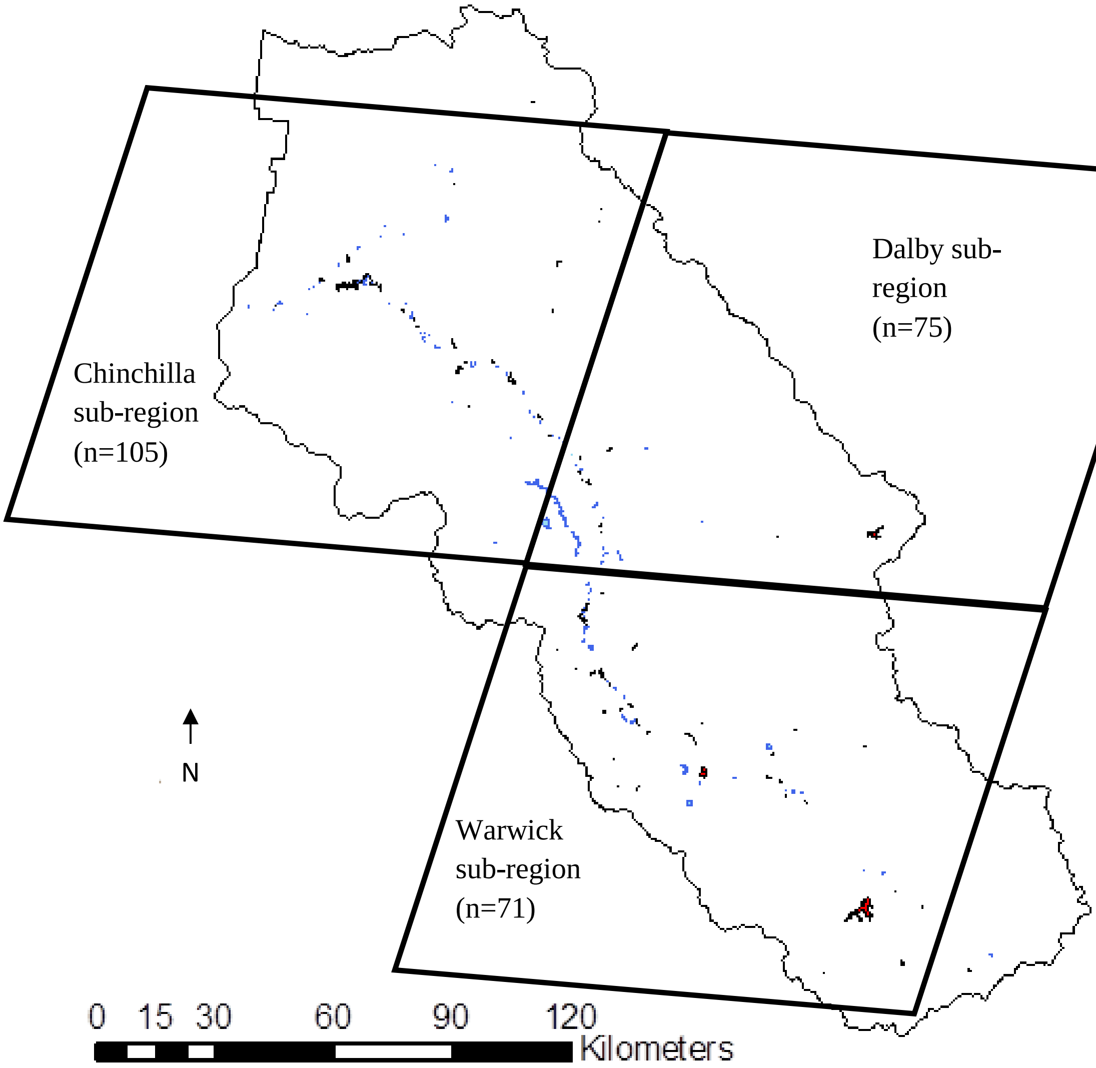


Figure 3.1 The Condamine Catchment showing the location of the 251 surveyed unmodified (blue) and modified (red) wetlands across the three sub-regions Chinchilla, Dalby and Warwick (Data source: Queensland Environmental Protection Agency 2008 and Queensland Department Environment and Natural Resources and Water 2005).

Each selected wetland was delineated as either ‘unmodified’ or ‘modified’ (after Clayton et al. 2006). Clayton et al. (2006) used a combination of satellite data and on-site assessments to classify wetlands as either modified or unmodified. Modified wetlands were those that were subject to identifiable and direct local hydrological modifications as a result of agriculture; these included weirs, dams, levees and pumps for water extraction (Clayton et al. 2006). In contrast, un-modified wetlands were those not subject to any identifiable and direct local hydrological modifications by agricultural activities (Clayton et al. 2006) (i.e. they are still potentially affected by broader landscape scale land use and hydrological changes but not by more local modifications, such as pumping). Of the 251 wetlands examined in this study, 109 (43%) were classified as modified and 142 (57%) unmodified.

3.2.2 Wetland inundation frequency

Following wetland selection, the QDWB (2005) dataset was utilised to derive hydrological metrics for each wetland. This dataset provided a yearly snap-shot of hydrological conditions (a binary representation of whether the wetland was inundated or non-inundated) from annual Landsat 5 satellite imagery for the period 1987-2005 (Appendix A1). Each wetland was classified as inundated or non-inundated for each year between 1987 and 2005 on the basis of this satellite imagery. As the data represents a single scene per year, the temporal resolution of the data is limited and as such, excludes any in depth intra-annual analysis. However, despite the limited temporal resolution within years, the spatial spread of the data and period of observation (1987-2005) provides a relative indication of hydrological conditions at wetlands, and hence, reasonable approximation of broad differences in hydrology between modified and unmodified wetlands.

The frequency of years each wetland was classified as inundated was calculated as a percentage, giving an indication of the time inundated (hereafter referred to as ‘inundation frequency’). For example, in Figure 3.2a, the wetland is inundated (wet) 7 out of 19 years and so has an inundation frequency of 37%; whereas, in Figure 3.2b, the wetland is inundated 14 out of 19 years and so, has an inundation frequency of 68%. Calculating wetland hydrology metrics in such a way provides a consistent metric for comparing wetland hydrology across different time periods.

In the Dalby and Warwick sub-regions, six and five scenes were missing, respectively. For these sub-regions years with missing scenes were excluded and only years with available data were used to calculate the inundation frequency (Appendix A2).

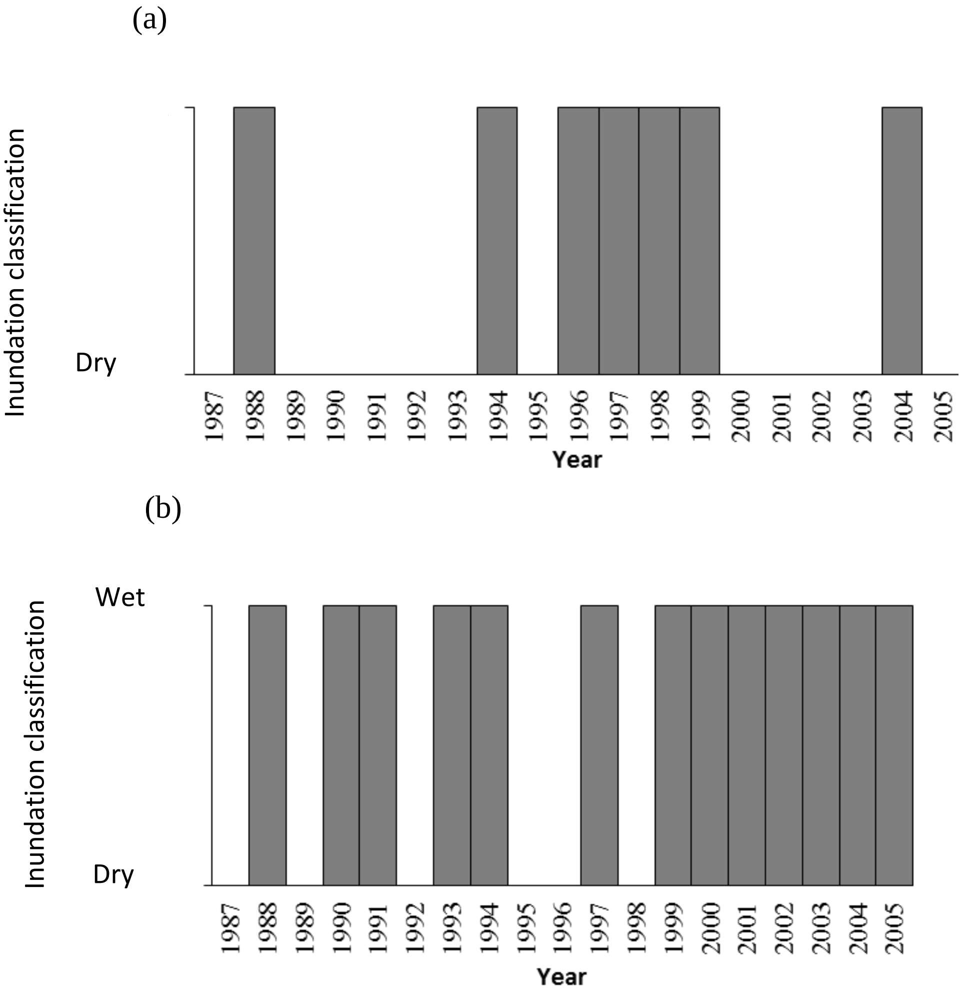


Figure 3.2 Examples of different inundation frequencies for individual wetlands (a - site 7 wetland ID# 279) & (b – site 112 wetland ID# 1736) from the Chinchilla and Dalby sub-regions respectively, 1987-2005 (Appendix A1). Data represent yearly classification of wetland inundation. In (a), wetland inundation frequency is 37%; whereas in (b), inundation frequency is 68%.

3.2.3 Developing landscape hydrological metrics

A geographical information system (GIS) was used to quantify hydrological landscape metrics. Data on rainfall and groundwater depth were interpolated across all wetlands, while a digital elevation model (DEM) (accuracy ±10 m on 25m horizontal grid (McDougall et al. 2008) was used to calculate connectivity with the river network. Although, the metrics derived from this approach will not give an absolute value of hydrological conditions at each wetland, it is anticipated that they will provide a useful measure of relative hydrological conditions for comparing conditions over broad spatial scales (e.g. 24,000 km^2 of the Condamine Catchment in this study). The full range of hydrological metrics used is given in Table 3.1. A detailed description of the hydrological metrics is given below.

Table 3.1 Name and brief description of hydrological metrics used

Hydrological metric name	Description
Inundation frequency (%)	Percentage of time wetland was inundated
Rain volume (ML)	Long term mean rain volume, based on each wetlands catchment area.
Rainfall (mm)	Average rainfall (mm) from 1987 to 2005
Groundwater depth (m) 1987	Represents past groundwater depths
Groundwater depth (m) 2000	Pre-drought groundwater depths
Groundwater depth (m) 2005	Mid-drought groundwater depths
Catchment area (ha)	Catchment area of each wetland. Determined using DEM
Wetland area (ha)	Area of each wetland
River connectivity (m)	Connectivity between the riverine system and non-riverine wetlands.

Groundwater metrics

Groundwater depth for three different years (1987, 2000 & 2005) was derived from the Queensland Groundwater Database (Queensland Department Environment Resource Management 2009b). This database contains information on groundwater depths at approximately 20,000 bores throughout the Condamine Catchment. Data on groundwater depths were taken from different times throughout the year, depending on availability. In instances where groundwater levels varied within a year, the greatest depth from that year was selected.

The years 1987, 2000 and 2005 were selected from the available database as they corresponded with the range of years for which wetland inundation data was available and indicate groundwater levels under different environmental conditions. Groundwater levels in 1987 represented historical levels before extraction caused dramatic and consistent declines in the area (Chapter 2; CSIRO 2008). Groundwater levels in the year 2000 represent conditions following a wet period and prior to drought, while 2005 groundwater levels provide an indication of prolonged drought conditions (Chapter 2, CSIRO 2008). Groundwater depth levels in 2009 were also available, however as they were strongly correlated (Pearson r = 0.89) (Appendix B1) with Groundwater depth in 2005 they were not used.

Measured groundwater depths at 694, 620 and 644 monitoring bores, respectively, for the years 1987, 2000 and 2005, were extracted and interpolated in Arc Map version 9.2 (ESRI 2006). Tests for clustering, using Moran's Index (MI) (Moran 1950), a statistic that measures the strength of spatial auto-correlation (Legendre and Fortin 1989), were completed preceding interpolation to ensure that the data were significantly clustered to allow interpolation. Groundwater depths were significantly clustered ($MI_{1987} = 0.15$; $MI_{2000} = 0.205$; $MI_{2005} = 0.16$; sig. <0.001), indicating strong positive spatial auto-correlation and hence, justifying interpolation (Legendre & Fortin 1989). The interpolated groundwater levels were overlayed with the selected wetlands for each year and the average depths calculated to give a metric which could be compared across modified and unmodified wetlands.

Rainfall & River connectivity

Variables relating to surface hydrological flows were derived using the Spatial Analyst tools in Arc Map version 9.2 (ESRI 2006). Measures of river connectivity and wetland catchment area were derived from a Queensland Department Resources and Water (QNRW) Digital Elevation Model (DEM) (2005). McDougall et al. (2008) found that the DEM for the Condamine Catchment had ±10m accuracy at a 90% confidence level, varying depending on slope and land utilisation characteristics. Wetland-river connectivity (hereafter referred to as ‘river connectivity’) and catchment area were quantified for each wetland using the DEM and the hydrology Spatial Analyst extension for Arc Map (ESRI 2006). Connectivity between the main river channel and non-riverine wetlands was derived using a digital elevation model (DEM) and the Path Distance function in Arc Map version 9.2 (ESRI 2006). Similar approaches, using distance from the main channel and elevation data have been utilised for modelling floodplain tree species in other landscapes (e.g. Turner et al. 2004).

Although this method for calculating river connectivity does not take into consideration commence to flow values or thresholds at which each wetland will fill, this is still considered a reasonable index, as it provides a simple, consistent and relative measure for comparing the influence of stream flow on wetlands throughout the region. More sophisticated analysis for determining commence to flow values requires precise on-site morphological data, such as stage heights, backwater curves, flow impedances and roughness coefficients (Overton 2005). These were unable to be collected due to the large number and broad spatial spread of wetlands and the low resolution of the DEM for the area. Consequently, while the methods used are relatively simple measures of river connectivity, they provide a useful means for comparing the influence of different hydrological inputs on floodplain wetlands across large areas, in this instance over the entire Condamine Catchment.

The mean annual rainfall for each wetland was calculated using Australian Bureau of Meteorology mean annual rainfall data (2009) from 1987 to 2005 and the Data Visualisation and Analysis software FERRET version 6.02 (Hankin et al. 1996).

FERRET provides a gridded interpolated output of rainfall data of the selected area in 25 x 25km grid output, which can be converted in Arc Map into a raster layer so that values specific to each wetland can be derived. The interpolated rainfall average for each wetland for each time period was then multiplied by each wetlands catchment area, to give rain volume (ML).

3.2.4 Hydrological characteristics of modified and unmodified wetlands

Analysis of variance (ANOVA) was used to compare differences in hydrological metrics (inundation frequency, groundwater depth, rainfall, catchment area, rain volume, wetland area and river connectivity) between modified and unmodified wetlands. Sub-region was also included as a factor in the analysis to account for spatial and temporal differences in scene capture. ANOVAs comparing modified and unmodified wetlands were carried out separately within sub-regions when there were differences between sub-regions were indicated or where there was a significant interaction between main effects. Inundation frequency was arc-sine transformed to correct for bounded data and non-normality (Ahrens et al. 1990). Data for groundwater depth, rain volume, river connectivity was log and/or square root transformed to fulfil normality and equality of variance assumptions for the ANOVA (Quinn and Keogh 2000). Prior to analysis, Bartlett’s test was used to test for equality of variance (Lim and Loh 1996). Based on Bartlett’s test, hydrological metrics that did not exhibit equality of variance were omitted from analyses. All analysis were performed in R version 2.10.1 (R Development Core Team, 2009) using the Biodiversity R package (Kindt 2009).

3.3 Results

Groundwater depth was excluded from ANOVA analysis due to unequal variances (Appendix A3). Inundation frequency differed significantly between modified and unmodified wetlands with means of 54 % and 43 %, respectively (Table 3.1; Figure 3.3a). Modified and unmodified wetlands were only significantly different within the Chinchilla sub-region (Table 3.2).

Rain volume and river connectivity differed significantly between modified and unmodified wetlands (Table 3.1). Modified wetlands had greater mean rain volume than unmodified ones, with approximately 2700 and 500 ML per annum respectively (Figure 3.3b). Catchment area also differed significantly between modified and unmodified wetlands, with modified wetlands being on average 300 ha larger (Table 3.1; Figure 3.3e). Modified wetlands had higher mean levels of river connectivity, being on average 150 m from the riverine network compared to 230 m for unmodified wetlands (Figure 3.3c). Neither rain volume nor river connectivity varied significantly between sub-regions (Table 3.1; Figure 3.3b & c). Rainfall and wetland area differed significantly between sub-regions, but not between modified and unmodified wetlands (Table 3.1; Figure 3.3d & f).

Table 3.2 ANOVA results for each hydrological metric in relation to the factors sub-region and modification and an interaction between them.

Hydrological metric	Factor	F-value
Inundation frequency (%)	Sub-region	5.00**
	Modification	5.88*
	Sub-region*Modification	3.18*
Rain volume (ML)	Sub-region	1.15
	Modification	14.01***
	Sub-region*Modification	0.71
Rainfall (mm)	Sub-region	7.64***
	Modification	2.15
	Sub-region*Modification	0.90
Catchment area (ha)	Sub-region	0.83
	Modification	14.39***
	Sub-region*Modification	0.59
Wetland area (ha)	Sub-region	7.27***
	Modification	1.72
	Sub-region*Modification	0.96
River connectivity (m)	Sub-region	1.97
	Modification	12.06***
	Sub-region*Modification	2.74

Degrees of freedom = 245; *p <0.05; **p<0.01; ***p<0.001.

Table 3.3 ANOVA results for differences in inundation frequency between modified and unmodified wetlands within sub-regions.

Sub-region	Degrees of freedom	F-value
Chinchilla	103	11.07**
Dalby	73	0.24
Warwick	69	3.10

*p <0.05; **p<0.01; ***p<0.001.

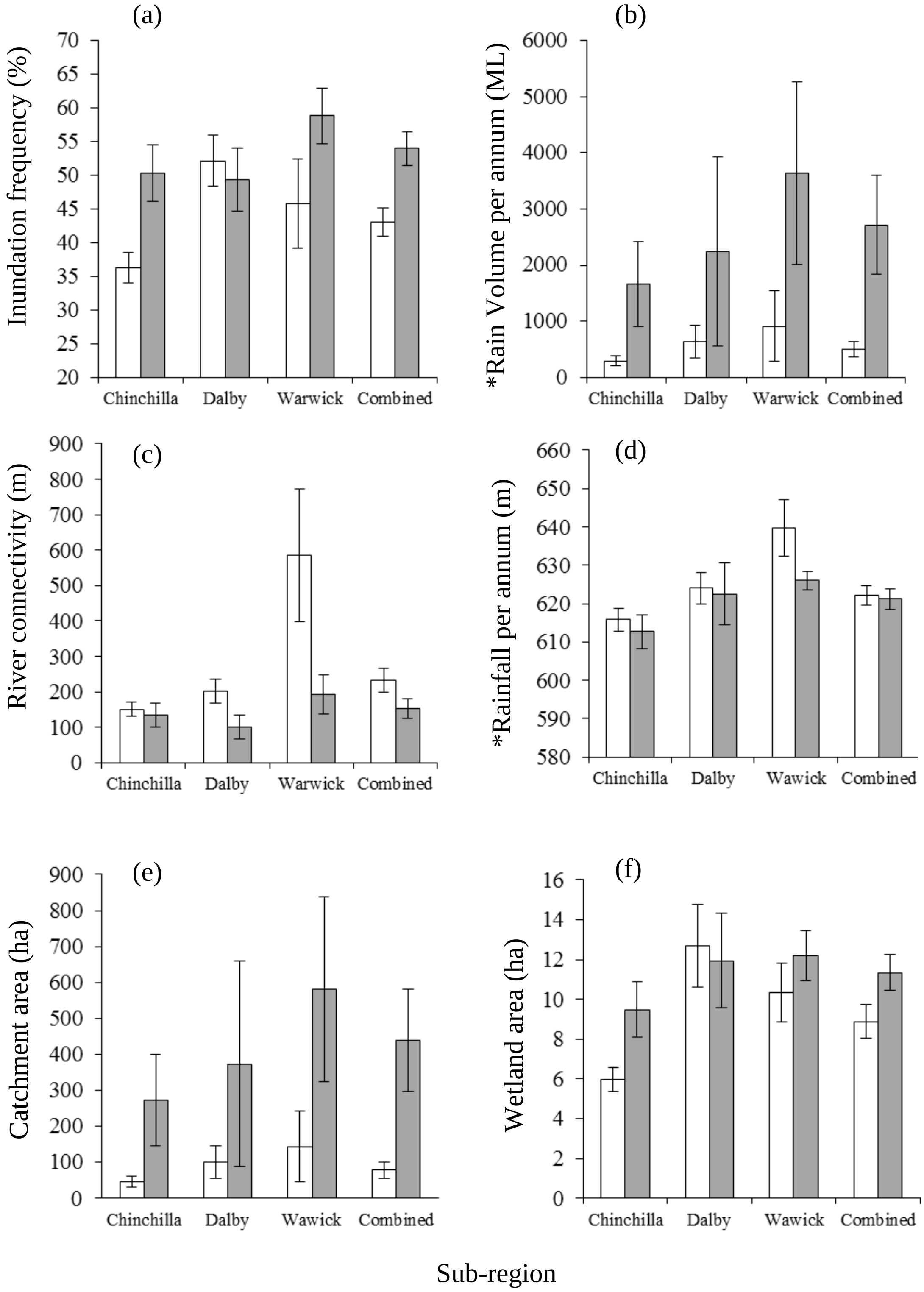


Figure 3.3 Mean (a) inundation frequency (b) rain volume (c) river connectivity (d) rainfall (e) catchment area and (f) wetland area for unmodified (white) and modified (grey) wetlands in each sub-region and for all wetlands combined. * Mean rainfall and rain volume from 1987 to 2005.

3.4 Discussion

3.4.1 Modified and unmodified wetlands

Modified wetlands are becoming increasingly prevalent in agricultural landscapes and may become more so in the future to help increase water supply security (Brock et al. 1999; Nielsen and Brock 2009). However, in many landscapes, there is little data on the hydrology of wetlands, let alone on how modified and unmodified wetlands may differ. The results of this study showed that unmodified and modified wetlands were both similar and different in a number of hydrological characteristics. Modified and unmodified wetlands had similar mean inundation frequencies, except in the Chinchilla sub-region. Modifed and undmodifed wetlands were also on average a similar area and in areas that received similar amounts of rainfall. However, compared to unmodified wetlands, modified wetlands did receive significantly higher mean rain volume, as a result of larger catchment areas, and were also closer to the riverine network (i.e. higher river connectivity).

3.4.2 Wetland inundation frequency

Previous research comparing modified and unmodified wetlands is rare. Although, in the Border Rivers Catchment in Queensland, Australia, Lutton et al. (2010) showed that modified wetlands are larger, deeper and have greater water holding capacity than natural unmodified wetlands. However, unlike the current study, Lutton et al. (2010) did not have inundation frequency data. In contrast, the current study did not have data on wetland morphology (e.g. depth) and so could not calculate water holding capacity. Nonetheless, the results of the two studies fit cogently, as significantly higher inundation frequencies would be expected to be facilitated by modified wetlands with greater water holding capacity. Others have proposed that modified wetlands are likely to be more permanently inundated compared to natural unmodified ones (Kingsford 2000; Neilsen and Brock 2009). The results of this study also suggest that relative to unmodified wetlands, modified wetlands may be inundated more frequently.

However, in this study, differences in inundation frequency between modified and unmodified wetlands were only evident in the Chinchilla sub-region. Differences in environmental characteristics, particularly land use, between the sub-regions may help explain these dissimilarities. The Dalby and Warwick sub-regions are more agriculturally intense with irrigated land covering approximately 9-10% of the land surface, compared to only 2% in the Chinchilla sub-region (Queensland Department of Environment and Resource Management 2005). Vegetation clearing has also been much higher in the Dalby and Warwick sub-regions: where only ~20% of native remnant vegetation remains, compared to 46% in the Chinchilla sub-region (Queensland Department of Environment and Resource Management 2005). In more agriculturally intensive areas, there is likely to have been changes to hydrological processes, which may influence wetland inundation frequency, such as increases in run-off (e.g. Thornton et al. 2007). As a consequence of being embedded within a more agriculturally intense sub-region, modified and unmodified wetlands within the Dalby and Warwick may be inundated more frequently and hence, be more similar to their modified counterparts. Although, data on temporal land use changes is needed before conclusions about differences in inundation frequency between modified and unmodified wetlands can be attributed to this.

3.4.3 Hydrological differences between modified and unmodified wetlands

While differences in inundation frequency were not evident between modified and unmodified wetlands, there were differences in river connectivity and rain volume (catchment area). Unmodified wetlands were on average less connected and received less overland flows (i.e. rain volume) per annum. In the Borders River catchment, Australia, Lutton et al. (2010) also showed that modified wetlands were significantly closer to the river than unmodified natural wetlands, with mean distances of 6.2 km and 11.1 km, respectively. In contrast, Daniels and Cummings (2008) observed along the Tempisque River Catchment of north western Costa Rica, that areas of higher elevation, further from the riverine network, had the greatest proportions of wetland conversion, while those in the lower lying wetter areas were more likely to remain natural.

The conflicting results between the current study and Lutton et al. (2010) with Daniel and Cummings (2008) may result from interactions between topographical influences and broader scale hydro-climatic factors. For example, in Costa Rica where wetland conversion was more frequent in higher elevation areas, mean annual rainfall is 1817 mm. In contrast, mean annual rainfall in the Condamine Catchment is much lower, at around 680 mm, while for the wetlands examined in Lutton et al. (2010) in the Borders River catchment, mean annual rainfall is 500 mm. Consequently, in contrast to the higher rainfall area of Costa Rica where water is likely more abundant, modification of wetlands in the more water limited Condamine Catchment may occur closer to the river to gain better access to water.

Daniels and Cummings (2008) also concluded that topography was an important predictor of wetland conversion, as it determined accessibility and suitability for human land use. Lutton et al. (2010) similarly argued that modified (storage) wetlands were built closer to the river to minimise the distance water had to be pumped. In more temperate Canada, the distribution of modified prairie wetlands is also thought to vary depending on topography and soils (Austin et al. 2003). Similarly, the findings of this study, showing that modified wetlands are closer to the river network and have larger catchment areas, suggest preferential development of wetlands which are of more hydrological utility for agriculture. However, as time of wetland modification and their specific utility for agriculture was not assessed, future research is needed to test this.

3.4.4 Significance and implications

This study indicates that wetland modification is not random throughout the floodplain and as a consequence, remaining unmodified wetlands are less connected to the riverine network and receive less overland flows (rain volume). These differences in hydrological characteristics could have significant ecological implications. Firstly, as unmodified wetlands received significantly less rain volume per annum than modified wetlands, it suggests that these wetlands are more water limited and less likely to be inundated by overland flows. Alterations in the relationships with landscape hydrology may change how wetlands are affected by future droughts and climate change.

Burkett and Kusler (2000) argue that wetlands dependent primarily on precipitation for their hydrological inputs are the most vulnerable to climate change. Similarly, Roshier et al. (2001) also suggest that the impacts of climatic changes that result in a drying or reduction in flood events, coupled with water extraction for agriculture, could be particularly detrimental for wetland ecosystems dependent on heavy rainfall events. If receiving lower rain volume from smaller catchment areas leads to a reduction in hydrological inputs this could exacerbate the ecological consequences of drought and overland flow extractions and diversions (Bond et al. 2008) for natural unmodified wetlands.

Secondly, relative to modified wetlands, unmodified wetlands were less connected to the riverine network. River connectivity is a fundamental aspect of floodplain ecology and its importance has been highlighted by various authors, including its importance for facilitating dispersion, transfer of organic matter and species diversity (Pringle 2001; Jenkins and Boulton 2003; Thoms 2003; Leyer, 2006; Cook and Hauer 2007; Vercoutere et al. 2007; Gallardo et al. 2008). As such, differences in connectivity between rivers and floodplains that result from river regulation structures (e.g. dykes, weirs, damns etc.) may have more significant implications for remaining ‘natural’ unmodified wetlands that are on average less connected to the riverine network.

Figure 3.4 schematically summaries the main hydrological differences between modified and unmodified wetlands in the production landscape of the Condamine Catchment, southern Queensland. Firstly, as a result of smaller catchment areas, unmodified wetlands tend to receive less rain volume and therefore may be more susceptible to drought and potentially to climate change (e.g. Burkett and Kusler 2000) ((1) in Figure 3.1)). In addition, unmodified wetlands further from the riverine network may experience lower flood frequency, and reduced species dispersion and exchange of organic matter, which all may have significant ecological implications ((2) in Figure 3.1) (e.g. Pringle 2001; Jenkins and Boulton 2003; Thoms 2003; Leyer, 2006; Cook and Hauer 2007; Vercoutere et al. 2007; Gallardo et al. 2008). Exploring what these differences mean for the biota wetlands will likely be important future step in understanding the ecological consequences of modifying wetlands in agricultural landscapes.

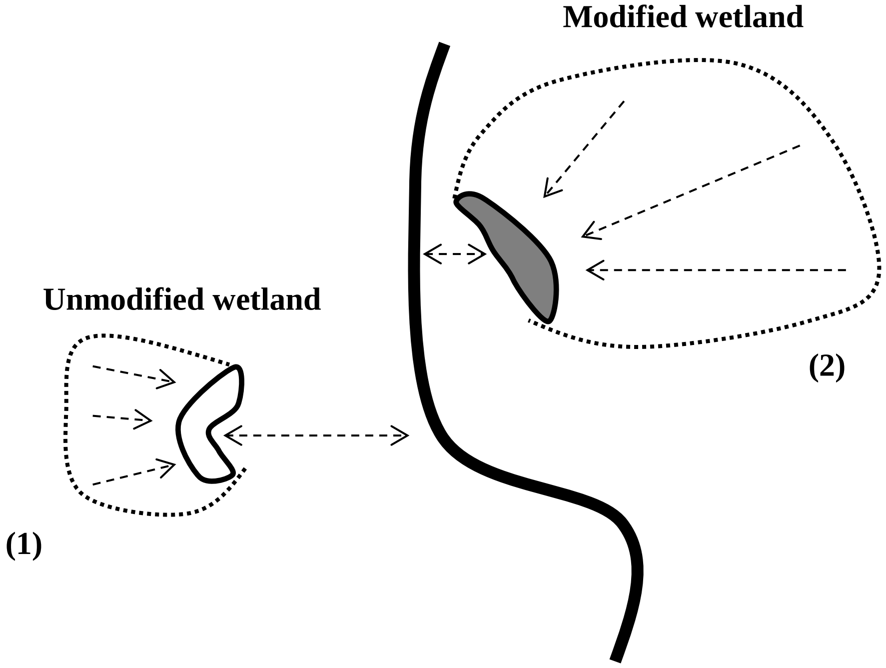


Figure 3.4 Diagrammatic summary of the dynamics of modified (shaded) and unmodified (unshaded) wetlands in the production landscape of the Condamine Catchment. Solid black line represents the river and the dotted line the wetland catchment. Dashed arrows indicate hydrological flows from overland flows within catchment and between the river and wetland. See text for explanation of characteristics and significance at (1) and (2).

3.4.5 Limitations and future directions

While this study showed significant hydrological differences between modified and unmodified wetlands, it was limited to only a few indices of wetland hydrology. For example, it did not take into account that modifications are also likely to make wetlands less suitable as a consequence of other hydrological changes (e.g. altered duration and depth of inundation Casanova and Brock (2000)), non-hydrological factors (e.g. pollution, McCormick and Laing (2003)), and morphological changes (e.g. deepening, Lutton et al. (2010)). Furthermore, the current research was restricted to a simple classification of wetlands as modified or unmodified and thus, failed to distinguish between the variety of ways in which these wetlands may be modified (e.g. pumps, weirs, morphological etc.).

The inundation frequency data used here, although covering broad spatial and temporal scales, was based on one snapshot per year and hence, precludes investigations into the intra-annual effects of wetland modification on hydrology. As such, intra-annual relationships with the duration, frequency and variability of inundation could not be quantified. Hydrologically, intra-annual variability in duration, timing, frequency and other aspects of the wetland water regime are all known to be important for the ecology of wetlands (Toner and Keddy 1997; Leck and Brock 2000; Pettit and Froend 2001; Warwick and Brock 2003; Capon and Brock 2006). However, even though these factors could not be investigated here, the extensive spatial and temporal coverage of available data was still useful for examining long term patterns in inundation frequency which is often unable to be examined in smaller spatial and temporal scale studies.

The ecological relevance of the wetland inundation data and landscape scale hydrological metrics developed needs to be tested before the ecological implications of differences between modified and unmodified wetlands can be more fully appreciated. The results of this study suggest that unmodified wetlands are potentially the most at threat from hydrological alterations, because they are on average, less connected to the riverine network and receive less water from overland catchment flows (rain volume). Consequently, from the standpoint of floodplain wetland conservation in agricultural landscapes, this may mean that the most ecologically intact wetlands are also those most threatened by the consequences of water resource development. As such, understanding how they relate to hydrological and land use factors may be of a greater priority for biodiversity conservation amongst remaining wetlands. Ideally, a full examination of the biota of both modified and unmodified wetlands would be carried out to investigate the consequences of these hydrological differences on wetland ecology. However, due to resource limitations this is not feasible, and as such the following chapters (4-6) will focus on unmodified wetlands to identify how they are affected by hydrological and land use factors in this agriculturally altered floodplain landscape.

3.5 Conclusion

The impacts of flow regulation and extraction on wetland hydrology are well known; however, in agricultural landscapes, there are often additional, smaller scale modifications to wetlands which may also alter their hydrology. To help address this knowledge gap, this study compared modified and unmodified wetlands in an agricultural landscape. Modified wetlands were on average, inundated more frequently, better connected to the river and received more rain volume per annum. It is concluded that ‘natural’ unmodified and modified wetlands represented significantly different systems in terms of hydrology. In the future, investigations into how the hydrological factors that differ between modified and unmodified wetlands influence species and ecological functioning will be an important step for improving understanding about the ecological conservation of floodplain wetlands

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Chapter 4. Hydrological and land use determinants of wetland tree condition in an agricultural landscape.

4.1 Introduction

In agricultural landscapes, changes to hydrology and land use have caused widespread loss and degradation of wetland ecosystems (Chapter 1; Zedler 2003; Vorosmarty et al. 2010). Tree dieback, a condition typified by rapid defoliation and progressive stem mortality (*sensu* Landsberg and Wylie 1983), exemplifies this degradation in river-floodplain and wetland ecosystems. Currently, research attributes hydrology and specifically, the influence of the wetland water regime, as the key driver of vegetation in wetlands (e.g. Toner and Keddy 1997; Capon 2003; Warwick and Brock 2003; Brooks 2005; van der Valk 2005; Capon and Brock 2006; Raulings et al. 2010). In a more general sense, it has also been argued that hydrology is a 'master variable' which controls the ecology of river-floodplain landscapes (Walker et al. 1995; Bunn and Arthington 2002; Lytle and Merritt 2004; Leigh et al. 2010). However, whether hydrological factors alone are suitable for explaining floodplain wetland degradation and declines in tree condition has rarely been tested. This chapter tests the premise that an exclusively hydrological perspective is suitable for understanding the tree condition of wetlands in an agricultural landscape.

4.1.1 Hydrology and tree condition

In concordance with a premise that a hydrological perspective is suitable for understanding wetland ecosystems, the water regime (defined as the timing, frequency, duration, variability, extent and depth of all hydrological inputs and outputs; *sensu* Mitsch and Gosselink 2000) has been shown to be a key determinant of the condition and composition of wetland vegetation species (e.g. Denton and Ganf 1994; Keeland and Sharitz 1997; Keeland et al. 1997; Keeland and Conner 1999; Ernst and Brooks 2003; Klein et al. 2005; Raulings et al 2010). In Bool Lagoon, South Australia, changed water regime conditions from increased inundation, increased juvenile *Melaleuca halmaturorum* mortality (Denton and Ganf

1994). In the Kenai Lowlands of south-central, Alaska, shifts towards dryer water regimes have caused changes in vegetation communities, with wetland species (i.e., *Carex lasiocarpa* and *Ledum palustre*) being replaced by upland forest species (e.g. *Rubus idaeus* and *Vaccinium vitis-idea*) better adapted to dryer conditions (Klein et al. 2005).

In addition to changes to wetland water regime in agricultural landscapes, broader hydrological changes to stream flows and groundwater may also be strong determinants of vegetation condition. In riparian and floodplain environments, much research has documented the impacts of water extraction and regulation on tree condition (e.g. Taylor et al. 1996; Benger 1997; O'Connor 2001; Horton et al. 2001; Stromberg 2001; Cooper et al. 2003; Rood et al. 2003b; Jones et al. 2006). For example, along the South Platte River, Colorado, United States, short-term declines in groundwater were linked with decreased shoot water potential, leaf mortality and branch dieback in *Populus deltoides* (Cooper et al. 2003). While studies have highlighted how water extraction and regulation cause changes to wetland vegetation community composition (e.g. Roberts and Ludwig 1991; Walker and Thoms 1993; Hudon 1997, Toner and Keddy 1997; Bunn and Arthington 2002), few have explicitly examined its impact on tree condition in smaller floodplain wetlands of agricultural landscapes (but see Bacon 1996). Bacon (1996) highlighted the importance of water supply and quality as key determinants of *E. camaldulensis* condition in the Macquarie Marshes of New South Wales. However, there are no similar studies focused on smaller floodplain wetlands in agricultural landscapes.

Hydrological influences on wetland vegetation may also be influenced by local scale site conditions, such as, increased insect attack and light, nutrient and water availability (Peet and Christensen 1987; Landsberg 1990; Kim et al. 1995; Davis et al. 1998). Vegetation structure may vary substantially at local scales and influence factors, such as water availability, which affect tree condition (Davis et al. 1998). For example, tree canopy cover may affect local microclimatic conditions and decrease soil evaporation and thus, increase water availability at the local scale (Ovalle and Avendano 1988; Caylor et al. 2005). This may be especially important for young trees in dry conditions (Davis et al. 1998). Alternatively, increased tree canopy cover may also increase evapotranspiration and precipitation interception and thus, decrease local water availability (Bréda et al. 1995; Raz-Yaseef et al. 2010). Despite the potential influence of local vegetation structure on water availability, no studies have examined its relationship with tree condition in wetland environments.

4.1.2 Land use and tree condition

Challenging the proposition that hydrology is the only driver of wetland condition, other studies have suggested that land use factors may also be important for understanding floodplain (Turner et al. 2004), riparian (Meeson et al. 2002) and wetland ecosystems (Ogden 2000). In the terrestrial components of production landscapes, changed land use cover (Fensham and Holman 1999; Reid and Landsberg 1999), livestock grazing (Davidson et al. 2007) and increased nutrient levels and insect attack (Landsberg 1990) have all been related to tree dieback. For example, in Australian agricultural landscapes insect outbreaks associated with changes in soils from chemical use have been linked with the 'dieback' of eucalypts (Landsberg 1990). At the local wetland scale, land use practices, such as grazing, may also influence tree condition (Davidson et al. 2007). Close et al. (2008) noted that increased levels of foliar nitrogen and phosphorus, associated with increased grazing intensity, were correlated with poor tree health in *Eucalyptus* woodlands of north-eastern Tasmania. However, the role that land use factors play in determining wetland tree condition and whether they need to be considered in conjunction with hydrological factors remains untested.

4.1.3 **E. camaldulensis** *condition in agricultural landscapes*

As a consequence of its wide extent and dominance, *E. camaldulensis* is an ideal species for examining the importance of hydrological and land use factors on wetland tree condition in agricultural landscapes. Previous studies that have examined *E. camaldulensis* condition have linked hydrology, and specifically, flooding and the impacts of river regulation, to declines in condition (e.g. Bren 1988; Bacon et al. 1993; Briggs and Thorton 1999; Cunningham et al. 2011; Steinfled and Kingsford 2011). Along reaches of the Murray-Darling River, changes to the hydrological nature of the system have been associated with the major deterioration of riparian forest, often dominated by *E. camaldulensis* (Bacon et al. 1993). Roberts and Marston (2000) state that established *E. camaldulensis* trees are highly dependent on the frequency and duration of flooding, the duration of the inter-flood period (or dry period) and the variability of these two factors. In Yanga National Park, Australia, Wen et al. (2009) observed that *E. camaldulensis* communities without direct access to stream water require overbank floods to maintain crown condition. In the Macquarie Marshes, New South Wales, Australia, low water availability was associated with poor condition stands of *E. camaldulensis* (Bacon 1996). However, while these studies illustrate will the importance of hydrology, they have not explicitly considered the additional impacts of land use factors as determinants of *E. camaldulensis* condition in floodplain wetlands.

