Floodplain Vegetation Productivity Response to Wetting and Drying: Testing the Adaptive Cycle Model

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Certification of Dissertation

Candidate’s Certification

I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification.

I certify that any help received in preparing this thesis and all sources used have been acknowledged in this thesis

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Abstract

Dryland floodplains are characterized by highly variable flooding and drying regimes. The spatial and temporal variability in flooding plays a significant role in the productivity of these ecosystems and is a key influence on the composition and distribution of vegetation in these floodplains. Dryland floodplains have been perceived to be boom and bust systems, in which the boom is characterised by an inundated floodplain and the bust is characterised by a dry floodplain in moisture deficit. The boom stimulates great primary and secondary production where as the bust brings contraction of the ecosystem into refugia and a reduction in primary and secondary production. This relatively simple two state model may not account for the transitions that may occur between flooding (boom) and dry (bust) floodplain states. Understanding the patterns of response at different scales is critical to our ability to manage these complex dryland systems and to be able to make predictions about their future condition over time.

This thesis applied an adaptive cycle model in order to understand change in floodplain vegetation productivity through multiple periods of flooding and drying. Adaptive cycles are a key component of resilience thinking. In this adaptive cycle model, vegetation productivity is the ecosystem responder and hydrology, or floodplain flooding and drying, the main driver of change. I derived a series of sequential hypotheses that explored the applicability of an adaptive cycle for the response of vegetation productivity in the Narran floodplain. The Normalized Difference Vegetation Index (NDVI) which measures vegetation greenness was used as a surrogate for vegetation productivity. In this adaptive cycle floodplain inundation was considered to drive vegetation productivity response through a cycle of exploitation, conservation, release and reorganization phases. The adaptive cycle starts as floodwater inundates the floodplain in the wetting phase. The wetting phase corresponds to the exploitation part of adaptive loop, where the area of vegetation productivity and quality will increase because of the availability of water as an exploitable resource. The wet phase is the phase of maximum inundation and corresponds to the conservation phase of the adaptive loop. The conservation phase is a period of increased vegetation productivity and a stability of vegetation productivity. The contraction of floodwater triggers the drying phase and corresponds to the release phase of an adaptive cycle. Further, desiccation of the floodplain occurs with the draining of floodwaters until the floodplain reaches a dry phase, a phase of no surface water availability. The dry phase corresponds to the reorganization phase of an adaptive cycle. The results of this thesis represents an advance on previous studies of dryland floodplains as an approach for characterising and understanding the response of vegetation communities in large floodplains.

The findings of this thesis demonstrated there to be marked differences in NDVI class area, number of transitions, directions of transitions, probability of transitions and NDVI class diversity between the dry phase and the combined wetting, wet and drying phases of inundation. Overall an anti-clockwise hysteresis relationship occurred between flooding and vegetation productivity, indicating a cyclic nature of vegetation response to floodplain inundation through dry, wetting, wet and drying phases. These results support the hypothesised adaptive cycle model for the response of vegetation productivity and its appropriateness for understanding the complexity of dryland floodplain vegetation response to wetting and drying. These results were also repeated over four flood events of different size. Although the four events exhibited an adaptive cycle, the duration and the nature of vegetation within each phase of the adaptive cycle differed. Likewise, the four different vegetation communities also exhibited response patterns in relation to flooding and drying that fit the adaptive cycle model. However, differences were evident in the timing of transitions between adaptive cycle phases and the duration spent in those phases in each vegetation community. The woodland community types of the Narran floodplain showed a higher productivity response during the drying or release phase. By comparison the highest productivity response for the grassland and shrubland was observed during the wetting or exploitation phase. Overall, the results showed the four vegetation communities are sensitive at different points in the adaptive cycle.

A unique finding of this study result was the location of the exit point from the adaptive cycle, which is the potential point for a state change. The exit point from an adaptive cycle is characterized by a period of enhanced high instability. In the Narran floodplain, the patterns of response in vegetation productivity to flooding and drying indicate this occurred between the conservation and release phases and not between the reorganization and exploitation phases as hypothesised by adaptive cycle theory. Thus, the potential for a change in state in dryland floodplains is highest between the wet (conservation) and drying (release) phases.

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Table of Contents

Certification of Dissertation i

Abstract ii

Acknowledgements iv

List of Figures xii

List of Tables xviii

Chapter 1 Introduction and aims 1

1.1. Introduction 1

1.1.1 Key knowledge gaps in understanding floodplain ecosystem change 6

1.1.2 Aims of this study 8

1.1.3 Thesis outline 8

Chapter 2 Literature review 11

2.1. Theories of change in vegetation communities 11

2.2. Resilience theory in understanding change 12

2.2.1 Adaptive cycles: a framework to understand change in ecosystems 14

2.2.2 Cross scale interaction (panarchy) or hierarchy in understanding change in ecosystems 17

2.2.3 Floodplain ecosystems and resilience 20

2.3. The role of disturbance in floodplain change 21

2.3.1 Disturbance in floodplain landscapes 22

2.3.2 The boom and bust model of hydro-ecological change in floodplains 24

2.3.3 Floodplain vegetation dynamics 25

2.3.4 Floodplain vegetation resilience 26

2.4. The use of satellite remote sensing and Geographical Information Systems in understanding spatial and temporal change 27

2.4.1 NDVI as a surrogate of vegetation productivity 30

Chapter 3 Study area and general methods 33

3.1. Study area 33

3.1.1 The Lower Balonne floodplain 33

3.1.2 The Narran floodplain 36

3.1.3 Wetting and drying of the Narran floodplain 42

3.2. General methods 44

3.2.1 Identifying wet and dry resource states and selection of satellite images 44

3.2.2 Satellite data pre-processing 44

3.2.3 Floodplain surface area inundation mapping 50

3.2.4 Calculation of the Normalized Vegetation Difference Index 51

3.2.5 Analysis of change in vegetation productivity 51

Chapter 4 The response of dryland floodplain vegetation productivity to flooding and drying 53

4.1. Introduction 53

4.2. Methods 56

4.2.1 Study area 56

4.2.2 Selection of satellite imagery 58

4.2.3 Calculation of NDVI 60

4.2.4 Statistical analysis 61

4.3. Results 62

4.3.1 Distribution of major vegetation communities 62

4.3.2 Differences in NDVI between wet and dry resource states at the landscape scale 62

4.3.3 Differences in NDVI between wet and dry resource states at the vegetation community scale 65

4.3.4 Climatic drivers of NDVI 68

4.4. Discussion 72

Chapter 5 An adaptive cycle hypothesis of semi-arid floodplain vegetation productivity in dry and wet resource states 79