In the Condamine Catchment, south east Queensland, Australia, the dominant *E. camaldulensis* vegetation of the agriculturally altered floodplains exhibits extensive dieback (Reardon-Smith 2011). As with other agricultural landscapes throughout the world, a range of factors, including hydrological, land use and biotic agents, have been associated with dieback and general declines in vegetation condition in the area (Voller 1996; Murray Darling Basin Commission 2005; Reardon-Smith 2011). However, no published studies have been able to attribute this decline to any specific factors, although salinity, psyllids (insect attack) and herbivory have been investigated and no significant link with these factors identified (Voller 1996). Recent work on riparian woodlands along the Condamine River have shown that the highest levels of tree dieback occur in the areas of the floodplain most significantly impacted by floodplain development and hydrological changes, particularly in relation to groundwater declines (Reardon-Smith 2011). To date, there has also been no investigation into the causes of dieback in *E. camaldulensis* dominated non-flowing wetlands of the Condamine Catchment.

To help address these knowledge gaps, this study examined the question as to whether a combination of hydrological and land use factors better explained tree decline (as measured by crown vigour of *E. camaldulensis* and stag abundance of all trees) than hydrological factors alone in the floodplain wetlands of the Condamine Catchment. The hydrological and land use factors chosen represent a suite of factors commonly linked to tree decline, not only in the study area, but in aquatic ecosystems in agricultural landscapes worldwide. The hydrological and land use variables selected cover a range of spatial and temporal scales, both local (e.g. grazing and inundation frequency) and landscape (e.g. agricultural land cover and river connectivity). Ideally, detailed data on all factors at all these scales would be used, however due to the resource intensive nature of collecting data at various different scales this is not possible. Furthermore, given the long lived nature of E. camaldulensis long term data would also be desirable. Nonetheless, the selection of different land use and hydrological variables at different scales is still likely to provide important insights about the focus of this study, namely testing the importance of both hydrological and land use factors.

4.2 Methods

4.2.1 Site selection

The 2008 Queensland Environmental Protection Agency (EPA) Wetland Mapping Version 1.2 (QEPA, 2008) and 2005 Department of Natural Resource and Water (DNRW) Queensland Dams and Water Body (QDWB) (DNRW 2005) datasets were used to select wetlands. Selection was restricted to small (< 50ha) non-flowing water bodies, as they are dominant and prevalent hydrological feature in the landscape present across a range of hydrological and land use conditions, making them ideal for comparing the importance of hydrology and land use.

Site selection was limited to unmodified wetlands (Chapter 3) as modified wetlands are predominantly devoid of fringing vegetation, making it difficult to assess tree condition over the range of hydrological and land use conditions present in the catchment. Following the identification of accessible unmodified wetlands, a subset of those best representing the range of hydrological and land use conditions present in the catchments floodplain were selected. Randomised selection of sites was not feasible: firstly, the number of accessible wetlands was limited (<60); and secondly, most accessible wetlands were located on private property and hence, permission (which was not always granted) for access was required. A total of 37 wetlands were selected for vegetation surveys (Figure 4.1).

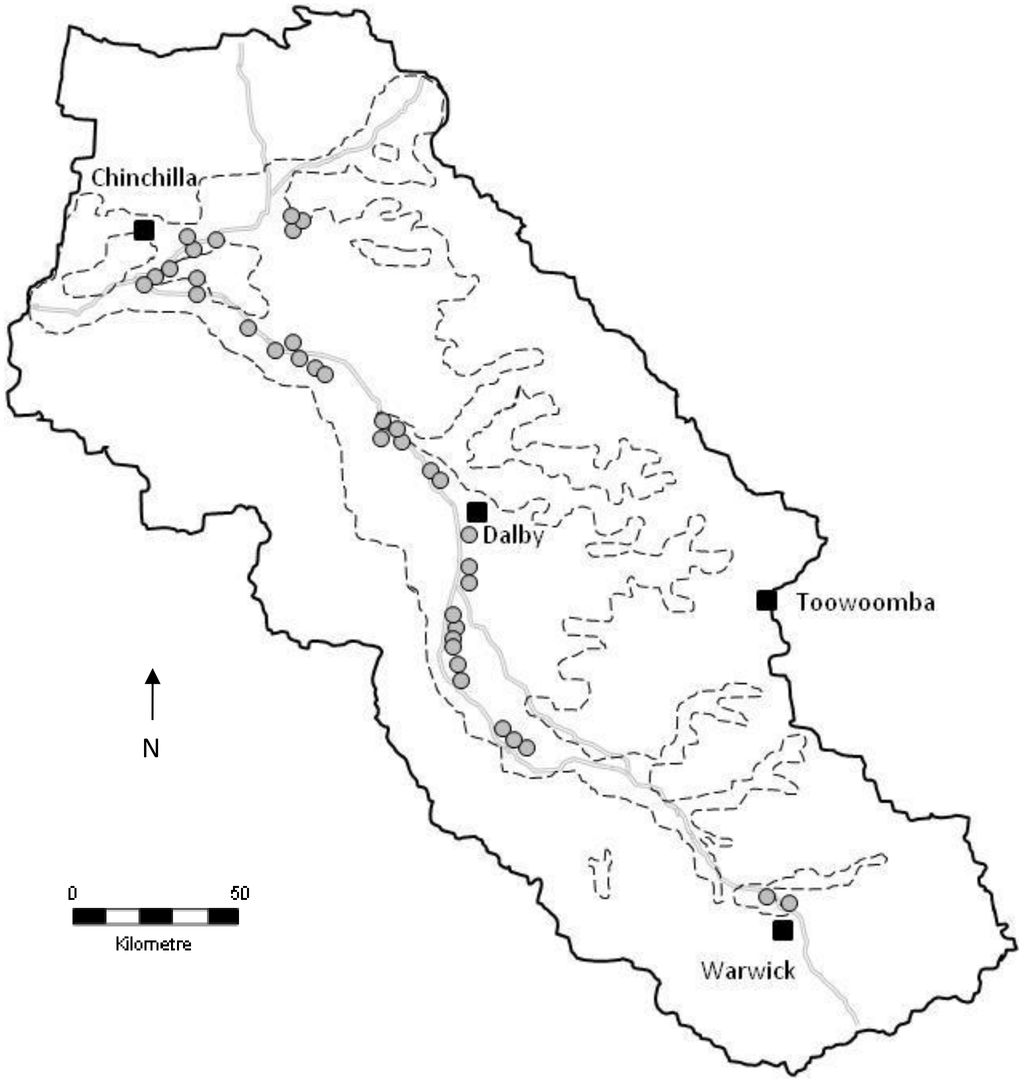


Figure 4.1 The location of wetlands surveyed in 2009 (n=37) (●). The alluvial floodplain throughout the catchment (---) and main river channel (—) is also shown.

4.2.2 Vegetation surveys

Fringing woody vegetation was surveyed at 37 floodplain wetlands across the Condamine Catchment in 2009. Most wetlands were in the Chinchilla (n=18) and Dalby (n=14) sub-regions, with only 5 wetlands were within the Warwick sub-region. The cover, condition and density of woody vegetation was assessed in three 150m^2 (5m x 30m) belt transects subjectively located around the perimeter of the wetland to enable the range of fringing vegetation variation to be sampled. A randomised placement of transects was not suitable due to the sparse vegetation coverage at many wetlands, often a result of selective clearing from agriculture. The 5 x 30m belt transect was chosen as remaining fringing vegetation patches were often <10m in width and often in sparse patches of around 30m length. The sparse cover of vegetation also meant that vegetation surveys on the understorey (e.g. shrubs and herbs) was often not possible and as such surveys were focused on tree species.

Tree crown vigour was used as indicator of tree condition at surveyed wetlands. Cunningham et al. (2007) assessed various measures of stand condition of *E. camaldulensis* and found that crown vigour was one of the best indicators of stand condition. Other indicators of tree condition, such as epicormic growth, leaf damage, water potential and chlorophyll fluorescence, were less reliable and showed little difference between sites of good and poor condition (Cunningham et al. 2007). In contrast, crown vigour provided a consistent and simple measure of tree condition that was responsive to changes in environmental conditions (Cunningham et al. 2007).

Within each transect, all trees were assigned to one of 6 different size classes (<10, 10-20, 20-50, 50-75 and >75cm circumference at breast height (cbh)). These were reclassified for analysis into three size classes reflecting three broad size classes (small trees: <20cm cbh; medium trees: 20-50cm cbh; and large trees: >50cm cbh). Preliminary analysis show no patterns when size classes were analysed together so analysis were carried in different size classes to account for any influence that tree size may have on relationships with the environmental factors tested (Dawson and Ehleringer 1991).

The crown vigour of each tree was assessed subjectively by visual estimation of the percentage of the potential crown containing foliage using a six level classification scheme (adapted from Cunningham et al. 2007; Figure 4.2). The score for each assessed tree was averaged to give average crown vigour at each wetland.

In addition to crown vigour, stag abundance (density of all standing tree stags (i.e. dead trees) within the 150m^2 quadrat) was also measured within each transect. Although not reflecting tree condition *per se* as time since tree death could not be calculated, stag abundance was assessed as it provided a metric which is likely less reflective of shorter term conditions than crown vigour and as such may give an indication of longer term impacts on wetlands. Stag abundance was also assessed and analysed within the same classes as crown vigour.

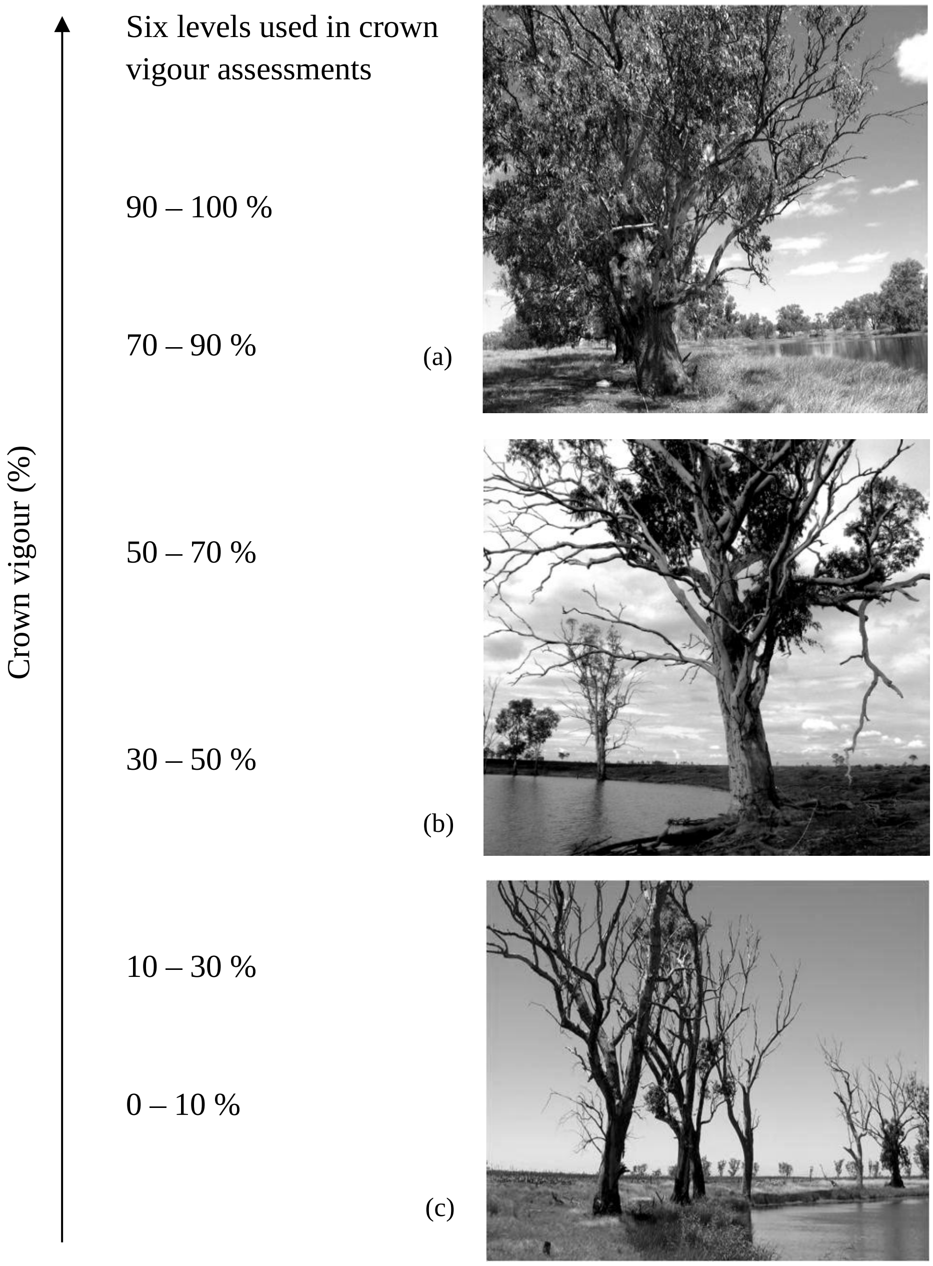


Figure 4.2 Representation of score system used to classify crown vigour as a measure of tree condition. The crown vigour of each tree was assessed (using the six level classification scheme) and averaged to give a mean value of crown vigour for each wetland. Mean crown vigour of trees in example photographs is (a) ~85%, (b) ~35% and (c) ~5%.

4.2.3 Hydrological and land use explanatory factors

Hydrological and land use data for each wetland was derived using Arc View 9.2 (ESRI 2006; Table 4.1). The survey procedure for each wetland is represented diagrammatically in Figure 4.3. Hydrological metrics, relating to river connectivity (connectivity, distance from weir), groundwater (groundwater depth) and rainfall (inundation frequency, rain volume) were calculated for each wetland utilising digital elevation models (to account for topographic influences) and interpolation procedures in Arc View 9.2 (ESRI 2006) (full hydrological methods given in Chapter 3). The impact of river regulation structures (weirs), were assessed by measuring the distance from the weir to each wetland (measured in Arc View 9.2 ESRI 2006). Weirs are small barriers across rivers, which pond water upstream to enable the extraction and diversion of water and as such effectively act as small dams (Kingsford 2000). It is acknowledged that weir impacts are likely to vary as size and extraction rates may differ. The simple metric distance from weir was selected to account for the broad impacts of weirs. More detailed information on each weir is unjustified, mainly due to the broad scale nature of the study which is focused on looking at a wide range of hydrological and land use factors and not so much focused on a detailed examination on any particular driver.

Land use factors, spatial extent of agriculture and remnant vegetation cover, were calculated as a percentage within the catchment of each wetland. These land use factors were not correlated and did not sum to 100% and so the contribution of each factor could be assessed individually (Allan 2004). Measures of grazing intensity and canopy cover were made on site within each vegetation transect. Measures of canopy cover were are an interrelated measure of larger tree crown vigour and so were only used in regressions for the smaller size classes. Although, canopy cover (>2m) measurements may have included some measures of crown vigour for the smaller size classes (<20cm cbh) the two were not correlated and as such were able to be used in multiple regression analysis together (Pearson $r = -0.15$, $df = 29$, $p = 0.40$). A description of each variable and quantification methods is given in Table 4.1.

Table 4.1 Description of hydrological and land use explanatory variables and their quantification methods.

Variables	Description	Analysis procedure and notes	Data Source
Inundation frequency (%)	Percentage of time wetland was inundated. Details Chapter 3	Inundation frequency data was not available at 4 sites. Details Chapter 3.	Queensland Dams and Water Body (QDWB) (DNRW 2005)
River connectivity (m)	Connectivity between the riverine system and non-riverine wetlands. Details Chapter 3	Derived using a DEM and the path distance function in Arc Map version 9.2 (ESRI, 2006). Details Chapter 3	Department Natural Resources and Water DEM 2005
Distance from weir (km)	Distance upstream (km) from a weir (river regulation structure).	Measured using Arc Map version 9.2 (ESRI, 2006)	Queensland Department Natural Resources and Water (2006)
Groundwater depth (m) 1987, 2000, 2005, 2009	Represents past (1987), pre-drought (2000), mid-drought (2005) and (2009) groundwater depths (m).	Interpolated groundwater depths from measurements made at bores throughout catchment. Details Chapter 3.	Queensland Department of Environment and Resource Management Groundwater data (2009)
Rain Volume (ML)	Long term mean rain volume, based on each wetlands catchment area.	Rainfall was used with catchment area values for each wetland to calculate rain volume (ML). $R_V = (L_R)(WC_A)$. Details Chapter 3	Australian Bureau of Meteorology (2009)
Canopy cover (%)	Canopy cover of trees > 2m high.	Estimated on site, measured as the total foliage projected cover of all vegetation > 2m in height within each transect. Mean values from three transects at each wetland were used for analysis.	On site assessment
Grazing intensity (cow pats per 150 m^2)	Measure of grazing intensity at wetland	Mean number of cow patties per 150 m^2 within the three vegetation transects (after Batterham, 2008)	On site assessment
Agriculture (%)	Represents a composite variable of irrigated, dryland and intense agricultural cover within each wetlands catchment.	Calculated as a proportion within each wetland's catchment area using Arc Map version 9.2 (ESRI, 2006).	Queensland government land use mapping data (Qld DERM 1999).
Remnant vegetation cover (%)	Percentage of remnant vegetation within each wetlands catchment.	Calculated as a proportion within each wetland's catchment area using Arc Map version 9.2 (ESRI, 2006).	Queensland Herbarium mapping data (Qld DERM 2005).

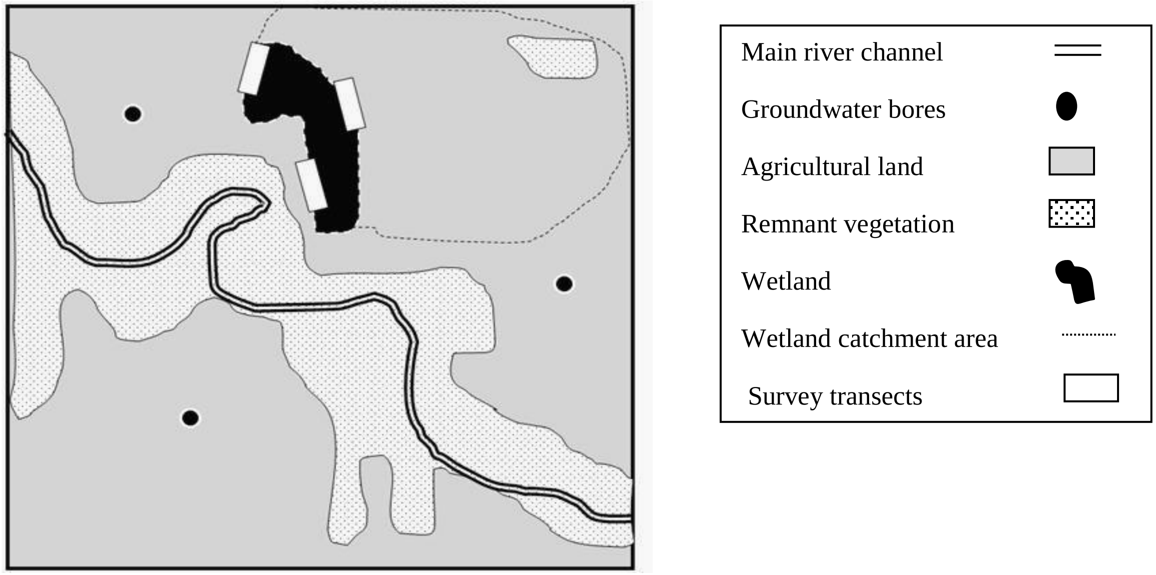


Figure 4.3 Representation of the vegetation sampling procedure and spatial distribution of landscape factors. Detailed vegetation assessments were undertaken in linear (5 x 30m) transects at three locations around the perimeter of each wetland.

4.2.4 E. camaldulensis *response to hydrology and land use*

Crown vigour was modelled using generalized linear models (GLMs; Kindt and Coe 2005). Only *E. camaldulensis* was modelled, as there were insufficient individuals of other surveyed tree species (Table 4.2). Stag abundance included all dead tree species surveyed. Crown vigour and stag abundance were modelled against each selected environmental variable (as continuous data) using both simple (single factor) and multiple (step-wise), regression to produce a ‘best model’. The significance and parsimony of the best model was evaluated using Akaike's information criterion (AIC) (Bozdogan 1987; Kindt and Coe 2005).

Initial models for crown vigour and stag abundance modelled with a normal distribution exhibited over and under dispersion and as such regression models were developed using a quasi-Poisson GLM. A quasi-Poisson GLM accounts for over and under dispersion by fitting a dispersion parameter to the dataset (Kindt and Coe 2005). Unimodal responses and interactions between different explanatory variable were also tested (Crawley 2003). Prior to analysis, explanatory factors were checked for multi-collinearity between explanatory variables using Pearson's correlation co-efficient (Appendix B1). Variables that were strongly correlated (Pearson's r > 0.40) were not used in multiple regressions together (Appendix B1).

All percentage data (e.g. inundation frequency) were arc-sine transformed to correct for bounded percentage data (Ahrens et al. 1990). All models were developed using R version 2.10.1 (R Development Core Team 2009) and the package Biodiversity R (Kindt 2009). Post-analysis diagnostic plots (residuals, q-q plots and cooks distance plot) (Kindt and Coe 2005) were used to check the assumptions of the model and to check for outliers or overly influential points which may have biased the analysis (after Kindt and Coe 2005). In significant models when strongly influential data points were identified the analysis was re-run without them to determine if they significantly biased results.

4.3 Results

In total, 1687 trees were surveyed, 395 of which were stags. *E. camaldulensis* was the most abundant species (912 individuals) (Table 4.2); *A. stenophylla* was the next most prevalent species, (276 individuals) and *E. coolabah* the least (104 individuals) (Table 4.2). Averaged across all individuals within a species, crown vigour was highest for *A. stenophylla* (67%), second highest for *E. coolabah* (66%) and lowest for *E. camaldulensis* (63%).

Table 4.2 Number of individuals surveyed for each species and size class cm (cbh)

Species	**<20cm**	**20-50 cm**	**>50cm**	**Total**
E. camaldulensis	404	244	264	912
**A. stenophylla*	209	50	17	276
**E. coolabah*	42	27	35	104
Stags (all species)	224	92	79	395
Total	879	413	395	1687

*occurrence and abundance too few for modelling.

4.3.1 **E. camaldulensis** ***condition in single factor hydrological and land use models***

There were no significant relationships between tree crown vigour and any of the explanatory factors tested (P > 0.05) (Table 4.3). There was a positive and significant relationship between stag abundance <20cm and canopy cover (Table 4.5). When outliers were removed this relationship was no longer significant (Table 4.5; Figure 4.4). The 20-50cm stag abundance size class was significantly (F = 6.82, df = 35, p = 0.01) and positively related to grazing intensity (Table 4.6; Figure 4.5).

Table 4.3 Crown vigour's relationship with hydrological variables and canopy cover in single factor regressions.

Factor	Size class (cbh)	Co-efficient	Standard error	F-value	df	Deviance explained (%)
*Inundation (%)	< 20 cm	0.00	0.00	0.47	26	1.73
	20 – 50 cm	0.00	0.00	0.11	26	0.40
	> 50 cm	0.00	0.00	2.60	27	8.49
Log River connectivity (m)	< 20 cm	-0.02	0.11	0.04	29	0.14
	20 – 50 cm	-0.07	0.11	0.40	30	1.28
	> 50 cm	-0.02	0.11	0.02	31	0.07
Distance from weir (km)	< 20 cm	0.00	0.00	1.31	29	4.30
	20 – 50 cm	0.00	0.00	0.00	30	0.01
	> 50 cm	0.00	0.00	0.02	31	0.04
Groundwater depth (m) 1987	< 20 cm	-0.01	0.02	0.61	29	1.95
	20 – 50 cm	-0.01	0.02	0.50	30	1.57
	> 50 cm	0.00	0.02	0.04	31	0.13
Groundwater depth (m) 2000	< 20 cm	-0.01	0.02	0.80	29	2.57
	20 – 50 cm	0.00	0.02	0.06	30	0.20
	> 50 cm	0.01	0.02	0.19	31	0.59
Groundwater depth (m) 2005	< 20 cm	-0.02	0.01	3.13	29	9.47
	20 – 50 cm	0.00	0.01	0.17	30	0.00
	> 50 cm	0.00	0.01	0.05	31	0.16
Groundwater depth (m) 2009	< 20 cm	-0.01	0.01	1.16	29	3.66
	20 – 50 cm	0.00	0.01	0.00	30	0.01
	> 50 cm	0.00	0.00	0.00	31	0.00
Rain volume (ML)	< 20 cm	0.03	0.05	0.32	29	1.05
	20 – 50 cm	-0.02	0.05	0.20	30	0.65
	> 50 cm	-0.06	0.05	1.73	31	5.02
#Canopy cover (> 2m) (%)	< 20 cm	0.00	0.00	0.76	29	2.43
	20 – 50 cm	0.00	0.00	0.46	30	1.45
	†> 50 cm	--------------------------NOT MODELLED---------------------------------				

*data on 4 sites missing;† canopy cover not modelled for tree crown vigour for > 50 cm cbh trees; *p <0.05; **p<0.01; ***p<0.001. #Not a hydrology variable

Table 4.4 Relationship of crown vigour with land use variables in single factor regressions.

Factor	**Size class (cbh)**	**Co-efficient**	**Standard error**	**F-value**	**df**	**Deviance explained (%)**
Grazing intensity (cow pats / 150 m^2)	< 20 cm	0.00	0.01	0.10	29	0.34
	20 – 50 cm	0.00	0.01	0.02	30	0.05
	> 50 cm	0.00	0.01	0.04	31	0.12
Agriculture (%)	< 20 cm	0.03	0.15	0.05	29	0.16
	20 – 50 cm	-0.02	0.14	0.03	30	0.09
	> 50 cm	-0.12	0.14	0.71	31	2.13
Remnant vegetation cover (%)	< 20 cm	-0.04	0.19	0.04	29	0.12
	20 – 50 cm	0.06	0.15	0.14	30	0.45
	> 50 cm	0.22	0.18	1.39	31	4.13

*p <0.05; **p<0.01; ***p<0.001.

Table 4.5 Stag abundances relationship with hydrological variables and canopy cover in single factor regressions.

Factor	Size class (cbh)	Co-efficient	Standard error	F-value	Deviance explained (%)
*Inundation (%)	< 20 cm	-0.02	0.02	1.45	6.90
	20 – 50 cm	-0.01	0.01	1.32	4.29
	> 50 cm	0.00	0.01	0.13	0.47
Log River connectivity (m)	< 20 cm	-0.75	0.82	0.88	4.23
	20 – 50 cm	-1.17	0.65	3.56	10.53
	> 50 cm	-0.32	0.44	0.52	1.60
Distance from weir (km)	< 20 cm	0.00	0.16	0.02	0.08
	20 – 50 cm	0.00	0.01	0.02	0.06
	> 50 cm	0.00	0.01	0.17	0.54
Groundwater depth (m) 1987	< 20 cm	-0.09	0.14	0.38	1.73
	20 – 50 cm	-0.05	0.12	0.19	0.67
	> 50 cm	-0.05	0.08	0.37	1.25
Groundwater depth (m) 2000	< 20 cm	-0.24	0.14	3.59	13.34
	20 – 50 cm	-0.16	0.11	2.29	7.49
	> 50 cm	-0.08	0.08	1.29	4.31
Groundwater depth (m) 2005	< 20 cm	-0.01	0.07	0.03	0.14
	20 – 50 cm	0.03	0.06	0.20	0.73
	> 50 cm	0.02	0.04	0.25	0.78
Groundwater depth (m) 2009	< 20 cm	0.01	0.08	0.01	0.05
	20 – 50 cm	0.07	0.07	0.99	3.63
	> 50 cm	0.04	0.05	0.91	2.72
Rain volume (ML)	< 20 cm	-0.44	0.39	1.51	6.23
	20 – 50 cm	-0.22	0.30	0.58	1.93
	> 50 cm	-0.21	0.21	1.07	3.27
Canopy cover (> 2m) (%)	< 20 cm	-0.13	0.04	6.30	21.73*
	#< 20 cm	0.02	0.02	1.15	3.70
	20 – 50 cm	-0.02	0.01	0.66	2.36
	> 50 cm	-0.14	0.02	2.90	7.76

Degrees of freedom = 35; *data on four sties missing df=31; # Results with outliers removed. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

Table 4.6 Stag abundances relationship with land use variables in single factor regressions.

Factor	Size class (cbh)	Co-efficient	Standard error	F-value	Deviance explained (%)
Grazing intensity (cow pats / 150 m^2)	< 20 cm	-0.14	0.09	3.46	11.82
	20 – 50 cm	-0.17	0.09	6.15	16.77*
	#20 – 50 cm	-0.18	0.09	6.82	17.72*
	> 50 cm	-0.08	-0.05	3.76	10.48
Agriculture (%)	< 20 cm	-0.21	-0.96	0.05	0.22
	20 – 50 cm	-0.67	-0.82	0.41	2.35
	> 50 cm	-0.33	-0.58	0.34	1.09
Remnant vegetation cover (%)	< 20 cm	0.82	-0.94	0.64	2.94
	20 – 50 cm	0.67	-0.79	0.64	2.17
	> 50 cm	-0.18	-0.77	0.05	0.18

Degrees of freedom = 35; # Results with outliers removed. *p <0.05; **p<0.01; ***p<0.001.

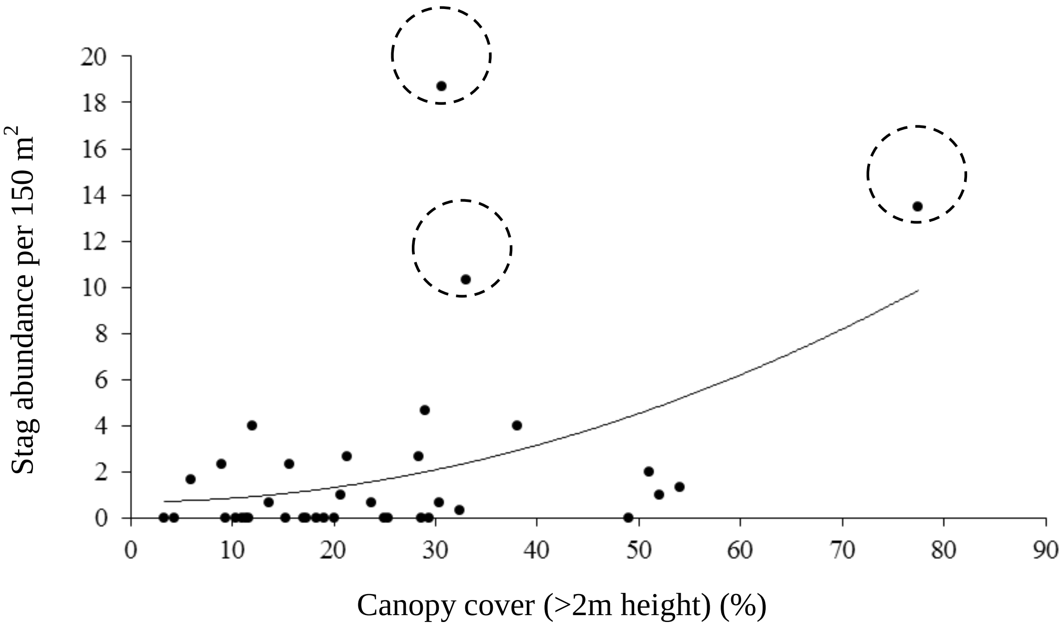


Figure 4.4 Relationship between canopy cover and stag abundance (< 20 cm cbh size class) Outliers are highlighted with dashed circles.

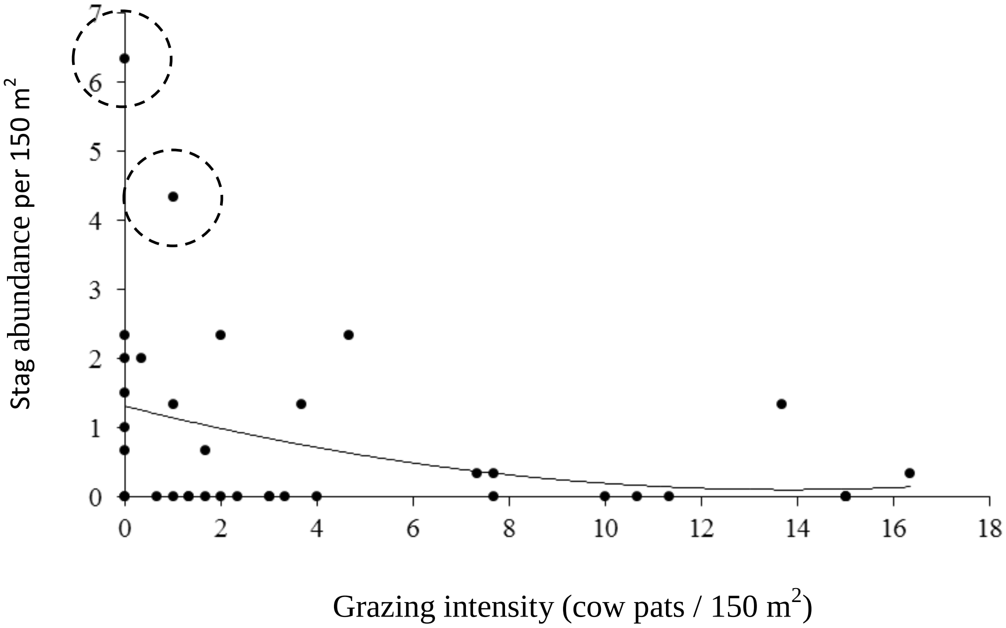


Figure 4.5 Relationship between grazing intensity and stag abundance (20-50cm cbh size class) Outliers are highlighted with dashed circles.

4.3.2 E. camaldulensis *crown vigour multiple-regression 'best models'*

Crown vigour for the <20cm cbh size class was best explained by inundation frequency, canopy cover and an interaction term between these factors (*F* = 7.83, df =24, p = 0.009) (Table 4.7). When canopy cover was high (~ >50%) and inundation frequency low (<40%), then crown vigour for the <20cm cbh size class was low (Figure 4.6). When canopy cover and inundation frequency were both either high (>50% cover and inundated >70%) or low (<20% cover and inundated <40%), then crown vigour was predicted to be high for the <20cm size class (Figure 4.6). No combination of factors was able to explain significant amounts of variation in crown vigour for the 20-50cm cbh size class (Table 4.7).

Table 4.7 Crown vigour multiple regression 'best model' results.

Size class cm (cbh)	**Best Model[#]**	**df**	**F-value**	**Deviance explained (%)**
< 20	Inundation frequency (1.7) + Canopy cover (3.3) + Inundation frequency^{x}Canopy cover (23.4)	24	7.83	28.4**
20 – 50	NS	-	-	-
> 50	Inundation frequency (8.4) + Distance from weir (0.3) + Inundation frequency^{x}Distance from weir (24.3)	25	9.06	33.0**

NS = no significant model; [#]values in parenthesis is individual deviance explained (%) by each term. *p <0.05; **p<0.01; ***p<0.001.

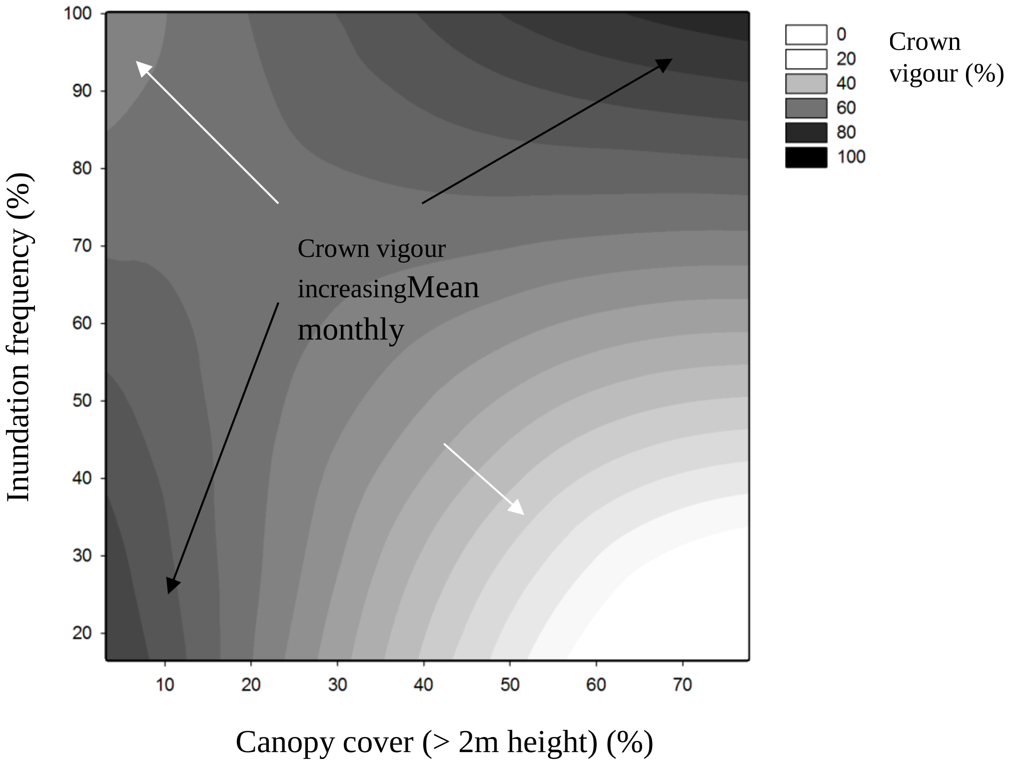


Figure 4.6 Contour plot of small tree crown vigour (<20cm cbh) in relation to inundation frequency (%) and canopy cover (>2m height) (%).

Crown vigour for the >50cm cbh size class was best explained by a model which included inundation frequency, distance from weir, and an interaction term between these two factors (*F* = 9.06, df =25, p = 0.006) (Table 4.7). When inundation was high (>70%) and distance from weir low (~<20km), or when inundation was low (<30%) and distance from weir high (>50km), then crown vigour for the > 50 cm cbh class was low (Figure 4.7). When distance from weir and inundation frequency were both either low or high, then crown vigour was high (Figure 4.7).

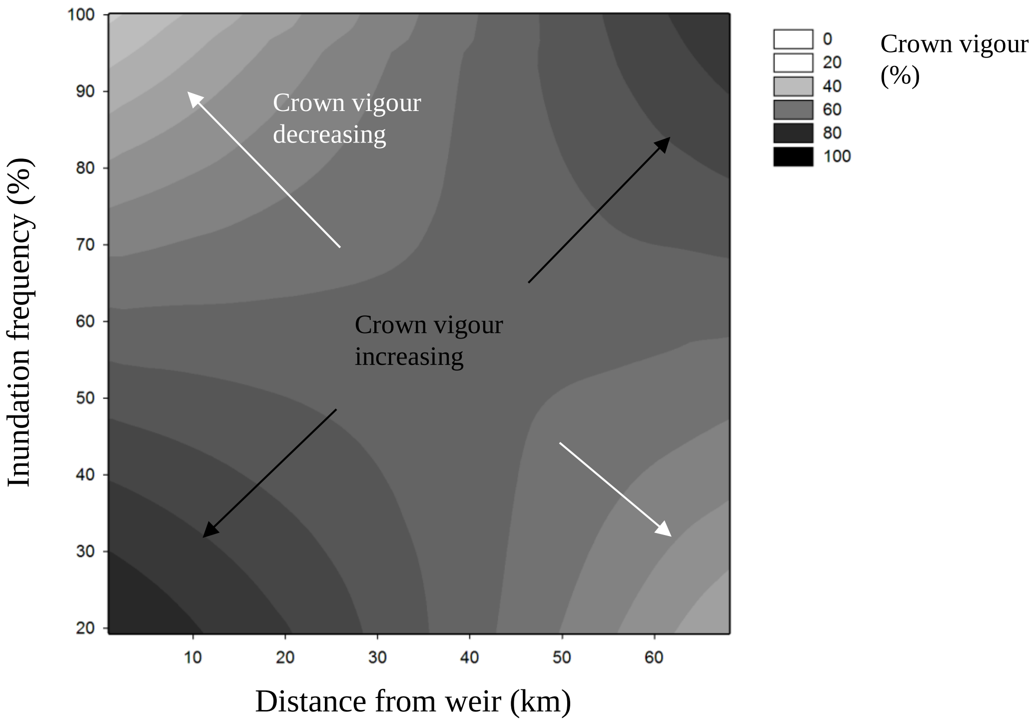


Figure 4.7 Contour plot of large tree crown vigour (>50cm cbh) in relation to inundation (%) and distance from weir (km).

4.3.3 Stag abundance multiple-regression 'best models'

The best model for <20cm cbh stag abundance was predicted by inundation frequency and canopy cover (Table 4.8). When outliers (high stag abundance sites) were removed, canopy cover and inundation frequency was still significant, explaining 30% of the variation in <20cm cbh stag abundance (*F* = 10.63, df = 27, p = 0.003) (Table 4.8). When canopy cover was high and inundation low, then the predicted abundance of <20cm cbh stags was at its highest (Figure 4.8). When canopy cover was low and inundation frequency high, then <20cm cbh stag abundance was low (Figure 4.8).

Table 4.8 Stag abundance multiple regression ‘best model’ results.

Size class (cm) cbh	**Best Model***	**df**	**F-value**	**Deviance explained (%)**
< 20	Inundation frequency (6.9) + Canopy cover (33.0)	30	16.49	39.9***
[#]< 20	Inundation frequency (24.1) + Canopy cover (7.2)	27	10.63	31.3**
20 – 50	Grazing (10.5) + log River Connectivity (17.6)	34	7.54	28.1**
[#]20 – 50	Grazing (17.72)	32	6.82	17.72*
> 50	Inundation frequency (0.5) + Groundwater 2000 (4.7) + Inundation frequency ^{x}Groundwater depth 2000 (19.0)	29	7.42	24.2*

[#] Analysis results with outliers removed. * Individual deviance explained (%) by each factor is given in parenthesis. *p <0.05; **p<0.01; ***p<0.001.