5.1. Introduction 80

5.2. Study area 81

5.3. Methods 84

5.3.1 Satellite image selection 84

5.3.2 Calculation of the Normalized Difference Vegetation Index 85

5.3.3 Analysis of vegetation productivity 86

5.4. Results 88

5.4.1 Floodplain inundation in the dry resource state and wet resource state 88

5.4.2 Vegetation productivity 89

5.4.3 Vegetation productivity change 90

5.4.4 Diversity of vegetation productivity 94

5.4.5 Cyclic change of vegetation productivity in relation to floodplain inundation...... 95

5.5. Discussion 98

5.5.1 Vegetation productivity responses to wetting and drying.................................... 98

5.6. Conclusion 102

Chapter 6 Adaptive cycles of floodplain vegetation response to flooding and drying .. 105

6.1. Introduction 106

6.2. Study area 109

6.3. Methods 111

6.3.1 Satellite image selection 111

6.3.2 Delineation of adaptive phases 115

6.3.3 Calculation of the Normalized Difference Vegetation Index 115

6.3.4 Analysis of vegetation productivity among adaptive cycle phases 116

6.4. Results 117

6.4.1 Floodplain inundation and adaptive cycle phases 117

6.4.2 Area and quality of vegetation productivity through the adaptive cycle phases .. 118

6.4.3 Number and direction of vegetation productivity transitions through the adaptive cycle phases 121

6.4.4 Probability of NDVI class transitions through the adaptive cycle phases 126

6.4.5 Diversity of vegetation productivity through the adaptive cycle phases 130

6.4.6 Vegetation productivity among flood events 130

6.5. Discussion 132

6.5.1 Conclusion 136

Chapter 7 Do adaptive cycles of floodplain vegetation response to inundation differ among vegetation communities?... 139

7.1. Introduction.. 140

7.2. Study area and methods 144

7.2.1 Study area.. 144

7.2.2 Methods... 147

7.3. Results.. 150

7.3.1 Differences between the coolibah woodland community adaptive phases.......... 150

7.3.2 Differences between the grassland community adaptive cycle phases 153

7.3.3 Differences between the lignum community adaptive cycle phases 156

7.3.4 Differences between the poplar box woodland community adaptive cycle phases 159

7.3.5 Multivariate analyses 162

7.4. Discussion... 166

7.4.1 Different vegetation communities have a different adaptive cycle 166

7.4.2 Implications for floodplain vegetation community resilience............................ 169

7.4.3 Conclusion.. 170

Chapter 8 Thesis synthesis 173

8.1. Introduction to synthesis 173

8.2. Summary of the key research results emerging from this thesis 177

8.3. Contribution to the broader scientific knowledge 182

8.3.1 Semi-arid floodplain ecosystems 182

8.3.2 Value of a landscape approach using remote sensing techniques 183

8.3.3 Floodplain resilience 185

8.3.4 Ecosystem change.. 187

8.4. Application of this study to management 189

8.5. Future research prospects emerging from this thesis 190

References... 193

APPENDICES 223

Appendix 1...224

Appendix 2...237

Appendix 3...243

List of Figures

Figure 2.1 Adaptive cycle of change, indicating transitions among four phases: exploitation or growth (r phase) to conservation (K phase) to release (Ω omega phase) to renewal (α alpha phase). The cycle reflects changes in connectedness and capital, where the X- axis is the degree of connectedness among the controlling variables and the Y-axis is the capital that is inherent in the accumulated resources of biomass and nutrients. The exit from the cycle indicated at the left of the figure is the stage where the potential can leak away and where a change in threshold is most likely (adapted and modified from Holling 1986). 15

Figure 2.2 Hierarchical organisation of hydrological and geomorphological patches within the riverine landscape (Taken from Thorp *et al*. 2008). A. Nested hierarchy and level of organization, patches at one scale are nested within the level of organization above. B. The spatial scale associated with a hierarchically organised system. C. Hierarchical level of organisation and scale of geomorphological and hydrological patches within the riverine landscape. 19

Figure 2.3 Hierarchical levels of organization in geomorphology, hydrology and ecology in a riverine system (taken from Dollar *et al*. 2007). 20

Figure 3.1 Location of the Condamine Balonne River Catchment within Australia (top) and the main river network within the catchment (bottom). 35

Figure 3.2 The Narran floodplain and its location within the Lower Balonne floodplain. 38

Figure 3.3 Long term variation in temperature and precipitation in the Narran floodplain at the Collarenebri (Danumbral 48038) station between 1940 and 2009. 39

Figure 3.4 Annual discharge of the Narran River at the Wilby Wilby gauging station between 1965 and 2009. 39

Figure 3.5 Distribution of vegetation community and land cover types within the Narran floodplain landscape. The vegetation map obtained for this study was produced for the region by the Northern Floodplain Regional Planning Committee (NFRPC 2004) and was verified and modified with the vegetation ground truth data collected in 2007 by the Narran ecosystem project (Thoms *et al*. 2007). 41

Figure 3.6 The Narran floodplain in a dry state (a) and wet state (b). Photos: Martin C. Thoms. 43

Figure 3.7 Flowchart showing the detail of the image pre-processing procedure adopted in this research to examine vegetation productivity and change response between images within the DRS and WRS. 48

Figure 4.1 The location of the Narran floodplain. 57

Figure 4.2 The distribution of major vegetation communities and general land cover types in the Narran Floodplain. Modified from NFRPC (2004). 59

Figure 4.3 NDVI for the Narran floodplain in different resource states. A) Combined values for all dry (DRS) and wet (WRS) resource states; and, B). Individual resource states. Box and whisker plot provide the median (solid line within the box), the 25th and 75th percentile (outer edges of the box) and 5th and 95th percentiles (end of each line) as well as main outliers. 64

Figure 4.4 NDVI for the four major vegetation communities in the Narran floodplain. a). Vegetation communities in the wet (WRS) and dry (DRS) resource states; and, b). Vegetation communities in the individual resource states. Box and whisker plots provide the median (solid line within the box), the 25th and 75th percentile (outer edges of the box) and 5th and 95th percentiles (end of each line) as well as main outliers. 67

Figure 4.5 The effect of monthly precipitation on NDVI of the major vegetation communities in the Narran floodplain; (a) Coolibah, (b) Lignum, (c) Poplar Box, and (d) Grass. Solid lines are the local regression lines while dashed lines are the 5th and 95th confidence intervals. 70

Figure 4.6 The effect of monthly discharge (GL) on NDVI of the major vegetation communities in the Narran floodplain; (a) Coolibah, (b) Lignum, (c) Poplar Box, and (d) Grass. Solid lines are the local regression lines while dashed lines are the 5th and 95th confidence intervals. 70

Figure 4.7 Combined effect of monthly discharge (GL) and monthly precipitation (mm) on NDVI of the major vegetation communities in the Narran floodplain. (a) Coolibah, (b) Lignum, (c) Poplar Box, and (d) Grassland. Contour lines are median NDVI values. 71

Figure 5.1. Location of the Narran floodplain within the lower reaches of the Condamine-Balonne River catchment. 83

Figure 5.2 Area of floodplain inundation during the dry resource states (DRS) and wet resource states (WRS). The WRS is further divided into wetting, wet and drying phases. Image numbers are explained in Table 5.1 88

Figure 5.3. Area of NDVI Classes 2-6 in the Narran floodplain in the dry, wetting, wet and drying phases of inundation. NDVI Class 1 is not shown because it represents bare ground or water. Image numbers are explained in Table 5.1. 90

Figure 5.4 Area of floodplain change among six NDVI classes for the dry, wetting, wet and drying phases of inundation. Floodplain change is divided into the area that increased or decreased in NDVI class between consecutive images. Periods are explained in Table 5.1 91

Figure 5.5 Markovian transition models of change between NDVI classes 1-6 in the dry (a) and wetting, wet and drying (b) phases of floodplain inundation. The area of floodplain in each NDVI class is shown by different sized circles, and labelled with area (ha). Arrows identify the changes between NDVI classes, where red arrows indicate decrease green arrows indicate increase in NDVI classes. The size of the arrowhead indicates the probability of change among NDVI classes. Periods are explained in Table 5.1. 93

Figure 5.6 Distribution of the probability of transitions between all NDVI classes in the dry and combined wetting, wet and drying phases of flood inundation. Probability transitions were tallied from the Markovian transition models shown in Figure 5.5. 94

Figure 5.7 Shannon-Wiener Diversity Index of change in NDVI classes 2-6 for the dry, wetting, wet and drying phases. Images are explained in Table 5.1.Figure 5.7. Shannon-Wiener Diversity Index of change in NDVI classes 2-6 for the dry, wetting, wet and drying phases. Images are explained in Table 5.1. 95

Figure 5.8 Cyclic change in (a) Normalized difference vegetation index (NDVI) Class 2 area, (b) NDVI Class 4 area, (c) total number of transitions, (d) two-way transitions, (e) transition probability 1-5 % and (f) diversity in relation to floodplain inundation. The dry, wetting, wet and drying phases correspond to the phases of floodplain inundation outlined in Figure 5.2. 96

Figure 5.9 The hypothesised adaptive cycle model of the Narran floodplain based on hydrology and vegetation productivity. 100

Figure 6.1 The hypothesised adaptive cycle model of vegetation productivity response to hydrology in semi-arid floodplains. The adaptive cycle starts as floodwater inundates the floodplain in the wetting (exploitation phase), the wet (conservation phase) is the phase of maximum inundation, the drying (release phase) starts with the contraction of floodwater, the dry (reorganisation phase) occurs with desiccation of floodplain. The adaptive cycle reflects changes in the two properties: i) 108

Figure 6.2 The Narran floodplain within the lower reaches of the Condamine Balonne Catchment, Australia. 110

Figure 6.3 Surface area inundation of the Narran floodplain divided into corresponding dry, wetting, wet and drying phases of the adaptive cycle (a). Image numbers are explained in Table 6.1. Inset graph (b) shows the total discharge in (ML) in the Narran River and corresponding Narran floodplain surface area inundation. 120

Figure 6.4 Area of NDVI Class 2 through 6 in the Narran floodplain during the dry, wetting, wet and drying phases of the adaptive cycle. NDVI Class 1 is not shown because it represents bare ground or water. Image numbers are explained in Table 6.1. 123

Figure 6.5 Non-metric multidimensional scaling (MDS) ordination comparing adaptive phases using (a) area and quality (b) number of transitions and (c) probability of transitions data. 124

Figure 6.6 An example of Markovian transition models of change between NDVI Classes 1-6 in the dry, wetting, wet and drying phases of floodplain inundation. The area of floodplain in each NDVI class is shown by different sized circles, and labelled with area (ha). Arrows identify the changes between NDVI classes, where red arrows indicate decrease and the green arrows indicate increase in NDVI classes. The size of the arrowhead indicates the probability of change among NDVI classes. Periods are explained in Table 6.1. 125

Figure 6.7 Total number transitions, one-way and two-way transitions between NDVI classes in the adaptive cycle phases. Periods are explained in Table 6.1. 127

Figure 6.8 The distribution of probability transition classes in a) events divided into flood an dry components and b) the dry, wetting, wet and drying adaptive cycle phases. 128

Figure 6.9 Shannon -Wiener Diversity of NDVI class area in the dry, wetting, wet and drying adaptive phases. Image numbers are explained in Table 6.1. 131

Figure 7.1 The hypothesised adaptive cycle model of semi-arid floodplain productivity. The adaptive cycle starts as floodwater inundates the floodplain in the wetting (exploitation) phase. The wet (conservation) phase is the phase of maximum inundation. The drying (release) phase starts with the contraction of water from the floodplain and the dry (reorganisation) phase occurs with desiccation of the floodplain. The cycle reflects changes in two properties: the X -axis corresponds to connectedness along a continuum from a dry floodplain to complete inundation and the Y- axis corresponds to low to high vegetation vigour. The exit from the cycle, indicated at the left of the figure, is the stage where there is potentiality a change in state (after Thapa *et al.* 2015) 141

Figure 7.2 Location of the Narran floodplain within the Condamine Balonne Catchment and the distribution of vegetation communities within the Narran floodplain. Vegetation communities are derived from (NFRPC 2004).......... 146

Figure 7.3 The area of NDVI Classes 2-6 for coolibah woodland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPC = wetting phase coolibah, WPC = wet phase coolibah, DRPC = drying phase coolibah and DPC = dry phase coolibah. 151

Figure 7.4 Direction of change (one-way or two-way) between coolibah woodland NDVI classes in the dry, wetting, wet and drying phases of the adaptive cycle. WEPC = wetting phase coolibah, WPC = wet phase coolibah, DRPC = drying phase coolibah and DPC = dry phase coolibah 152

Figure 7.5 Distribution of the probability of NDVI class changes for coolibah in the wetting, wet, drying and dry phases of the adaptive cycle. WEPC = wetting phase coolibah, WPC = wet phase coolibah, DRPC = drying phase coolibah and DPC = dry phase coolibah. 153

Figure 7.6 The area of NDVI Classes 2-6 for grassland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPG = wetting phase grassland, WPG = wet phase grassland, DRPG = drying phase grassland and DPG = dry phase grassland. 154

Figure 7.7 Direction of change (one-way or two-way) between grassland NDVI classes in the dry, wetting, wet and drying phases of the adaptive cycle. WPG = wet phase grassland, DRPG = drying phase grassland and DPG = dry phase grassland. 155

Figure 7.8 Distribution of the probability of NDVI class changes for grassland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPG = wetting phase grassland, WPG = wet phase grassland, DRPG = drying phase grassland and DPG = dry phase grassland. 156