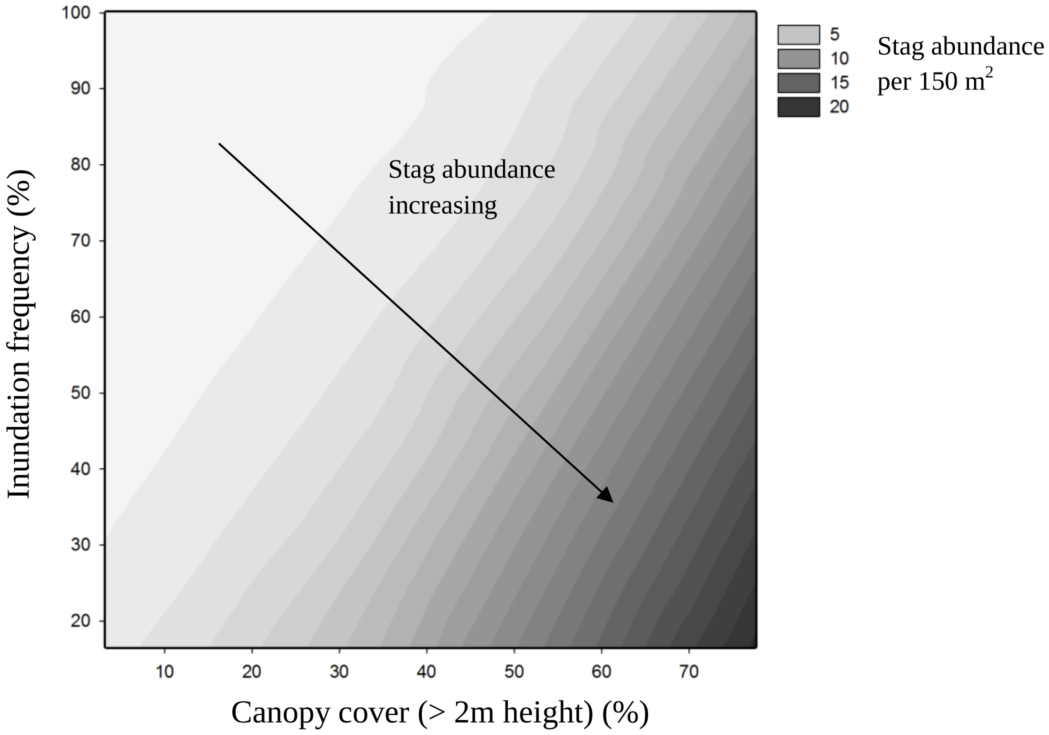


Figure 4.8 Contour plot of small stag (<20cm cbh) abundance in relation to inundation (%) and total woody vegetation cover (%).

Stag abundance in for the 20-50cm cbh size class was best explained by grazing intensity and river connectivity (Table 4.8). As grazing intensity increased, the number of stags decreased, while as river connectivity increased (lower values reflect wetlands closer to the river), stag abundance increased (Figures 4.5 and 4.9) (Table 4.8). When outliers (high stag abundance sites) were removed from analysis, grazing was the only a significant factor in the model (*F* = 6.82, df = 32, p=0.01) (Table 4.8).

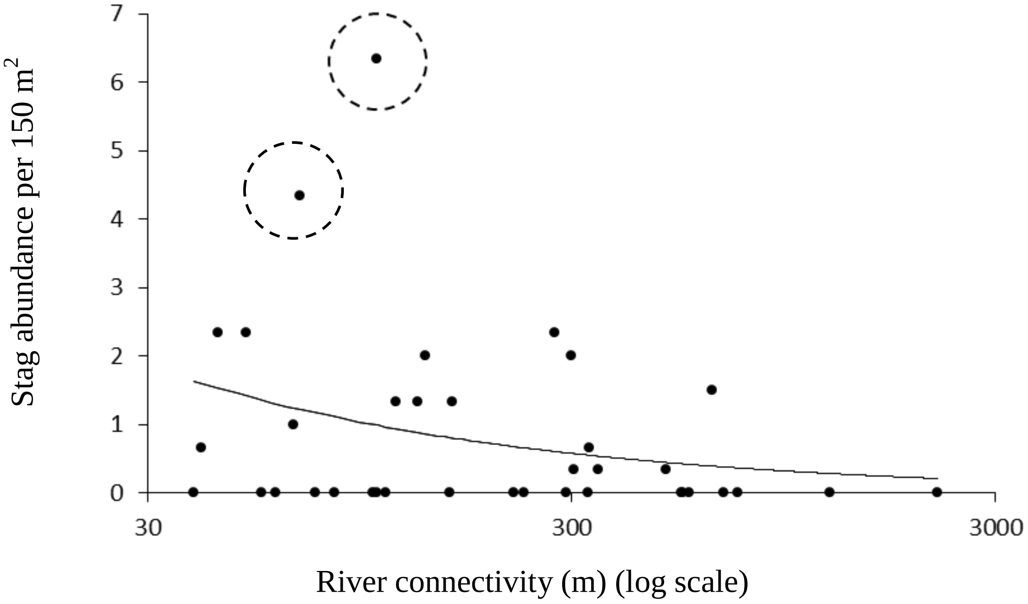


Figure 4.9 Relationship between river connectivity and stag abundance (20 – 50 cm cbh). Outliers are highlighted with dashed circles.

The best model for >50cm cbh stag abundance included inundation frequency and groundwater depth 2000, as well as an interaction term between these factors (F = 7.42, df = 29, p = 0.01) (Table 4.8). At deep, groundwater 2000 depths (<-16m) and low inundation frequencies (<40%), >50cm cbh stag abundance was at its highest. High >50cm cbh stag abundance was also predicted when groundwater depth was relatively shallow (>-10m) and inundation frequency high (>90%) (Figure 4.10). Conversely, stag abundance was low at shallow groundwater depths (>-15m) and low inundation and / or also when inundation frequency was high (>80%) and deep (<-18m) groundwater (Figure 4.10).

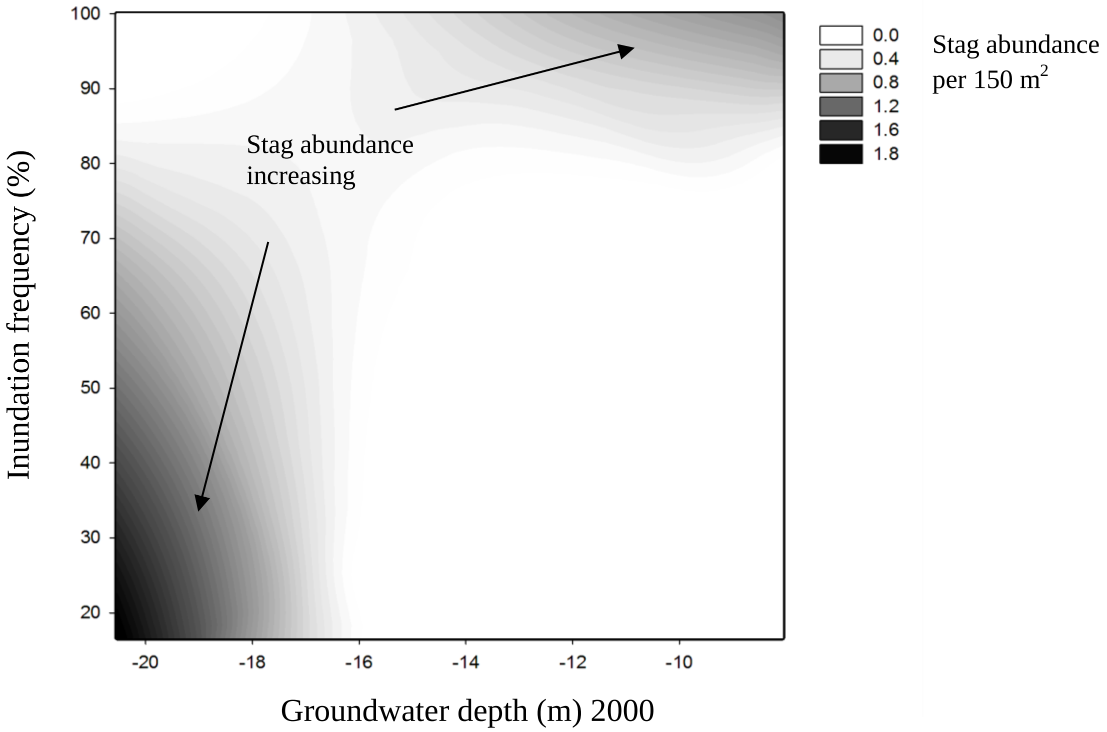


Figure 4.10 Contour plot of stag abundance (> 50 cm cbh) in relation to inundation frequency and Groundwater depth (m) in year 2000.

4.4 Discussion

In agricultural landscapes, declines in vegetation condition have been attributed to various factors, from the local impacts of insects, nutrients and grazing, to the wide reaching impacts of diseases, pathogens and drought (Landsberg 1990; Fensham and Holman 1999; Reid and Landsberg 1999; Martin et al. 2001; Holdenrieder et al. 2004; Davidson et al. 2007). However, for the aquatic components of agricultural landscapes, such as wetlands, declines in vegetation condition are often attributed to hydrological factors, with the water regime thought to be particularly important in this regard (e.g. Denton and Ganf 1994; Ernst and Brooks 2003; Jones et al. 2006). In this study, inundation frequency was present in all but one of the significant models explaining tree condition. Other hydrological factors, such as groundwater depth and distance from weir, were also present in models that explained significant variation in tree crown vigour and stag abundance. Models for small tree crown vigour and stag abundance also included a biotic variable, canopy cover. However, canopy cover may have also affected crown vigour through it influence on water availability and as such its inclusion in models could not justify the rejection of the hydrology hypothesis. Thus, in concordance with the premise that hydrology is the primary driver of floodplain river and wetland ecosystems (e.g. Walker et al. 1995; Bunn and Arthington 2002; Lytle and Merritt 2004; Leigh et al. 2010), the tree condition of wetlands examined in this study was best explained by solely hydrological factor models.

4.4.1 Tree condition and wetland inundation frequency

This study is in general agreement with others showing the importance of the water regime and specifically, inundation frequency, for tree condition (Denton and Ganf 1994; Ernst and Brooks 2003; Jones et al. 2006). For example, in wetlands of Louisiana, South Carolina, wetland water regime explained differences in tree growth and condition for *Nyssa sylvatica var. biflora* and *Taxodium distichum,* with the former preferring rarely inundated sites and the later more permanently inundated ones (Keeland et al.

1997). In swamps along the Myakka River, south eastern United States, increased flooding was associated with increased mortality and decline in tree communities (Ernst and Brooks 2003). The results of this study similarly show that inundation was an important factor for explaining variation in the stand condition of *E. camaldulensis*.

However, in contrast to the above studies, there was not a clear or direct relationship between wetland inundation and tree condition. For example, high inundation frequency was not directly related to low condition or vice versa, but instead was only significantly related to tree condition when interactions with other factors, such as distance from weir, canopy cover and groundwater depth were taken into account.

Two contrasting features of this study that may account for these differences with previous research showing direct relationships between inundation frequency and tree condition are firstly, the metrics used to represent inundation frequency and secondly, a broader spatial scale. Ernst and Brooks (2003), used elevation as a surrogate measure for the amount of flooding tree communities were subject to, and measured this along a gradient of tree condition (from low to high mortality) along a 500m linear transect. Denton and Ganf (1994) flooded juvenile *Melaleuca halmaturorum* for periods of 3 to 14 weeks in a controlled experiment and were thus able to precisely measure inundation frequency. In contrast, the present study utilised lower resolution inundation frequency metrics based on annual inundation frequency and compared wetlands over much a broader spatial scale of ~350km.

The lower resolution data utilised in this study was unable to account for differences in inundation frequency over smaller intra-annual time scales, which is likely to be an important short term determinant of tree condition. Nonetheless, although tree condition, as measured by crown vigour, is likely to reflect short term hydrological conditions, patterns in longer term conditions of inundation frequency should also be reflected to some degree in this attribute. Furthermore, inundation frequency was still able to explain tree condition when in interactive relationships, suggesting that, although a coarse measure of inundation, it was still indicative of inundation patterns at the wetland scale.

The differences with other studies may therefore result from the larger spatial scale of the current study. Many studies comparing the impacts of inundation on tree condition are carried out experimentally or at much smaller scales (Keeland et al. 1997) and as such, are unable to account for the environmental variation that occurs between wetlands over large spatial scales (e.g. Denton and Ganf 1994; Ernst and Brooks 2003). In this study, differences in both hydrology and land use conditions are present across the wetlands examined and may explain why tree condition relates to inundation frequency only when interactive relationships with these other varying environmental factors (e.g. distance from weir) are taken into account. Consequently, while this study suggests that inundation frequency is important, it also suggests that its influence varies with other factors (i.e. canopy cover, distance from weir and groundwater depth).

4.4.2 Land use and wetland tree condition

In contrast to studies on vegetation in the terrestrial components of agricultural landscapes (e.g. Davidson et al. 2007; Close et al. 2008), there was no consistent relationship between grazing or broader land use patterns (e.g. agricultural and remnant vegetation cover) and tree condition for the wetlands examined in this study. Although, grazing did explain significant variation in stag abundance for the 20-50cm size class, no other indicators of tree condition were related to the land use factors tested. Furthermore, while increased grazing was positively associated with stag abundance (i.e. high grazing occurred when stag abundance was low), in other studies, it is often negatively associated with measures of tree condition (e.g. Close et al. 2008). Time lag effects are one possible explanation for these counterintuitive results, so that previously, while low grazing may have helped the establishment of more trees (e.g. Robertson and Rowling 2000), it may also mean that there is a greater abundance trees and hence, potentially stags. However, as time since death was not assessed, the analysis of other aspects, such as the presence and absence of live trees, is likely needed to help understand this relationship. Analysis on the presence and absence of live trees is investigated in Chapter 5.

4.4.3 Hydrology and wetland tree condition

Attributing hydrological factors as the only determinants of tree condition is also supported by other studies which have implicated hydrology and specifically, flooding and river regulation to changes in *E. camaldulensis* condition (Bren 1988; Bacon et al. 1993; Briggs and Thorton 1999). Furthermore, other studies, although not explicitly examining tree condition, have also observed strong relationships between groundwater and *E. camaldulensis* (Mensforth et al. 1994; Thorburn and Walker 1994). The results presented here also suggest that hydrology is a key determinant of *E. camaldulensis* tree condition in the wetlands examined.

Hydrology as the key determinant of tree condition also fits cogently with studies which have linked water availability to tree condition (Bacon et al. 1993; Kozlowski 1997; Kozlowski 2002; Segura et al. 2002; Turnbull et al. 2002). The factors interacting with inundation frequency (distance from weir and groundwater depth) are likely to affect water availability and have also been linked to tree condition in river-floodplain landscapes (e.g. Stromberg et al. 1996; O’Connor 2001; Horton et al. 2001). Although this study did not directly measure water availability, the factors measured here and the interactions observed suggest differences in water availability may be an underlying mechanism driving the patterns in tree condition observed.

Canopy cover and water availability

Canopy cover of large trees is likely correlated with local soil moisture and thus, water availability for younger trees. Ter-Mikaelian et al. (1999) found that canopy cover was a robust measure of biomass growth for a variety of plant species and argued that measures of above ground plant material are likely correlated with resource use (e.g. water and nutrients). Similarly, O'Grady et al. (1999) also showed a strong link between vegetation structure and water use, observing that increasing tree water use was strongly correlated with leaf area and diameter at breast height. In this study, sites high canopy cover may indicate overall greater tree water use and hence, lower local water availability. Such a mechanism may explain why at wetlands with low inundation frequencies and high canopy cover small tree crown vigour was at its lowest. However, this mechanism must be more thoroughly tested as high levels of canopy cover may also influence the crown vigour of small trees in various other ways which were not measured nor controlled for in this study (e.g. insect attack, competition, light and nutrient availability, rainfall interception and soil evaporation etc. (Peet and Christensen 1987; Ovalle and Avendano 1988; Landsberg 1990; Bréda et al. 1995; Kim et al. 1995; Caylor et al. 2005).

Distance from weir and water availability

Differences in water availability may also explain the response of large tree crown vigour to inundation frequency and distance from weir. Wetlands closer to weirs are likely to have higher water availability as their shallow groundwater levels may be supplemented by increased infiltration from pooling water (e.g. Lane and Zinn 1980). In contrast, wetland sites further downstream may be subject to lower water availability as a consequence of water extraction and reduced flows to the floodplain (Kingsford 2000; e.g. O'Connor 2001). Increased infiltration closer to weirs supplementing local shallow groundwater, may therefore counter low water availability in rarely inundated wetlands and in turn, facilitate higher crown vigour for large trees. In contrast, for wetlands further from weirs, the lower water availability may be exacerbated by low wetland inundation frequency, leading to relatively lower tree condition. Conversely, when inundation frequency is high, increased water availability may lead to 'too much' water for wetlands close by weirs and thus, increased physiological stress from waterlogging (e.g. Megonigal et al. 1997; Kozlowski 2002).

Groundwater and water availability

The response of large stag abundance to interactions between groundwater depth and inundation frequency also suggest that complementing hydrological factors which alter water availability may be an underlying mechanism driving patterns in tree condition. The role of groundwater in determining tree condition has been highlighted in several studies (Stromberg et al. 1992; Stromberg et al. 1996; Shafroth et al. 2000; Cooper et al. 2003; Xu et al. 2010). In the Sonoran Desert of Arizona, USA, the condition of riparian woodlands (*Prosopis velutina*) was highly dependent on groundwater, with tree stress increasing at depths of -15 to -18m and becoming sub lethal at depths of -18 to -30m (Stromberg et al. 1992). Likewise, in this study, depths less than -16m were associated with increased stag abundance, but only at wetlands with inundation frequencies lower than 80%.

In contrast to this study, the aforementioned studies linking groundwater and tree condition did not assess interactions with wetland inundation frequency; although Stromberg et al. (1992) did note that precipitation and surface flows temporarily offset water stress from groundwater decline for some trees in *P. velutina* woodlands. In the current study, stag abundance was explained by inundation frequency and groundwater levels in the year 2000, which was the beginning of an intense and long duration drought in the study area (Chapter 2; Australian Bureau of Meteorology 2010). This drought likely reduced water availability and may have made large trees more dependent on groundwater, particularly at wetlands that are inundated less often. Consequently, groundwater levels in the year 2000 may indicate how well trees were buffered against drought, with wetlands with high inundation frequencies performing a similar function as precipitation and stream flow in *P. velutina* woodlands, potentially mitigating increased water stress for trees in wetlands with deep groundwater. Trees at rarely inundated wetlands with deep groundwater may be less able to survive and thus, show greater relative increases in stag abundance.

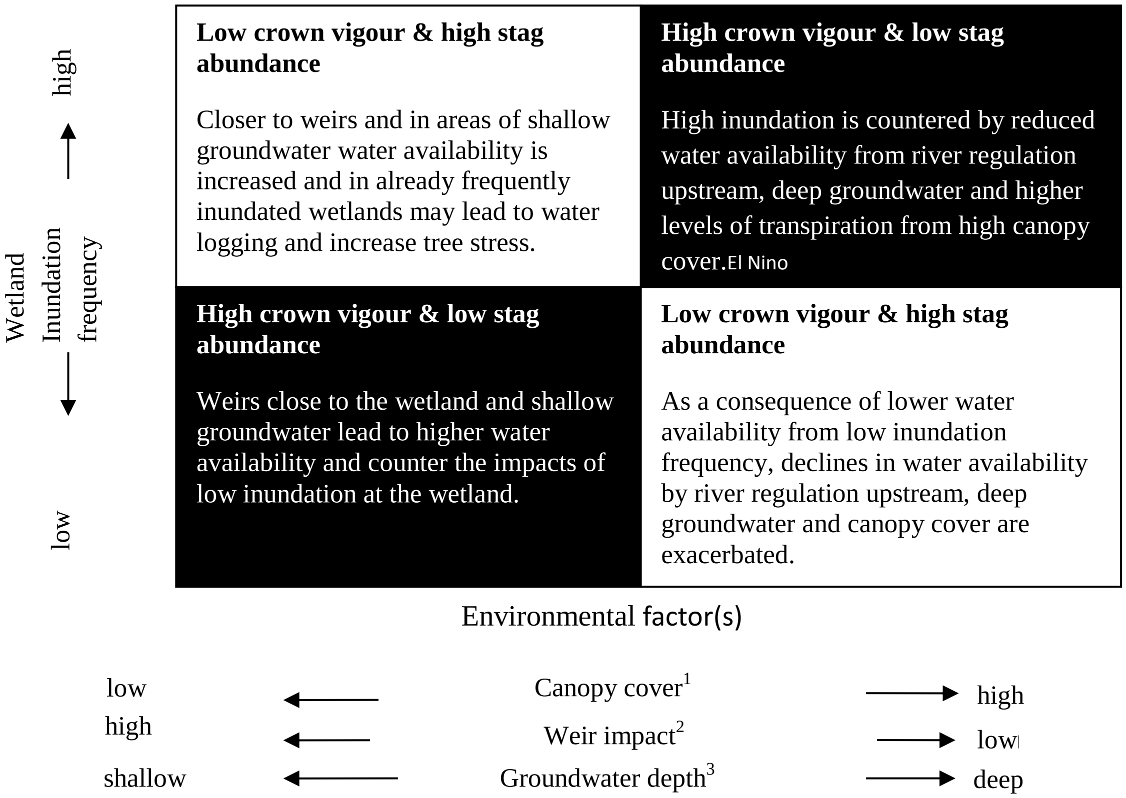
In the Great Basin and Range region of the USA, perennial alkali meadow vegetation is also thought to be buffered from the impacts of precipitation variability and drought by groundwater (Elmore et al. 2006). However, in some areas, pumping has caused groundwater levels to decline below the average plant rooting depth (-2.5m), which in turn has made the vegetation community more dependent on precipitation and hence more susceptible to changes in rainfall (Elmore et al. 2006). In a plantation of *E. camaldulensis* in the Barmah-Millewa Forest, on the Murray River, south-eastern Australia, declining groundwater levels from -12 to -15m, during drought have also been suggested as playing a role in *E. camaldulensis* mortality (Horner et al. 2009).

However, not measuring changes in stag abundance through time, as in other studies (e.g. Horner et al. 2009), limits the ability of the current study to decipher whether groundwater buffers *E. camaldulensi*s against drought conditions. In this study, stag abundance represented a snapshot of conditions during 2009, and as such, no measurement of time since death was made. As such, the measure of stag abundance in this study likely represents trees that have died at different times. Future research which monitors mortality rates through both wet and drought periods across gradients of groundwater depth would help clarify groundwater's importance in buffering wetland vegetation against the impacts of drought.

In addition to observing increased stag abundance at rarely inundated wetlands with deep groundwater, increased stag abundance was also predicted at shallow groundwater depths (<10m) at frequently inundated wetlands (>80%). Other studies have highlighted how increased inundation can lead to tree death (e.g. Ernst and Brooks 2003), but this has not been linked to interactions with groundwater depth. Although, Cunningham et al. (2011) did note that *E. camaldulensis* response to groundwater depth varied regionally, with dieback both increasing and decreasing with increasing groundwater depth, depending on salinity levels. Cunningham et al. (2011) also argued that the condition of floodplain forests is likely determined by interactions between groundwater, flooding, rainfall and soil properties. Salinity is minimal throughout most areas in the Condamine catchment (Searle 2007) and soil properties are similar between the wetlands examined. Nonetheless, this study does also suggest that *E. camaldulensis* response to groundwater varies depending on interactions, but in this instance, interactions that determine water availability (i.e. wetland inundation frequency). Again, before groundwater depths and inundation frequently can be more confidently attributed to causing increased stag abundance, further research on mortality rates, which was lacking in this study, is needed. In the interim, models based on the presence and absence of live *E. camaldulensis* may also help clarify the importance of groundwater, as presumably if the abundance of stags is greater in wetlands of deeper groundwater depths, then the likelihood of live trees being present may also be lower. Analysis on *E. camaldulensis* occurrence is carried out in Chapter 5.

4.4.4 Significance and implications

Collectively, the aforementioned relationships suggest that interactions between hydrological factors which determine water availability are key drivers of wetland tree crown vigour and stag abundance. Under this conceptualisation, the interactions of wetland inundation frequency with canopy cover, weirs and groundwater depth potentially influence water availability to produce conditions which differentiate between wetlands with ‘high condition’ (i.e. high crown vigour and low stag abundance) and ‘low condition’ (i.e. low crown vigour and high stag abundance) trees (Figure 4.11). Future research which could measure local water availability and tree water use in addition to the tree condition and hydrological factors assessed in this study, would be able to test the below conceptualisation and in doing so would provide further insights for the research and management of wetlands in agricultural landscapes.



Low crown vigour & high stag abundance Closer to weirs and in areas of shallow groundwater water availability is increased and in already frequently inundated wetlands may lead to water logging and increase tree stress.	**High crown vigour & low stag abundance** High inundation is countered by reduced water availability from river regulation upstream, deep groundwater and higher levels of transpiration from high canopy cover.El Nino
High crown vigour & low stag abundance Weirs close to the wetland and shallow groundwater lead to higher water availability and counter the impacts of low inundation at the wetland.	**Low crown vigour & high stag abundance** As a consequence of lower water availability from low inundation frequency, declines in water availability by river regulation upstream, deep groundwater and canopy cover are exacerbated.

Figure 4.11 Summarised schematic of the potential consequences of interactions between inundation frequency and environmental factors which may alter water availability and hence determine the crown vigour of small trees[1], large trees[2] and stag abundance[3]. Numbers (1,2,3) correspond to the environmental factors which explain each response; for example 1 indicates that small tree crown vigour was explained by canopy cover.

Most significantly, the results of this study highlight how changes to the hydrological nature of wetlands (e.g. inundation frequency) and the broader landscape (e.g. groundwater depth and distance from weir) drive patterns in wetland tree condition. These findings fit cogently with hydrological concepts which emphasise the importance of temporal hydrological dynamics, such as the wetland water regime (e.g. Chapter 1; Mitsch and Gosselink 2000), as well as those that highlight the importance of hydrological connectivity with groundwater (e.g. Chapter 1; Pringle 2003). Furthermore, as has been illustrated for tree species in other floodplain systems throughout the world, the results suggest that future alterations to the hydrology of floodplain groundwater (extraction) and river flows (weirs) will have significant implications for the future condition of wetland tree species in the Condamine Catchment. This could be a particularly pertinent point in the Condamine Catchment, where hydrological alterations to the river, floodplain and groundwater aquifers have been substantial and may intensify in the future (Chapter 2).

However, while the results of this study suggest that wetland tree condition is sensitive to hydrological changes it also showed that interactions between hydrological factors were important determinants of tree condition. As such, the consequence of changes to hydrology (i.e. changed wetland inundation frequency, increased river regulation, groundwater decline etc.) may not influence wetland tree condition independently, but instead through interactions. These interactions appeared to both exacerbate and mitigate relationships with hydrological factors. Future research and management, which is able to reconcile the impacts of hydrological interactions so that the impacts of hydrological changes can be directly understood is likely an important future step for the conservation of these systems. However, for wetlands in agricultural landscapes rarely has research explicitly illustrated how interactions between hydrological factors determine tree condition. The implications of interactions for understanding wetlands in agricultural landscapes are discussed in more detail in Chapter 6.

Hydrological factors were consistently the only determinant of tree condition among the factors examined. Targeted management and research at factors influencing hydrology may therefore prove the most beneficial for understanding and alleviating declines in the tree condition of wetlands in agricultural landscapes. From a research and management perspective, wetland tree conditions consistent relationship with hydrological factors may also distinguish it from the stressors that cause tree decline in the terrestrial components of agricultural landscapes. This suggests that declines in the tree condition of wetland ecosystems embedded within agricultural landscapes should be managed specifically and not necessarily assumed to be related to broader scale patterns of tree dieback in the terrestrial components of agricultural landscapes.

4.4.5 *Limitations and future directions*

Although the results of this study showed that land use factors were not significant, these results should not be generalised. Light availability, nutrients, insects and pathogens are all non-hydrological factors which may influence tree condition that were not assessed in this study. Although previous investigations in the study area showed no relationship between insects, herbivory and tree condition (Voller 1996), these factors, as well as nutrients, may still be important determinants of wetland tree condition that should be examined in the future. Furthermore, the best models in this study explained less than 40% of the variation in tree condition, suggesting that other hydrological and potentially land use factors may also be important for understanding declines in tree condition. Future research which examines these other factors is needed to more fully test the hypothesis that only hydrological factors need to be considered to understand the condition of wetland tree species. In particular importance in this regard may be the use of detailed and longer term (+30 year) floodplain inundation metrics, which are currently unavailable for the study area. Nonetheless, the insights gained from modelling a range of hydrological and land use factors still provided important information for understanding tree condition in wetlands of the Condamine Catchment, as well as further showing the fundamental importance of hydrology in driving the ecology of floodplain wetlands.

Another key limitation of the current study that should be considered before accepting the hypothesis that a hydrological focused perspective is justified is the metrics used to assess tree condition. Both crown vigour and stag abundance, while providing indications of wetland tree condition, do not represent other ways in which tree communities relate to environmental factors in agricultural landscapes. Declines in tree condition, if severe and long lasting, presumably result in the complete disappearance of that species from that wetland or landscape. In such situations, if hydrology determined tree condition then it may be plausible to treat hydrology as the sole and primary driver of tree communities more generally. However, declines in tree condition may not directly correlate to the future absence of trees (Tominaga et al. 2008; Doody and Overton 2009). For example, Tominaga et al. (2008) argue that while crown vigour (dieback) is a good indicator of tree condition it is not well known how it relates to future tree survival, for example in the next 10-20 years. In Australia and North America, distinctions between the causes of dieback and tree absence have been made (e.g. Jurskis 2005; Tominaga et al. 2008), suggesting that the two should be considered separately. In North America, Tominaga et al. (2008) observed over an 18 year period, that even though *Acer saccharum* crown condition improved, mortality rates did not. Consequently, in addition to tree condition an examination of other factors, namely the presence and absence of live trees and their abundance is needed to gain a fuller understanding of how hydrological and land use change relate to the trees of floodplain wetlands (Chapter 5 and 6).

4.5 Conclusion

The condition of wetland ecosystems and their dominant tree species are degraded in many agricultural landscapes worldwide. Hydrological factors are often purported as the main reason for tree declines in wetland ecosystems. However, in agricultural landscapes various non-hydrological factors are also known to cause declines in the condition of remaining vegetation and may also influence the vegetation of wetlands. Current research prioritises hydrological factors, broadly considering hydrology as a ‘master variable’ which shapes the ecology of river-floodplain-wetland ecosystems. However, it is not known whether such generalisations about the importance of hydrology justify an exclusively hydrological perspective for understanding the tree condition of wetlands in agricultural landscapes. This study tested the premise that hydrological factors are the sole determinants of tree condition in floodplain wetlands in an agricultural landscape.

Models consistently included hydrological factors, with interactions between inundation frequency and other hydrological factors (i.e. canopy cover, groundwater depth and distance from weir) explaining significant amounts of variation in tree condition. Small tree condition was best explained by interactions between inundation frequency and canopy cover, while large tree condition was best explained by inundation frequency, distance from weir and groundwater depth. The results of this study support the hypothesis that an exclusively hydrological perspective is suitable for understanding wetland tree condition, even in agricultural landscapes where potentially detrimental land use factors are also present. However, these conclusions are limited to the land use factors tested and importantly, to the two metrics of tree condition assessed. The metrics in particular may not reflect how other aspects of *E. camaldulensis* occurrence relate to hydrological and land use factors. As such, other measures of *E. camaldulensis* response, such as occurrence, should be considered. These limitations are addressed in Chapter 5.

Chapter 5. Is land use important for *Eucalyptus camaldulensis* occurrence in wetlands in an agriculturally altered floodplain?

5.1 Introduction

Hydrology plays a fundamental role in shaping species distributions in floodplain landscapes, and accordingly much research seeks to understand how species relate to hydrological processes in these habitats (e.g. Hughes 1990; Toner and Keddy 1997; Vervuren et al. 2003; Lite et al. 2005). As such, current research regarding the conservation and distribution of floodplain vegetation often focuses exclusively on hydrology and the consequences of hydrological changes, such as river regulation and groundwater extraction (e.g. Taylor et al. 1996; Benger 1997; Horton et al. 2001; Stromberg 2001; Rood et al. 2003b; Rood et al. 2005; van der Valk 2005; Renofalt et al. 2007; Raulings et al. 2010). Conservation management in these landscapes has followed a similar path, with the re-instatement of hydrological flows often seen as a priority for the future persistence and conservation of degraded floodplains, rivers and wetlands (Stromberg 2001; Bunn and Arthington 2002; Rood et al. 2005). Today, addressing anthropogenic alterations to hydrological regimes is considered a central tenant of ensuring the future ecological persistence of river-floodplains and their associated wetlands (Sparks 1995; Ward et al. 1999; Bunn and Arthington 2002).

However, while hydrological changes undoubtedly have significant consequences for species in floodplain habitats, concurrent land use changes, which are often given a lower priority, may also have substantial impacts (Zedler 2000). Challenging the exclusive importance of hydrology, it has also been argued that land use factors may also be critical determinants of ecological communities in freshwater habitats of floodplain landscapes (Robertson 1997; Houlahan et al. 2006).

Several studies have illustrated significant impacts from land use practices, such as grazing (e.g. Robertson and Rowling 2000; Meeson et al. 2002; Jones et al. 2011) and the influence of adjacent land use practices (Roth et al. 1996; Lammert and Allan 1999;

Houlahan et al. 2006) on the species of floodplain, rivers and wetlands. As such, the utility of research and management in river-floodplain ecosystems based solely on hydrological factors, without consideration of land use, has been questioned, especially in landscapes altered by agriculture (e.g. Ogden 2000; Robertson and Rowling 2000). However, in contrast to hydrological alterations, changing land use patterns in floodplain landscapes are less well understood and documented in many landscapes (Northcott et al. 2007). Furthermore, studies which consider the consequences of hydrological alterations and land use practices simultaneously are generally lacking, especially for floodplain wetland habitats (but see Meeson et al. 2002; Andersen et al. 2007). Additional to this, studies which have considered both land use and hydrology (e.g. Meesone et al. 2002; Anderson et al. 2007), have often not considered groundwater, nor have they focused on floodplain wetlands.

The significance of considering land use may be particularly important in floodplains where intensive and wide spread agriculture is a relatively recent and novel disturbance. For example, changes to soils and landscape processes associated with grazing by recently introduced large herbivores (i.e. sheep and cattle) has negatively affected many native fauna and flora species poorly adapted to these types of disturbance in Australia (Lunt et al. 2007). In many landscapes, grazing is also of particular concern for wetlands, as domestic stock and feral grazing herds often congregate around water sources (Jansen and Robertson 2001). However, in places where grazing is a relatively new disturbance, such as in Australia, there have been relatively few studies on the impacts of grazing on wetlands (Jenkins et al. 2005; but see Robertson and Rowling 2000 and Jansen and Robertson 2001). Furthermore, studies which have examined grazing, such as Robertson and Rowling 2000 and Jansen and Robertson 2001, were restricted to the local impacts of grazing; with the broader scale impacts from land use were not examined.

The impacts of catchment and local scale land use has also been noted for riparian and wetland species in floodplain, rivers, and wetlands (Roth et al. 1996; Lammert and Allan 1999; Houlahan et al. 2006; Northcott et al. 2007). Agricultural land use may, among other things, increase non-point pollution, sedimentation and nutrient inputs, all of which may negatively impact on the biota of floodplains, rivers and wetlands (Allan 2004). In the Upper Colorado River Basin, USA, Northcott et al. (2007) examined the regeneration of cottonwood forest and found that land use development reduced the likelihood of observing forest regeneration by 65%. Along the River Raisin in the Midwestern United States, the extent of agriculture within upstream catchment areas was also negatively correlated with the biotic integrity (for fish species) and the habitat quality of streams (Roth et al. 1996). Consequently, land use may have significant impacts on wetland species across various different scales.

Despite research demonstrating both hydrological and land use impacts on floodplain systems, rarely has the importance of hydrological and land use factors been simultaneously compared, let alone for wetlands in agricultural landscapes (but see Northcott et al. 2007; Andersen et al. 2007). Andersen et al. (2007), in the Colorado River Basin, USA, examined riparian cottonwood forest extent in relation to both river regulation level and the extent of floodplain development and found no relationships, arguing that confounding effects from development, time lags and contrasting effects from flow alteration in different sub-basins may have obscured patterns. At smaller scales along the Murrimbidgee River, Australia, Meeson et al. (2002) examined the impacts of grazing, flooding and seed predation by ants and observed that in areas of high cattle grazing, seed predation was higher and that this may exacerbate the effects of reduced flooding on *E. camaldulensis* recruitment. In the River Raisin catchment, Michigan, USA, Lammert and Allan (1999) more explicitly tested the importance of land use by relating agricultural and forest cover at 100m and 250m buffer widths and at catchment scales to biotic integrity indexes of macro-invertebrate and fish species. Catchment scale land use had minimal impact and although local agriculture cover at 100m buffers had significant negative impacts on biotic measures, in many cases land use did not explain any additional variation for models which included hydrological related stream habitat factors, such as substrate and flow stability (Lammert and Allan 1999). However, all three studies cited above were significantly limited in extent and methodology (i.e. scale, species, factors examined).

The conflicting results from these very limited studies highlight the uncertainty about the important of considering land use in addition to hydrology for floodplain river and wetland species. If studies examining both hydrological and land use factors consistently show that land use factors do not significantly improve models considering only hydrological factors, then research and management focused exclusively on hydrology, as is often the current case, may be well justified. In contrast, if studies show that the addition of land use factors improves models, then a sole focus on hydrology may not be adequate for understanding factors limiting and threatening the occurrence of wetland species.

To determine the importance of land use for wetland species, this study explores the relative contribution of hydrological factors and land use context for the occurrence of *E. camaldulensis* in the Condamine Catchment. Like many other dominant floodplain tree species, *E. camaldulensis* has been explained by a range of hydrological (Bren 1988; Bacon et al. 1993) and land use factors (Jansen and Robertson 2001; Meeson et al. 2002). However, research comparing hydrological and land use impacts concurrently are rare (but see Meeson et al. 2002). Furthermore, when research has been undertaken, only a few factors have been examined simultaneously. For example, while Meeson et al. (2002) has examined flooding and grazing together, other important hydrological factors, such as groundwater depth, have only been examined in isolation (e.g. Cunningham et al. 2011) or with other hydrological factors (Mensforth et al. 1994) and not in combination with coinciding land use contexts, such as grazing and agricultural land cover in the broader landscape.

Results from Chapter 4, examining the condition (crown vigour and stag abundance) of *E. camaldulensis* suggest that hydrological factors were of overriding importance, with land use factors (grazing, agricultural land cover and remnant vegetation cover) not improving models. However, whether this also applies to the occurrence (presence/absence) of *E. camaldulensis* in wetlands throughout the Condamine Catchment, and more generally in wetlands throughout agricultural landscapes, is untested. To examine the importance of hydrology and land use, species distribution modelling was used to determine *E. camaldulensis*, relationship with a range of hydrological and land use factors in an agricultural landscape of south-east Queensland, Australia. Specifically, this study asked whether hydrological plus land use factor models improve upon exclusively hydrological factor models for explaining patterns in the occurrence of *E. camaldulensis* in floodplain wetlands?

5.2 Methods

5.2.1 Vegetation surveys

E. camaldulensis abundance was surveyed at 37 wetlands in 2009 that varied in hydrology and land use context (Figure 4.1). The full suite of explanatory hydrological and land use variables used for modelling are outlined in Chapter 4 (Table 4.1).

Abundance data on *E. camaldulensis* from surveys in 2009 (Chapter 4) was converted to presence and absences. Preliminary analysis with abundance data showed few relationships with hydrological and land use factors (Appendix C1) and as such, analysis was only carried out on presence absence data for *E. camaldulensis*.

5.2.2 Species distribution modeling - **E. camaldulensis** *occurrence, hydrology and land use*

Presence/absence data was used to model the occurrence of *E. camaldulensis* using generalized linear models with a binomial error structure based on a logic link (logistic regression). A presence was classified as when one or more trees was present in any of the three surveyed transects at a wetland. The hydrological and land use factors outlined in Chapter 4 (Table 4.1) were used as explanatory factors.

Five different size classes (<10, 10-20, 20-50, 50-75 and >75cm circumference at breast height (cbh). More size classes were utilised in this study, compared to Chapter 4 to ensure a sufficient number of absences, which is important for logistic regression modelling (Vittinghoff and McCulloch 2007). As the data set was based on 37 sites the number of events per variable (EPV; that is, number of presences and absences) restricts the number of explanatory variables that can be modelled without biasing results. Typically, a minimum of 10 EPV is recommended for logistic regression analysis, as below this point there is increasing bias and unreliability in confidence interval coverage (e.g. Peduzzi et al. 1996). However, more recent studies have highlighted that a rule of thumb of 10 or more EVP may be too conservative and that an EPV greater than 4 may still yield reliable results (Vittinghoff and McCulloch 2007). In this study, due to the limited number events per variable, logistic models were restricted to two explanatory factors.