Figure 7.9 The area of NDVI Classes 2-6 for lignum shrubland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPL = wetting phase lignum, WPL = wet phase lignum, DRPL = drying phase lignum and DPL = dry phase lignum. 157

Figure 7.10 Direction of change (one-way or two-way) between lignum shrubland NDVI classes in the dry, wetting, wet and drying phases periods of the adaptive cycle. WEPL = wetting phase lignum, WPL = wet phase lignum, DRPL = drying phase lignum and DPL = dry phase lignum. 158

Figure 7.11 Distribution of the probability of NDVI class changes for lignum shrubland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPL = wetting phase lignum, WPL = wet phase lignum, DRPL = drying phase lignum and DPL = dry phase lignum. 159

Figure 7.12 The area of NDVI Classes 2-6 for poplar box woodland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPP = wetting phase poplar box, WPP = wet phase poplar box, DRPP = drying phase poplar box and DPP = dry phase poplar box. 160

Figure 7.13 Direction of change (one-way or two-way) between poplar box woodland NDVI classes in the dry, wetting, wet and drying phases of the adaptive cycle. WEPP = wetting phase poplar box, WPP = wet phase poplar box, DRPP = drying phase poplar box and DPP = dry phase poplar box. 161

Figure 7.14 Distribution of probability NDVI class changes for poplar box woodland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPP = wetting phase poplar box, WPP = wet phase poplar box, DRPP = drying phase poplar box and DPP = dry phase poplar box 162

List of Tables

Table 3.1 Satellite images comprising the dry and wet resource state of four events, with corresponding hydrology, rainfall and 46

Table 4.1 Pair-wise comparisons of NDVI in different Dry and Wet resource states for the Narran floodplain. D = dry resource state and W = wet resource state; * = significant difference ($p < 0.05$) and NS = not significant. 63

Table 4.2 Pair-wise comparisons of NDVI for Coolibah, Poplar Box, Lignum and Grassland vegetation communities in different resource states. D = dry resource state and W = wet resource state; * = significant difference ($p < 0.05$)and NS = not significant. 65

Table 4.3. Associations between resource state, monthly precipitation, monthly discharge and NDVI values in the Narran floodplain. Results were generated from a Generalised Estimating Equation Model where * = a significant association ($p < 0.05$) and NS = not-significant. 68

Table 5.1 Satellite images comprising the dry and wet resource states, with corresponding hydrology, rainfall and temperature conditions. A period refers to the comparison of two images, where the comparison of image 1 and 2 becomes period 1. 86

Table 5.2 Pattern of cyclic change in vegetation productivity measures in response to floodplain inundation. NDVI = Normalised Difference Vegetation Index. For hysteresis direction AC = anti-clockwise and C = clockwise. Example hysteresis loops are given in Figure 5.8.. 97

Table 6.1 Satellite images for the four events, with corresponding hydrology, rainfall and temperature conditions. A period refers to the comparison of two images, where the comparison of Image 1 and 2 becomes Period 1. Hydrology data were obtained from the Department of Primary Industries (NSW) Office of Water Information and climatic data were acquired from the Australian Bureau of Meteorology. 113

Table 6.2 Differences in NDVI class area and quality, number and direction of NDVI class transitions, probability of NDVI class transitions and NDVI class diversity among adaptive cycle phases of four events. NS = not significant ($p > 0.05$).. 121

Table 6.3 Multivariate dispersion index values of different adaptive cycle phases for NDVI class area and quality, number and direction of NDVI class transitions and probability of NDVI class transitions data. 129

Table 6.4 Matrices of group centroid distances between the adaptive cycle phases using NDVI class area and quality, number and direction of NDVI class transitions and probability of NDVI class transition data. 129

Table 6.5 Differences in NDVI class area and quality, number and directions of NDVI class transitions, probability of NDVI class transitions and NDVI class diversity among events for each adaptive phase. NS = not significant (p>0.05). No test = replication unavailable for a test. 132

Table 7.1 Pairwise permutation MANOVAs for individual vegetation communities, adaptive cycle phases and vegetation communities within adaptive cycle phases using NDVI area and quality data. p values are provided and p > 0.05 is non-significant (NS). 163

Table 7.2 Pairwise permutation MANOVAs for individual vegetation communities, adaptive cycle phases and vegetation communities within adaptive cycle phases using direction of change data. p values are provided and p > 0.05 is non-significant (NS). 164

Table 7.3 Pairwise permutation MANOVAs for individual vegetation communities, adaptive cycle phases and vegetation communities within adaptive cycle phases using probability of change data. p values are provided and p > 0.05 is non-significant (NS); * no p value 165

Table 8.1 A summary of research undertaken in this thesis and the contributions emerging from this thesis.. 175

Chapter 1 Introduction and aims

1.1. Introduction

Change is a natural feature of any system. Globally, during the last five decades unprecedented changes have occurred in ecosystems due to human activities (MEA 2005, Chapin *et al*. 2009) resulting in loss of biodiversity, altered ecosystem processes and reduced resilience (Chapin *et al*. 2000). However, changes in ecosystems are rarely simple, because responses to drivers of change are mediated through a range of interactions and feedbacks between biotic and abiotic components and processes that make up most ecosystems. Ecosystem processes change at multiple scales (Forman and Godron 1986, Turner 2005) because different controls and processes are characteristic of each scale in time and space (Wu 1999) and are differentiated by biotic and abiotic structure (Pickett and Cadenasso 1995). Thus, understanding how and why ecosystems change requires an understanding of the key drivers of change at different scales, and is central to ecosystem science (Sutherland *et al*. 2013).

The theory of ecosystem change has been a major focus of ecological research since Clements (1916) introduced his theory of ecological succession in relation to vegetation, where the focus was on orderly successional change within communities. This theory was later criticised by Gleason (1926), who emphasised that ecosystem change is unpredictable and fluctuates with time and space. However, Cooper (1926) described ecosystem change as a constant process that is like a “flowing braided stream” that changes over time in a dynamic manner as a result of a complex interaction between abiotic and biotic processes. Cooper’s (1926) approach to the properties of change in ecosystems was far beyond his time. He emphasised that vegetation change is dynamic and transient, has short term predictability and long term unpredictability, is irreversible and changes with the scale of observation. This view of the process of change in ecosystems has only just been recognised in contemporary ecosystem science through theories of hierarchical organization, ecological heterogeneity, complex adaptive systems and disturbance driven patchiness (O'Neill *et al*.1989, Wu and Loucks 1995, Pickett *et al*. 2003). Of these, complex adaptive system theory has been adopted in ecology to examine the change in ecosystems and to understand the relationships between pattern and process.

Complex adaptive systems are characterised by nonlinear dynamics, multiple stable states, fast and slow drivers and self-organisation (Holling 1986, Gunderson and Holling 2002, Dearing 2008, Folke *et al*. 2010, Walker and Salt 2012). Complex systems are also characterised by resilience, or the capacity to recover from disturbances and maintain the same structure, function and feedbacks (Holling 1973, Holling and Gunderson 2002). Resilience theory proposes that complex adaptive systems have dynamic trajectories that do not tend towards stable or equilibrium conditions (Holling 1973, Carpenter and Gunderson 2000). Rather, they possess trajectories of change through an adaptive cycle (Holling, 1986, Gunderson and Holling 2002). The adaptive cycle is a key component of resilience theory, and provides a framework for understanding processes of change in complex systems (Holling 1986, Gunderson *et al*. 2010, Jax 2010, Walker and Salt 2012). Adaptive cycles characterise change as a cyclic process comprised of four phases: exploitation, conservation, release and reorganisation (Holling and Gunderson, 2002).

The majority of past studies that have used succession theory also focus on patterns arising from change, and less attention has been given to the processes of change (Stienhard and Volk 2003). Where processes have been examined, they are generally studied at smaller plot or transect scales (Brock and Casanova 1997, Warwick and Brock 2003, Capon 2005, Capon *et al*. 2009, Reid *et al*. 2011). According to Pickett *et al.* (2003), to better understand the dynamics of ecosystem change it is necessary to focus on functional connections, hierarchical structure, boundaries and scale of resolution of processes. The adaptive cycle concept of Holling (1986) and Holling and Gunderson (2002) provides an alternative framework for understanding the functional processes of change in a complex system; however, much remains to be studied, particularly in relation to the empirical testing of the theory of adaptive cycles (Walker and Meyers 2004).

Floodplains can be defined from many different perspectives. Hydrologists, for example, view the floodplain as the surface area that is inundated by a return flow of a certain magnitude (e.g. the 100 year return flood). Geomorphologists view the floodplain as the area of alluvial deposits adjacent to a river channel. Ecologists view floodplains as flat featureless areas adjacent to river channels that provide habitat for a distinct suite of interacting plants and animals adapted to cope with and exploit periodic inundation (Wiens 2002). The common theme in all these perspectives is the important role of periodic inundation as a manifestation of a hydrological regime, as the means by which alluvial sediments are exchanged, and as a driver of ecological processes such as biomass accumulation and loss, biochemical transformation, fluxes and connectivity. Exchanges of water, sediment, nutrients and biota between river channels and their floodplain are driven by hydrological connections that create a dynamic mosaic of inundated patches during the expansion and contraction of floodwaters (Thoms 2003, Murray *et al*. 2006). Change is especially noticeable in floodplain landscapes because they are subject to periodic inundation and drying, which, in turn, results in contrasting aquatic, terrestrial and transitional phases (Junk *et al*. 1989, Naiman and Decamps 1990, Tockner *et al*. 2008). The high biodiversity of floodplain ecosystems is maintained, in part, by variation in hydrological regimes and highly productive soils, all of which influence the abundance, spatial organisation and resilience of floodplain plant and animal species over time (Whited *et al*. 2007).

Floodplain ecosystems are among the most threatened globally by human activities and climate change (MEA 2005, Whited *et al*. 2007, Tockner *et al*. 2008, Tockner *et al*. 2010). The ecological integrity of floodplains has been compromised by activities such as flow regulation, the construction of levees, direct land clearing and upstream catchment land use changes (Kingsford 2000, Tockner and Stanford 2002). Resulting changes in flow regime have drastically altered spatial and temporal patterns of wetting and drying, resulting in reduced mean annual flows, changes in the frequency and duration of floods, and changes in the shape of individual flood hydrographs (Thoms *et al*. 2005), shifts in flooding seasonality (Maheshwari *et al*.1995, Thoms *et al*. 2005) and channel instability (Walker and Thoms, 1993). A review of pressures influencing large river floodplain ecosystems by Nilsson *et al*. (2005) indicated that more than half (172 out of 292) of the world's major floodplain ecosystems are affected by some form of human-induced hydrological alteration and have substantially altered natural wetting and drying regimes (Baldwin *et al*. 2013). Alteration of flow patterns in rivers is a key driver of riverine and floodplain riparian ecosystem change. Flow regulation alters sediments transportation and reduces the magnitude and frequency of flow (Naiman *et al*. 2005, Stromberg *et al*. 2007), that ultimately results in lower water tables, reduced lateral connectivity and modification of successional processes. Further, reduced flow has known consequences for the ecology of dryland rivers, including refugia loss, conversion of aquatic ecosystems to terrestrial ecosystems and decline in biodiversity of riverine ecosystems (Naiman *et al*. 2005, Bunn *et al*. 2006, Sheldon *et al*. 2010).

Seventy three percent of Australia's large rivers are semi-arid systems and exist as a network of temporary channels and waterholes (Thoms and Sheldon 2000) which are important refugia for aquatic biota (Bunn *et al.* 2006) and are highly productive ecosystems compared to terrestrial environments (Sims and Colloff 2012). Australian floodplain ecosystems are a valuable resource in terms of the ecosystem services they provide. The ecosystem services provided by the floodplain wetlands of the Murray-Darling Basin have been valued at $187-302 million per year (Thoms and Sheldon 2000), and support economically valuable agricultural and recreational activities (CSIRO 2008).

Semi-arid floodplains are often referred to as boom (flooding or wetting) and bust (dry) ecosystems (Walker *et al.* 1995, Bunn *et al.* 2006) as a result of highly variable and unpredictable hydrology. Australian semi-arid river floodplain ecosystems are amongst the most hydrologically variable in the world (McMahon 1978, Finlayson and McMahon 1988, Puckridge *et al.* 1998) and this variability plays a major role in the integrity of floodplain ecosystems (Kingsford 2000, Leigh *et al.* 2010). The variability in flooding and drying of a floodplain is a key influence on the composition and distribution of semi-arid floodplain vegetation (Nightingale and Phinn, 2003, Brock *et al.* 2006, James *et al.* 2007, Hassler *et al.* 2010).