Initially, single factor species distribution models for the different size classes of *E. camaldulensis* were developed only including hydrological explanatory variables. Following the development of hydrological factor only models, land use factors were also examined, both individually, and in combination with hydrological factors using multiple regression. To compare a hydrological versus hydrological plus land use perspective, multiple-regression models which most parsimoniously explained the greatest variation in *E. camaldulensis* occurrence within size classes were developed (hereafter referred to as the 'best model') using only hydrological factors and hydrological and land use factors together. Model factors were selected using stepwise regression and the significance and parsimony of the best model evaluated using Akaike's information criterion (AIC; Bozdogan 1987). Unimodal responses were also tested by including a quadratic term (Crawley 2003). All binomial GLM models were developed using the Biodiversity R package (Kindt 2009) in R (R Development Core Team, 2006). Variables that were strongly correlated (Pearson $r > 0.40$) were not used together in multiple regressions.

5.2.3 Model validation

Model performance was assessed using internal bootstrap validation (1000 iterations) using the Design Package in R (Harrell 2009; R Development Core Team, 2006). The procedure provides a range of bias-corrected indices of model performance (e.g. for R^2

and AUC) for each model (Harrell 2009). Internal validation using bootstrapping has shown to be a more reliable and efficient means of evaluating model performance than other methods, such as using training and testing data sets (Harrell 2001; Steyerberg et al. 2001; Brunelli and Rocco 2006).

In addition to measures of model fit, such as R^2, an important aspect that should be considered when assessing the performance of a species occurrence models is discrimination (Harrell 2001; Vernier et al. 2008). Discrimination refers to the ability of a model to accurately discriminate between presences and absences at a site (Vernier et al. 2008). Discrimination was assessed using the area under curve (AUC) of the receiver operating characteristic (ROC), which gives the relative proportions of correct and incorrect predictions over a wide and continuous range of threshold levels that divides calculated probability of occurrences into presences and absences (Pearce and Ferrier 2000). AUC values of 0.5 indicate a model with no predictive power, while models with a value of 1 signify perfect discrimination (Swets 1988). An AUC value of 0.7 or greater indicates acceptable levels of model discrimination (Swets 1988).

5.3 Results

In total, 912 individuals of *E. camaldulensis* were surveyed (Table 5.1). Across the 37 wetlands surveyed the 20-50cm size class was the most prevalent, with 244 individuals and the >75 cm size class the least so with 117 individuals (Table 5.1). The 20-50cm size class was most often present at a wetland, being absent from only 6 wetlands surveyed in 2009. The 10-20 cm size class was the least frequently present, occurring at only 22 of the 37 wetlands surveyed.

Table 5.1 Mean abundance and number of presences and absences at surveyed wetlands for *E. camaldulensis* in each size class.

Size class (cbh)	Mean (per 150 m^2)	Standard error	Number of individuals	Number of wetlands	
				Absent	Present
< 10 cm	4.68	1.44	173	12	25
10 to 20 cm	6.24	1.45	231	15	22
20 to 50 cm	6.59	1.27	244	6	31
50 to 75 cm	3.97	0.69	147	10	27
>75 cm	3.16	0.44	117	8	29

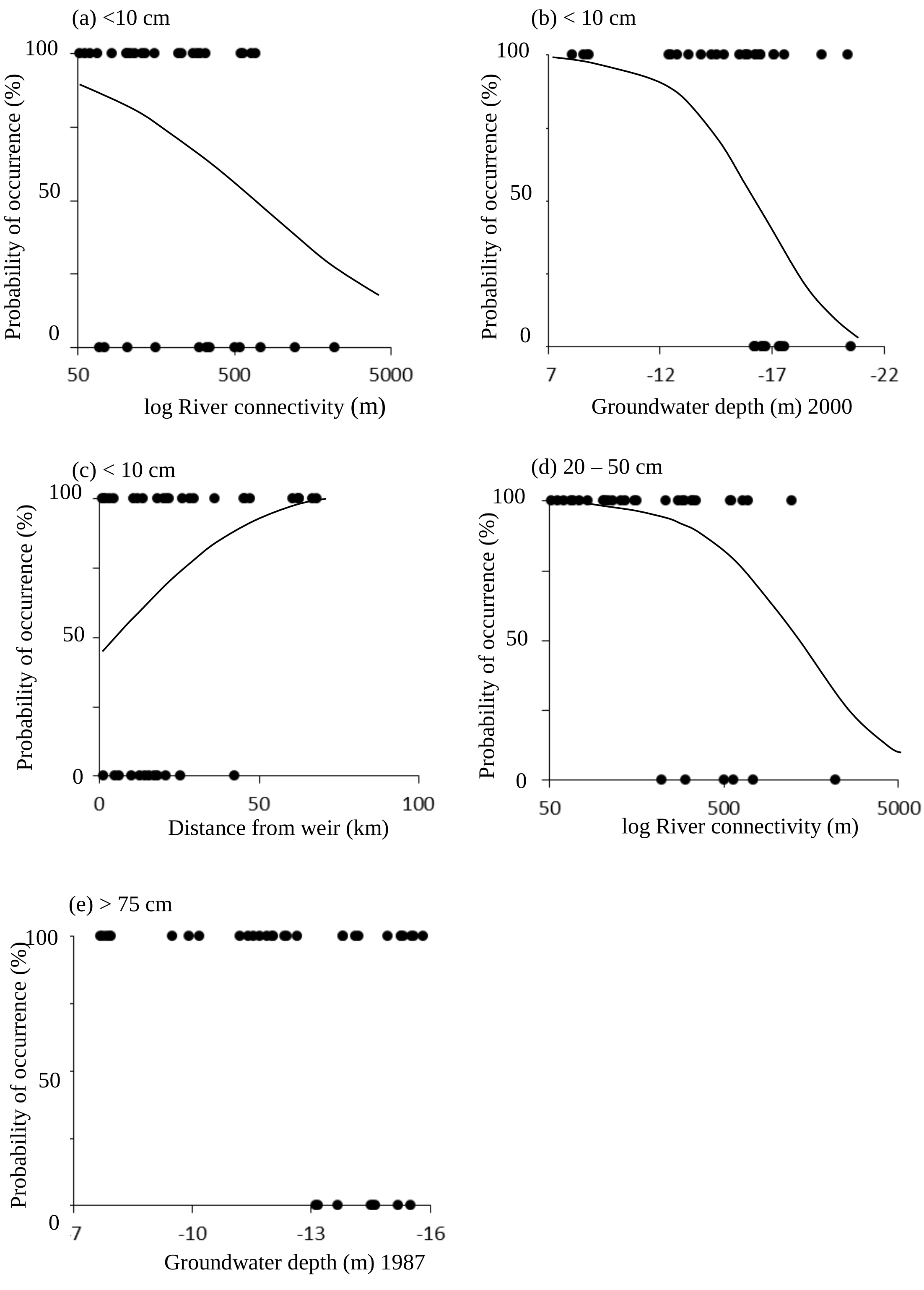
5.3.1 **E. camaldulensis** ***relationship with hydrology in single factor models***

The <10cm and 20-50cm cbh size classes were both significantly explained by log river connectivity (Table 5.2; $R^2 > 0.16$, $p < 0.02$). As river connectivity increased, the likelihood of *E. camaldulensis* in the <10 and 20-50cm cbh size classes occurring also increased (Figure 5.1 a & d). The <10cm cbh size class was also explained by groundwater depth 2000 and distance from weir, with probability of occurrence declining closer to weirs and as groundwater depth declined (Table 5.2, Figure 5.1b & c; $R^2 = 0.16$, $p = 0.03$ and $R^2 = 0.25$, $p = 0.004$ respectively). The 50-75cm cbh size class was not significantly explained by any of the hydrological factors (Table 5.2; $R^2 < 0.03$, $p > 0.1$). The >75cm cbh size class was significantly explained by groundwater depth in 1987, with the likelihood of occurrence declining as depth increased (Table 5.2; Figure 5.1e; $R^2 = 0.2$, $p = 0.02$). At groundwater depths between -13 and -16m the >75cm cbh *E. camaldulensis* showed the greatest decline in likelihood of occurrence (Figure 5.1e). None of the *E. camaldulensis* size classes were significantly explained by inundation frequency, rain volume or groundwater depth in 2005 or 2009 (Table 5.3; $R^2 < 0.1$, $p > 0.05$). Apart from the distance from weir model for the <10cm cbh size class and, all significant single factor hydrological models had acceptable or better discrimination ability, with AUC values greater than 0.7 (Table 5.2).

Table 5.2 Results of logistic regressions for *E. camaldulensis* with single hydrological factors as explanatory variable.

Factor	**Size class (cbh)**	**Co-efficient**	**Standard error**	**Deviance explained (%)**	**Index corrected and validated model performance measures**	
					AUC	**R^2**
Log River connectivity (m)	<10 cm	-1.99	0.93	11.59	0.72	0.16*
	10- 20 cm	-1.24	0.81	4.94	0.49	0.01
	20 -50 cm	-3.64	1.56	26.83	0.84	0.36**
	50 -75 cm	-1.34	0.89	5.47	0.57	0.03
	> 75 cm	0.52	0.94	0.80	0.47	-0.05
Distance from weir (km)	<10 cm	0.05	0.02	10.63	0.69	0.16*
	10- 20 cm	0.03	0.02	7.33	0.62	0.11
	20 -50 cm	0.05	0.04	9.82	0.68	0.12
	50 -75 cm	0.02	0.02	1.76	0.65	0.05
	> 75 cm	-0.01	0.02	0.13	0.42	-0.05
Groundwater depth 1987 (m)	<10 cm	0.12	0.15	1.65	0.52	-0.01
	10- 20 cm	-0.03	0.13	1.32	0.42	-0.04
	20 -50 cm	-0.20	0.17	4.21	0.56	0.06
	50 -75 cm	0.25	0.18	5.37	0.68	-0.02
	> 75 cm	0.52	0.27	15.17	0.73	0.20*
Groundwater depth 2000 (m)	<10 cm	0.52	0.25	18.06	0.81	0.25*
	10- 20 cm	-0.07	0.11	0.88	0.39	-0.01
	20 -50 cm	-0.16	0.14	4.18	0.53	0.06
	50 -75 cm	0.12	0.14	1.92	0.68	-0.02
	> 75 cm	0.26	0.19	6.45	0.64	0.07

Degrees of freedom = 35; *p <0.05; **p<0.01; ***p<0.001.


(a) <10 cm

(b) < 10 cm

(c) < 10 cm

(d) 20 – 50 cm

(e) > 75 cm

Figure 5.1 Response curves of *E camaldulensis* size classes (a, b, c) < 10 cm, (d) 20 – 50 cm and (e) > 75 cm in relation to significant hydrological factors.

Table 5.3 Non-significant results of logistic regressions for *E. camaldulensis* with single hydrological factors as explanatory variable.

Factor	**Size class (cbh)**	**Co-efficient**	**Standard error**	**Deviance explained (%)**	**Index corrected and validated model performance measures**	
					AUC	**R^2**
*Inundation (%)	<10 cm	0.02	0.02	3.76	0.58	0.03
	10- 20 cm	-0.01	0.14	1.11	0.48	-0.03
	20 -50 cm	0.01	0.02	1.76	0.54	-0.02
	50 -75 cm	-0.01	0.02	0.07	0.40	-0.06
	> 75 cm	0.01	0.02	0.03	0.42	-0.05
Groundwater depth 2005 (m)	<10 cm	-0.01	0.07	0.13	0.40	-0.02
	10- 20 cm	-0.04	0.07	0.78	0.47	-0.02
	20 -50 cm	-0.10	0.11	2.93	0.54	0.04
	50 -75 cm	-0.01	0.08	0.00	0.37	-0.02
	> 75 cm	0.04	0.08	0.72	0.44	-0.02
Groundwater depth 2009 (m)	<10 cm	-0.03	0.08	0.34	0.46	-0.02
	10- 20 cm	-0.16	1.51	0.28	0.44	-0.03
	20 -50 cm	-0.03	0.11	0.18	0.44	0.01
	50 -75 cm	0.01	0.83	0.00	0.47	-0.02
	> 75 cm	0.08	0.09	1.94	0.45	-0.02
Rain volume (m^3)	<10 cm	-0.43	0.36	3.19	0.52	0.02
	10- 20 cm	-0.68	0.39	7.03	0.65	0.10
	20 -50 cm	-0.42	0.42	2.96	0.63	0.04
	50 -75 cm	-0.35	0.37	2.11	0.58	0.00
	> 75 cm	0.33	0.45	1.45	0.48	-0.01

Degrees of freedom=35; *data not available at 4 sites (df=31). *$p < 0.05$; **$p<0.01$; ***$p<0.001$.

5.3.2 **E. camaldulensis *relationship with land use in single factor models***

None of the *E. camaldulensis* size classes were significantly related to remnant vegetation cover (Table 5.4; $R^2 < 0.05$, $p > 0.1$). The <10, 10-20 and 20-50cm cbh size classes were all significantly explained by agricultural land cover (Table 5.4; $R^2 > 0.12$, $p < 0.05$). As agricultural land cover increased, the probability of occurrence for these size classes declined (Figure 5.2a - c). The <10, 10-20 and 20-50cm cbh size classes likelihood of occurrence declined as agricultural land cover increased (Figure 5.2a-c). The 20-50cm and 50-75cm cbh size classes were both significantly explained by grazing intensity (Figure 5.2d & e; $R^2 > 0.13$, $p < 0.05$). As grazing intensity increased, the likelihood of occurrence for the 20-50 and 50-75cm cbh size classes declined (Figure 5.2d & e). Except for the 20-50cm cbh size class models with grazing intensity and agricultural land cover, single factor land use models had poor predictive ability with AUC values below 0.7 (although it should be noted that the agricultural land cover model for the < 10 cm cbh size class did have an AUC value very close to the 0.7 threshold, with an AUC of 0.69) (Table 5.4).

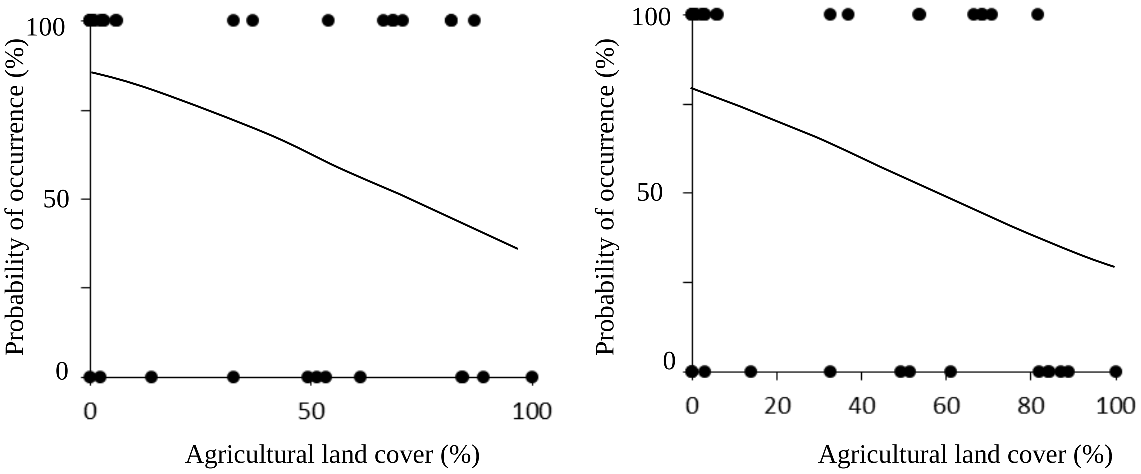
Table 5.4 Land use factor relationships with *E. camaldulensis* occurrence in logistic regressions.

Factor	Size class (cbh)	Co-efficient	Standard error	Deviance explained (%)	Index corrected and validated model performance measures	
					AUC	R^2
Remnant vegetation cover (%)	<10 cm	1.28	1.64	1.69	0.42	0.01
	10- 20 cm	-0.01	1.22	0.00	0.05	-0.04
	20 -50 cm	3.98	4.97	4.66	0.40	0.03
	50 -75 cm	-0.64	1.25	0.56	0.61	-0.04
	> 75 cm	-1.98	1.28	6.21	0.62	0.05
Grazing intensity (cow pats / 150 m^2)	<10 cm	0.04	0.07	0.77	0.50	-0.02
	10- 20 cm	-0.09	0.07	4.16	0.51	0.05
	20 -50 cm	-0.17	0.08	13.75	0.73	0.17*
	50 -75 cm	-0.14	0.07	9.87	0.66	0.13*
	> 75 cm	-0.10	0.07	4.69	0.57	0.03
Agriculture land cover (%)	<10 cm	-2.11	1.08	8.98	0.69	0.13*
	10- 20 cm	-2.04	1.03	8.47	0.66	0.12*
	20 -50 cm	-3.19	0.16	16.16	0.73	0.20*
	50 -75 cm	-0.90	1.06	1.67	0.48	-0.01
	> 75 cm	-0.40	1.14	0.31	0.60	-0.04

Degrees of freedom=35, $^*p < 0.05$; $^{**}p<0.01$; $^{***}p<0.001$.

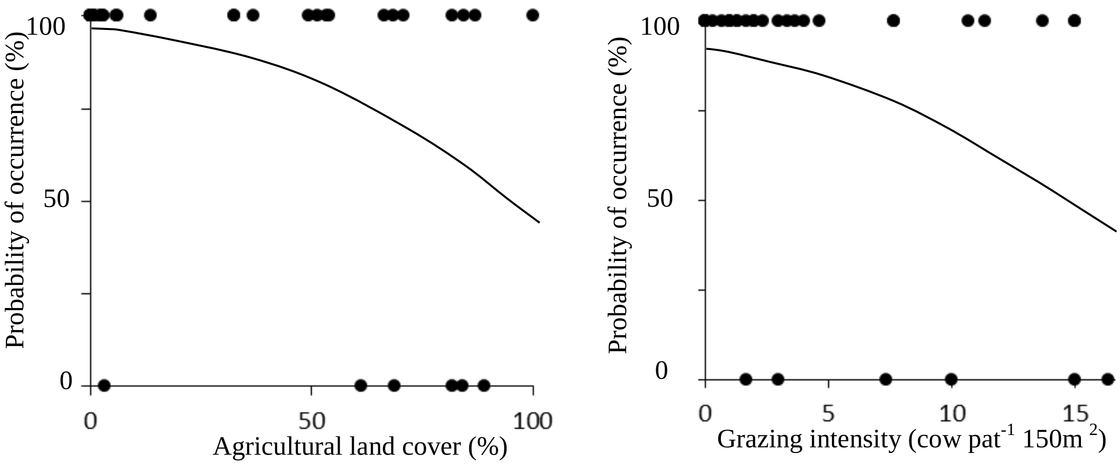
(a) <10 cm

(b) 10 -20 cm



(c) 20 -50 cm

(d) 20 -50 cm



(e) 50 – 75 cm

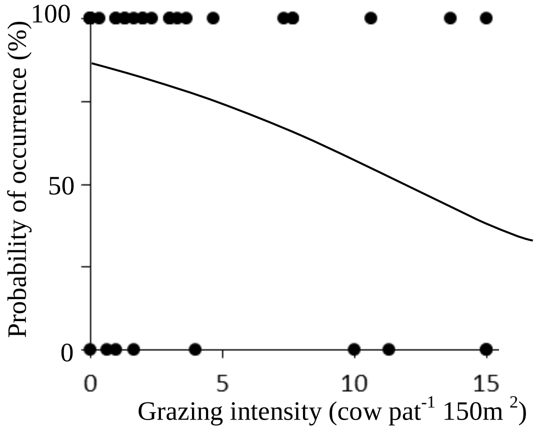


Figure 5.2 Response curves of *E camaldulensis*. size classes (a) < 10 cm, (b) 10 – 20 cm (c,d) 20 – 50 cm and (e) 50-75 cm in relation to significant land use factors

5.3.3 **E. camaldulensis** ***occurrence, hydrology and land use: multiple regression best models***

Best models developed using only hydrological factors for the <10cm cbh size class included groundwater depth 2000 and distance from weir (Table 5.5). Twenty-four per cent of the variation in the occurrence of <10cm cbh *E. camaldulensis* was explained by a combination of groundwater depth in 2000 (18%) and distance from weir (6%) (Table 5.5; $R^2 = 0.30$, $p = 0.004$). The model for the <10cm cbh size class had good predictive ability, with an AUC value of 0.8 (Table 5.5). The hydrological factor only best model for <10cm cbh *E. camaldulensis* was not significantly improved by the addition of land use factors (Table 5.5).

The 10-20cm cbh size class was best explained (15%) by distance from weir and rain volume when using only hydrological factors (Table 5.5; $R^2 = 0.17$, $p = 0.03$). Validation results showed that the model performance was poor, with an AUC value below 0.7 (Table 5.5). The inclusion of a land use factor, agricultural land cover, increased the total amount of variation explained to 17% (Table 5.5; $R^2 = 0.21$, $p = 0.014$). When the land use factor, agricultural land cover was also included the models predictive performance improved (AUC=0.75; Table 5.5).

Log river connectivity, individually, best explained variation in the 20-50cm cbh size class for the hydrological factor only model (Table 5.5; $R^2 = 0.36$, $p = 0.003$). The 20-50cm model was improved by the addition of the land use factor, grazing, which explained, 44% (Table 5.5; $R^2 = 0.48$, $p = 0.0008$). The hydrological plus land use factor model for the 20-50cm size class performed well with an AUC of 0.9 (Table 5.5).

The best hydrological factor only model for the 50-75cm cbh size class included log river connectivity and groundwater depth 1987, which explained 10% of the variation in occurrence (Table 5.5). The best hydrological factor only for the 50-75cm cbh model was not significant and performed poorly with an AUC of 0.6 (Table 5.5; $R^2 = 0.01$, $p = 0.23$). The addition of the land use factor, grazing, increased the total amount of variation explained to 24% (Table 5.5; $R^2 = 0.25$, $p = 0.006$). In the hydrological plus land use factor model, groundwater depth 1987 explained 15% of the variation and grazing 9% (Table 5.5). The groundwater depth

1987 and grazing model for the 50-75cm cbh size class had reasonable predictive performance, with an AUC of 0.76 (Table 5.5).

Groundwater depth 1987 was the only hydrological factor which explained significant variation in the >75cm cbh size class (Table 5.5; $R^2 = 0.21$, $p = 0.015$). The groundwater depth 1987 model explained 15% of the variation in the >75cm cbh class and had acceptable predictive performance (AUC=0.73) (Table 5.5). The addition of a land use factor, grazing, increased the amount of variation explained to 30% and increased the performance of the model (AUC=0.8) (Table 5.5; $R^2 = 0.34$, $p = 0.003$). In the hydrology plus land use model, groundwater depth 1987 explained 25% and grazing 5% of the variation in occurrence of the >75cm cbh size class (Table 5.5).

Table 5.5 Summary of best models for multiple regressions for hydrology only and hydrology plus land use ‘best models’.

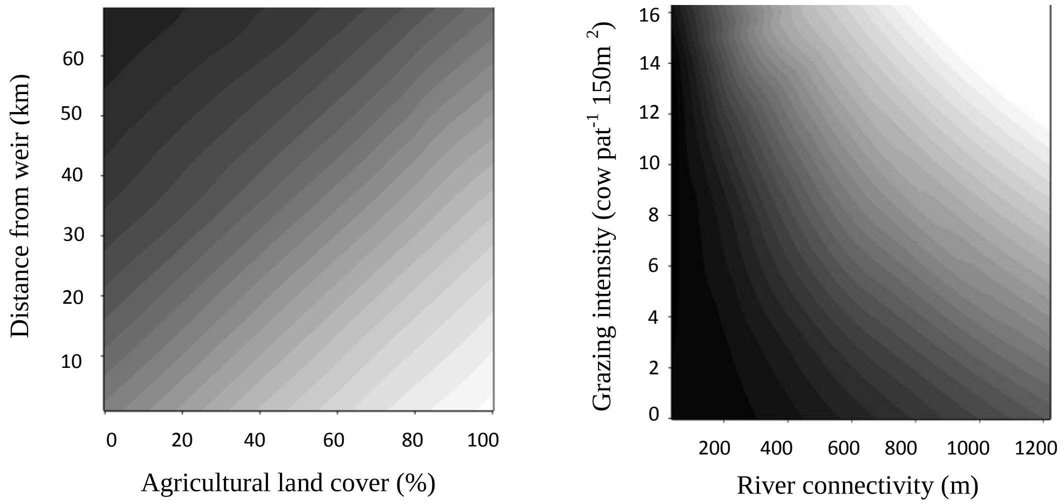
Size class (cbh)	Best model*	AIC	df	Total deviance explained (%)	Index corrected and validated model performance measures AUC	R^2
Hydrology only ‘best models’:						
<10cm	Groundwater 2000 (18.0%) + Distance from weir (5.9%)	41.49	30	23.9	0.81	0.30**
10 - 20 cm	Distance from weir (7.3%) + Rain Volume (7.1%)	48.81	34	14.4	0.68	0.17*
20 - 50 cm	Log River connectivity (26.8%)	28.00	35	26.8	0.84	0.36**
50 - 75 cm	Groundwater 1987 (5.4%) + Log river connectivity (5%)	44.69	34	10.4	0.60	0.01
> 75 cm	Groundwater 1987 (15.2%)	36.78	35	15.2	0.73	0.21*
Hydrology and Land use ‘best models’:						
#<10 cm	Groundwater 2000 (18.0%) + Distance from weir (5.9%)	41.49	30	23.9	0.81	0.30**
10 - 20 cm	Agriculture (9.96%) + Distance from weir (7.4%)	47.36	34	17.0	0.75	0.21*
20 - 50 cm	Log River connectivity (26.8%) + Grazing intensity (16.8%)	24.48	35	44.0	0.9	0.48***
50 - 75 cm	Groundwater 1987 (14.18%) + Grazing intensity (9.86%)	38.80	34	24.0	0.76	0.25**
> 75 cm	Groundwater 1987 (25.29%) + Grazing intensity (4.69%)	33.05	34	30.0	0.8	0.34**

*Deviance explained by each factor individually is given in parenthesis. #Same as hydrological factor only model. *p <0.05; **p<0.01; ***p<0.001.

All best models that included land use factors showed that *E. camaldulensis* relationship with hydrological factors changed as the corresponding land use factor did (Figure 5.3). The probability of occurrence for the 10-20cm cbh size class was highest at a distance from weir of 60 km when agricultural land cover was low, but when agricultural land cover was high (>60%) then its probability of occurrence decreased (Figure 5.3a). As river connectivity declined (distances further from the river) and grazing intensity increased the probability of occurrence the 20-50cm cbh size class declined (Figure 5.3b).

The probability of occurrence for the 50-75cm and >75cm cbh size classes with groundwater depth in 1987 differed depending on grazing intensity (Figure 5.3c & d). At groundwater depths lower than -13 m (for 50-75cm cbh trees) and -14m (for >75cm cbh trees), when grazing intensity was less than 10 cowpats per 150m^2, the probability of occurrence was relatively high (Figure 5.3c & d). At similar groundwater depths of -13 to -14m, when grazing intensity was greater than 10 cowpats per 150m^2, the likelihood of occurrence was low, declining as groundwater depth and grazing intensity increased (Figure 5.3c & d).

(a) 10 – 20 cm (b) 20 – 50 cm



(c) 50 –75 cm (d) > 75 cm

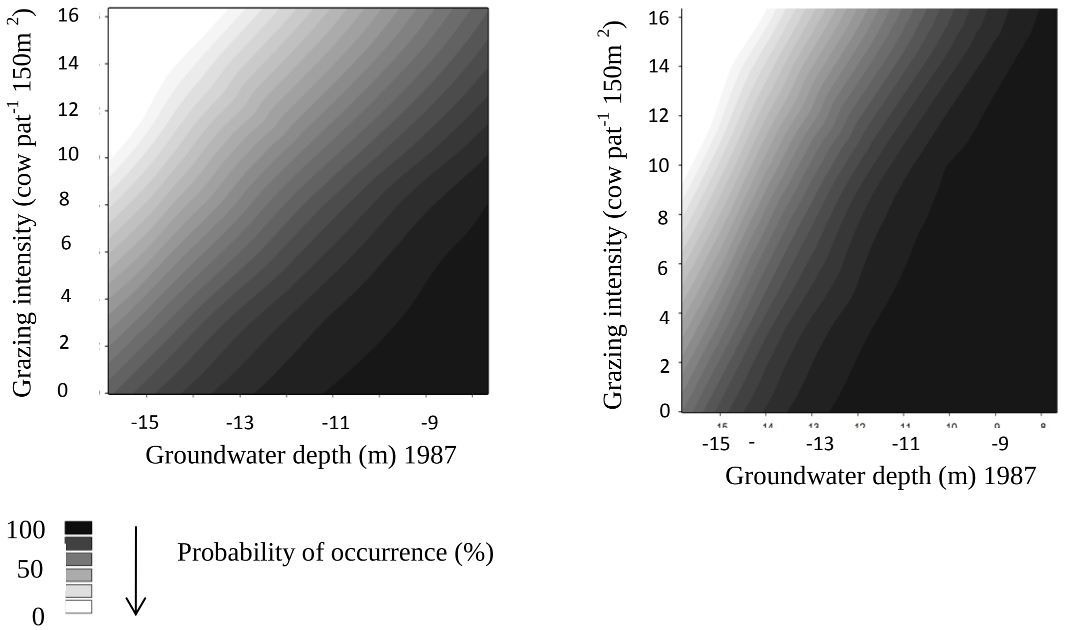


Figure 5.3 Contour plots showing the probability of occurrence for *E. camaldulensis* size classes for best models that included both a hydrological and land use factor.

5.4 Discussion

The importance of hydrology in shaping the ecology of floodplain rivers and wetlands is well recognised, with research and management often solely focusing on hydrological influences (e.g. Hughes 1990; Walker et al. 1995; Toner and Keddy 1997; Stromberg 2001; Bunn and Arthington 2002; Vervuren et al. 2003; Lytle and Merritt 2004; Rood et al. 2005; Leigh et al. 2010; Raulings et al. 2010). However, other studies have challenged a hydrology only perspective, showing that non-hydrological factors, such as land use, may also be important ecological determinants in floodplains, rivers and wetlands (Ogden 2000; Meeson et al. 2002; Turner et al. 2004). Previous research simultaneously comparing the impacts of hydrological and land use factors has showed varied results, with some showing that a focus on hydrology may be justified in some instances (e.g. Lammert and Allan 1999), while others suggesting that both hydrology and land use should be considered (e.g. Meeson et al. 2002; Northcott et al. 2007).

This study was in general agreement with research indicating that the additional consideration of land use factors is important (e.g. Meeson et al. 2002; Northcott et al. 2007), showing that land use significantly explained the occurrence of the wetland tree species *E. camaldulensis.* In addition, this study also showed the importance of multiple hydrological (distance from weir, river connectivity and groundwater) and land use factors (grazing and agricultural land cover) simultaneously, not just agricultural land cover and river regulation (e.g. Andersen et al. 2007) or grazing and flooding (e.g. Meeson et al. 2002). Furthermore, this study also showed that except for trees <10cm, models incorporating land use factors explained up to twice as much variation and had better predictive performance than models developed using only hydrological factors. Consequently, the hypothesis that only hydrological factors need to be examined for understanding the occurrence of *E. camaldulensis* could not be supported, across all the size classes examined.

5.4.1 **E. camaldulensis** ***occurrence and land use***

Both the land use factors (agricultural land cover and grazing intensity) that improved the performance of *E. camaldulensis* distribution models in this study, have been observed as important factors in shaping vegetation distribution in floodplain environments elsewhere (e.g. Clary and Kinney 2002; Meeson et al. 2002; Northcott et al. 2007; Jones et al. 2011). Along the River Raisin in the Midwestern United States, the extent of agriculture within upstream catchment areas was negatively correlated with the biotic integrity for fish species and the habitat quality of streams (Roth et al. 1996). Along the Murrumbidgee River, Robertson and Rowling (2000) observed that relative to sites with grazing, areas without grazing had significantly higher mean densities of *Eucalyptus* spp. seedlings. Also along the Murrumbidgee River, Jansen and Robertson (2001) observed a strong negative relationship between cow pat density and an index of riparian habitat condition, which included a measure of *E. camaldulensis* regeneration. Likewise, this study showed that the land use factors, proportion of agricultural land cover within the wetlands catchment and grazing intensity at the local scale, were negatively related to the likelihood of occurrence of *E. camaldulensis* at wetlands.

However, contrasting with previous research (e.g. Robertson and Rowling 2000; Jansen and Robertson 2001), in this study, grazing intensity explained significant variation in the presence of large trees (>20cm cbh), but not smaller trees (<20cm cbh). Taking into account the results of previous studies, explaining why grazing would be impacting the presence of larger trees rather than smaller trees needs to be considered, especially given that large herbivores, such as cattle often consume and trample seedlings (Zamora et al. 2001; Chauchard et al. 2007). One methodological difference with previous studies that may account for this is an analysis based on presence/absence data and not abundance (e.g. Robertson and Rowling 2000; Jansen and Robertson 2001). In this study, there were few relationships between abundance and the hydrological and land use factors tested, with regressions between grazing and < 10 cm cbh *E. camaldulensis* abundance not significant (Appendix C1). Consequently, other factors aside from the choice of response variable may be causing the discrepancies between the current study and others.

Another potential explanation for the lack of relationship between smaller size classes and grazing may be the climatic conditions under which sampling occurred. In the current study, sampling was carried out after a dry period, with minimal flooding and average rainfall approximately 100mm below median in the preceding 5 years (Chapter 2; Australian Bureau of Meteorology 2011). This low rainfall likely limited recruitment and hence, may have masked impacts of grazing on these smaller size classes. In agriculturally developed floodplains, recruitment of *E. camaldulensis* is rare (Meeson et al. 2002) and in drought conditions this is likely to be even more so. Consequently, under other conditions, for example following flooding and more widespread recruitment, then grazing may have also been a limiting factor for smaller size classes of *E. camaldulensis.*

Also contrasting with previous research, the presence of large *E. camaldulensis* was explained by grazing intensity. There are no studies which have linked the occurrence of *E. camaldulensis* to grazing intensity, although in *Eucalyptus* woodland of north-eastern Tasmania, grazing intensity has been correlated with increased levels of foliar nitrogen and phosphorus and subsequently, with poor tree health (Close et al. 2008). In addition to possible negative impacts from increased nutrient inputs, grazing is also known to disturb soil structure, through compaction and erosion, which can decrease water infiltration (Belsky and Blumenthal 1997). Consequently, in intensively grazed sites, disturbances to soil structure and increased nutrient inputs may decrease large *E. camaldulensis* health and reduce their ability to persist. However, Chapter 4 showed no relationship between tree health (crown vigour) and grazing, suggesting that other mechanisms may be responsible.

One alternative is that the response of large trees to grazing intensity may be a consequence of past land use practices. For example, when grazing is present, other factors such as firewood and timber collection, thinning, burning and utilisation of the wetland for other agricultural uses may also be more likely. Jansen and Robertson (2001) also cautioned that indicators of grazing intensity likely reflect past land use management, with stocking rates generally higher in areas where *E. camaldulensis* had been heavily cleared in the past. Likewise, in this study, the measure of grazing intensity utilised may also relate to local scale past land management and may explain why large *E. camaldulensis* are less likely to occur in areas of high grazing intensity.

Disentangling the independent effects of current grazing and past land use management is likely an important avenue for future research if land use impacts on freshwater habitats are to be more fully understood. In the interim, measures of grazing intensity, such as cowpat density, are still likely to provide useful measures of local land use impacts on vegetation communities (e.g. Jansen and Robertson 2001) and therefore still provide important insights for understanding land use impacts on freshwater ecosystems. In the context of this study the relatively small sample size, and hence relatively few sites with high levels of grazing, should also be considered when interpreting the relationships between grazing and E. camaldulensis. In the future surveys of *E. camaldulensis* across a greater number of sites covering a wider range of grazing sites, especially high intensity ones, would be beneficial for elucidating this relationship.

5.4.2 E. camaldulensis occurrence and hydrology

Despite the additional importance of land use, hydrological factors still had strong relationships with *E. camaldulensis* occurrence. Furthermore, in agreement with research highlighting the importance of hydrological processes, such as river-floodplain connectivity and the impacts of river regulation on floodplain functioning and species distribution (Junk et al. 1989; Tockner et al. 2000; Ward et al. 2002; Pringle 2003; Thoms et al. 2005), hydrological factors generally explained more variation than land use factors. Consequently, even though land use factors were important additional explanatory factors, in relative terms hydrological factors were still the most important determinants of *E. camaldulensis* occurrence in the wetlands studied.

In this study, two of the significant hydrological factors identified, river connectivity and distance from weir are two factors well known for the influence on floodplain and riparian vegetation (Stromberg 1998; Leyer 2006; Stella et al. 2010). In the upper Colorado River basin, DeWine and Cooper (2007) observed that the extent of *Acer negundo* forest recruitment was restricted to lower landscape positions along regulated rivers compared to unregulated rivers with greater peak flows. In an examination of riparian species in South Africa, O’Connor (2001) also observed that at greater distances from the river, individuals of *Combretum imberbe* suffered the highest levels of water stress. Likewise in this study, there was a lower likelihood of <20cm cbh size trees occurring close to weirs potentially reflecting a reduction in peak flows. Furthermore, as river connectivity decreased the probability of occurrence of *E. camaldulensis* <50cm cbh decreased. However, this research did not quantify how weirs and declines in river connectivity impacted on peak flows, local water availability or tree water use (e.g. Horton et al. 2001; O' Connor 2001; DeWine and Cooper 2007). Consequently, future investigations into how river connectivity and weirs influence peak flows and water availability at wetlands in the Condamine Catchment is needed to test the above mechanisms.

In addition to relationships with river connectivity and distance from weir, large *E. camaldulensis* was also significantly explained by groundwater depths in 1987 and the smallest size class <10cm, by groundwater depths in 2000. This suggests that past groundwater conditions are an important determinant of the current distribution of *E. camaldulensis*. Kingsford (2000) has argued that the consequences of a loss of hydrological connectivity with the river may take years until they are evident in wetlands, in the case of long lived tree species, such as eucalypts up to 20 years. Similarly, groundwater conditions from over 20 years ago in the Condamine Catchment appear to be an important explanatory factor for the current occurrence of large *E. camaldulensis*.

However, as abilities to access water likely change as tree size increases (Dawson and Ehleringer 1991), the mechanisms behind these relationships and the time scale they operate on likely differ between the large and small size classes. For example, larger trees likely have deeper roots allowing direct relationships with groundwater (Dawson and Ehleringer 1991; Mensforth et al. 1994). In contrast, the smaller trees (<10cm cbh) unlikely have roots which reach deep groundwater. One possible explanation is that groundwater in the year 2000 influenced the condition of larger mature trees and potentially their seed output (e.g. George et al. 2005) and thus the occurrence of small trees (<10cm cbh). Chapter 4 also showed that lower groundwater depths in 2000 explained higher levels of stag abundance, which may be an indication of the longer term condition of wetlands. Future research which investigates the relationship between wetland tree condition, occurrence, fecundity and groundwater is needed to test this mechanism.

The influence of size class aside, in other parts of the world, floodplain vegetation occurrence and condition has been linked to groundwater depth (e.g. van Tol et al. 1998; Horton et al. 2001; Leyer 2005). For example, in the southwest of the United States of America, declines in groundwater have been frequently linked to the degradation of riparian habitats (Busch and Smith 1995; Stromberg et al. 1996; Patten et al. 2008). In the Hissayampa River, Arizona, Horton et al. (2001) observed that deep groundwater levels were detrimental for *Populus fremontii* and *Salix gooddingii*, with increases in depth to groundwater leading to increased dieback and mortality. In more temperate areas, such as The Netherlands, declines in groundwater have also been linked to the local extinction of many plant species (van Tol et al. 1998).

No previous research has linked groundwater depth with the occurrence of *E. camaldulensis* in floodplain wetlands. However, throughout the Murray Darling Basin, Australia, changes in the condition of *E. camaldulensis* floodplain forests have been linked with groundwater declines (Cunningham et al. 2011; Reardon-Smith 2011). In addition to the above studies, the results of this study also suggest that groundwater plays a key role in the occurrence of large (>50cm cbh) *E. camaldulensis*. To date, no studies have utilised species distribution modelling to model *E. camaldulensis* responses to groundwater depth. However, the results of this study indicate that this may be an important avenue for future research in floodplains where groundwater depths are declining, as in the Condamine catchment (Chapter 2). If groundwater depths continue to decline then not only may the vigour of *E. camaldulensis* decline (e.g. Reardon-Smith 2011), but also the number of wetlands able to support large *E. camaldulensis.*

5.4.3 Significance and implications

Observing that land use is an important additional determinant of the wetland species *E. camaldulensis* has significant implications for ecological research and management. It suggests that while current hydrological concepts (Chapter 1) are able to predict *E. camaldulensis* response to river connectivity, groundwater depth and distance from weir, they do not account for land use factors, which were also significant determinants. Consequently, the results of this study suggest that models developed using only hydrological factors may be too narrowly focused and may not adequately explain relationships universally across *E. camaldulensis* age classes. This is likely to be particularly so for the size classes > 20 cm cbh, for which the model R^2 increased by 0.12 to 0.24. It should also be noted that the inclusion of land use factors, while significantly improving model performance, was not substantial, in most cases increasing the variation explained by only 10 to 20%. While this is important for ecological models, which typically only explain 50% of the variation, given the large variability in data, this should be kept in mind when considering the additional importance of land use factors. Nonetheless, the results do suggest in general that following a hydrology hypothesis, where only hydrological factors are considered, may compromise understanding about wetland ecosystems in agricultural landscapes.