Most research on spatial patterns of floodplain vegetation distribution in relation to floodplain inundation has adopted a gradient approach (Whittaker 1967, Austin and Gaywood 1994, Friedman *et al.* 2006, Petty and Douglas, 2010). More recent research, however, suggests that spatial patterns in floodplain vegetation do not necessarily follow simple gradients (Southwell and Thoms 2011, Thoms and Parsons 2011), and that a gradient approach may not deal effectively with the complexity of the floodplain vegetation structure arising from hydrological processes (van Coller *et al.* 2000). An alternative to the gradient approach is that floodplains are better viewed as dynamic, shifting mosaics (Stanford *et al.* 2005, Whited *et al.* 2007, Thorp *et al.* 2008, Thoms and Parsons 2011). Recent studies describe floodplains as heterogeneous and as a dynamic spatial mosaic where water plays a significant role in connecting and regulating the exchange of energy, materials, nutrients and biota between different patches of a floodplain (Poole 2002, Thoms 2003, Parsons *et al.* 2005, Thorp *et al.* 2006). These exchanges are driven by hydrological connections which create a dynamic mosaic of inundated-patches during the expansion and contraction of floodwaters (Murray *et al.* 2006). In particular, the wetting and drying of a floodplain plays a significant role in maintaining the spatial heterogeneity of floodplain vegetation communities (Osterkamp and Hupp 2010). The connectivity between terrestrial and riverine ecosystems during flooding is an important process in floodplain ecology and a foundation for understanding variation in pattern and process of riverine ecosystems (Ward *et al*. 1999). Any changes in flow variability over time may result in a loss of vegetation functionality such as the provision of habitat features (Capon, 2003).

Much of the current knowledge of floodplain vegetation dynamics in relation to inundation comes from small-scale studies, based on information collected at sites, transects or plots (e.g. van Coller *et al*. 2000, Capon 2003, Capon 2005, Capon *et al*. 2009, Reid *et al*. 2011). Yet flooding in low gradient semi-arid floodplains can cover large areas (Thoms 2003), and be highly patchy (Murray *et al*. 2006). Given that what is observed at one scale may not be applicable at other scales of observation (Wu and Loucks 1995), examination of vegetation in relation to inundation is needed at large scales in addition to smaller scales. Developments in remote sensing techniques for assessing vegetation at large scales, such as the NDVI measure of vegetation vigour, provide an avenue to undertake the types of large-scale, whole-of-landscape studies required for large scale, whole of floodplain ecosystem-level assessments of vegetation. Thus, remote sensing is an approach that can explore pattern across scales more effectively than plot or transect-based studies.

Floodplain vegetation is one of the key components of floodplain productivity and plays a major role in riverine ecosystem processes (Casanova and Brock 2000, Reid *et al*. 2011, Parsons and Thoms, 2013). The productivity of floodplain vegetation is determined by the availability of water, local geomorphology, soil conditions and human interference (Hutley *et al*. 2011, Sims and Colloff 2012). Increased vegetation growth in response to flooding is one of the most important processes controlling the carbon and nutrient dynamics on floodplains and in the adjacent terrestrial and riverine ecosystem (Naiman and Decamps 1990, Sims and Thoms 2002, Tockner *et al*. 2008). Flooding provides water to vegetation which stimulates a rapid increase in floodplain productivity that may last for months across large areas of the floodplain (Kingsford 1999, Thoms 2003, Leigh *et al*. 2010). In addition, flooding also contributes to elevation of soil nutrients, which further increases vegetation productivity (Baldwin and Mitchell 2000, Ogden and Thoms 2002,Westbrooke *et al*. 2005, Reid *et al*. 2011, Parsons and Thoms 2013, ,). The dry state, when water is limited, may last for years and may also influence the distribution and composition of floodplain vegetation communities (Arthington *et al*. 2010, Parsons and Thoms 2013). Water table fluctuations can also exert controls on vegetation growth depending on the plants capacity to tolerate anoxic or saline conditions (Naumburg *et al*. 2005). Decline in groundwater below the rooting zone can lead to moisture stress on the vegetation followed by reduced growth and increased mortality (Asbjornsen *et al*. 2011). Vegetation that does not have physiological mechanisms to withstand drought conditions will not survive extended periods of drought (Xu *et al*. 2010). However, the response of vegetation mostly depends on plant adaptations, and there is a threshold at which the system is able to cope. If this threshold is crossed, then the system will change its state (Gunderson 2000, Scheffer and Carpenter 2003). Some vegetation is not able to cope with irregular disturbances, whereas others maintain the same function and structure after disturbances (Lichtenthaler 1996).

1.1.1 Key knowledge gaps in understanding floodplain ecosystem change

Understanding the role of water in sustaining natural ecosystems, protecting biodiversity and restoring rivers degraded by over-abstraction has become a key water resource management issue worldwide (Murray *et al*. 2006). Studies on the effect of water stress or inundation on floodplain vegetation dynamics have mostly been small-scale studies that focus on the scale of sites, plots and transects or in the narrow riparian corridors; however, knowledge of long-term floodplain vegetation productivity and community responses to wetting and drying at the floodplain landscape scale is relatively scant. Better floodplain vegetation management requires a focus on the whole floodplain landscape (Thoms and Parsons 2011). Floodplain landscapes are heterogeneous, complex ecological systems that operate over multiple spatio-temporal scales (Ward 1989). Most environmental and resource management problems can only be dealt with effectively at the broad scales on which they typically occur (Wu 1999). The appearance of different patterns at different scale reveals the hierarchy of structuring processes (O’Neill *et al*. 1989, Dollar *et al*. 2007). Thus, any attempt at understanding pattern and process linkages in ecosystems within the context of complex adaptive system must be aware of scale.

Semi-arid floodplain vegetation is conceived to respond to a wet (boom) state of abundant water availability and a dry (bust) state of limited water availability. This simple two-state model does not address the potentially important processes and patterns that may arise through the transition between the two states (boom and bust). Ecosystems respond in a complex manner to the availability of resources (Schwinning and Sala 2004, Smith *et al.* 2009) and may show multiple stable states, nonlinearity and self-organization (Holling 1973, Folke *et al.* 2010). Thus, emphasis on floodplain productivity as consisting of two states may not account for the potential complexity in response to water availability. To facilitate a better understanding of the process of change Holling (1986) and Gunderson and Holling (2002) proposed the adaptive cycle as a model of ecosystem change derived from complex adaptive systems theory. Applying an adaptive cycle model to semi-arid floodplain vegetation assumes that the dynamics of these systems are more complex than the two-state boom and bust model of change. Further, understanding of temporal patterns is critical to the ability to manage complex semi-arid systems, as well as to make predictions about future dynamics as the pattern may vary over time. Thus, an adaptive cycle framework may help us to better understand these complexities; however there has been no empirical research to date that uses an adaptive cycle framework to understand change in floodplain vegetation productivity over time.

Satellite data in combination with Geographic Information Systems (GIS) have proven extremely useful for detecting change in vegetation pattern and process over various scales. These technologies provide an avenue for investigating the relationship between pattern and process (Walsh and Davis 1994, Farina 2006). Further, multispectral satellite images and remote sensing (RS) and GIS analysis techniques have the capability to manage, retrieve and combine large amounts of spatio-temporal data and provide avenues to undertake whole-of-landscape scale studies. Many studies have recognised the potential of RS and GIS for analysing landscape patterns, gradients and trajectories of landscape patterns and processes (Farina 2006, Jensen 2007, Campbell and Wynne 2011). Field based ground observations are impractical over large areas because they are time consuming and are often very expensive, while RS potentially allows for more cost-effective and regular monitoring of vegetation cover change over large areas (Lillesand and Kiefer 1994). Therefore, RS and GIS are powerful instruments for understanding ecosystem change. No other survey methods can operationally provide a standardised survey of the landscape with which to analyse landscape-level pattern and change (Burnett and Blaschke 2003, Steinhardt 2003).