Observing that the inclusion of hydrology and land use into models provides a more complete understanding of the ecology of floodplain wetlands suggests that future research in the production landscape of the Condamine Catchment should not be restricted to identifying the influence of hydrology factors only. The Condamine Catchment, as with many agriculturally productive areas, has been subject to extensive hydrological and land use changes. In the future, the impacts of these changes on the ecology of the catchment may be further exacerbated by newly developing industries (e.g. mining and groundwater pumping) (Queensland Department of Environment and Resource Management 2010). However currently, much of the environmental concern about the Condamine River and its floodplain is in regards to hydrological impacts (e.g. from water extraction and climate change) (MDBA 2005; CSRIO 2008; but see Reardon-Smith 2011). While, Reardon-Smith (2011) did examine a range of hydrological and land use factors, this study was restricted to the Condamine River; to date there have been no similar studies on the catchments wetlands. Contrasting with a focus on hydrology the results of this study suggest that if the impacts current environmental changes on floodplains and their wetlands are to be more fully understood, then it is imperative that land use factors are also considered. The failure to do so may not only lead to models which have less predictive and explanatory power, but also management which is sub-optimal and inefficient.

To address current and future limits on *E. camaldulensis* distribution, this study suggests strategies that integrate current hydrological concepts with the impacts of agricultural land use activities may prove the most beneficial. The management implications of acknowledging both land use and hydrological factors has been considered for different ecological components of floodplain ecosystems (e.g. Ogden 2000; Robertson and Rowling 2000; Meeson et al. 2002; Allan 2004; Jenkins et al. 2005; Houlahan et al. 2006). A common observation of these studies is that actions aimed solely at ameliorating hydrological changes may be suboptimal, if concurrent land use practices are not also addressed (Robertson 1997; Ogden 2000), arguing that even if environmental flows are restored various negative impacts from agriculture are likely to persist (Ogden 2000). Indeed, Nias et al. (2003) has questioned whether in some agricultural lands it is even possible to recover habitat values just by re-instating hydrological flows. Houlahan et al. (2006) also argued that failure to incorporate adjacent land use practices which impact on wetlands makes some current management practices inadequate.

5.4.4 Limitations & Future directions

Support for the hypothesis that both land use and hydrology should be considered when examining the biota of floodplain rivers and wetlands, is limited by the focus on a dominant perennial tree species in this study. Various studies which have highlighted the importance of land use by focussing on tree species (e.g. Robertson and Rowling 2000; Meeson et al. 2002; Andersen et al. 2007; Northcott et al. 2007). The risks of focusing research on one or a few species are highlighted by Wiens (2002) who suggests that as all species exhibit unique relationships with their environment, a species-based approach for understanding riverine landscapes may lead to situation-specific findings, with limited generality. This statement may hold equally true even if these species are seen as an indicator (*sensu* Noss 1990) or keystone species (*sensu* Simberloff 1998) with research highlighting the risks of attempting to use species as indicators or surrogates of ecological condition (e.g. Mills and Soule 1993; Ormerod et al. 2000; Cushman et al. 2010). However, the ecological importance of *E. camaldulensis*, is well recognised and as such, using it as a focus species to test the hydrology only hypothesis is still highly relevant for the broader ecological functioning and persistence of various species (Chapter 2), which depend on it for providing habitat and resources (Boulton and Lloyd 1991; Briggs et al. 1997; Mac Nally et al. 2001; Wen et al. 2009).

Another important avenue for future research could be examining how the hydrological and land use factors tested operate in concert and specifically whether they interact. In this study, the relationships between both grazing and groundwater, and agricultural land cover and distance from weir, were strengthened when modelled together, suggesting that they may augment each other’s influence. While studies examining how both hydrological and land use factors interact to influence riparian and wetland communities are rare, Meeson et al. (2002) has argued that grazing likely exacerbates the impacts of hydrological changes from water extraction and river regulation on *E. camaldulensis* recruitment. However, aside from this there is little research on how hydrological and land use factor interactions influence wetland species (but see Leyer 2005 who examined interactions between hydrological factors, but not between hydrological and land use factors). How different hydrological and land use factors interact and whether they exacerbate or mitigate each other’s impacts is explored in more detail in Chapter 6.

5.5 Conclusion

Much research examining floodplain, riparian and wetland vegetation has focused solely on hydrological factors. However, other studies in floodplain environments have also highlighted the importance of land use factors, such as grazing. This chapter tested two hypothesises reflecting these different perspectives (1) the hydrology hypothesis reflecting research focused on hydrology and (2) the interactive hydrology-land use hypothesis. Hydrological factors (river connectivity, groundwater depth and distance from weir) and land use factors (grazing intensity and agricultural land cover) all explained significant variation in *E. camaldulensis* occurrence.

However, except for the <10cm cbh size class, all models which included a land use factor performed better (R^2 0.04 to 0.24 and AUC 0.06 to 0.16 greater than hydrology factor only models in predicting *E. camaldulensis* occurrence. Consequently, both hydrological and land use factors should be examined to understand the distribution of *E. camaldulensis* in the wetlands of the current study and possibly for floodplain, riparian and wetland species more broadly. Models developed using only hydrological factors may fail to consider important factors limiting the distribution of wetland species in agricultural landscapes and therefore be sub-optimal for research and management.

Chapter 6. A Bayesian network model describing independent and interactive effects of hydrology and land use on *E. camaldulensis* in floodplain wetlands

6.1 Introduction

It has been argued that one of the key challenges for future research in human modified floodplains is distinguishing between the direct effects of hydrological changes, such as modified flow regimes, from coinciding land use changes (Bunn and Arthington 2002). However, environmental factors causing a negative change in an ecological variable may not always operate directly (i.e. independently), but instead, interactively (Breitburg et al. 1998). Across most ecological studies, the focus has been on the independent effects of factors, with studies on the nature of interactions between multiple factors much less frequent (Sala et al. 2000; Crain et al. 2008; Tylianakis et al. 2008; Poff and Zimmerman 2010). As such, Tylianakis et al. (2008) has argued that the importance of interactions between multiple stressors is unknown in many environments, with research across a broader range of systems that explicitly tests interactions needed. Floodplains, which are often highly altered by anthropogenic activities, provide an ideal system for studying the impacts of multiple stressors (Tockner et al. 2010). This chapter examines the interaction of environmental factors and the consequences for the functionally dominant wetland tree species, *E. camaldulensis,* using a Bayesian network model.

6.1.1 Interactions in floodplain systems

In floodplain landscapes, interactions between multiple stressors play a key role in shaping the distribution of species (e.g. Leyer 2005; Matthaei et al. 2010). In agricultural streams in New Zealand, Matthaei et al. (2010) noted synergistic interactions, with equivalent amounts of sediment having more negative effects at lower flow rates than at higher flow rates on aquatic biota. Along the Elbe River, Germany, Leyer (2005) observed that in recent (‘hydrological active’) and older (‘hydrological inactive’) floodplains, interactions with average groundwater levels influenced the distribution of herbaceous plant species (e.g. *Poa palustris* and *Deschampsia cespitosa*), so that in the older floodplain, optimum conditions occurred at shallower average groundwater levels than in the recent floodplain (Leyer 2005). It was concluded that older floodplain areas acted synergistically with average groundwater levels, which exacerbated the plants susceptibility to groundwater declines (Leyer 2005). Consequently, considering interactions between factors is likely to be an important part of understanding how species responding to their environment.

6.1.2 Conceptualizing qualitative interactions in ecological systems

Conceptually, research about interactions has classified them as: (i) additive (ii) synergistic or (iii) antagonistic (Folt et al. 1999; Crain et al. 2008; Didham et al. 2007; Darling and Côté 2008) (Figure 6.1). Additive interactions represent a model where the effects of each stressor, say, x and y, are independent and as such, can be simply represented by their additive effects (x + y = effect) (Crain et al., 2008; Darling and Côté 2008; Scenario 1 in Figure 6.1). Antagonistic models represent situations where the effect of one (or both) of the stressors is reduced in the presence of another (Crain et al. 2008; Darling and Côté 2008; Scenario 2 in Figure 6.1). Synergistic interactions occur when the effect of the stressors is increased in each other's presence (Crain et al. 2008; Darling and Côté 2008; Scenario 3 in Figure 6.1).

One aspect of interactions that has thus far been neglected in ecological research is qualitative interactions; or interactions which are not only associated with a change in the magnitude of response in the presence of another factor, as with synergistic and antagonistic interactions, but also a directional change. In medical research, the importance of qualitative interactions is well recognised and has been frequently examined (e.g. Zelterman 1990; Piantadosi and Gail 1993; Jatoi et al. 2008; Williamson et al. 2010). In a medical context, qualitative interactions may, for example, drastically change the effect of a drug, so that for one subset of patients it may have negative effects, while for others positive (Gail and Simon 1985).

Although rarely considered, there are indications that qualitative interactions may also be equally important in ecological systems (e.g. Leyer 2005; Crain et al. 2008;

Daleo and Iribarne 2009; Bozelli et al. 2009). Bozelli et al. (2009) noted for benthic invertebrate species richness in Brazilian lakes, that low-water periods had positive effects in natural areas, while low-water periods had negative effects in high human impact areas. Similarly, Daleo and Iribarne (2009) observed that the effects of the burrowing crab (*Neohelice granulate*) effects on *Spartina alterniflora* in salt marshes along the south western Atlantic coastline, Argentina, varied from positive to negative, depending on sand grain size. These examples, while limited in scope, highlight how qualitative interactions may lead to vastly different ecological outcomes and therefore may be an essential part of understanding the consequence of multiple interacting factors on species. Consequently, qualitative interactions may occur when there is a change in both the magnitude and direction of response (Scenario 4 in Figure 6.1).

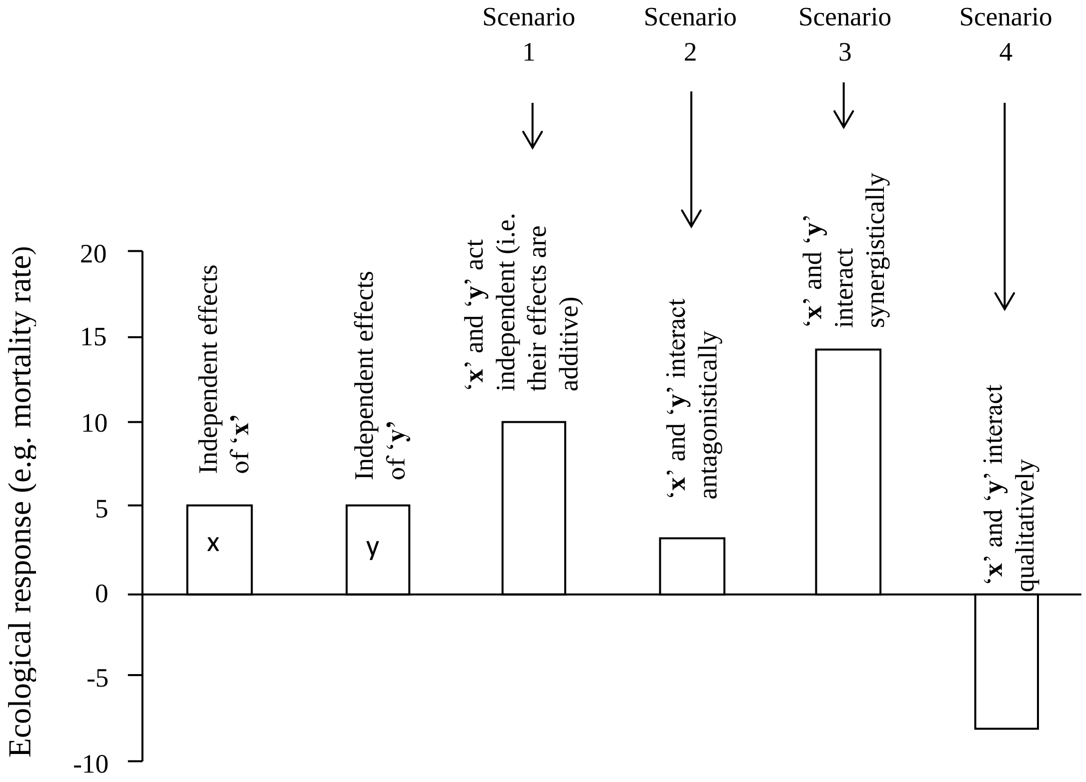


Figure 6.1 Graphical representation of different types of interactions. From left to right showing the effects of stressors 'x' and 'y' in isolation (independent effects), their effects if additive; antagonistic; synergistic and qualitative (adapted from (Crain et al. 2008).

In an ecological context, broadening current hydrological concepts about floodplain systems to take account of qualitative interactions could play an important role in understanding the consequences of multiple interacting factors on species. This may be particularly so in highly modified landscapes with multiple novel stressors. For example, Jackson and Pringle (2010) have argued that the impact of hydrologic connectivity may change qualitatively between intensively and non-intensively developed landscapes. In non-intensive landscapes, hydrologic connectivity has a strong positive effect, playing a critical role in many ecological processes important for the distribution of species in floodplain landscapes (e.g. Jackson and Pringle 2010). However, in intensively managed landscapes, such as urban and irrigated agricultural areas, increased hydrological connectivity may increase the spread of invasive species or toxic elements and cause declines in ecological function and be negative for certain species (Presser 1994; Pringle 2001; Jackson and Pringle 2010). This qualitative shift, from positive to negative (or vice versa), in the role of hydrological connectivity highlights the potential importance of qualitative interactions in ecosystems, especially in human altered floodplain landscapes.

6.1.3 Modeling interactions between multiple factors

Assessing the impacts of multiple factors and interactions on ecological response variables has been carried out using a range of statistical approaches. Darling and Côté (2008) and Bozelli et al. (2009) have used log response ratios to compare the null additive model with other possibilities (i.e. synergistic and antagonistic). In contrast, Crain et al. (2008) and Coors and De Meester (2008) utilised ANOVAs, while Christensen et al. (2006) and Townsend et al. (2008) have made use of multiple linear regression techniques, testing for interactions between factors and using the sign of the co-efficient of interactive relationships to determine whether relationships were synergetic or antagonistic.

In addition to the above methods, Bayesian statistics, and specifically, Bayesian network modelling, offers another approach which may be highly suitable for testing the importance of interactions and may also help overcome some of the limitations of traditional statistical approaches. For example, in traditional statistics, a p-value may overstate the evidence against the null hypothesis (Reckhow 1990). In contrast, a Bayesian Network (BN) approach provides a direct measure of the probability of a certain event occurring and thus is less biased (Reckhow 1990).

A Bayesian approach also allows the quantification of both independent and interactive effects (Stewart-Koster et al. 2010). A BN also enables relationships between various factors to be modelled graphically (Jensen and Nielsen 2007). Relationships between different factors, representing conditional dependencies, allow independent and interactive effects of a change in one factor, for example a change in one environmental variable, to be modelled in other factor(s) (Stewart-Koster et al. 2010). To date, a Bayesian network model approach has not been utilised to examine different types of interactions (i.e. synergistic, antagonistic and qualitative) in ecological research.

To assist understanding about different ways of conceptualising ecological systems and whether qualitative interactions occur, this study uses a Bayesian network modelling approach to understand whether hydrological and land use factors effect *E. camaldulensis* independently or interactively. Additionally, this study also asks, if environmental factors do act interactively, then what models best characterise *E. camaldulensis* response (i.e. additive models, synergistic, antagonistic and / or qualitative models as outlined in Figure 6.1.). Specifically, this study tests the hypothesis that the effects of multiple environmental factors are best characterised by different types of interactive relationships (i.e. antagonistic, synergistic and qualitative) and not by their independent or additive effects.

6.2 Methods

Study area, site selection and survey methods for vegetation and explanatory hydrological and land use data are outlined in Chapter 3, 4 and 5.

6.2.1 Advantages and limitations of Bayesian network models

While BNs have numerous advantages for modeling ecological systems there are also several limitations, which should be carefully considered. Two of the main disadvantages of BNs relevant to this study are the need to discretize continuous variables and its inability to support feedback loops (Uusitalo 2007). Generally the discretization of continuous variables is undesirable (Pollino et al. 2007) and may cause a loss in statistical power if the relationship being tested is in fact linear (Myllmyäki et al. 2002). How to successfully discretize data for use in Bayesian networks remains an issue, with no satisfactorily automatic techniques known (Uusitalo 2007). BNs are also unable to support feedback loops and as such temporal and spatial dynamics can only be modeled through the tedious task of building numerous separate BNs (Uusitalo 2007). Despite, BNs limitations they have various advantages over many other statistical methods (Ellison et al. 2004), which is leading to an increase in the use in ecological research.

Bayesian network models are becoming increasingly popular in environmental and ecological science (e.g. Howes et al. 2010). This is likely a consequence of the numerous advantages they provide when dealing with high levels of uncertainty and variability which characterize the data used to build models of ecological systems. For example, BNs allow the probabilistic presentation of interactions, which allows risks and uncertainties to be better estimated than in models which are limited to only expected values (Reckhow 1999; Uusitalo 2007). Additional to this BNs are also will equipped for dealing with missing values and small datasets (Uusitalo 2007). This is because the expectations maximization method used in Bayesian learning can cope with missing observations regardless of whether they are random or not (Heckerman 1995).

6.2.2 Building the Bayesian network model

To assess the effects of multiple environmental factors, a Bayesian network (BN) model was developed (Norsys 2008). The structure of a BN can be established using pre-existing knowledge and/or empirical data (Norsys 2008). In this study, the underlying structure of the BN was based on field data and previous regression modelling on four different vegetation response variables (child nodes) and six explanatory variables (parent nodes) (Chapter 4 & 5) (Table 6.1). In addition, a node reflecting long term rainfall was also included to help account for the potential bias of climatic conditions as data was collected during one drought period. The four vegetation nodes represented the crown vigour and abundance of small (<20cm cbh) and large (>50cm cbh) trees. Intermediate size (20-50cm cbh) trees were excluded as previous analysis revealed that they were less responsive to the environmental factors tested (Chapter 4). Stag abundance was also excluded because it included species apart from *E. camaldulensis*. Each child and parent node was classified into two states, representing 'low' and 'high'. In this study, cut-off points for the low and high states for each explanatory and response variable were derived on the basis of histograms and previous regression analysis (Chapters 4 & 5; Table 6.1). In instances where there was a clear break evident in the distribution then this was used to delineate states, otherwise the states were chosen as to reflect the spread of the data available. The discretisation of variables is often undesirable, however it nonetheless helps to highlight and make explicit our rudimentary understanding of the data we are using (Pollio et al. 2006).

In addition to the four child vegetation nodes representing crown vigour and abundance for small (<20cm cbh) and large (> 50cm cbh) trees, three index nodes representing a combined index of site crown vigour, age structure and overall wetland tree condition were also developed (Table 6.1). The three index nodes were:

(1) a node representing site crown vigour (combing small and large tree crown vigour);

(2) a node representing site age structure (combing small and large tree abundance); and,

(3) a node representing overall wetland tree condition at the site (combining site crown vigour and site age structure).

Each of these index nodes was assigned to either 'low' or 'high' states based on their parent vegetation nodes. A low crown vigour site occurred when both small and large trees had 'low' crown vigour; otherwise it was a high crown vigour site (Table 6.1). Similarly, a low age structure site occurred when both small and large trees had ‘low’ abundance; otherwise it was a ‘high’ age structure site. The overall wetland tree condition node was classified as low, only when both site crown vigour and site age structure were low. When either site crown vigour or site age structure were high then overall wetland tree condition was classified as high (Table 6.1). These index nodes, while simplifying the different measures of trees at the wetlands, allowed for the influence of the seven different environmental factors to be compared in one response variable (i.e. overall wetland tree condition).

Bayesian learning

Conditional probability tables (CPTs) quantify the relationship between different variables (i.e. between the parent and child nodes; Smith et al. 2007). Using field data, Bayesian learning was used to determine the relationships between parent and child nodes to populate the CPT (Marcot et al. 2006). The field data (case files) were based upon the surveys of *E. camaldulensis* abundance and vigour as outlined in Chapters 4 & 5. In Netica, Bayesian learning utilises an expectation maximization algorithm to iteratively process data until model fit is maximised or the desired number of iterations is reached (Norsys 2008). The expectation maximization algorithm also has the ability to deal with missing data, by finding the parameterisations that give the greatest likelihoods based on the data available (Pollino et al. 2007). In this study, the BN learnt from the data with 1,000,000 iterations (after (Howes et al. 2010). Following Bayesian learning, the relationships between each variable were represented as probabilities in the CPTs of the BN (Appendix D1). The BN was constructed using the Netica software package (Norsys 2008).

Model validation

Model performance for predicting the vegetation child nodes was assessed in Netica using the ‘test with cases’ function (Norsys 2008). This function evaluates a BN using real cases to assess how well the predictions of the net match the observed cases (Norsys 2008). Using case data, a confusion matrix, which compares predicted and actual outcomes, was developed (Marcot et al. 2006). During model validation, the data case file was split into training (80%) and testing (20%) sets. This procedure was repeated randomly 10 times and the results averaged to account for variability in model validation results.

Table 6.1 Nodes and states used in Bayesian network model.

Environmental Parent Node(s)	**Description**	**BN states**
Groundwater depth	Interpolated depths from 1987 groundwater data	Shallow <11 m Deep >11 m
Canopy cover	Foliage projected woody vegetation cover > 2m (height)	Low <20 % High >20 %
Inundation frequency	Frequency, as % number of years (1987-2005) wetland classified as inundated (Ch. 3)	Intermittent < 75 % Frequent > 75 %
Weir impact	Distance from weir (km)	Low >40 km High <40 km
Grazing intensity	Number of cow pats per 150 m^{-2}	Low < 5 cow pat.150 m^{-2} High > 5 cow pat.150 m^{-2}
Agricultural land cover	Percentage of agricultural land in each wetlands catchment	Low <40 % High >40 %
Long term rainfall	Mean annual rainfall (mm) at each wetland from 1950-2009	Low < 634 mm High > 634 mm
Vegetation Child Node(s)		
Small tree crown vigour	Crown vigour (%) of small trees < 20 cm cbh	Low < 65 % crown vigour High > 65% crown vigour
Large tree crown vigour	Crown vigour (%) of large trees > 50 cm cbh	Low < 65 % crown vigour High > 65% crown vigour
Small tree abundance	Abundance of trees < 20 cm cbh	Low > 5 / 150 m^2 High > 5 / 150 m^2
Large tree abundance	Abundance of trees > 50 cm cbh	Low > 4 / 150 m^2 High > 4 / 150 m^2
Combined Index Vegetation Child Node(s)		
Site crown vigour	Index node representing crown vigour at the site, based on the crown vigour of small and large trees.	Low = Either or both small & large trees have low crown vigour High = Both small & large trees have high crown vigour
Site age structure	Index node, which gives an indication of age structure based on the abundance of small and large trees.	Low = Either or both small and large trees have low abundance High = Both small and large trees have high abundance
Overall wetland tree condition	Index node, which gives an indication of overall tree condition at the wetland	Low =Both site age structure & site crown vigour are low High = Either site age structure & site crown vigour are high

Scenario and sensitivity analysis

Following the construction and population of the BN, sensitivity analysis was used to quantify the relative influence of the environmental factors on the vegetation response variables (e.g. Pollino et al. 2007; Smith et al. 2007; Dlamini 2010; Liedloff and Smith 2010). Sensitivity analysis can be used to quantify the sensitivity of nodes of interest (i.e. response variables) to changes in the parameters of input nodes (i.e. explanatory variables) and also allows for the sensitivity of a node to a particular factor(s) to be evaluated under different conditions (Pollino et al. 2007). For example, using sensitivity analysis Howes et al. (2010) showed that the abundance of small passerines (response variable) was more sensitive to the abundance of a larger avian competitor than other factors (e.g. grazing, understorey density). In this study, changes in the sensitivity of vegetation to environmental factors were calculated using entropy reduction (expressed as a percentage of total entropy), which indicates the degree to which findings at one node alter those at another (Marcot et al. 2006; Dlamini 2010).

To help understand how interactions between environmental factors may change the response of *E. camaldulensis* crown vigour, age structure, and overall wetland tree condition, scenario analysis was used to determine the impact of changes in the environmental nodes on the probability of different vegetation states occurring. For example, the probability of 'high' large tree abundance occurring under different environmental scenarios represented by either 'high' or 'low' grazing intensity. In Netica, when a particular state (scenario) is selected (e.g. high grazing), it is assumed that the probability of that state occurring is 100%. When a scenario is selected, the coinciding change in the probability of all other variables also changes, allowing the impact of that particular scenario to be quantified as a percentage. For example, when the state of an environmental node is changed (e.g. from low to high grazing), then the probability (change in belief) of vegetation occurring in a particular state (e.g. high abundance) may also change. This change in probability indicates the likelihood of the child nodes being in a certain state given the scenarios selected. Changes in the probability of states within child vegetation nodes were calculated for both individual effects (e.g. high grazing only) and for combination scenarios (e.g. high grazing and shallow groundwater together).

6.2.3 Interaction classifications

To determine the extent and nature of interactions, changes in the probability of each vegetation variable were compared under individual and combined effect scenarios. The changes in probability from individual effects scenarios were added to give an expected change in probability if effects were additive, that is, when each factor is assumed to act independently (e.g. x + y, scenario 1 in Figure 6.1). The change in probability, under the simple additive model was then compared with the observed change in probability under the combination scenarios. The difference in probability between the additive and combined scenarios was then used to classify interaction types. If, under the combined scenario, the change in probability was equal to that under the additive model, then the interaction was classified as additive. If the change in probability was lower than expected (i.e. combinations of stressors are less negative than compared if they acted additively), then the interaction was classified as antagonistic. If the change in probability was greater than expected (i.e. combinations of stressors are more negative than compared to if they acted additively), it was classified as synergistic. If a strong directional change was evident, for example, under additive conditions a positive relationship was expected, but a negative relationship observed, then the relationship was classified as a qualitative interaction.

6.3 Results

All Bayesian network results for each environmental factors low and high scenario are given in diagrammatic network form in Appendix D2. The following summarises the scenario analysis results for each of the vegetation nodes.

6.3.1 **E. camaldulensis** *abundance scenario analysis*

Under neutral conditions, there was a 67% probability of small trees and 75% probability of large trees having high abundance (Figure 6.3). The probability of small trees being in a high abundance state declined by 9%, to 58%, under the high weir impact scenario, while under the low weir impact scenario, it increased by 24%, to 91% (Figure 6.2a; Figure 6.3). Under the high and low agricultural land cover scenarios the, probability of small tree abundance being high, declined to 48% and increased to 82%, respectively (Figure 6.2a). The probability of large tree abundance being high increased to 93% under the shallow groundwater scenario and decreased to 69% under the deep groundwater scenario (Figure 6.2b). Under the low grazing intensity scenario, the probability of large tree abundance being high increased to 89%, while under the high grazing intensity scenario it decreased to 39% (Figure 6.2b; Figure 6.3). The small and large tree abundance models had average error rates less than 30 and 20 % respectively (Table 6.2). The BN was able to predict high abundance sites well (>85% correctly predicted), but not low abundance sites (<50% correctly predicted) (Table 6.2).

6.3.2 **E. camaldulensis** ***crown vigour scenario analysis***

Under neutral conditions, the probability of small and large trees having high crown vigour was 45 and 55%, respectively (Figure 6.3). The probability of high small tree crown vigour increased by 5% when canopy cover was low and decreased by 5% when it was high. When inundation was intermittent, the probability of high small tree crown vigour declined from 45 to 30%, but when inundation was frequent it increased to 72% (Figure 6.2c). The probability of large tree crown vigour being in a high state declined by 2%, under the high weir impact scenario and increased by 5% under the low weir impact scenario (Figure 6.2d). When inundation was intermittent, there was a 9% increase in the probability of high large tree crown vigour (Figure 6.2d). When inundation was frequent, there was a 17% decline in the probability of high large tree crown vigour (Figure 6.2d). The models for tree crown vigour had error rates of 35 to 40% (Table 6.2). Validation results indicated that the model was able to predict low crown vigour sites reasonably well, but not high crown vigour ones (Table 6.2).

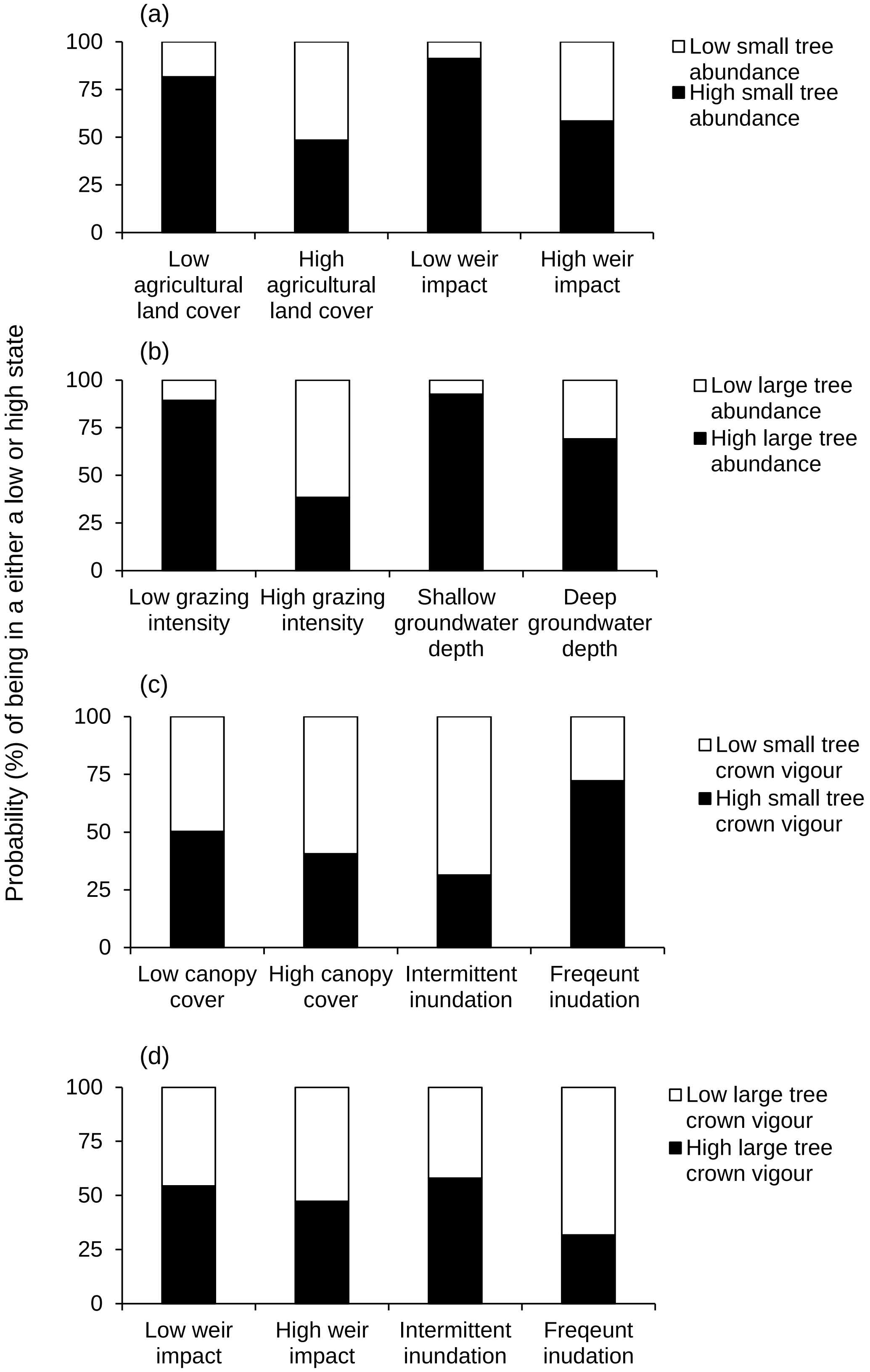


Figure 6.2 Probability of vegetation nodes (a) small abundance (b) large tree abundance (c) small tree crown vigour and (d) large tree crown vigour being in a particular state under different environmental scenarios.

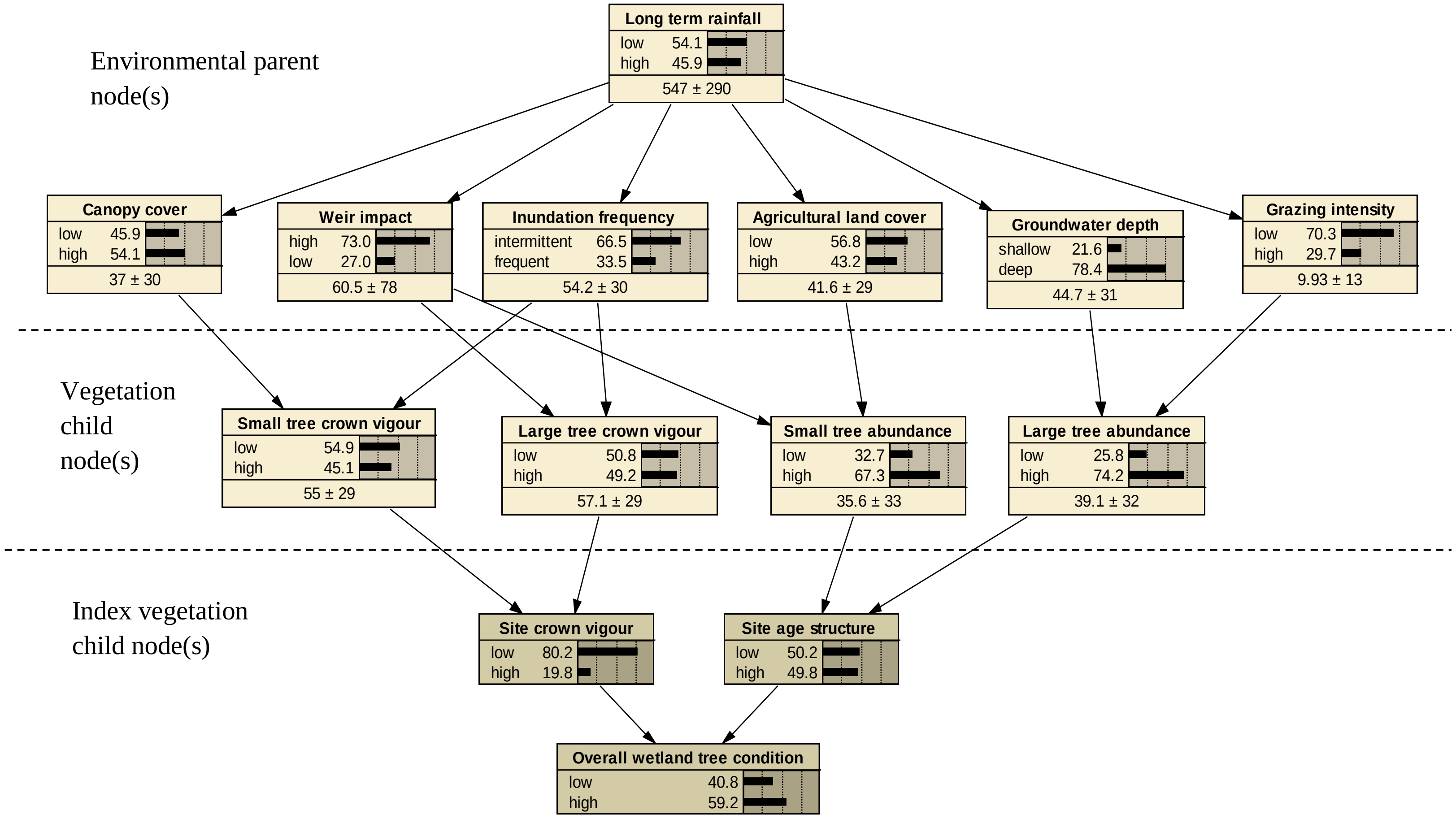


Figure 6.3 Bayesian network, showing each vegetation components relationship with environmental node(s). Values shown represent the probability (%) of the node being in a particular state; model shown is a neutral model where no scenarios are selected.

Table 6.2 Summarised confusion matrix results for each vegetation response variable showing averaged error rate (from 10 random splits of the dataset) of the BN model for each respective vegetation response variable.

Vegetation variable	**Error rate (%)**			**Correctly predicted**	
	Average	**Standard error**	**Range**	**Low state**	**High state**
Small tree crown vigour	38.28	3.79	16.67 – 50	28/39 (71.8%)	16/32 (50%)
Large tree crown vigour	34.82	2.39	28.57 – 50	31/43 (72.1%)	14/31 (45.2%)
Small tree abundance	26.25	3.46	12.5 – 50	13/27 (48.1%)	46/52 (88.5%)
Large tree abundance	18.75	3.84	0 – 37.5	9/20 (45%)	56/60 (93.3%)

6.3.3 Overall wetland tree condition scenario analysis results

Fifty nine per cent of sites had high overall wetland tree condition under neutral conditions (Figure 6.3). There was an 8% increase in the likelihood of high overall wetland tree condition when grazing was low, and a 19% decrease when grazing was high. Low agricultural land cover was associated with an 11% increase in the probability of high overall wetland tree condition, while high agriculture caused an 11% decrease in high overall wetland tree condition. When there was low weir impact, there was a 16% increase in the probability of high overall wetland tree condition and a 5% decline when the high weir impact scenario was selected. Deep groundwater was associated with a 2% decline in the probability of high overall wetland tree condition, while shallow groundwater was associated with a 7% increase. When canopy cover was low, there was a 4% increase in the probability of high overall wetland tree condition, while when canopy cover was high there was a 3% decrease. Intermittent and frequent inundation states changed the probability of high overall wetland tree condition by less than 1% (Figure 6.3).

6.3.4 Overall wetland condition sensitivity analysis results

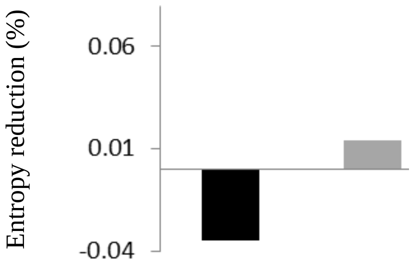
Grazing was the most influential factor on overall wetland tree condition, with 4.7% entropy reduction. Agricultural land cover and weir impact were respectively the next most influential factors, with around 3% entropy reduction each. The remaining factors all had a relatively small influence on overall wetland tree condition, each accounting for less than 0.5% entropy reduction (Table 6.3).

Table 6.3 Sensitivity analysis results ranked in increasing order of influence on overall site condition based on entropy reduction.

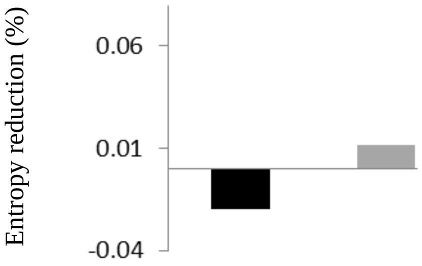
Node (Environmental variable)	**Entropy reduction (%)**
Grazing intensity	4.67
Agricultural land cover	3.10
Weir impact	2.99
Groundwater depth	0.41
Canopy cover	0.32
Long term rainfall	0.02
Inundation frequency	< 0.01

Relative to neutral conditions, the sensitivity of overall wetland tree condition to environmental factors changed under different scenarios (Figure 6.3). Overall wetland tree condition was more sensitive to grazing intensity under the deep groundwater scenario (Figure 6.3a), agriculture under high weir impact (Figure 6.3b), weir impact under high agriculture and frequent inundation (Figure 6.3c & d), canopy cover under both the intermittent and frequent inundation scenarios (Figure 6.3f) and inundation under low weir impact and both canopy cover scenarios (Figures 6.3g & h). Overall wetland tree condition was less sensitive to grazing under shallow groundwater (Figure 6.3a), agriculture under low weir impact (Figure 6.3b), weir impact under low agriculture and intermittent inundation scenarios (Figures 6.3c & d) and ground water depth under low grazing (Figure 6.3e).

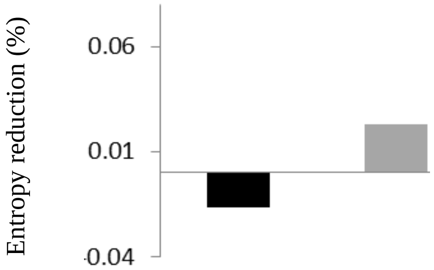
(a) Grazing intensity (■ shallow groundwater ▨ deep groundwater)



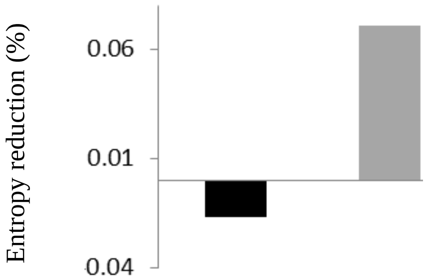
(b) Agricultural land cover (■ low weir impact, ▨ high weir impact)



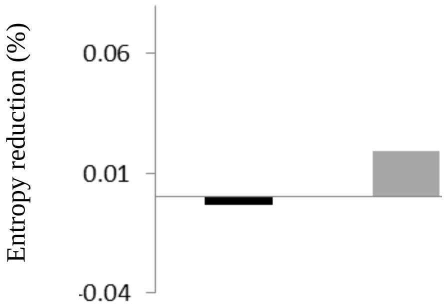
(c) Weir impact (■ low agriculture, ▨ high agriculture)



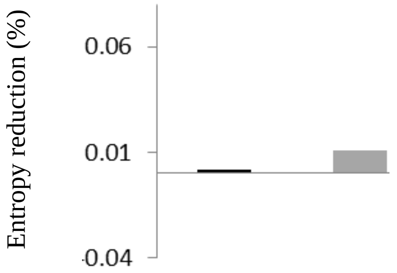
(d) Weir impact (■ intermittent inundation, ▨ frequent inundation)



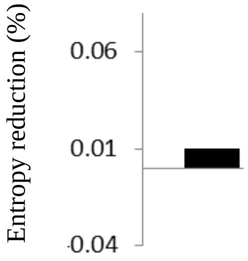
(e) Groundwater depth (■ low grazing, ▨ high grazing)



(f) Canopy cover (■ frequent inundation, ▨ intermittent inundation)



(g) Inundation frequency (■ low canopy cover, ▨ high canopy cover)



(h) Inundation frequency (■ low weir impact, ▨ high weir impact)

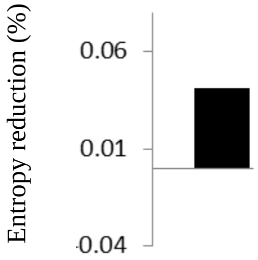


Figure 6.4 Change (relative to ‘neutral’ conditions) in sensitivity of overall wetland tree condition to different factors under different environmental scenarios.

The sensitivity of overall wetland tree condition to environmental factors changed under low and high rainfall scenarios (Figure 6.4). Under the low rainfall scenario, overall wetland tree condition was more sensitive to inundation, canopy cover, weir impact and grazing intensity than under the high rainfall scenario (Figure 6.4). Overall wetland tree condition was more sensitive to groundwater depth and agricultural land cover under the high rainfall scenario than the low rainfall scenario (Figure 6.4).

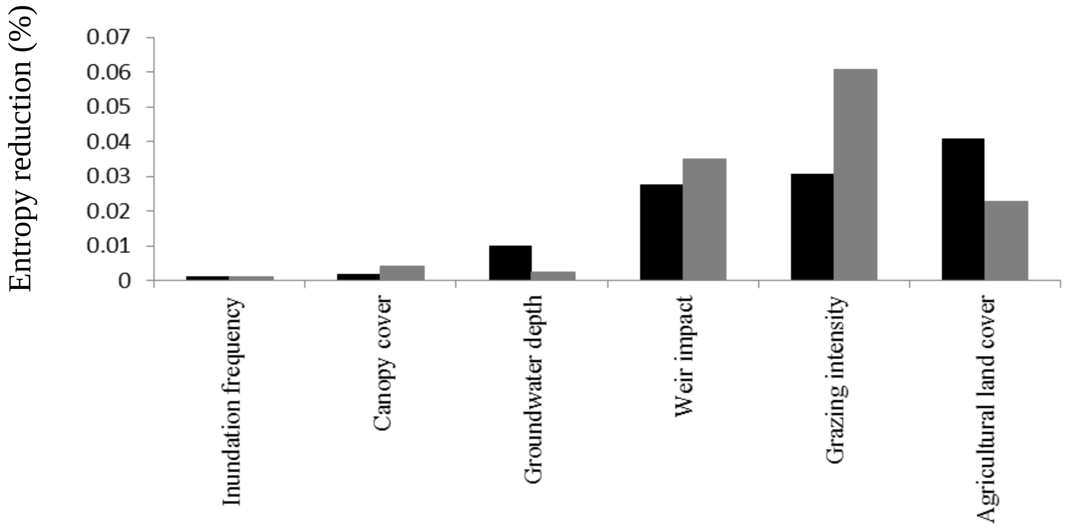


Figure 6.5 Sensitivity of overall wetland tree condition to environmental factors under high (black bars) and low (grey bars) rainfall scenarios.

6.3.5 **E. camaldulensis** ***abundance and interactions***

The observed change in the probability (relative to neutral conditions) of both small tree and large tree crown vigour and abundance, differed under the combination scenario compared to the expected (additive) effects (Table 6.4; Figures 6.5 & 6.6).

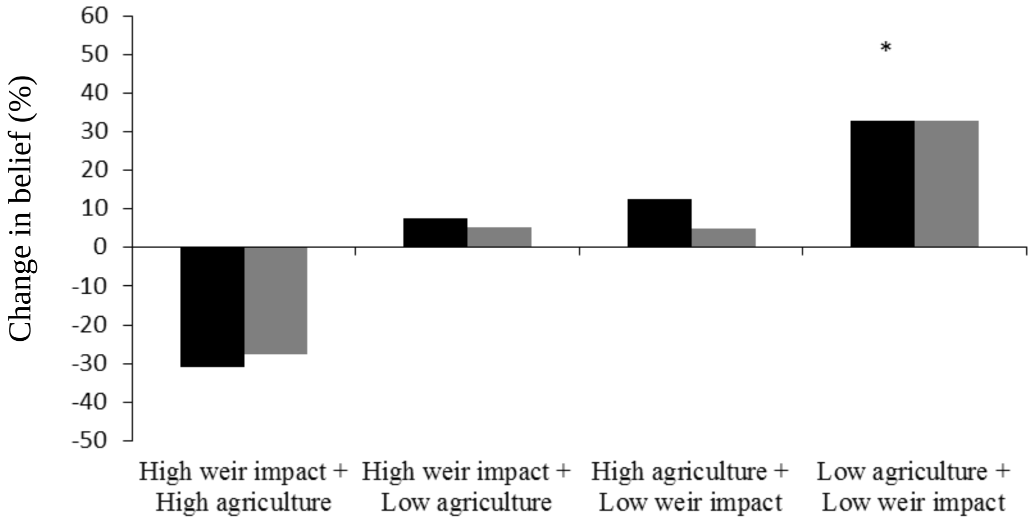
Under high weir impact and high agricultural land cover scenarios, the probability of high small tree abundance was lower than expected if effects were additive (Figure 6.5a) and so, the interaction was classified as synergistic (Table 6.4). Under high weir impact and low agricultural land cover and low weir impact and high agricultural land cover, the probability of small tree abundance being high was greater than expected if these factors interacted additively (Figure 6.5a) and as such, the interaction was classified as antagonistic (Table 6.4). Under combination scenarios of shallow groundwater and high grazing intensity, as well as deep groundwater and low grazing intensity, large tree abundance was more likely to be high compared to if these factors acted additively and as such the interactions were classified as being antagonistic (Figure 6.5b; Table 6.4). Under high grazing and deep groundwater scenarios the probability of large tree abundance being in a high state was lower relative to if effects were additive (Figure 6.5b). High grazing and deep groundwater scenarios had a more negative effect on large tree abundance than expected and were classified as acting synergistically (Table 6.4).

Table 6.4 Summary of interactive relationships in Bayesian network model for each vegetation variables and their corresponding environmental factors.

Vegetation response and Environmental factor(s) models	**Difference from additive (expected)**	**Interaction type**		
		Synergistic	**Antagonistic**	**Qualitative**
Small tree abundance				
High weir + High agriculture	(-) 3.1	YES	-	-
High weir + Low agriculture	(+) 2.3	-	YES	-
High agriculture + Low weir	(+) 7.7	-	YES	-
Low agriculture + Low weir	0*	NA	NA	NA
Large tree abundance				
Shallow groundwater + High grazing	(+) 18.1	-	YES	-
High grazing + Deep groundwater	(-) 4.8	YES	-	-
Low grazing + Shallow groundwater	0*	NA	NA	NA
Low grazing + Deep groundwater	(+) 2.2	-	YES	-
Small tree crown vigour				
Intermittent inundation + Low canopy cover	(+)19	-	-	YES
Intermittent inundation + High canopy cover	(-) 15.8	YES	-	-
Frequent inundation + Low canopy cover	(-) 37.4	-	-	YES
Frequent inundation + High canopy cover	(+) 32.3	-	YES	-
Large tree crown vigour				
Intermittent inundation + Low weir	(-) 25.7	-	-	YES
Intermittent inundation + High weir	(+) 10.6	-	YES	-
Frequent inundation + Low weir	(+) 63.1	-	-	YES
Frequent inundation + High weir	(-)17.3	YES	-	-

* If combined factor scenarios exceed 100% differences between observed and expected effects cannot be calculated (Folt et al., 1999; Darling and Cote, 2008).

(a) Small tree abundance



(b) Large tree abundance

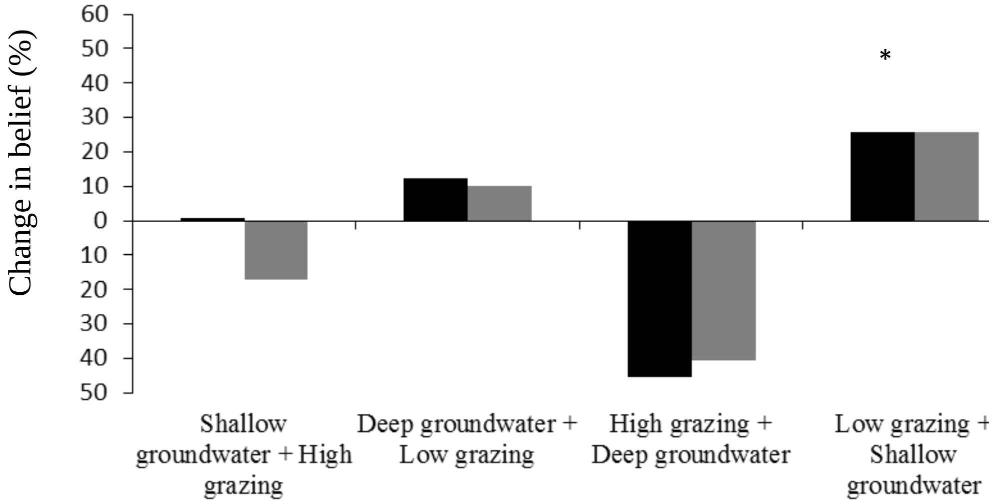


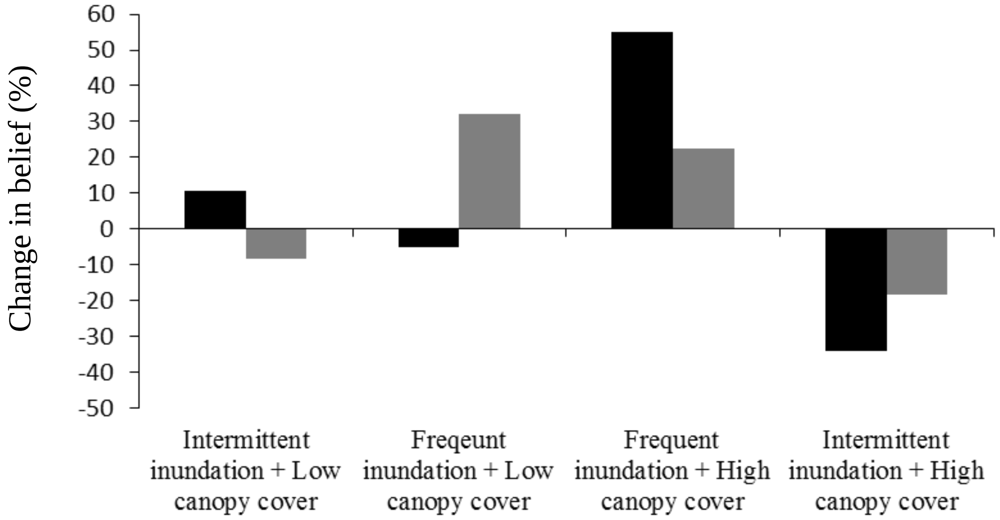
Figure 6.6 Observed (black bars) and expected (grey bars) representing change in belief (probability) of high abundance for (a) small trees and (b) large trees relative to ‘neutral conditions’. *When combined factor scenarios exceed 100%, interactions cannot be interpreted (Folt et al. 1999; Darling and Cote 2008).

6.3.6 **E. camaldulensis** ***crown vigour and interactions***

Under frequent inundation and high canopy cover scenarios, as well as intermittent inundation and high weir impact scenarios, observed effects were less negative than expected for both small and large tree crown vigour and were classified as antagonistic (Figure 6.6a & b; Table 6.4). Observed effects on small and large tree crown vigour were more negative than expected under intermittent inundation and high canopy cover and frequent inundation and high weir impact scenarios and were classified as synergistic (Figure 6.6a & b; Table 6.4).

Under intermittent inundation and low canopy cover scenarios and under frequent inundation and low weir impact scenarios, the probability of small and large tree crown vigour being high was positive respectively, not negative as was expected if combined effects were additive (Figure 6.6a & b). Under frequent inundation and high canopy cover scenarios and intermittent inundation and low weir impact scenarios, the probability of small and large tree crown vigour being high was negative, while it was positive if expected effects were additive (Figure 6.6a & b). In the above instances, as there was directional change between observed and expected effects (i.e. the observed effect was positive while the expected was negative (or vice versa)), the interactions were classified as qualitative (Table 6.4).

(a) Small tree crown vigour



(b) Large tree crown vigour

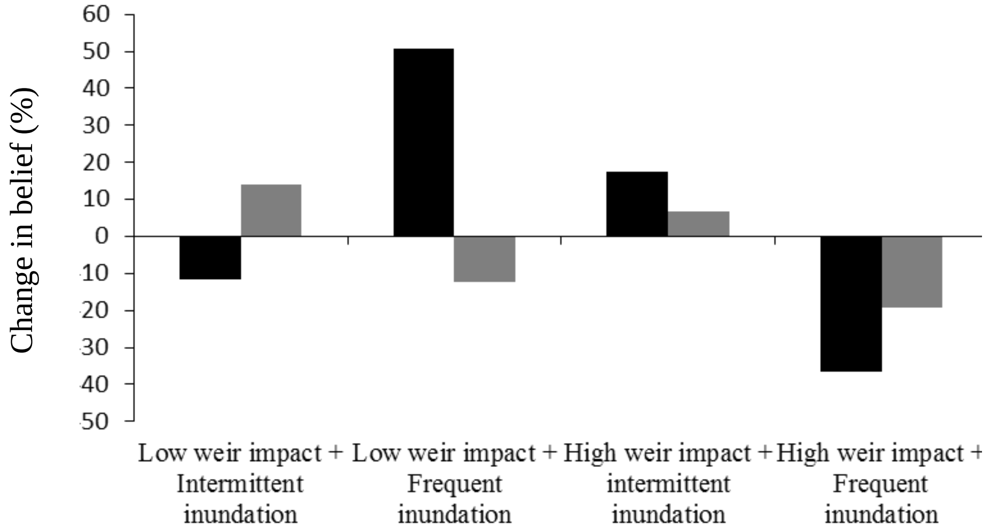


Figure 6.7 Observed (black bars) and expected (grey bars) representing change in belief (probability) of high crown vigour for (a) small trees and (b) large trees relative to ‘neutral conditions’.

6.4 Discussion

Much research has documented the independent effects of hydrological and land use factors on floodplains, rivers, wetlands and ecosystems more broadly (e.g. Taylor et al. 1996; Robertson and Rowling 2000; Stromberg 2001; van der Valk 2005; Renofalt et al. 2007). However, while studying the direct impacts of environmental factors is important for understanding and managing ecological systems, it may not always reflect how species respond to their environment, and especially, whether they respond to interactions (Sala et al. 2000; Crain et al. 2008; Tylianakis et al. 2008; Matthaei et al. 2010; Poff and Zimmerman 2010). Failure to consider interactions and how they vary (e.g. synergistic, antagonistic and qualitative), may lead to an over or under estimation of how species relate to their environment and potentially counterproductive management actions (Crain et al. 2008). In this study, small and large *E. camaldulensis* crown vigour and abundance response to combinations of hydrological and land use factors differed from what would be expected if environmental factors operated independently (additively). Consequently, the results of this study support the hypothesis that the effects of multiple environmental factors are best characterised by different types of interactive relationships (i.e. antagonistic, synergistic and qualitative) and not by their independent or additive effects.

6.4.1 Interactions between environmental factors

Numerous studies have highlighted the influence of interacting environmental factors on species responses and ecological processes, observing both synergistic and antagonistic responses (e.g. Folt et al. 1999; Christensen et al. 2006; Didham et al. 2007; Bancroft et al. 2008; Brook et al. 2008; Coors and De Meester 2008). Folt et al. (1999) examined the effects of multiple stressors on the reproduction and survival of two species of cladaceran zooplankton and observed both synergistic and antagonistic interactions. Crain et al. (2008) reviewed studies on the cumulative effects of multiple stressors in marine and coastal environments for various key ecological variables (i.e. species richness, biomass, abundance, disease severity) by classifying effects as additive, synergistic or antagonistic. They found that relationships were relatively evenly distributed over additive (26%), synergistic (36%) and antagonistic (38%). Crain et al. (2008) argue that, collectively, these studies in marine communities provide robust evidence that multiple stressors generally interact in marine ecosystems. Similarly, in an assessment of the effects of multiple stressors in boreal lakes in north western Canada, it was observed that interactions between drought, warming and acidification, better explained changes in planktonic consumer and producer biomass than the sum of their individual additive effects (Christensen et al. 2006).

The results of this study also fit with previous research in floodplain systems, which have shown antagonistic and synergistic responses of species to interactions between the environmental factors (Leyer 2005; Matthaei et al. 2010). In broad agreement with Leyer (2005) and (Matthaei et al. 2010), this study also observed a variety of interactive relationships for a floodplain species, *E. camaldulensis* response to environmental factors. These similarities suggest that regardless of the species and factors examined, interactions could be a frequent occurrence in ecological systems (Hames et al. 2006).

6.4.2 Interactions in floodplain systems

In addition to being characterized by interactive models, *E. camaldulensis* responses fit well with studies in environments exposed to similar factors, such as grazing. For example, in Murrumbidgee River, southern Australia, grazing may act synergistically on *E. camaldulensis* recruitment as it exacerbates the consequences of reduced water availability from river regulation (Meeson et al. 2002). This may be because interactions between grazing and climate may result in an overall decline in water availability, as grazing can increase moisture loss from the soil (Landsberg et al. 2002; Hulme 2005). In a general sense, the relationships between grazing and groundwater, and agriculture and weir impacts in this study suggest a similar situation; namely that declines in water availability may make species more susceptible to other environmental stressors, such as grazing and or those associated with agriculture at the catchment scale. (Folt et al. 1999) also hypothesized that when stressors interacted synergistically, it may be because any factor that reduces vigour is also likely to reduce that individual's ability to withstand further stressors. Consequently, the effects of multiple negative environmental stressors may be synergistic for many species.

Antagonistic responses to combinations of stressors have also been noted in floodplain environments (e.g. Matthaei et al. 2010). In small streams converted to pasture in southern New Zealand, Townsend et al. (2008) noted that the negative effects of sedimentation on *Deleatidium* spp. abundance, which impacted their habitat quality and physiology, was partially offset by high nutrient levels that increased algal productivity to the benefit of *Deleatidium* spp. However, in this instance, Townsend et al. (2008) argued that the negative effects of sedimentation strongly outweighed any positive antagonistic impacts of higher nutrients for *Deleatidium* spp. In the present study, when shallow groundwater or low weir impact was present, the coinciding negative impacts of high grazing intensity or high agriculture were also less detrimental (i.e. the combination was antagonistic) relative to when effects of these factors were simply additive. Christensen et al. (2006) also argued that in some instances exposure to one factor may improve tolerance to another stress and as such, lead to potential antagonistic interactions between stressors. This study in combination with others (e.g. Townsend et al. 2008; Matthaei et al. 2010) supports this conjecture.

6.4.3 Qualitative interactions

Contrasting with previous research, this study utilised a conceptual scheme, which classified interactions not only as synergistic and antagonistic, but also as qualitative. A qualitative interaction was defined as a response that was directionally different from that expected under independent additive effects. Qualitative interactions are seldom described in the ecological literature; however, there are recent examples of where species responses to a certain factors have qualitatively changed when compared under different conditions (e.g. Leyer 2005; Bozelli et al. 2009; Crain et al. 2008; Daleo et al. 2009). In this study, the relationship between canopy cover and weir impact on the crown vigour of small and large *E. camaldulensis* qualitatively changed, in terms of direction of effect, depending on whether the wetland was intermittently or frequently inundated. Expanding current conceptualizations to include qualitative interactions, although unlikely to lead to different conclusions about the extent of interactions versus independent effects in ecosystems, is still likely to have significant implications for ecological understanding.

6.4.4 Significance and implications – Conceptualizing interactions in ecosystems

Current ecological thinking is predominantly restricted to synergistic and antagonistic interactions (e.g. Christensen et al. 2006; Crain et al. 2008; Townsend et al. 2008; Matthaei et al. 2010); however, expanding conceptual thinking to include qualitative interactions could play an important role in helping to understand the consequences of multiple factors on species. Jackson and Pringle (2010) also highlighted how the influence of other factors, namely hydrological connectivity, may switch from positive to negative in different landscape contexts. Hydrological connectivity is generally seen as a fundamental part of restoring the ecological functioning in river floodplain ecosystems. However, it may interact qualitatively in different landscape settings, having positive effects in relatively unmodified landscapes, but negative effects in highly modified (e.g. urbanised and intensively used agricultural landscapes) where it may facilitate the spread of pollution and invasive species (Jackson and Pringle 2010). Similarly, the results of other studies suggest that in certain situations, factors thought to have positive effects on a particular species (e.g. increased water period Bozelli et al. (2009)); or reduced grazing by burrowing crabs Daleo et al. (2009)), may actually have negative effects as a consequence of interactions

More broadly, there are also significant ecological implications if species responses are better characterised by considering different types of interactions between environmental factors, rather than by a simple consideration of their independent effects. If multiple environmental factors influencing a species are assumed to act independently, when they in fact operate interactively, then it is likely that effects will be either under or overestimated (Sala et al. 2000; Christensen et al. 2006; Crain et al. 2008). As such, the effects of stressors on species may be only partially understood by studying their individual and independent effects (Townsend et al.

2008; Matthaei et al. 2010). Consideration of interacting effects is therefore also likely to be an important step in leading to a more complete understanding of the consequences of environmental changes, which often occur concurrently and therefore may interact (e.g. changes to hydrology and land use often occur together (Miller et al. 1995; Thompson and Polet 2000; Nilsson et al. 2005)).

In floodplain, river and wetland environments, the explicit consideration of different interaction types is also likely to improve understanding of how species respond to changes in their environment, including how they respond to hydrology. However, much research aimed at understanding the effects of anthropogenic activities in floodplain environments often focuses on the individual impacts of hydrological changes (e.g. reductions in stream flow) without considering how interactions with other factors may alter species responses (but see Townsend et al. 2008; Matthaei et al. 2010). For example, Matthaei et al. (2010) concluded that as a result of interactions, the effects of water extraction from streams is likely to be more severe for invertebrate fauna affected by high sedimentation compared to those with lower sediment levels. In New Zealand, stream habitats Townsend et al. 2008 also noted that the negative effects of sedimentation on *Deleatidium* spp. abundance, which impacted their habitat quality (i.e. decline in water quality), was partially offset by high nutrient levels that increased algal productivity to the benefit of *Deleatidium* spp. Resonating with the above conclusions, this study suggests that groundwater decline and weir impacts on *E. camaldulensis* will be far more detrimental in wetlands with high grazing and agricultural land cover, relative to ones with low grazing and agricultural land cover. If ecological management of floodplain systems does not take account of the nature of interactions, then restoration efforts may be limited and in some instances, even counterproductive, if species respond to qualitative interactions.

Within the Condamine Catchment, the failure to consider interactions is also likely to have significant implications for management. If a range of interaction types are present, as suggested by this results study, then investigations into the environmental consequences of for example, deepening groundwater (Barnett and Muller 2008) in the catchment will not be fully appreciated unless interactions with other hydrology and land use factors are considered. In the future, research and management of floodplain wetlands within the Condamine Catchment needs to careful consider synergistic, antagonistic and potentially qualitative interactions between factors (e.g. groundwater and grazing) or else the consequences of future environmental changes (e.g. mining, Queensland Department of Environment and Resource management 2010) may over or under estimated.

6.4.5 Limitations and future directions

Although in broad agreement with previous studies examining interactions amongst environmental factors, there are several limitations of this study that should be addressed in future research. Firstly, while the selected factors were based on previous regression analysis (Chapter 4 & 5), under the categorisations used in the BN model developed, high abundance and low crown vigour could be predicted well, but not low abundance and high crown vigour. Consequently, it is likely that other factors not modelled would explain additional variation in sites classified as low abundance and high vigour. However, the implications of model performance are dependent on how the model will be used (Marcot et al. 2006). As such, future models with better predictive ability should be built before extrapolating specific findings in a quantitative form (e.g. before saying an agricultural land cover of certain value causes wetlands to have *E. camaldulensis* present in either low or high condition). Nonetheless, the conceptual framework and methods outlined in this study provides a starting point for exploring the consequences of interactions in floodplain landscapes and more broadly in human modified landscapes where multiple interacting factors are likely to influence species.

In addition, as the model developed utilised data from surveys during relatively dry periods, it remains uncertain as to whether the interactions observed here are temporally consistent. The variable sensitivity of overall wetland tree condition to grazing, agricultural land cover and weir impact scenarios under low and high rainfall scenarios suggests that the relationships observed may change under different climatic conditions. Surveying vegetation under different climatic conditions is thus likely an important future step. If sampling was carried out during a wet period then results may have differed, especially for measures of tree condition, such as crown vigour. Eldridge and Lunt (2010) also argue that estimates of site condition or degradation in dry periods may differ greatly to estimates in wet periods. Consequently, care should be taken before the relationships identified for *E. camaldulensis* floodplain wetland are extrapolated to other agricultural landscapes and to different climatic conditions.

Finally, the dataset used to construct the BN was limited to 37 sites. Although, BNs require no minimum sample size and are still able to show high predictive accuracy even with small sample sizes (Kontkanen et al. 1997; Uusitalo 2007). Nonetheless, the limited dataset does mean that the confidence and generalisations which are valid to make from the models constructed here limited and in the future the model would benefit from the inclusion of data over greater spatial and temporal scales.

Despite the data and temporal limitations, the general approach outlined, which considers both hydrological and land use factors, still provides a starting point for future studies. These limitations may also be addressed in some part by the use of BN model, which allows future data (e.g. data collected wet periods) to be directly integrated with current data. Consequently, using a BN approach and scenario analysis the integration of data sets from different climatic periods would help elucidate how important variation in broad scale climatic conditions are in driving *E. camaldulensis* response to the factors examined and the interactions between them.

6.5 Conclusion

This study examined how a dominant wetland tree species, *E. camaldulensis* responded to multiple hydrological and land use factors, to assess firstly, whether factors acted independently or interactively and secondly, the nature of any interactions. *E. camaldulensis* relationships with environmental factors varied depending on the state of other factors (e.g. large *E. camaldulensis* abundance was more sensitive to grazing in deep groundwater compared to shallow groundwater areas), suggesting that the effects of environmental factors are best understood by examining the interactive effects and not just their independent effects. Furthermore, through an examination of the nature of interactions, this study expanded current conceptual thinking and showed that interactions between environmental factors may be classified not only as synergistic or antagonistic, but also as qualitative when two environmental factors interact to cause not only a decrease or increase in the effect of certain factors, but also a direction change from positive to negative or vice versa. The failure to consider interactions, and how they vary (e.g. synergistic, antagonistic and qualitative), may lead to an over or under estimation of how species relate to their environment and potentially counterproductive management actions.

Chapter 7. General discussion and conclusions

7.1 Thesis summary

The principle aim of this thesis was to evaluate two hypotheses: the hydrology hypothesis, that floodplain wetlands are best understood by exclusively focusing on hydrological factors; and, in contrast, the interactive hydrology-land use hypothesis, that the ecology of floodplain wetlands requires an examination of the impacts of both hydrological and land use factors, as well as interactions between them. To help achieve this, four studies examining the fringing (riparian) vegetation of wetlands in the Condamine Catchment of south east Queensland, Australia, were undertaken.

Initially, Chapter 3 developed a range of hydrological metrics and compared how modified and unmodified wetlands differed in relation to hydrology. Modified wetlands were on average closer to the river and received more rain volume per annum, as a consequence of having large catchment areas. It was concluded that 'natural' unmodified and modified wetlands represented significantly different systems in terms of their hydrology.

Utilising the hydrological metrics in Chapter 3, as well as a range of biotic and land use factors, Chapter 4 tested the hydrology hypothesis, by investigating whether hydrological factors are the only determinants of *E. camaldulensis* crown vigour and tree stag abundance of floodplain wetlands in an agricultural landscape. Multiple-regression models explaining crown vigour and stag abundance were consistently composed of hydrological factors, with inundation frequency, groundwater depth and distance from weir, explaining significant amounts of variation in tree crown vigour and stag abundance. Models for small tree crown vigour and stag abundance also included canopy cover. Canopy cover may affect crown vigour through it influence on water availability and as such its inclusion in models could not justify the rejection of the hydrology hypothesis. The results of Chapter 4 therefore support the hydrology hypothesis and suggest that an exclusive focus on hydrological factors for understanding tree crown vigour and stag abundance was not compromised by not considering the impacts of land use factors.

Chapter 5 modelled how hydrological and land use factors influenced the occurrence (presence/absence) of *E. camaldulensis.* Both hydrological and land use variables were significant determinants of *E. camaldulensis* occurrence. Hydrological factors (river connectivity, groundwater depth and distance from weir) and land use factors (grazing and agricultural land cover) all explained significant variation in *E. camaldulensis* occurrence. However, aside from < 10 cm cbh trees, hydrology plus land use factor models had consistently better predictive performance and explained more variation than hydrology factor only models. It was concluded that the failure to consider both hydrology and land use factors will lead to an incomplete understanding of the factors limiting the occurrence of *E. camaldulensis* in the floodplain wetlands of the Condamine Catchment.

Chapter 6 used a Bayesian network modelling approach to integrate the results from Chapters 4 and 5 to examine whether hydrological and land use factors influenced *E. camaldulensis* independently or through interactive relationships. The observed effects when two factors were modelled together consistently differed from what would be expected if each factor operated independently (i.e. additively). The relationships between *E. camaldulensis* crown vigour and abundance and overall wetland condition with the hydrological and land use factors examined was best characterised by different types of interactions (synergistic, antagonistic and qualitative).

7.2 Hydrology hypothesis versus interactive hydrology- land use hypothesis

The results of thesis provide conflicting evidence about the two opposing hypotheses tested. The failure to reject the hydrology hypothesis was not universal for all of the different aspects of *E. camaldulensis* examined. Measures of crown vigour and stag abundance in Chapter 4 only showed significant relationships with hydrological factors. Furthermore, in Chapter 5, logistic regression models for the occurrence of the smallest size class (<10cm cbh) were not improved by the addition of land use factors. In contrast, Chapter 5 and 6 provided evidence against the hydrology hypothesis. All size classes examined in Chapter 5, aside from the <10cm cbh class, showed that land use factors significantly improved models explaining the occurrence of *E. camaldulensis*. Chapter 6 also showed that hydrology factors interacted with other environmental factors and as such, their impacts could not be quantified or understood independently, as would be assumed under the hydrology hypothesis.

The conflicting responses of the variables tested suggest that neither the hydrology hypothesis nor interactive hydrology – land use hypothesis was universally applicable for understanding all aspects of *E. camaldulensis* in the floodplain wetlands examined. The two hypothesises are therefore not mutually exclusive; both are applicable depending on the aspect examined (i.e. crown vigour or occurrence). Nonetheless, the results do show that it is not valid to assume that only hydrological factors are important drivers of all ecological aspects in these systems. Consequently, the additional consideration of land use factors is needed to give a more complete understanding of how this species relates to its environment. Without this broader examination, then other factors (e.g. land use) limiting the occurrence of *E. camaldulensis*, as well as how it responds to interactions, may be overlooked and as such ecological understanding and management compromised

7.3 Significance and implications

Current hydrological concepts (e.g. hydrological connectivity, water regime etc.) success in understanding and predicting the consequences of hydrological changes, such as water extraction and regulation, have highlighted the critical role that hydrological processes play in floodplain systems. However, the success of these concepts has arguably led to much research being exclusively focused on the role that hydrology plays in shaping floodplain, river and wetland ecology (e.g. Hughes, 1990; Toner and Keddy 1997; Vervuren et al. 2003; Lite et al. 2005).

However, despite the utility of current hydrological concepts for understanding and predicting losses and degradation of river-floodplains and their dependent species, it has been argued that current concepts would benefit from a more interdisciplinary approach, which takes better account of other potential drivers such as land use and interactions (Robertson 1997). Other studies on riparian and wetland vegetation have also suggested that land use factors are important determinant of the ecology of floodplain systems (Ogden 2000; Meeson et al. 2002; Turner et al. 2004), potentially challenging the proposition that a hydrology focused perspective is the only driver that needs to be examined to understand wetland ecosystems. This study similarly showed that hydrology only research is limited for understanding *E. camaldulensis* in the wetlands of the Condamine Catchment of southern Queensland.

Observing that the inclusion of hydrology and land use into models provides a more complete understanding of the ecology of floodplain wetlands suggests that future research in the production landscape of the Condamine Catchment should not be restricted to identifying the influence of hydrology factors only. The Condamine Catchment, as with many agriculturally productive areas, has been subject to extensive hydrological and land use changes. In the future, the impacts of these changes on the ecology of the catchment may be further exacerbated by newly developing industries (e.g. mining and groundwater pumping) (Department of Environment and Resource Management 2010). However currently, much of the environmental concern about the Condamine River and its floodplain is in regards to hydrological impacts (e.g. from water extraction and climate change) (MDBA 2005; CSIRO 2008; but see Reardon-Smith 2011 who has recently examined the impacts of hydrological and land use factors on riverine riparian vegetation).

Contrasting with the approach outlined above, the results of this thesis suggest that if the impact of current and future environmental changes is to be more fully understood, then it is imperative that land use factors should be considered in addition to hydrological factors. Furthermore, the different types of interactions observed suggest that investigations into the environmental consequences of for example. deepening groundwater in the catchment will not be fully appreciated unless interactions with other hydrology and land use factors are considered. In the Condamine Catchment, the failure to do consider land use and interactions may not only lead to models which have less predictive and explanatory power, but also management which is sub-optimal and inefficient.

However, it is important to note that the alternate interactive hydrology-land use hypothesis suggested here does not understate the importance of hydrology. The relationships between *E. camaldulensis,* river connectivity and groundwater depth observed in this research, fit cogently with current hydrological concepts, particularly those highlighting the importance of connectivity (Amoros and Roux 1988; Amoros and Bornette 2002; Pringle 2003). Instead, an interactive hydrology and land use perspective, simply contends that a hydrological (and river-centric) perspective may be improved by the consideration of land use factors and interactions, which are sometimes overlooked in the research and management of floodplains systems.

7.4 Management implications

The management implications of acknowledging a range of land use and hydrological factors has been considered for different ecological components of floodplain ecosystems (e.g. Ogden 2000; Robertson and Rowling 2000; Meeson et al. 2002; Allan 2004; Jenkins et al. 2005; Houlahan et al. 2006). A common observation of these studies is that actions aimed solely at ameliorating hydrological changes may be suboptimal, if concurrent land use practices are not also addressed (Robertson 1997; Ogden 2000), arguing that even if environmental flows are restored various negative impacts from agriculture are likely to persist (Ogden 2000). Indeed, Nias (2003) has questioned whether in some agricultural landscapes, it is even possible to recover habitat values just by re-instating hydrological flows. Houlahan (2006) also argued that failure to incorporate adjacent land use practices which impact on wetlands makes some current management practices inadequate. The results of this research also suggest that hydrology-focused management may be limited for floodplain wetlands within agricultural landscapes.

This study suggests that the nature of interactions between drivers of ecological patterns may have significant consequences for management, particularly if it is exclusively focused on hydrological factors. If it is assumed that multiple stressors interact independently (or additively), then management actions (e.g. application of environmental flows) may be carried out directly with a relatively high degree of confidence about the outcomes of these actions (Crain et al. 2008). Conversely, if synergistic, antagonistic and qualitative interactions are considered (or present) then the benefits of any given management action may be far greater or less than expected (Crain et al. 2008; Matthaei et al. 2010).

Broadening perspectives to include land use as well as explicitly recognising interactions does not exclude the use of hydrologically focused management, such as environmental flows in other areas for other goals (geomorphic, socio-economic etc.), nor detract from its fundamental importance in the ecological restoration of river-floodplain systems. On the contrary, the broader perspective advocated in this thesis, should help highlight where the application of scant environmental flows will have the most mutual benefits. In instances where large scale hydrological changes have limited water availability in the environment and where socio-economic priorities exclude the possibility of reversing such changes, then a perspective which considers interactions may also help identify where reducing the impacts of non-hydrological stressors may mitigate current hydrological stressors and be highly beneficial for remaining ecological communities. This may be particular so if qualitative interactions are prevalent.

Qualitative interactions represented a novel way of conceptualising interactions in ecological systems and were defined as two environmental factors interacting to cause not only a decrease or increase in the effect of the factors, but also a directional change (from positive to negative or vice versa). If qualitative interactions are evident, as may result in polluted agricultural landscapes (e.g. Jackson and Pringle 2010) or from interactions between weirs and wetland inundation (Chapter 6), then the application of environmental flows may in fact have a ‘negative’ effects on overall ecological condition and thus, be counterproductive.

7.5 Limitations

Limitations are discussed in more detail in the relevant chapters; however, there are three key limitations of this study, which should be considered. Firstly, sampling was restricted to one off surveys during an extended dry period. Secondly, a focus on the wetland tree species, *E. camaldulensis*. Finally, only a limited number of hydrology and land use factors were tested. The implications of the above limitations are discussed below.

Spatial and temporal dynamics are a universal problem when studying ecological communities and call into question the validity of extrapolating information from one study to different spatial and temporal scales and contexts (Wu and Li 2006). This issue may be especially pertinent in floodplain rivers and wetlands that are largely driven by spatial and temporal hydrological dynamics (Tockner and Stanford 2002; Chapter 1). For example, if sampling was carried out during a wet or neutral period then results may have differed considerably, especially for measures, such as crown vigour. Eldridge and Lunt (2010) have also argued that estimates of site condition or degradation in dry periods may differ greatly to estimates in wet periods. Nonetheless, even though the results of this study may have varied if carried out under different climatic conditions, they still show that even if only under dry conditions the additional consideration of land use and interactions is important for floodplain wetlands. In the future, surveying vegetation under different climatic conditions will be an important step in further testing the hydrology hypothesis presented here, as well the importance of considering land use and interactions for floodplain systems.

The focus of this study on a dominant perennial tree species *E. camaldulensis* should also be considered. The risks of focusing research on one or a few species are highlighted by Wiens (2002) who suggests that as all species exhibit unique relationships with their environment. A species-based approach for understanding riverine landscapes may lead to situation-specific findings with limited generality. However, while this is a significant limitation of the current study, the importance of *E. camaldulensis* as a structurally and functionally ecological important species, is well recognised (Boulton and Lloyd 1991; Briggs et al. 1997; Mac Nally et al. 2001; Wen et al. 2009). As such, using it as a focus species to test the hypotheses is still highly relevant for the broader ecological functioning and persistence of various species (Chapter 2) which depend on *E. camaldulensis* for providing habitat and resources. Nonetheless, future research that concurrently examines different biota (e.g. fish, water birds and vegetation etc.) is important for further examining the hydrology and interactive hydrology – land use hypothesis usefulness for understand floodplain wetland ecology.

Finally, the hydrology and land use factors utilised, while explaining significant variation in different aspects of *E. camaldulensis,* were limited to five hydrology and three land use factors. Models were developed with these factors as they cover a range of factors, known to be important for the ecology of floodplain systems. Nonetheless, there are various hydrological (e.g. timing, variability and duration of inundation) and land use factors (e.g. pollution, grazing type and intensity) that are also known to be important for floodplain systems, but were unable to be tested as data was lacking. Nevertheless, the hydrology and land use factors tested in this study were still highly valuable for testing the competing hypotheses and the approach outlined will serve as valuable step for further research.

7.6 Future directions

The above issues, while limiting the generality of this study's findings, do highlight some important directions for future research. Potential avenues for future research that may help to both address some of the limitations mentioned above, as well as increase understanding for ecological theory and management of floodplain wetlands in agricultural landscapes, are discussed below.

Firstly, a broader examination of the hydrology hypothesis tested as presented in this thesis. Specifically, the suitability of a hydrology-only hypothesis for understanding specie richness, composition and functional diversity of various biota (vegetation, fish, invertebrates, birds) in floodplain wetlands should be tested. In addition, a wider range of hydrology (e.g. inundation timing and variability etc.) and land use (e.g. pollution) factors should be considered. Although studies concurrently comparing a range of hydrology and land use factors are limited, a meta-analysis of existing studies may still be particularly elucidating in this regard and help identify whether a hydrology-only hypothesis is limited only in a few instances (e.g. only for tree species, such as *E. camaldulensis* Chapter 5; Meeson et al. 2002) or consistently across a range of landscapes and species.

Further testing of the hydrology hypothesis could also be linked with additional investigation into the suitability of the different interaction types outlined in Chapter 6. For example, do the interaction types (synergistic, antagonistic and qualitative) account for other species as well as broader vegetation responses (e.g. species richness, composition, stand structure) to a wider range of interacting factors. The interaction framework outlined in Chapter 6, building upon the work of others (e.g. Crain et al 2008), should also be tested across not only a broader range of species and landscapes settings in floodplain systems, but more broadly across other ecological systems. This is particularly important for testing the prevalence of qualitative interactions, which are seldom considered in current ecological thinking about interactions. Testing if species responses to multiple factors can be characterized by qualitative, as well as synergistic and antagonistic interactions, is likely to have important implications in novel and natural ecosystems exposed to an increasing range of interacting human stressors and may have important implications for deciphering the impacts of new and novel stressors, such as climate change. The Bayesian network approach in Chapter 6 offers a method in which to pursue this, although a range of other statistical techniques should also be applied and tested to account for limitations of this approach (e.g. the use of categories).