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1.1.2 Aims of this study

The aim of this PhD research is to examine changes in the productivity of floodplain vegetation in response to wetting and drying in a semi-arid region of Australia. Specifically, the study will examine the vegetation productivity response over four wetting and drying cycles over 20 years at the floodplain landscape and vegetation community scales and use the observed patterns to empirically test the adaptive cycle model and thus assess its value as a means to understand change in floodplain vegetation.

To achieve this aim, four broad research questions are asked:

1. Is there a difference in floodplain vegetation productivity response between and within dry and wet periods and what is the spatial pattern of their response at the floodplain landscape scale and for individual vegetation communities?
2. How does floodplain vegetation productivity change through a wetting and drying state? In particular, can the pattern of change be characterised as a boom-bust pattern, or is it better and more usefully characterised as an adaptive cycle?
3. During multiple wetting and drying events does the floodplain adaptive cycle repeat and how is it influenced by different size flooding events? Are there any changes in the adaptive cycle and its stability over time in semi-arid floodplains?
4. Do adaptive cycles over multiple wetting and drying events, vary between the major vegetation communities of the floodplain and if so, can this variation be attributed to the strategies that the species within those communities employ to cope with variation in water availability?

1.1.3 Thesis outline

The aims of this PhD thesis are addressed through a literature review, four main data analysis chapters, and a synthesis. The data chapters have been developed as stand-alone papers, that has either been published or submitted for publication in an international scientific journal. The thesis is organised as follows:

Chapter 2 contains the literature review that explores existing knowledge surrounding the subject areas relevant to the research being undertaken. The literature review has four sections. The first section explores the theory of change and the process of understanding those changes. The second section highlights the role of disturbance in floodplains and how that causes change, and is followed by a conceptual model of change in floodplain vegetation based on floodplain vegetation dynamics and resilience. The third section of the literature review describes the application of remote sensing (RS) and Geographic Information Systems (GIS) and how these tools have been used to investigate spatial and temporal changes, with a focus on vegetation productivity change over time and the use of the Normalised Vegetation Difference Index (NDVI) as a surrogate of vegetation productivity.

Chapter 3 contains a description of the Condamine-Balonne catchment followed by a description of the Narran floodplain ecosystem study area. The general methods employed in this thesis are also presented in this chapter.

Chapter 4 (Manuscript 1) is a research article titled *"Semi-arid floodplain vegetation productivity response to wetting and drying".* This manuscript examines the Normalised Difference Vegetation Index (NDVI) values over 20 years on a monthly basis over four dry and four wet states. The main aim of this paper was to compare NDVI values of Narran floodplain vegetation for wet and dry states and to explore the relative influences of rainfall and inundation on NDVI responses. This comparison was carried out at the landscape scale and within the four major vegetation community types of the Narran floodplain landscape: lignum *(Duma florulenta*) shrubland, coolibah (*Eucalyptus coolabah*) woodland, poplar box (*Eucalyptus populnea*) woodland and grassland. A series of univariate statistics were applied to examine differences in the NDVI values between the wet and dry resource states and between and within each sequence, at the Narran floodplain landscape scale and between and within vegetation communities. This manuscript has been submitted to the Journal of Arid Environments.

Chapter 5 (Manuscript 2) is a research article titled *"An adaptive cycle hypothesis of semi-arid floodplain vegetation productivity in dry and wet resource states".* This manuscript quantifies the change in vegetation productivity through a dry and wet state with the aim of testing whether the vegetation productivity response can be characterised as a boom-bust response, or if the response is better characterised as an adaptive cycle. The vegetation change was tracked through the dry and wet cycle at approximately monthly intervals by analysis of the pair-wise change in NDVI on a pixel by pixel basis, which then led to the development of the Markovian Transition Model that tracked the change in vegetation productivity across the floodplain. This manuscript has been published in *Ecohydrology*. A copy is provided as Appendix 1.

Chapter 6 (Manuscript 3) is a research article titled *"Adaptive cycles of floodplain vegetation response to flooding and drying".* This manuscript examines multiple wet-dry events over 20 years to test whether the adaptive cycle model of floodplain vegetation productivity response to flooding and drying (developed in Manuscript 2) repeats and how it is influenced by the character of different flood events, particularly flood size. This manuscript has been submitted to Hydrology and Earth System Sciences.

Chapter 7 (Manuscript 4) is a research article titled "*Do adaptive cycles of floodplain vegetation response to inundation differ among vegetation communities*?" This manuscript examines vegetation productivity response at the vegetation community level, using the same 20 years multiple event data used in Manuscript 3. This manuscript further tests the hypothesised adaptive cycle model (developed in Manuscript 2) with a focus on response of individual vegetation communities. This manuscript has been submitted to PLOS ONE.

Chapter 8, the final chapter of this thesis, is a synthesis of the research undertaken in the four preceding manuscripts. This chapter synthesises the main findings with respect to the aims, discusses the implications of these findings and identifies areas for further research.

Chapter 2 Literature review

This thesis is concerned with floodplain vegetation productivity responses to multiple wetting and drying events at two scales: the floodplain landscape scale and individual vegetation communities. This literature review outlines the existing knowledge surrounding the subject areas relevant to the research being undertaken. The literature review has four sections. The first section explores the theories of change and the various models that have been used in understanding change. The second describe the resilience theory of change including the concept of resilience. The third section highlights the role of disturbances in floodplains and how that causes change, and is followed by conceptual models of change in floodplain vegetation, floodplain vegetation dynamics and resilience. The fourth section of the literature review describes the application of Remote Sensing (RS) and Geographic Information Systems (GIS) and how these tools have been used in understating the spatial and temporal changes in ecosystems, with a focus on vegetation productivity change over time and the use of Normalised Vegetation Difference Index (NDVI) as a surrogate of vegetation productivity.

2.1. Theories of change in vegetation communities

Change is an intrinsic feature of an ecosystem (Pickett and White 1985, Likens 1992, Holling and Gunderson 2002). Change in vegetation communities is rarely simple and involves interaction between biotic and abiotic factors (Pickett *et al.* 2003, Sutherland *et al.* 2013).The theory of change and understanding the process of change has been a major focus of ecological research, beginning with Clements (1916) model of ecological succession, where the focus was on orderly change within communities and not as a function of a dynamic environment. Vegetation communities were seen as moving through a series of predictable successional stages. On the other hand Gleason (1926) emphasised vegetation change as unpredictable, and driven by fluctuating phenomena that change in time and space. Succession, according to Gleason (1926), is not an orderly process. Cooper (1926) also describes vegetation change as a constant "flowing braided stream" where change occurs over time in a dynamic manner as a result of complex interaction between abiotic and biotic processes. Two decades later Watt (1947) emphasised spatial pattern and the dynamic processes responsible for the pattern and concluded that a vegetation community maintains and regenerates itself as a disturbance driven dynamic mosaic of patches, that change over time in a cyclic manner (Watt 1947).