Finally, the development and testing of practical management options which consider multiple hydrological and land use factors that interact should be pursued. For example, are management strategies which incorporate multiple interacting stressors more conducive with other priorities of water and land use in agricultural landscapes? Are there novel combinations of management practices that may produce ecological benefits with less socio-economic conflicts as a consequence of ‘non-intuitive’ response of species to interactions between multiple environmental factors?

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Appendix A1. Annual inundation data by year for all wetlands.

Site	ID #	Sub - region	Year																			Inundation frequency
			1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
1	135	Chinchilla	0	1	1	1	1	1	0	0	0	1	1	1	1	1	0	0	0	0	0	52.63
2	138	Chinchilla	0	1	0	0	0	1	0	1	0	1	1	1	0	0	0	0	0	0	0	31.58
3	140	Chinchilla	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	1	1	1	1	42.11
4	141	Chinchilla	0	1	1	1	1	0	0	1	1	1	1	1	1	1	1	0	0	1	1	73.68
5	277	Chinchilla	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	15.79
6	278	Chinchilla	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	21.05
7	279	Chinchilla	0	1	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	0	36.84
8	282	Chinchilla	0	0	0	1	0	1	0	1	0	1	1	1	1	0	0	0	0	1	0	42.11
9	283	Chinchilla	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	1	0	26.32
10	998	Chinchilla	1	1	1	1	0	0	0	1	0	1	0	1	1	0	1	0	0	1	0	52.63
11	999	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	10.53
12	1004	Chinchilla	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	31.58
13	1005	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	10.53
14	1062	Chinchilla	0	1	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	1	0	31.58
15	1063	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	15.79
16	1064	Chinchilla	0	1	1	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	0	52.63
17	1065	Chinchilla	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	0	1	0	42.11
18	1067	Chinchilla	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	15.79
19	1069	Chinchilla	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	89.47
20	1073	Chinchilla	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	100.00
21	1098	Chinchilla	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	15.79
22	1100	Chinchilla	0	1	1	0	1	0	0	1	0	1	1	0	1	0	0	0	0	1	0	42.11
23	1101	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	15.79
24	1137	Chinchilla	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1	68.42
25	1204	Chinchilla	0	0	0	1	1	1	0	1	0	1	1	1	1	0	0	0	0	1	1	52.63
26	1206	Chinchilla	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	21.05
27	1207	Chinchilla	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	15.79
28	1216	Chinchilla	0	0	1	1	1	1	1	1	0	1	0	0	1	0	0	1	1	1	1	63.16

Site	ID #	Sub - region	Year																			Inundation frequency
			1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
29	1220	Chinchilla	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	42.11
30	1222	Chinchilla	0	1	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	36.84
31	1223	Chinchilla	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	26.32
32	1225	Chinchilla	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	0	31.58
33	1239	Chinchilla	0	1	1	1	1	0	0	1	0	1	1	1	1	1	1	0	0	1	1	68.42
34	1242	Chinchilla	0	0	1	1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	31.58
35	1345	Chinchilla	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	89.47
36	1347	Chinchilla	0	1	1	1	1	0	0	1	0	1	0	0	1	1	1	1	1	1	1	68.42
37	1352	Chinchilla	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	31.58
38	1358	Chinchilla	0	1	1	1	1	1	0	1	0	1	1	1	1	1	0	0	0	0	0	57.89
39	1359	Chinchilla	0	1	0	0	1	0	0	0	0	1	1	1	1	0	0	0	0	0	0	31.58
40	1360	Chinchilla	0	1	1	1	1	1	0	1	0	1	1	1	1	1	1	0	0	1	1	73.68
41	1365	Chinchilla	0	1	1	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	36.84
42	1366	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	15.79
43	2213	Chinchilla	0	1	1	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	31.58
44	2214	Chinchilla	0	1	1	1	0	0	0	1	0	1	1	1	1	0	1	0	0	1	0	52.63
45	2219	Chinchilla	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	26.32
46	2222	Chinchilla	0	1	0	1	0	1	0	1	0	1	0	0	1	0	1	0	0	0	0	36.84
47	2223	Chinchilla	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	0	36.84
48	2224	Chinchilla	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	15.79
49	2226	Chinchilla	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	15.79
50	2228	Chinchilla	1	1	1	1	0	1	0	0	0	1	0	1	1	1	1	1	0	0	0	57.89
51	4622	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	15.79
52	4623	Chinchilla	0	1	1	1	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	36.84
53	4625	Chinchilla	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	21.05
54	4813	Chinchilla	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	1	52.63
55	5076	Chinchilla	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	36.84
56	5141	Chinchilla	0	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	42.11
57	5283	Chinchilla	0	1	0	1	0	0	0	1	0	1	0	1	0	0	0	1	0	1	1	42.11

Site	ID #	Sub - region	Year																			Inundation frequency
			1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
58	5284	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	10.53
59	5619	Chinchilla	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	63.16
60	7014	Chinchilla	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	1	1	1	42.11
61	7015	Chinchilla	0	1	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1	1	63.16
62	8694	Chinchilla	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	1	0	31.58
63	8697	Chinchilla	0	1	1	1	1	0	0	1	0	1	0	0	1	0	0	0	0	1	0	42.11
64	8700	Chinchilla	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	15.79
65	9654	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	10.53
66	9655	Chinchilla	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	15.79
67	9660	Chinchilla	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	36.84
68	10525	Chinchilla	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	21.05
69	10526	Chinchilla	0	1	0	1	1	1	0	1	0	1	1	1	1	0	1	0	0	1	0	57.89
70	57601	Chinchilla	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	15.79
71	57602	Chinchilla	0	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	0	1	1	42.11
72	57802	Chinchilla	0	0	0	0	0	1	0	1	0	0	1	1	1	0	0	0	0	0	0	26.32
73	57810	Chinchilla	0	1	0	1	0	1	0	1	0	1	1	1	1	0	1	0	0	0	1	52.63
74	57812	Chinchilla	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	21.05
75	57838	Chinchilla	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	84.21
76	57841	Chinchilla	0	1	1	0	0	1	0	1	0	1	1	1	0	0	0	0	0	1	1	47.37
77	57842	Chinchilla	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	42.11
78	57995	Chinchilla	1	1	1	1	0	1	0	1	0	1	0	1	1	1	1	0	0	0	0	57.89
79	57996	Chinchilla	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	21.05
80	58077	Chinchilla	1	1	1	1	1	0	0	1	0	1	1	1	1	1	1	0	1	1	1	78.95
81	58507	Chinchilla	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	15.79
82	59302	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	15.79
83	69373	Chinchilla	0	1	1	1	0	1	1	1	0	1	1	1	1	1	0	0	1	1	1	73.68
84	69383	Chinchilla	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	1	0	26.32
85	69422	Chinchilla	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	84.21
86	69426	Chinchilla	0	1	1	1	0	1	0	1	0	1	1	1	1	1	1	0	0	1	1	68.42

Site	ID #	Sub - region	Year																			Inundation frequency
			1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
87	69455	Chinchilla	0	1	0	0	0	0	0	1	0	1	1	1	1	1	0	0	1	1	1	52.63
88	69458	Chinchilla	0	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	1	0	31.58
89	69626	Chinchilla	0	1	1	1	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	52.63
90	69628	Chinchilla	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	100.00
91	70071	Chinchilla	0	1	0	1	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1	47.37
92	70140	Chinchilla	0	1	0	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0	1	42.11
93	71003	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	15.79
94	71201	Chinchilla	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	21.05
95	71368	Chinchilla	0	1	0	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1	0	63.16
96	80819	Chinchilla	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	36.84
97	80826	Chinchilla	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	21.05
98	80848	Chinchilla	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	31.58
99	80849	Chinchilla	0	1	1	1	0	0	0	1	0	1	1	1	1	1	0	0	0	1	1	57.89
100	80878	Chinchilla	0	1	1	1	0	1	0	1	0	1	1	0	1	0	0	0	0	0	0	42.11
101	81060	Chinchilla	0	1	1	1	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	42.11
102	81522	Chinchilla	0	1	1	1	0	0	0	1	0	1	1	1	1	1	0	0	0	0	1	52.63
103	81544	Chinchilla	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	21.05
104	81566	Chinchilla	1	1	1	1	0	1	0	1	1	1	1	1	1	1	0	0	0	1	1	73.68
105	82426	Chinchilla	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	15.79
106	72	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	1	0	1	0	1	1	0	53.85
107	1668	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	0	0	0	0	0	0	0	23.08
108	1695	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	1	0	0	0	1	1	0	46.15
109	1699	Dalby	NA	1	NA	1	1	NA	1	1	NA	NA	1	NA	1	1	1	1	1	1	1	100.00
110	1700	Dalby	NA	0	NA	0	1	NA	0	0	NA	NA	1	NA	1	1	1	1	0	1	0	53.85
111	1701	Dalby	NA	1	NA	1	1	NA	0	1	NA	NA	1	NA	1	1	1	1	0	0	1	76.92
112	1736	Dalby	0	1	0	1	1	0	1	1	0	0	1	0	1	1	1	1	1	1	1	68.42
113	1744	Dalby	0	0	0	0	1	0	0	1	0	0	1	0	1	1	1	1	1	1	1	52.63
114	1749	Dalby	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	1	1	1	1	52.63
115	1886	Dalby	NA	1	NA	1	1	NA	0	1	NA	NA	1	NA	1	1	0	0	0	0	0	53.85

Site	ID #	Sub - region	Year																			Inundation frequency
			1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
116	1943	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	1	NA	0	1	0	0	0	1	1	53.85
117	1945	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	0	0	0	1	0	1	0	38.46
118	1946	Dalby	NA	1	NA	1	0	NA	0	0	NA	NA	0	NA	0	0	0	0	0	1	0	23.08
119	1947	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	0	1	0	0	0	0	0	30.77
120	2494	Dalby	NA	1	NA	1	1	NA	0	1	NA	NA	0	NA	1	1	1	1	0	1	0	69.23
121	2495	Dalby	0	1	0	1	1	0	0	1	0	0	1	0	1	1	1	0	1	1	1	57.89
122	2496	Dalby	0	1	0	1	1	0	0	1	0	0	1	0	1	1	1	1	1	1	1	63.16
123	2861	Dalby	0	1	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	31.58
124	2863	Dalby	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	21.05
125	3702	Dalby	NA	1	NA	1	1	NA	1	1	NA	0	1	NA	1	1	1	1	1	1	1	92.86
126	3703	Dalby	NA	1	NA	1	1	NA	1	1	NA	0	1	NA	1	1	1	0	0	0	0	64.29
127	3704	Dalby	NA	1	NA	1	1	NA	0	1	NA	0	1	NA	1	1	1	1	1	1	0	78.57
128	4801	Dalby	NA	0	NA	0	0	NA	0	0	NA	NA	1	NA	1	1	0	0	0	1	0	30.77
129	4867	Dalby	NA	1	NA	0	1	NA	0	0	NA	NA	1	NA	1	1	0	0	0	0	0	38.46
130	5036	Dalby	NA	1	NA	0	0	NA	0	1	NA	NA	0	NA	0	0	0	0	0	0	0	15.38
131	5040	Dalby	NA	1	NA	1	1	NA	1	1	NA	NA	1	NA	1	1	1	1	0	1	1	92.31
132	5328	Dalby	NA	1	NA	1	1	NA	0	1	NA	NA	0	NA	1	1	0	0	0	1	0	53.85
133	5655	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	0	0	0	0	0	0	0	23.08
134	5656	Dalby	NA	1	NA	0	0	NA	0	1	NA	NA	0	NA	0	0	0	0	0	1	0	23.08
135	5766	Dalby	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	15.79
136	5768	Dalby	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	26.32
137	5769	Dalby	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	10.53
138	6932	Dalby	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5.26
139	6948	Dalby	NA	1	NA	1	1	NA	1	1	NA	0	1	NA	1	1	1	1	0	1	0	78.57
140	6949	Dalby	NA	1	NA	1	1	NA	1	1	NA	0	1	NA	1	1	1	1	0	0	0	71.43
141	6950	Dalby	NA	1	NA	1	0	NA	1	1	NA	0	1	NA	1	1	1	0	0	0	0	57.14
142	7058	Dalby	NA	1	NA	1	0	NA	0	0	NA	NA	1	NA	1	1	1	0	1	1	0	61.54
143	7061	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	1	0	0	1	0	0	1	46.15
144	7064	Dalby	NA	1	NA	1	1	NA	1	1	NA	NA	1	NA	1	1	1	1	1	1	1	100.00

Site	ID #	Sub - region	Year																			Inundation frequency
			1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
145	7066	Dalby	NA	0	NA	1	0	NA	0	1	NA	NA	0	NA	0	0	0	0	0	0	0	15.38
146	7229	Dalby	NA	1	NA	0	0	NA	0	1	NA	NA	0	NA	0	0	0	0	0	0	0	15.38
147	7276	Dalby	NA	0	NA	0	0	NA	0	0	NA	NA	0	NA	1	1	1	0	1	1	0	38.46
148	7278	Dalby	NA	1	NA	1	1	NA	0	1	NA	NA	1	NA	1	1	1	1	1	1	1	92.31
149	7327	Dalby	NA	1	NA	0	1	NA	0	0	NA	NA	1	NA	1	1	0	0	0	1	1	53.85
150	7328	Dalby	NA	1	NA	1	1	NA	0	0	NA	NA	1	NA	1	1	0	0	0	0	0	46.15
151	7479	Dalby	NA	0	NA	0	0	NA	1	1	NA	NA	1	NA	1	1	1	1	1	1	1	76.92
152	9695	Dalby	NA	1	NA	0	0	NA	0	1	NA	NA	0	NA	0	0	1	0	1	1	1	46.15
153	57914	Dalby	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	21.05
154	58287	Dalby	NA	0	NA	0	0	NA	0	0	NA	0	1	NA	1	1	1	1	1	1	1	57.14
155	58288	Dalby	NA	1	NA	1	1	NA	0	1	NA	0	1	NA	0	0	1	0	0	1	1	57.14
156	58515	Dalby	NA	1	NA	0	1	NA	0	0	NA	NA	1	NA	1	1	0	0	0	0	0	38.46
157	58615	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	1	NA	0	0	1	0	0	1	0	46.15
158	58616	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	0	0	0	0	0	0	0	23.08
159	58618	Dalby	NA	1	NA	1	1	NA	0	1	NA	NA	0	NA	0	0	0	0	0	1	1	46.15
160	59517	Dalby	NA	1	NA	1	1	NA	1	1	NA	NA	1	NA	1	0	0	0	0	1	0	61.54
161	69515	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	0	0	0	0	0	0	0	23.08
162	69516	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	0	1	0	0	0	0	0	30.77
163	69683	Dalby	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	15.79
164	69962	Dalby	NA	1	NA	1	1	NA	1	1	NA	0	1	NA	1	1	1	1	1	1	1	92.86
165	69963	Dalby	NA	1	NA	1	0	NA	0	1	NA	0	1	NA	0	1	0	0	0	0	0	35.71
166	69965	Dalby	NA	1	NA	1	1	NA	1	1	NA	0	1	NA	1	1	1	1	1	1	1	92.86
167	70378	Dalby	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	42.11
168	70647	Dalby	NA	1	NA	1	1	NA	1	1	NA	0	1	NA	1	1	1	0	0	1	0	71.43
169	70704	Dalby	NA	1	NA	0	0	NA	0	1	NA	NA	0	NA	0	0	0	0	0	0	0	15.38
170	71153	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	0	1	0	1	0	1	1	53.85
171	71211	Dalby	NA	1	NA	1	1	NA	1	1	NA	NA	1	NA	1	1	1	1	0	1	0	84.62
172	80952	Dalby	NA	1	NA	1	1	NA	0	1	NA	NA	1	NA	1	1	1	1	0	1	1	84.62
173	80960	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	0	0	0	0	1	1	0	38.46

Site	ID #	Sub - region	Year																			Inundation frequency
			1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
174	80999	Dalby	NA	1	NA	1	1	NA	0	1	NA	NA	1	NA	1	1	1	1	1	1	0	84.62
175	81014	Dalby	NA	1	NA	1	0	NA	0	1	NA	NA	0	NA	0	0	0	0	0	1	0	30.77
176	81686	Dalby	NA	1	NA	1	1	NA	0	1	NA	NA	1	NA	1	1	0	0	0	1	0	61.54
177	81790	Dalby	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	31.58
178	81919	Dalby	NA	1	NA	1	1	NA	0	1	NA	1	1	NA	1	1	1	1	0	1	0	78.57
179	82636	Dalby	NA	1	NA	1	1	NA	1	1	NA	NA	1	NA	1	1	1	1	0	1	1	92.31
180	82637	Dalby	NA	1	NA	1	1	NA	1	1	NA	NA	1	NA	1	1	0	1	0	1	1	84.62
181	6380	Warwick	NA	1	NA	0	0	NA	0	1	NA	1	0	NA	0	0	0	0	0	0	0	21.43
182	6381	Warwick	NA	1	NA	1	1	NA	0	1	NA	1	1	NA	1	1	1	1	0	1	0	78.57
183	7630	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	1	1	1	100.00
184	7633	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	1	NA	1	1	1	1	1	1	1	85.71
185	7655	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	0	1	1	1	1	1	92.86
186	7683	Warwick	NA	0	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	1	1	1	92.86
187	7769	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	0	NA	0	0	0	0	0	1	0	35.71
188	7783	Warwick	NA	1	NA	0	0	NA	0	0	NA	0	0	NA	1	0	1	1	1	1	1	50.00
189	7888	Warwick	NA	0	NA	0	0	NA	0	1	NA	1	0	NA	0	0	0	0	0	0	0	14.29
190	7889	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	0	NA	1	0	1	1	0	1	0	57.14
191	7890	Warwick	NA	1	NA	1	1	NA	0	1	NA	1	1	NA	1	1	1	1	0	1	0	78.57
192	7891	Warwick	NA	1	NA	1	1	NA	0	1	NA	1	1	NA	1	1	1	1	0	1	0	78.57
193	8017	Warwick	NA	1	NA	0	0	NA	0	1	NA	1	0	NA	0	0	0	0	0	0	0	21.43
194	8018	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	0	NA	0	0	0	1	1	1	1	57.14
195	8019	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	1	1	1	100.00
196	8021	Warwick	NA	1	NA	1	0	NA	0	0	NA	1	0	NA	0	0	0	0	1	1	1	42.86
197	8037	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	1	NA	1	0	1	1	1	1	0	71.43
198	8038	Warwick	NA	1	NA	1	0	NA	0	0	NA	1	0	NA	1	0	0	0	0	0	0	28.57
199	8039	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	1	NA	1	0	1	1	1	1	0	71.43
200	8113	Warwick	NA	1	NA	1	0	NA	1	0	NA	1	1	NA	1	1	1	1	0	0	1	71.43
201	8623	Warwick	NA	0	NA	1	0	NA	0	1	NA	0	0	NA	0	0	0	0	1	0	0	21.43
202	8625	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	1	1	1	100.00

Site	ID #	Sub - region	Year																			Inundation frequency
			1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
203	9107	Warwick	NA	1	NA	1	0	NA	0	0	NA	0	1	NA	1	0	0	0	1	0	0	35.71
204	9110	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	0	NA	0	0	0	0	1	1	1	50.00
205	9348	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	1	1	1	100.00
206	9818	Warwick	NA	1	NA	0	0	NA	0	0	NA	1	0	NA	1	1	0	0	0	0	0	28.57
207	10004	Warwick	NA	1	NA	0	0	NA	0	0	NA	1	0	NA	1	0	0	0	0	0	0	21.43
208	10009	Warwick	NA	1	NA	0	0	NA	0	0	NA	0	0	NA	1	0	0	0	0	0	0	14.29
209	10010	Warwick	NA	1	NA	0	0	NA	0	0	NA	0	0	NA	1	0	0	0	0	0	0	14.29
210	10011	Warwick	NA	0	NA	0	0	NA	0	0	NA	0	0	NA	1	1	1	1	1	0	0	35.71
211	10015	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	1	1	1	100.00
212	10016	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	1	1	1	100.00
213	10165	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	0	NA	1	0	0	0	0	0	0	35.71
214	10166	Warwick	NA	1	NA	1	1	NA	0	1	NA	1	0	NA	1	1	1	0	0	1	0	64.29
215	10167	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	0	NA	0	0	0	0	0	0	0	28.57
216	10278	Warwick	NA	1	NA	1	0	NA	0	0	NA	1	0	NA	1	0	0	0	0	0	0	28.57
217	10766	Warwick	NA	1	NA	1	1	0	1	0	0	1	1	0	1	1	1	1	0	1	1	70.59
218	11422	Warwick	NA	0	NA	0	0	NA	0	0	NA	0	0	NA	0	0	1	1	1	1	1	35.71
219	11527	Warwick	NA	0	NA	0	0	NA	0	0	NA	1	0	NA	1	0	0	0	0	0	0	14.29
220	12432	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	0	1	1	92.86
221	12433	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	0	1	1	92.86
222	13382	Warwick	NA	0	NA	0	0	NA	0	0	NA	0	0	NA	1	0	0	0	0	1	1	21.43
223	13399	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	0	NA	1	0	1	1	0	1	0	57.14
224	59077	Warwick	NA	0	NA	0	0	NA	0	0	NA	0	0	NA	1	0	0	1	0	0	0	14.29
225	59135	Warwick	NA	0	NA	0	0	NA	0	1	NA	1	0	NA	0	0	0	0	0	0	0	14.29
226	59162	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	0	NA	1	0	1	1	1	0	0	57.14
227	59299	Warwick	NA	1	NA	1	0	NA	0	0	NA	0	0	NA	1	0	0	0	0	1	0	28.57
228	59536	Warwick	NA	1	NA	1	0	NA	0	0	NA	1	0	NA	1	0	0	0	0	0	0	28.57
229	59538	Warwick	NA	1	NA	0	0	NA	0	1	NA	1	0	NA	1	0	1	0	0	0	0	35.71
230	59579	Warwick	NA	0	NA	0	0	NA	0	0	NA	1	0	NA	1	0	0	0	0	0	0	14.29
231	59580	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	0	1	1	1	1	1	1	92.86

Site	ID #	Sub - region	Year																			Inundation frequency
			1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	
232	59637	Warwick	NA	1	NA	0	0	NA	0	1	NA	1	0	NA	1	0	1	0	0	1	0	42.86
233	59854	Warwick	NA	1	NA	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	41.18
234	60003	Warwick	NA	1	NA	1	1	NA	1	0	NA	1	1	NA	0	1	1	1	1	1	1	85.71
235	70774	Warwick	NA	1	NA	1	1	NA	0	1	NA	1	1	NA	1	1	1	1	1	1	1	92.86
236	70778	Warwick	NA	0	NA	0	0	NA	0	0	NA	0	0	NA	0	1	1	1	1	1	1	42.86
237	70862	Warwick	NA	1	NA	1	0	NA	0	0	NA	1	0	NA	0	0	0	0	1	0	0	28.57
238	70994	Warwick	NA	1	NA	1	0	NA	0	0	NA	1	1	NA	1	0	1	1	0	1	0	57.14
239	71088	Warwick	NA	1	NA	1	1	NA	0	1	NA	1	1	NA	1	1	1	1	1	1	1	92.86
240	71320	Warwick	NA	1	NA	1	1	NA	0	1	NA	1	1	NA	1	1	1	1	1	1	1	92.86
241	71726	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	0	1	1	92.86
242	71999	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	0	NA	1	0	0	0	0	1	0	57.14
243	82107	Warwick	NA	1	NA	1	1	NA	0	1	NA	NA	1	NA	1	1	1	1	1	1	1	92.31
244	82250	Warwick	NA	0	NA	0	0	NA	0	1	NA	1	0	NA	0	0	0	1	0	1	0	28.57
245	82284	Warwick	NA	1	NA	1	0	NA	0	1	NA	1	1	NA	1	0	0	0	1	1	0	57.14
246	82422	Warwick	NA	0	NA	0	0	NA	0	1	NA	1	0	NA	1	0	1	0	1	1	1	50.00
247	82542	Warwick	NA	1	NA	1	1	NA	1	1	NA	1	1	NA	1	1	1	1	0	1	1	92.86
248	82653	Warwick	NA	1	NA	0	0	NA	0	0	NA	1	0	NA	1	0	0	0	0	0	0	21.43
249	82684	Warwick	NA	1	NA	0	0	NA	0	0	NA	1	0	NA	0	0	0	0	0	0	0	14.29
250	82685	Warwick	NA	1	NA	1	1	NA	0	0	NA	1	1	NA	0	0	1	0	0	0	0	42.86
251	82851	Warwick	NA	1	NA	1	1	NA	0	0	NA	1	1	NA	1	1	1	1	0	1	1	78.57

Appendix A2. Wetland inundation scene dates (data source Queensland Dams and Waterbody dataset 2005)

Region	Chinchilla	Dalby	Warwick
Year	**Scene dates**	**Scene dates**	**Scene dates**
1987	9/25/1987	No data	No data
1988	5/6/1988	9/20/1988	9/20/1988
1989	12/19/1989	No data	No data
1990	3/9/1990 &9/1/1990	7/8/1990	5/5/1990
1991	9/4/1991	9/29/1991	10/15/1991
1992	7/4/1992	No data	No data
1993	6/21/1993	4/27/1993	4/27/1993
1994	7/26/1994	6/17/1994 & 3/13/1994	6/17/1994
1995	7/13/1995	No data	No data
1996	2/6/1996 &9/1/1996	No data	1/30/1996
1997	6/16/1997	8/12/1997	8/12/1997
1998	8/6/1998	No data	No data
1999	9/18/1999	11/14/1999	11/14/1999
2000	9/20/2000 & 10/6/2000	10/15/2000 & 3/5/2000	10/15/2000
2001	2/11/2001 &8/6/2001	8/15/2001	8/15/2001
2002	7/24/2002	7/17/2002	7/17/2002
2003	9/5/2003	7/28/2003	7/28/2003
2004	3/31/2004 &9/23/2004	4/9/2004 & 10/2/2004	4/9/2004 & 10/2/2004
2005	8/25/2005	7/17/2005	7/17/2005

Appendix A3. Results of Bartlett's test for equality of variance between modified and unmodified wetlands.

Factor	Bartlett's k-squared
#Inundation frequency (%)	0.01
Rainfall (mm)	0.10
*River connectivity (m)	<0.01
#*Rain volume (ML)	2.36
Wetland area (ha)	0.22
#*Catchment area (ha)	1.61
Groundwater depth (m)	28.73***

#Arcsine and *log transformed for analysis; *p <0.05; **p<0.01; ***p<0.001

Appendix B1. Pearson r correlations between explanatory factors.

	Inundation frequency	Grazing intensity	Groundwater depth 1987	Groundwater depth 2000	Groundwater depth 2005	Groundwater depth 2009	Rain volume	Agricultural land cover	Remnant vegetation cover	River connectivity	Distance from weir	Canopy cover
Inundation frequency	1.00	-0.04	0.12	0.15	0.11	0.21	0.25	-0.13	-0.40	-0.09	-0.28	0.11
Grazing intensity		1.00	0.37	**0.44**	0.21	-0.01	0.05	0.32	0.04	0.06	-0.08	-0.10
Groundwater depth 1987			1.00	**0.80**	**0.54**	**0.41**	0.03	0.11	-0.28	-0.05	-0.29	-0.22
Groundwater depth 2000				1.00	**0.43**	0.28	0.18	0.12	-0.24	-0.04	0.10	-0.19
Groundwater depth 2005					1.00	**0.89**	0.10	0.04	0.00	-0.05	-0.19	-0.23
Groundwater depth 2009						1.00	0.08	-0.19	-0.02	-0.08	-0.31	-0.17
Rain volume							1.00	**0.47**	**-0.35**	**0.52**	-0.10	-0.22
Agricultural land cover								1.00	-0.15	**0.42**	-0.01	-0.04
Remnant vegetation cover									1.00	-0.36	0.26	-0.11
River connectivity										1.00	-0.26	-0.15
Distance from weir											1.00	0.09
Canopy cover												1.00

Strongly correlated (r> 0.4) variables are bolded.

Appendix C1 Regression results with *E. camaldulensis* abundance

Factor	Size class (cbh)	F-value
*Inundation (%)	< 10 cm	0.50
	10 – 20 cm	0.6
	20 – 50 cm	0.01
	50 – 75 cm	0.01
	>75cm	0.55
Log River connectivity (m)	< 10 cm	0.53
	10 – 20 cm	2.11
	20 – 50 cm	2.72
	50 – 75 cm	0.87
	>75cm	0.75
Distance from weir (km)	< 10 cm	0.07
	10 – 20 cm	0.71
	20 – 50 cm	0.62
	50 – 75 cm	0.75
	>75cm	1.45
Groundwater depth (m) 1987	< 10 cm	0.65
	10 – 20 cm	0.21
	20 – 50 cm	0.11
	50 – 75 cm	0.03
	>75cm	0.03
Groundwater depth (m) 2000	< 10 cm	0.52
	10 – 20 cm	1.37
	20 – 50 cm	1.80
	50 – 75 cm	0.77
	>75cm	0.69
Groundwater depth (m) 2005	< 10 cm	0.85
	10 – 20 cm	1.50
	20 – 50 cm	0.70
	50 – 75 cm	0.02
	>75cm	0.20
Groundwater depth (m) 2009	< 10 cm	0.39
	10 – 20 cm	0.15
	20 – 50 cm	0.11
	50 – 75 cm	0.02
	>75cm	0.55
Rain volume (ML)	< 10 cm	2.28
	10 – 20 cm	1.22
	20 – 50 cm	0.66
	50 – 75 cm	3.38
	>75cm	0.57

Factor	Size class (cbh)	F-value
Grazing intensity (cow pats / 150 m^2)	< 10 cm	0.58
	10 – 20 cm	5.67*
	20 – 50 cm	3.29
	50 – 75 cm	6.70*
	>75cm	1.89
Agriculture (%)	< 10 cm	5.33*
	10 – 20 cm	1.10
	20 – 50 cm	0.12
	50 – 75 cm	0.70
	>75cm	0.31
Remnant vegetation cover (%)	< 10 cm	0.87
	10 – 20 cm	0.29
	20 – 50 cm	0.19
	50 – 75 cm	0.03
	>75cm	0.74

Degrees of freedom = 35; *data on four sites missing df=31; *p <0.05; **p<0.01; ***p<0.001.

Appendix D1. Conditional Probability Tables for each vegetation node.

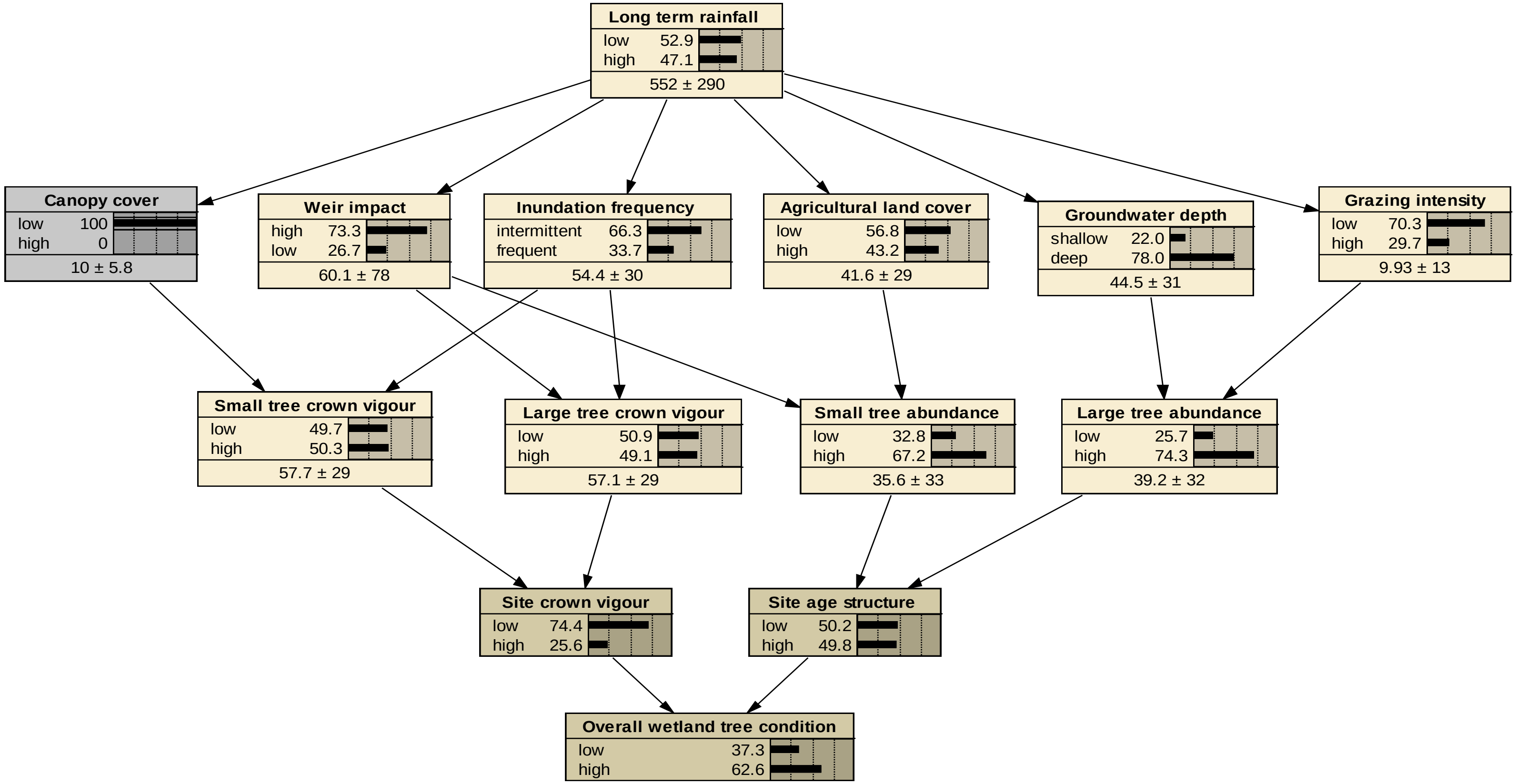
Environmental factor and state		Probability (%) of small tree crown vigour being:	
Canopy cover	**Inundation frequency**	**Low**	**High**
low	intermittent	44.44	55.56
low	frequent	60.00	40.00
high	intermittent	88.89	11.11
high	frequent	0.00	100.00

Environmental factor and state		Probability (%) of large tree crown vigour being:	
Inundation frequency	**Weir impact**	**Low**	**High**
intermittent	high	33.33	66.67
intermittent	low	62.5	37.50
frequent	high	87.5	12.50
frequent	low	0.01	99.99

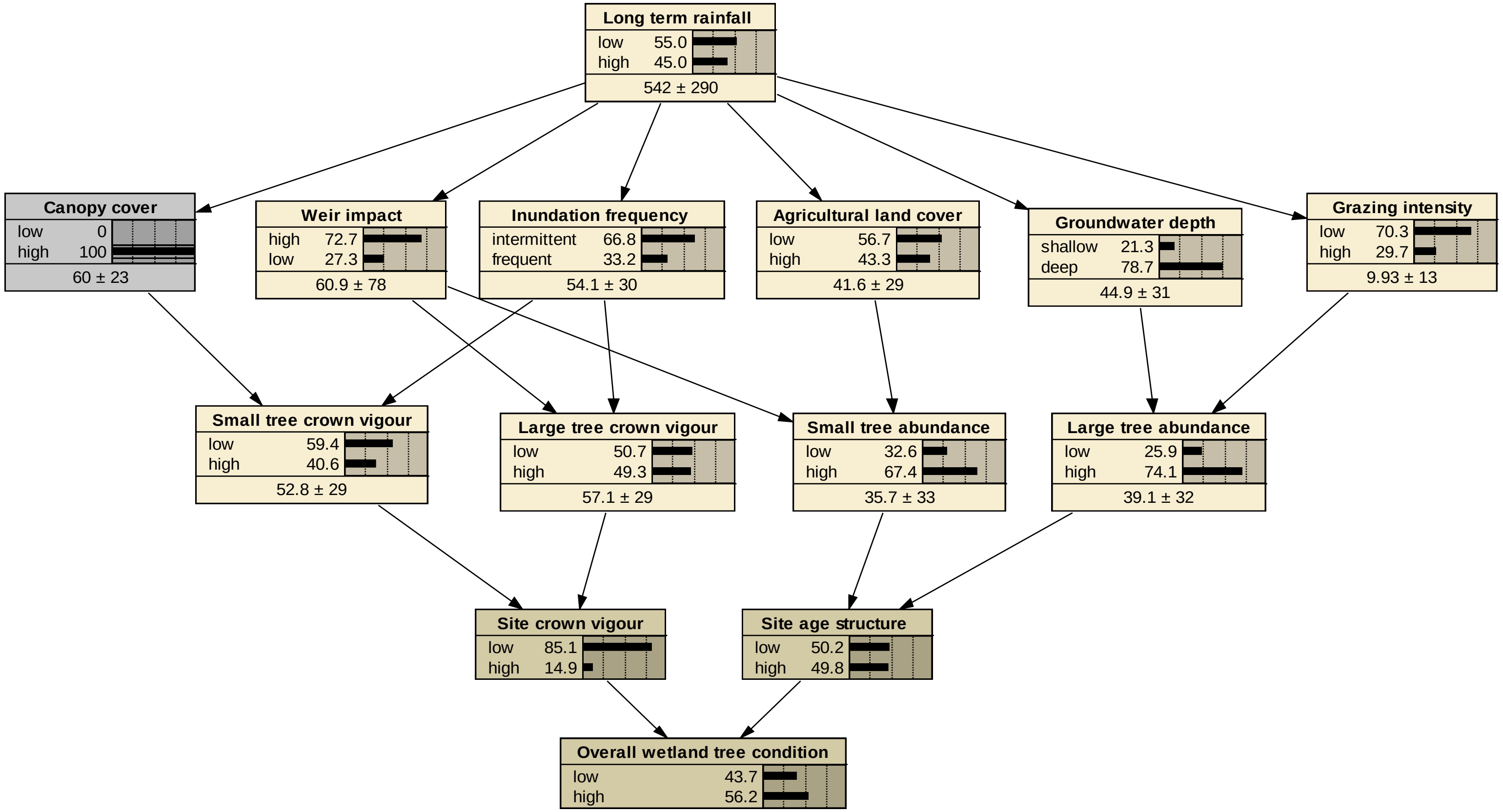
Environmental factor and state		Probability (%) of small tree abundance being:	
Weir impact	**Agricultural land cover**	**Low**	**High**
high	low	25	75.00
high	high	63.64	36.36
low	low	0.00	100.00
low	high	20	80.00

Environmental factor and state		Probability (%) of old tree abundance being:	
Grazing intensity	**Groundwater depth**	**Low**	**High**
low	shallow	0.00	100.00
low	deep	13.64	86.36
high	shallow	25	75.00
high	deep	71.43	28.57

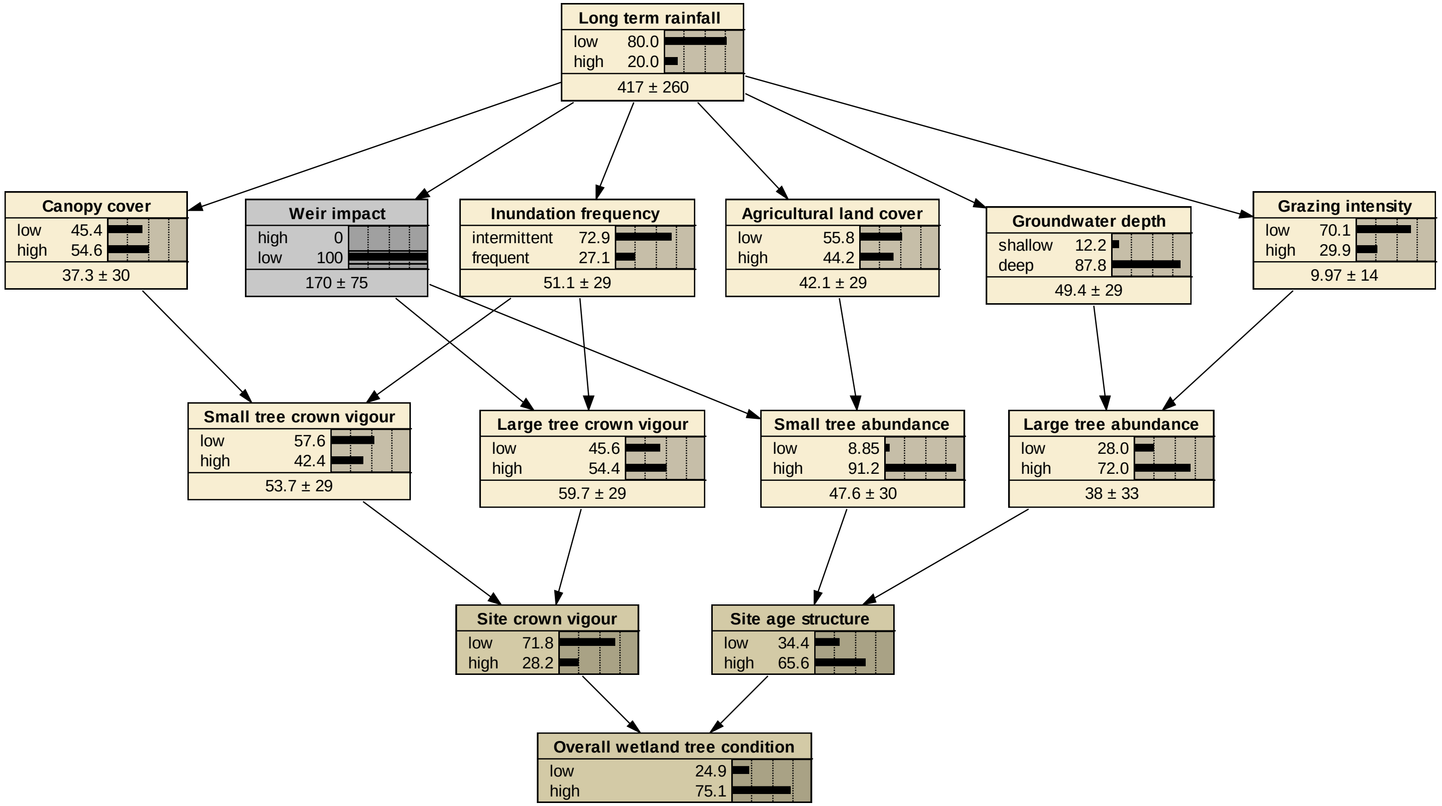
Appendix D2. Bayesian Network scenario analysis - Low canopy cover



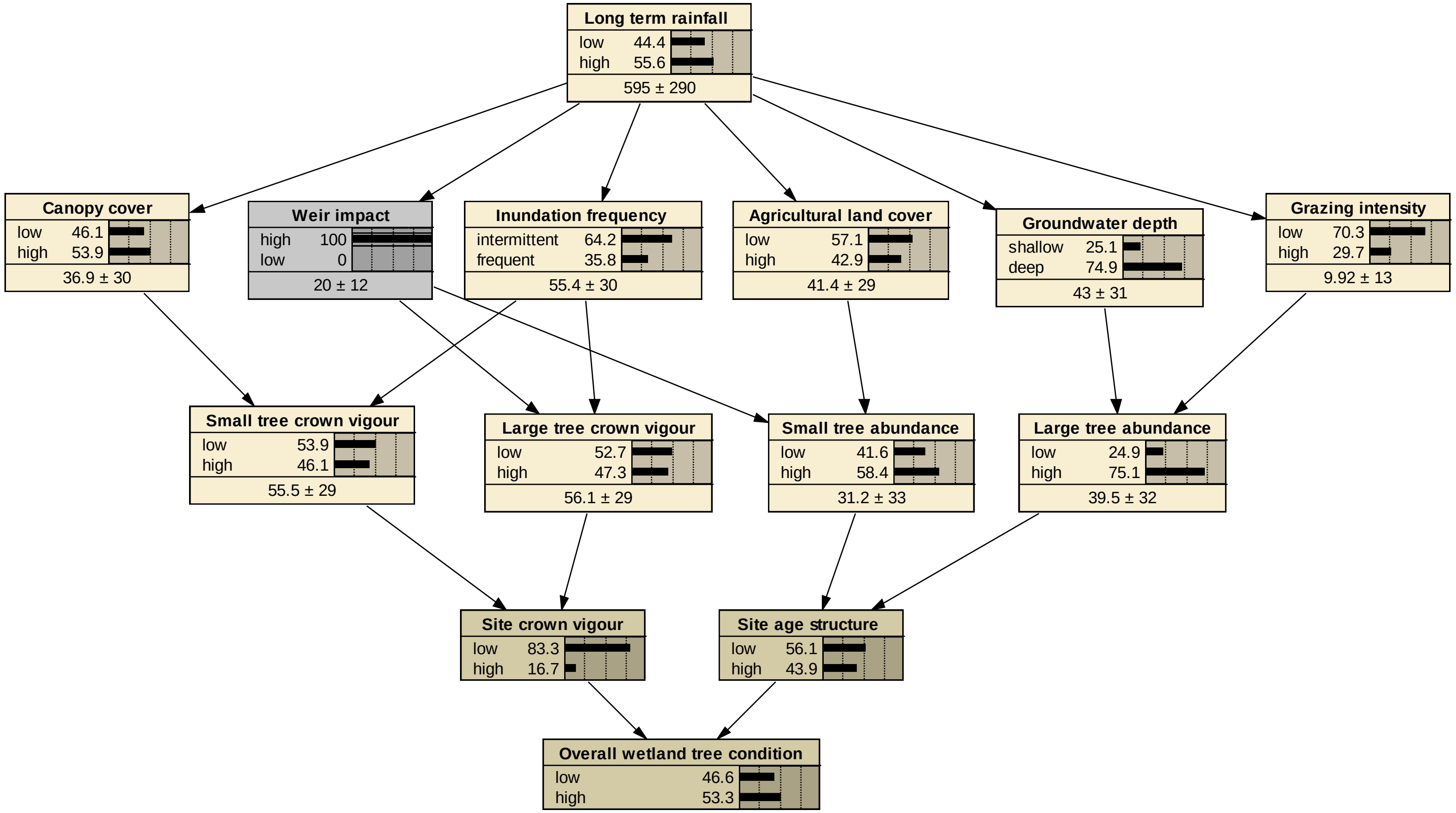
Appendix D2 contd. Bayesian Network scenario analysis – High canopy cover



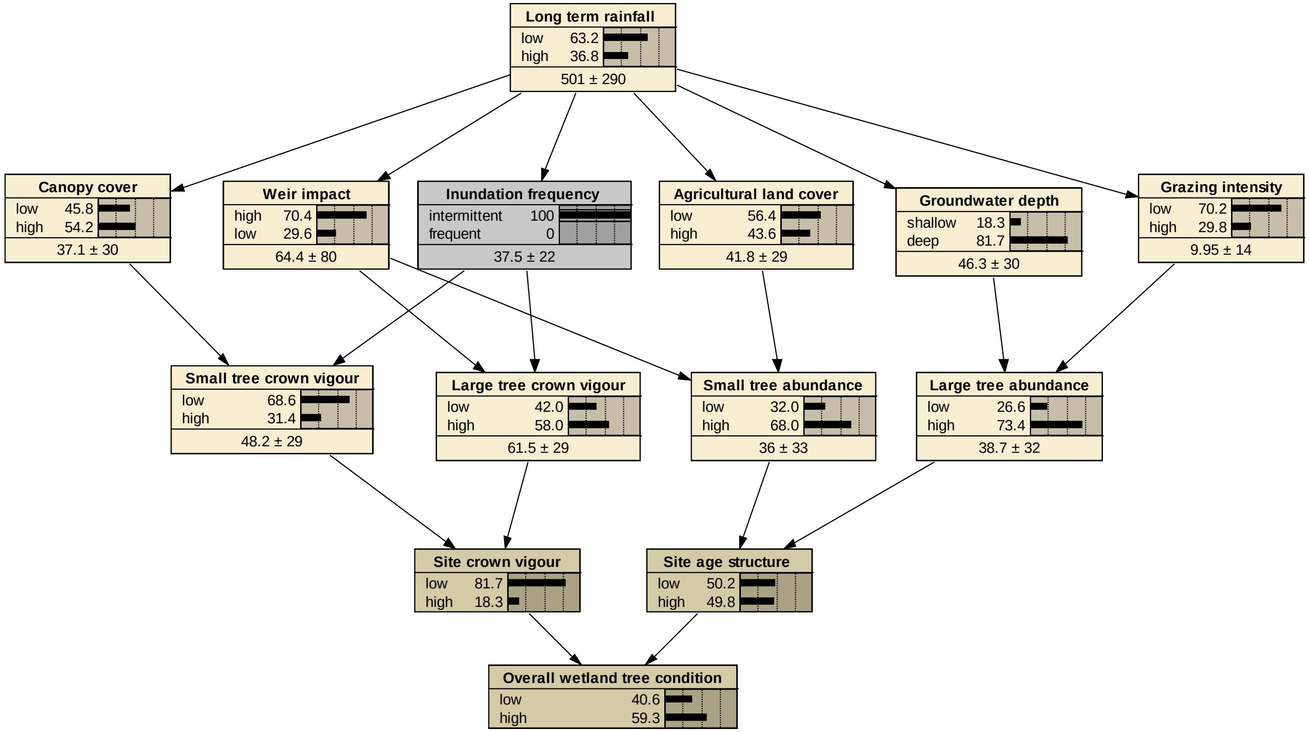
Appendix D2 contd. Bayesian Network scenario analysis – low weir impact



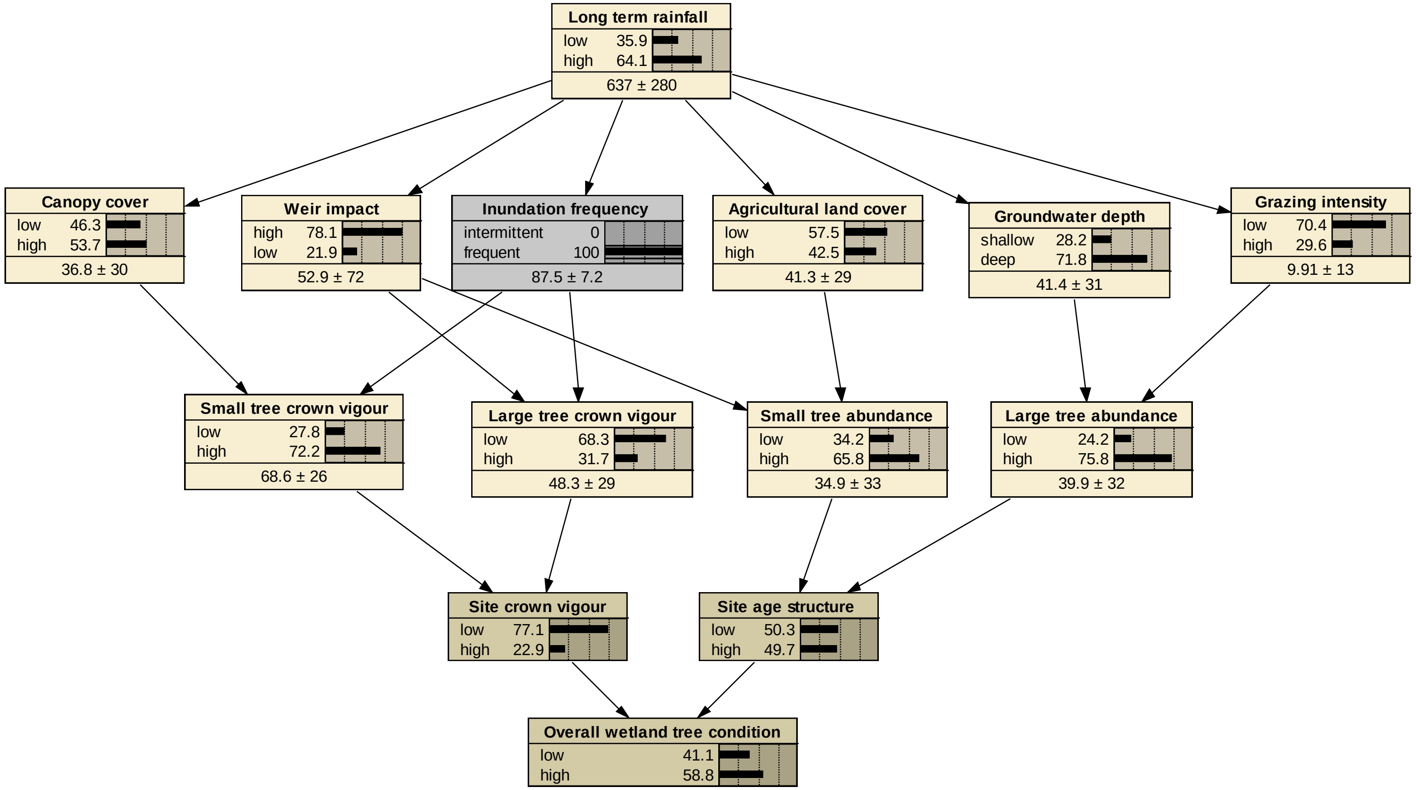
Appendix D2 contd. Bayesian Network scenario analysis – high weir impact



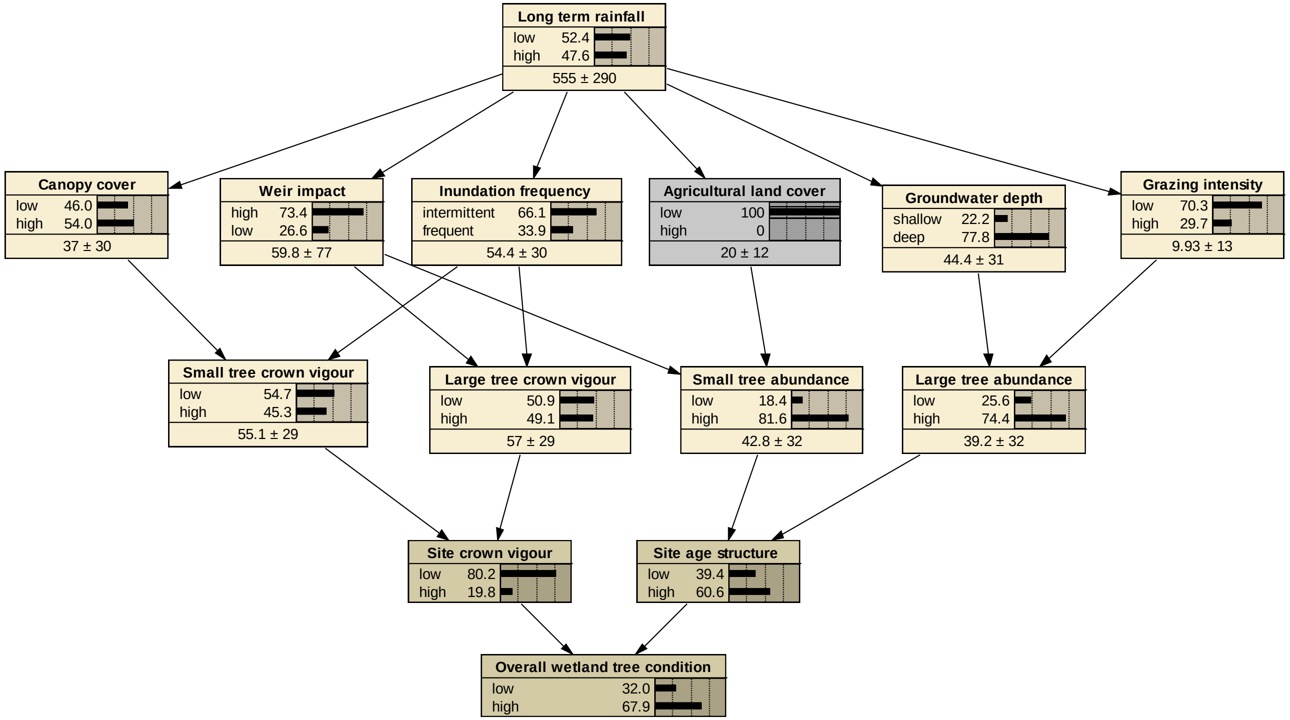
Appendix D2. Bayesian Network scenario analysis – intermittent inundation frequency



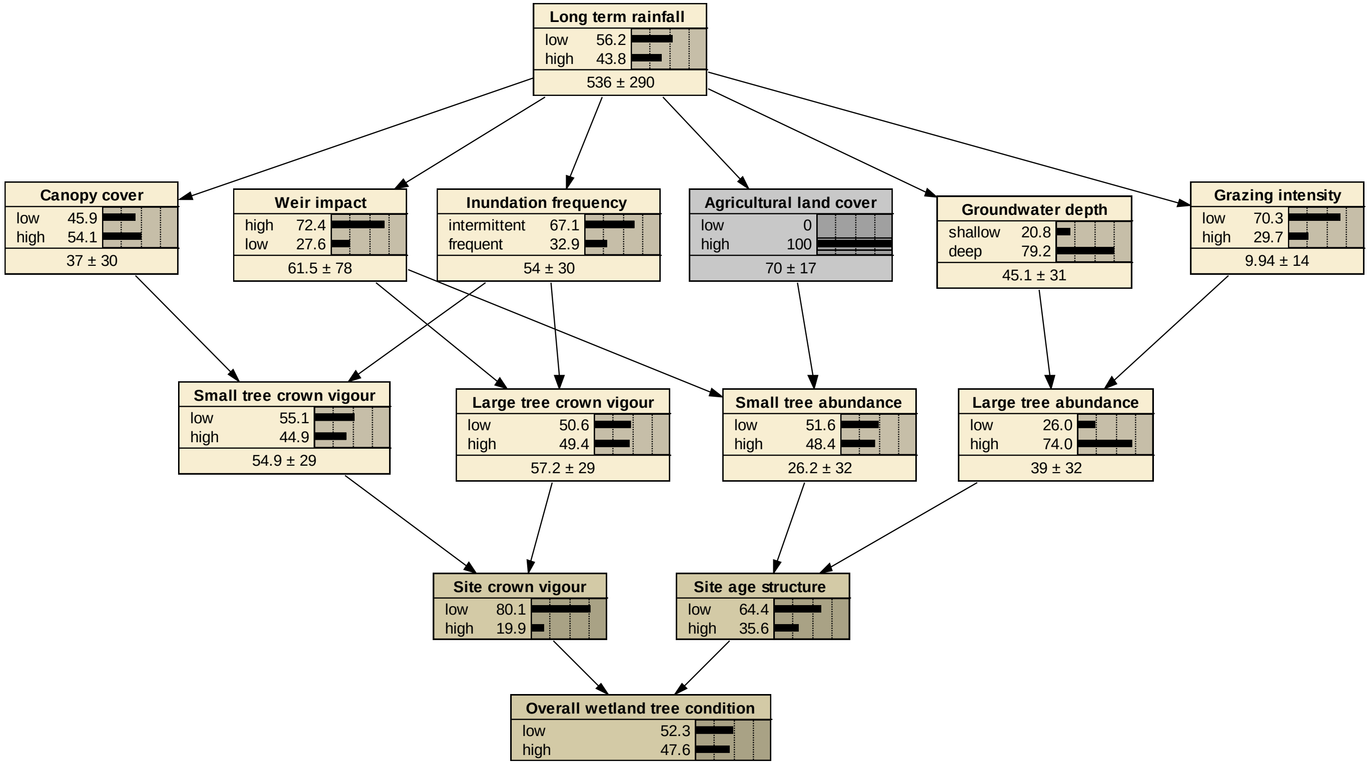
Appendix D2. Bayesian Network scenario analysis – frequent inundation frequency



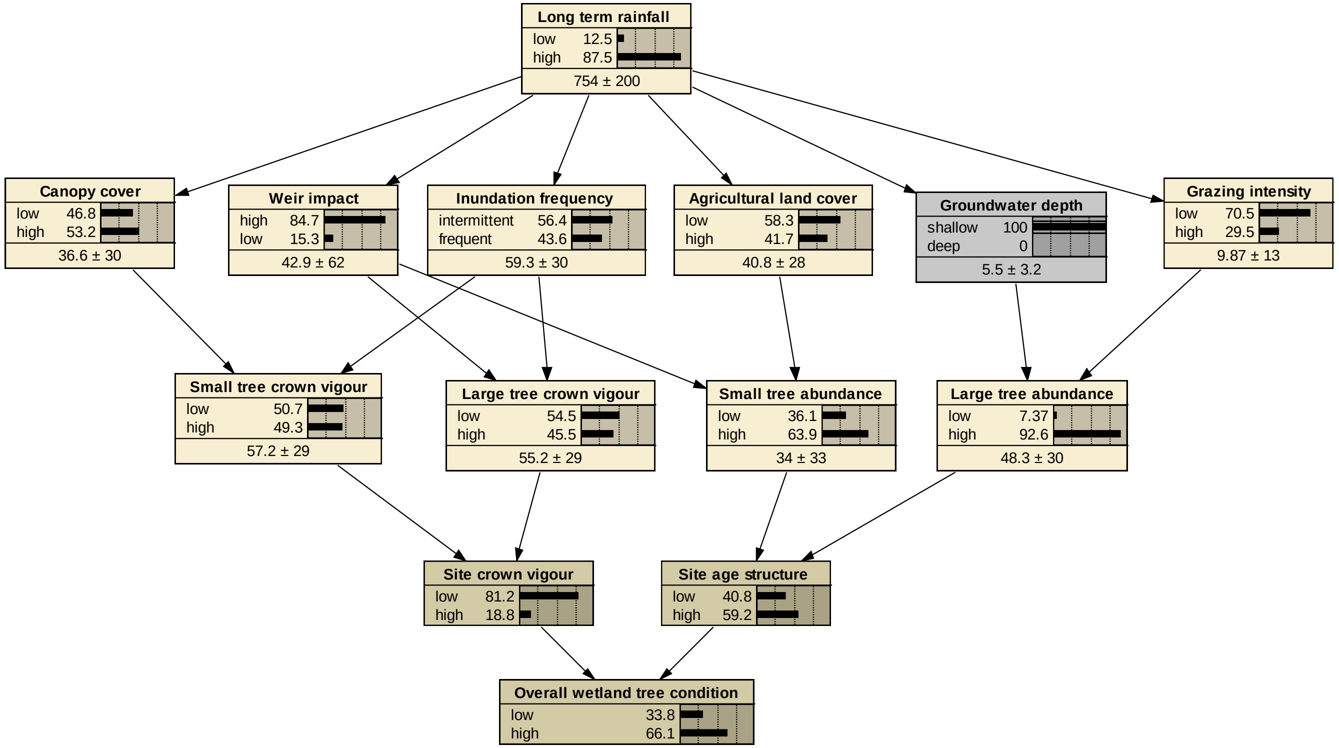
Appendix D2 contd. Bayesian Network scenario analysis – low agricultural land cover



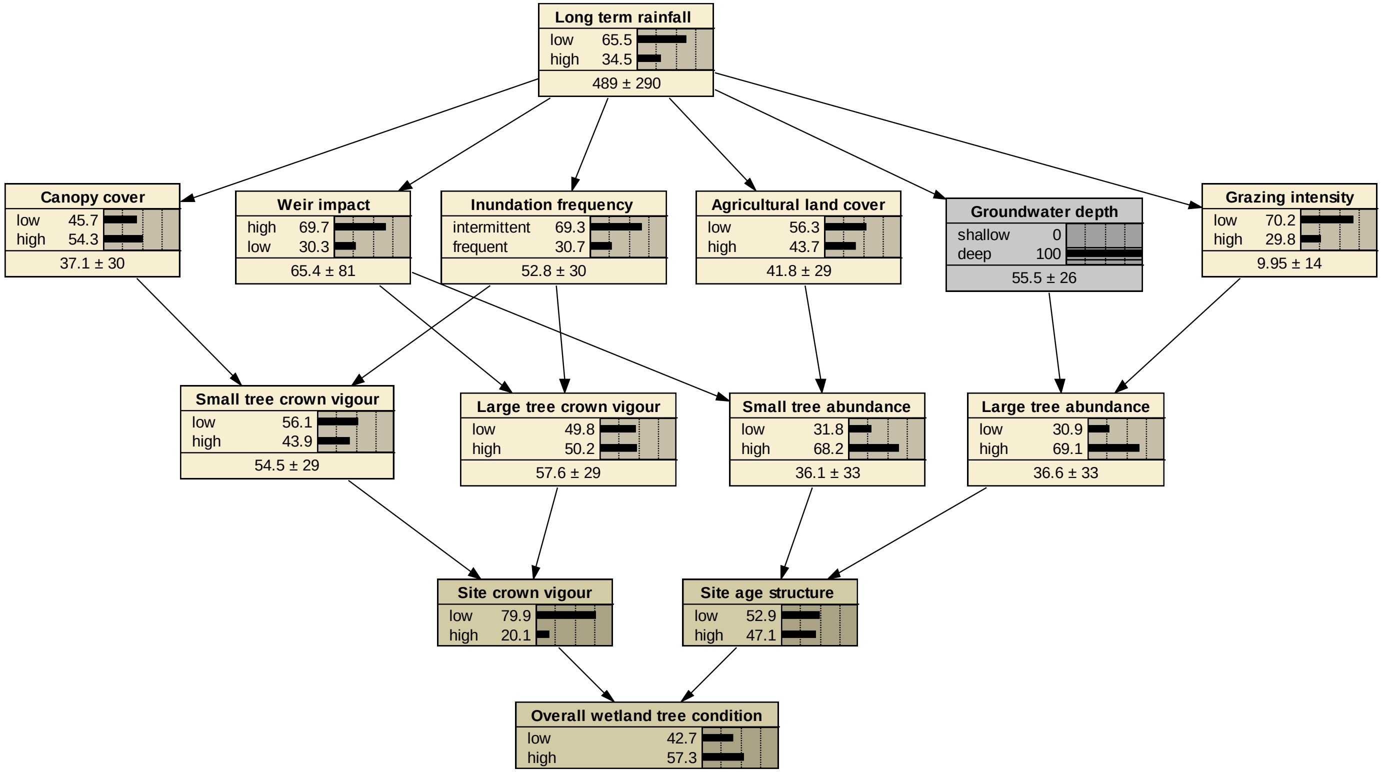
Appendix D2 contd. Bayesian Network scenario analysis – high agricultural land cover



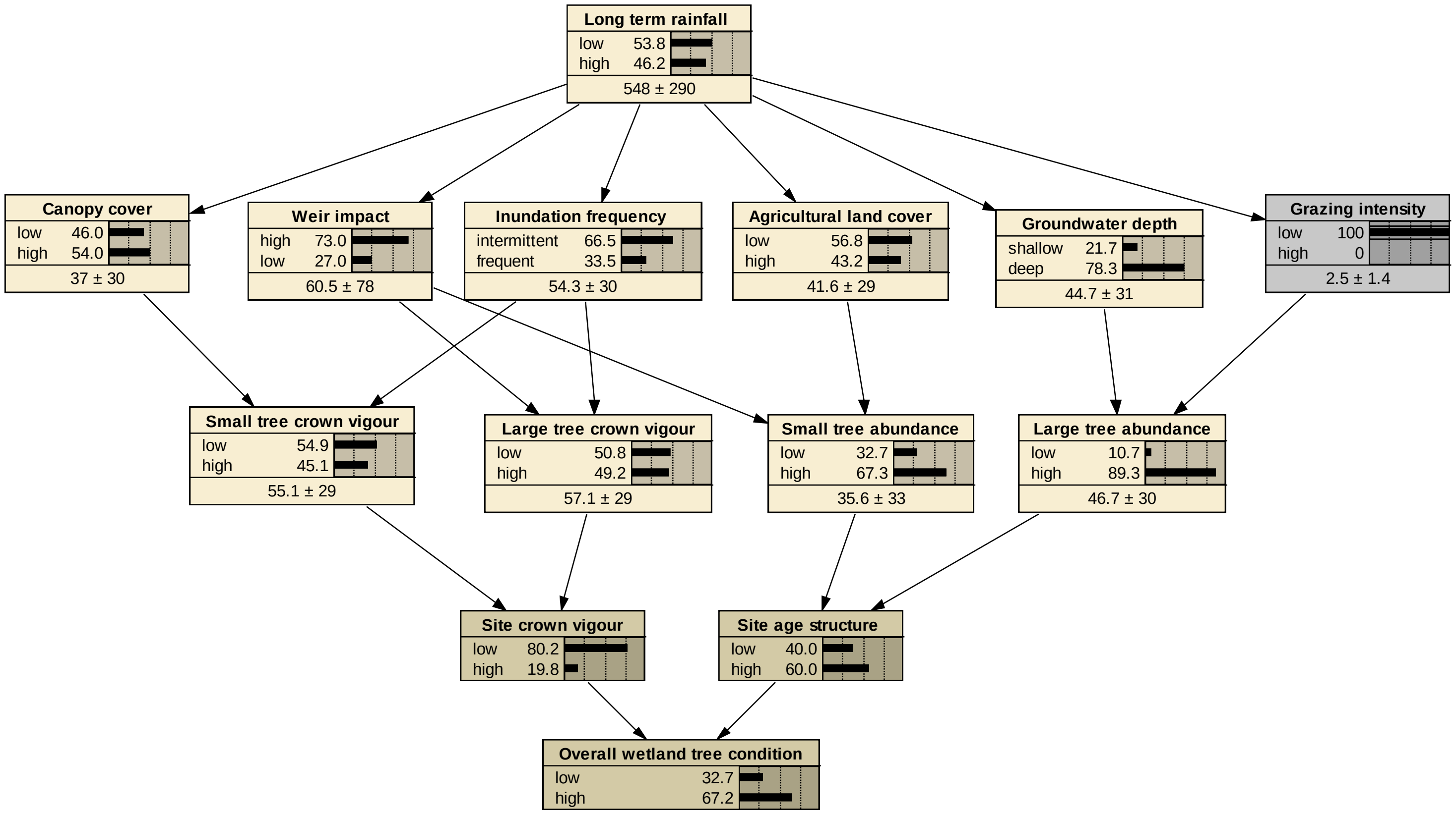
Appendix D2 contd. Bayesian Network scenario analysis – shallow groundwater depth



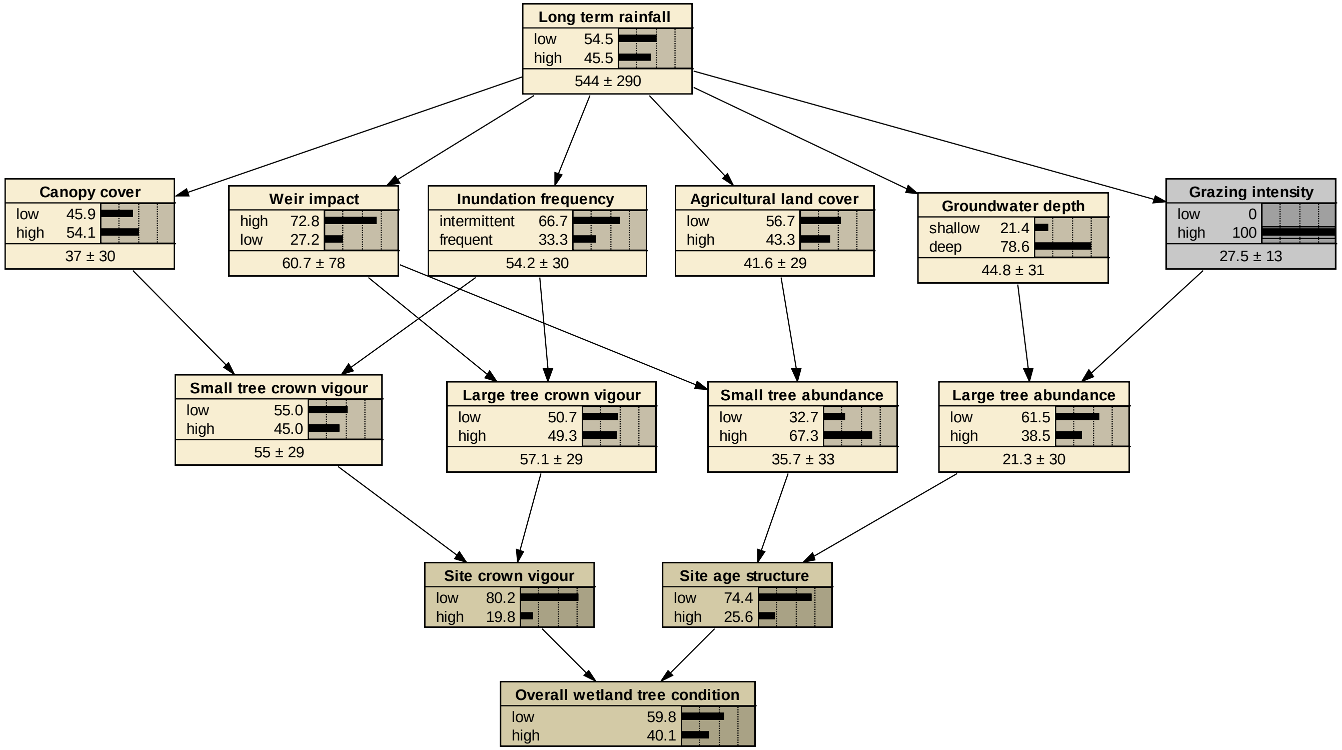
Appendix D2 contd. Bayesian Network scenario analysis – deep groundwater depth



Appendix D2 contd. Bayesian Network scenario analysis – low grazing intensity



Appendix D2 contd. Bayesian Network scenario analysis – high grazing intensity



Appendix E1. Means, standard error and range for hydrology and land use variables.

Environmental variables	Units	n	Mean	Standard error	Minimum	Maximum
Inundation frequency	(%)	33	58.39	4.41	16.67	100.00
Grazing intensity	(cow pats / 150 m^2)	37	4.53	0.86	0.00	16.33
Groundwater depth 1987	(m)	37	-12.60	0.42	-15.82	-7.68
Groundwater depth 2000	(m)	37	-15.36	0.50	-20.54	-8.07
Groundwater depth 2005	(m)	37	-18.38	0.80	-30.46	-9.75
Groundwater depth 2009	(m)	37	-19.16	0.73	-29.78	-10.19
Rain volume 1900 - 2007	(ML)	37	5.75	0.17	4.15	9.01
Remnant vegetation cover	(%)	37	0.14	0.05	0.00	1.00
River connectivity	(m)	37	322.98	66.86	38.64	2184.79
Agricultural land cover	(%)	37	35.04	5.80	0.00	100.00
Distance from weir	(km)	37	25.88	3.47	1.00	68.01
Canopy cover (> 2 m height)	(%)	37	24.43	2.63	3.33	77.50

Appendix E2. Count data for dominant tree species surveyed at each wetland

Site	Species and size class (cbh cm)														
	Eucalyptus camaldulensis					*Acacia stenophylla*					*Eucalyptus coolabah*				
	< 10	**10 - 20**	**20 -50**	**50 - 75**	**> 75**	**< 10**	**10 - 20**	**20 -50**	**50 - 75**	**> 75**	**< 10**	**10 - 20**	**20 -50**	**50 - 75**	**> 75**
1	2	0	4	0	6	2	0	1	0	0	0	0	0	0	0
2	6	1	3	3	7	0	0	0	0	0	0	0	0	0	0
3	13	27	13	6	1	18	2	1	0	0	3	2	5	1	0
5	2	1	8	7	4	0	1	1	1	0	0	0	0	0	0
6	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
7	4	0	1	3	6	0	0	0	0	0	0	0	0	0	0
8	1	0	0	5	4	0	0	0	0	0	0	0	0	0	0
9	6	1	0	1	0	2	0	1	1	0	10	7	6	0	0
10	0	0	0	0	8	5	1	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	1	0	0	5	0	1	7	1
13	2	1	2	0	0	1	0	0	0	0	1	8	6	1	0
14	41	1	6	5	5	2	0	0	0	0	0	0	0	0	0
15	2	14	15	1	5	0	0	0	0	0	0	0	0	0	0
16	5	5	2	3	2	0	0	0	0	0	0	0	2	1	0
17	0	0	1	0	3	2	5	6	0	0	1	0	0	0	0
18	8	25	20	6	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
20	31	1	1	5	4	0	0	0	0	0	0	0	0	0	0
21	7	20	9	12	4	7	5	6	5	1	0	0	0	0	0
22	2	19	22	19	0	0	0	0	0	0	0	0	0	0	0
23	4	0	2	4	7	0	0	0	0	0	0	0	0	0	0
25	0	0	2	5	4	2	1	1	1	0	0	0	0	0	0
26	1	23	17	5	1	6	6	9	0	0	0	0	0	0	0
27	0	19	27	4	4	25	0	0	2	0	0	0	0	0	0

Site	Species and size class (cbh cm)															
	Eucalyptus camaldulensis					***Acacia stenophylla***						***Eucalyptus coolabah***				
	< 10	**10 - 20**	**20 -50**	**50 - 75**	**> 75**	**< 10**	**10 - 20**	**20 -50**	**50 - 75**	**> 75**		**< 10**	**10 - 20**	**20 -50**	**50 - 75**	**> 75**
29	0	0	3	0		5	0	0	3	0	0	0	0	0	0	0
30	23	1	3	12		9	13	0	2	0	2	0	0	0	0	0
31	2	22	16	12		0	1	5	1	1	0	0	0	1	1	0
32	0	0	5	2		5	0	0	0	0	0	0	0	0	0	0
33	0	4	9	8		1	0	0	0	0	0	0	0	0	1	0
34	2	5	4	5		8	0	0	0	0	0	0	1	0	0	0
35	1	5	3	4		4	1	0	1	2	0	0	0	0	0	0
36	1	0	1	0		0	21	1	0	0	0	1	0	2	4	8
37	3	18	26	5		1	8	30	7	0	0	0	0	0	0	0
38	2	13	14	2		3	13	14	9	0	1	0	0	0	0	0
39	0	0	2	2		3	4	4	0	0	0	0	0	0	0	0
40	0	5	1	1		1	1	0	0	0	0	0	0	0	0	0
41	2	0	0	0		1	0	0	0	0	0	3	0	4	9	1

Appendix E3. Crown vigour and stag abundance data for dominant tree species surveyed at each wetland.

Site	Species and size class (cbh cm)											
	Eucalyptus camaldulensis			*Acacia stenophylla*			*Eucalyptus coolabah*			Stag abundance		
	< 20 cm	**20 – 50 cm**	**>50 cm**	**< 20 cm**	**20 – 50 cm**	**>50 cm**	**< 20 cm**	**20 – 50 cm**	**>50 cm**	**< 20 cm**	**20 – 50 cm**	**>50 cm**
1	0.68	0.71	0.33	0.67	0.17	-	-	-	-	0.00	0.00	1.33
2	0.83	0.50	0.63	-	-	-	-	-	-	0.00	0.00	1.00
3	0.51	0.68	0.78	0.65	0.50	-	0.78	0.73	0.67	4.00	2.33	0.67
5	0.76	0.79	0.72	0.75	0.67	0.67	-	-	-	0.67	1.00	1.67
6	0.42	0.83		-	-	-	-	-	-	0.00	0.00	1.33
7	0.50	0.33	0.64	-	-	-	-	-	-	0.00	0.00	0.00
8	0.50	0.00	0.74	-	-	-	-	-	-	0.00	0.00	0.00
9	0.59	0.00	0.67	0.42	0.67	0.83	0.42	0.81	-	0.00	0.33	0.33
10	-	0.00	0.77	0.82	-	-	-	-	-	0.00	0.00	0.33
12	-	0.00	-	-	0.83	-	0.77	1.00	0.74	0.00	0.33	1.00
13	0.55	0.67	-	0.33	-	-	0.44	0.78	0.83	2.33	0.00	0.00
14	0.83	0.61	0.67	0.72	-	-	-	-	-	2.67	1.33	1.00
15	0.63	0.74	0.59	-	-	-	-	-	-	0.00	0.67	0.33
16	0.71	0.83	0.83	-	-	-	-	0.83	0.83	0.00	0.00	0.00
17	0.83	0.83	0.45	0.82	0.39	-	0.83	-		4.00	4.33	3.67
18	0.52	0.71	0.73	-	-	-	-	-	-	1.00	0.00	0.33
19	0.82	0.00	0.50	-	-	-	-	-	-	0.00	0.00	0.67
20	0.67	0.67	0.30	-	-	-	-	-	-	0.00	1.33	3.33
21	0.68	0.56	0.66	0.79	0.56	0.63	-	-	-	2.00	2.00	0.00
22	0.63	0.73	0.79	-	-	-	-	-	-	13.50	1.50	0.50
23	-	0.67	0.78	-	-	-	-	-	-	0.00	0.00	0.00
25	-	0.67	0.47	0.50	0.67	0.33	-	-	-	2.33	0.00	0.67
26	0.58	0.70	0.77	0.74	0.63	-	-	-	-	18.67	6.33	0.33
27	0.46	0.57	0.51	0.71	0.00	0.75	-	-	-	1.00	0.33	0.33
29	0.71	0.83	0.47	0.00	0.83	0.00	-	-	-	0.00	0.00	0.67
30	0.25	0.61	0.65	0.48	0.33	0.67	-	-	-	0.33	0.00	0.67

Site	**Species and size class (cbh cm)**											
	Eucalyptus camaldulensis			***Acacia stenophylla***			***Eucalyptus coolabah***			**Stag abundance**		
	< 20 cm	**20 – 50 cm**	**>50 cm**	**< 20 cm**	**20 – 50 cm**	**>50 cm**	**< 20 cm**	**20 – 50 cm**	**>50 cm**	**< 20 cm**	**20 – 50 cm**	**>50 cm**
31	0.60	0.76	0.78	0.80	0.50	0.83	-	0.17	0.83	4.67	2.33	1.00
32	-	0.33	0.43	-	-	-	-	-	-	1.67	2.00	0.00
33	0.63	0.48	0.60	-	-	-	-	-	0.33	0.67	0.00	0.67
34	0.70	0.58	0.44	-	-	-	0.83	-	-	0.00	0.00	0.67
35	0.41	0.78	0.55	0.83	0.50	0.58	-	-	-	0.67	0.00	0.00
36	0.67	0.83		0.74	-	-	0.33	0.83	0.76	0.00	0.00	0.00
37	0.44	0.59	0.74	0.71	0.50	-	-	-	-	10.33	2.33	0.00
38	0.60	0.58	0.73	0.73	0.61	0.50	-	-	-	1.33	0.00	0.33
39	-	0.92	0.88	0.90	-	-	-	-	-	2.67	1.33	1.33
40	0.65	0.50	0.59	0.83	-	-	0.39	0.83	0.82	0.00	0.67	1.67
41	0.67	0.75	0.51	0.83	-	-	0.59	0.72	0.75	0.00	0.00	0.33