By the mid-1970s, ecologists recognised the inadequacy of both Clement's and Gleason's theories. This lead to two major conceptual trends in understanding the dynamics of change in ecosystems particularly the dynamics of vegetation change: (i) a shift away from holistic explanations of successional phenomena towards mechanistic approaches and (ii) a shift away from an equilibrium paradigm towards a non-equilibrium paradigm (Holling 1973). Holling (1973) suggests that the equilibrium view is essentially static and does not fully describe the transient behaviour of ecosystems that are far from equilibrium. The observations that Cooper (1926) and Watt (1947) made about the properties of change in vegetation were far beyond their time, where they emphasise that vegetation change is dynamic, transient, irreversible and changes with scale of observation. Watt's (1947) concept of vegetation mosaics formed a basis for the theory of patch dynamics (Pickett and White 1985). Patch dynamic theory views vegetation change as disturbance driven, with patches of different successional stages arrayed as a landscape mosaic. The composition and configuration of the patches influences ecosystem function in heterogeneous landscapes.

Other recent theories express the dynamics of change in relation to hierarchy and complex systems. O'Neill *et al.* (1989) proposed a hierarchical approach as an appropriate means of viewing change in ecosystems. Hierarchy theory proposes that change in ecosystems arises from processes operating at discrete hierarchical levels (O'Neill *et al.* 1989). As a result, higher levels of a hierarchy are associated with longer temporal and larger spatial scale changes while lower levels of a hierarchy are associated with shorter temporal and smaller spatial scale changes (Bergkamp 1995). Complex systems are characterized by nonlinear dynamics, multiple stable states, fast and slow drivers and self-organization (Holling and Gunderson 2002, Dearing 2008; Folke *et al.* 2010, Walker and Salt 2012). Complex systems are resilient systems because they appear to resist major threshold change by observing and responding to changes associated with systems dynamics (Garmestani *et al.* 2009). Thus, the theory of change has a long history in ecology, indicating that it is central in understanding the dynamics of change in vegetation. However, there is a lack of temporal understanding of semi-arid floodplain vegetation productivity change in response to wetting and drying at multiple scales.

2.2. Resilience theory in understanding change

Resilience theory has its foundation in complex systems theory. Complex systems are organised at a range of scales from the interaction of a set of socio-ecological systems

(Gunderson *et al*. 2010). Resilience is central to understanding the change of these systems. Resilience is defined in two ways in the ecological literature. Engineering resilience refers to dynamics close to equilibrium and ecological resilience refers to dynamics far from any equilibrium steady state (Holling 1973, Holling and Gunderson 2002). This thesis focuses on ecological resilience. In ecological terms resilience can be defined as the capacity of a system to undergo change and still retain essentially the same fundamental function, structure, identity and feedbacks either through recovery or reorganization in a new context without moving into an alternate regime or crossing a threshold (Holling 1973, Holling and Gunderson 2002, Walker *et al*. 2004, Folke *et al*. 2010). If systems cross a threshold, this change is are often irreversible, and management intervention may be needed to bring those systems to their original state (Scheffer *et al*. 2001, Folke *et al*. 2004). Systems that are not resilient cannot absorb disturbance and may collapse into a qualitatively different state that is controlled by a different structure, functions and feedbacks (Walker *et al*. 2004). Resilient systems can experience more disturbances without shifting into an alternate state (Walker and Salt 2006). Holling (1973) introduced the word resilience to describe the three aspects of transitional change that may occur in an ecosystem over time. First, the amount of change the system can undergo and the ability of the systems to absorb those changes by maintaining the same function and structure. Second, the degree to which the system is capable of self-organization. Third, the degree to which the system can build and increase the capacity to learn and adapt (Holling and Gunderson 2002, Walker and Salt 2012). The resilience of a system is a function of several interacting properties (Walker and Salt 2006). Cross scale interaction (panarchy) or hierarchy, adaptability and transformability are the main building blocks that are essential in order to manage system resilience (Folke *et al*. 2010, Walker and Salt 2012). Cross-scale interactions (panarchy) or hierarchy is a conceptual term, where large and small-scale events can impact the resilience of a system at a level of interest (Holling and Gunderson 2002, Walker *et al*. 2004). Adaptability or the adaptive capacity of actors in a system to respond to change also influences its resilience (Folke *et al*. 2010). Transformability is the capacity to reconceptualise and create a fundamentally new system with different functional characteristics. These dynamic properties of complex systems move through an adaptive cycle over time through phases of exploitation, conservation, release and reorganisation (Holling 1986, Holling and Gunderson 2002).

2.2.1 Adaptive cycles: a framework to understand change in ecosystems

The adaptive cycle concept of Holling (1986) is a key component of resilience theory, and provides a framework for understanding change in complex systems (Holling and Gunderson 2002). An adaptive cycle describes how structure and function changes over time in an ecosystem (Figure 2.1). According to the adaptive cycle concept, ecosystem change over time is driven by both internal system dynamics and external influences, resulting in four phases: exploitation (r phase), conservation (K phase), release (Ω omega phase) and renewal (α alpha phase) (Holling 1986). Transitions between phases are accompanied by variation in key properties of change through the adaptive cycle: potential, connectedness and resilience (Holling 1973, Holling and Gunderson 2002). Potential relates to the accumulated resources (biomass or capital) available to the system; connectedness relates to the internal connections between the resources within the system; and resilience refers to the system's ability to respond to change by maintaining the same function, structure and feedbacks (Holling and Gunderson 2002). These three properties prime and catalyse the system to further change. When a system becomes more connected it is more susceptible to shock, and systems with higher potential and higher connectedness are associated with lower resilience (Holling 1986, Holling and Gunderson 2002). Systems move from low connectivity and low potential for change in the r phase to a state of high connectivity and high potential for change in the K phase. The release phase (Ω or omega phase) is one of creative destruction where the loss of structure continues due to break in linkages, and is more dynamic and chaotic with no stability. The transition from K to Ω omega phase can happen in a very short period of time (Holling and Gunderson 2002, Walker and Salt 2006). After the phase of release or destruction the system again moves back to the first part of the cycle in the reorganization or the renewal α alpha phase, where all options are open and novelty can thrive. In α alpha phase ecosystems, pioneer species may appear from elsewhere or from previously suppressed vegetation; buried seeds can germinate and new species may invade the system (Walker and Salt 2006).

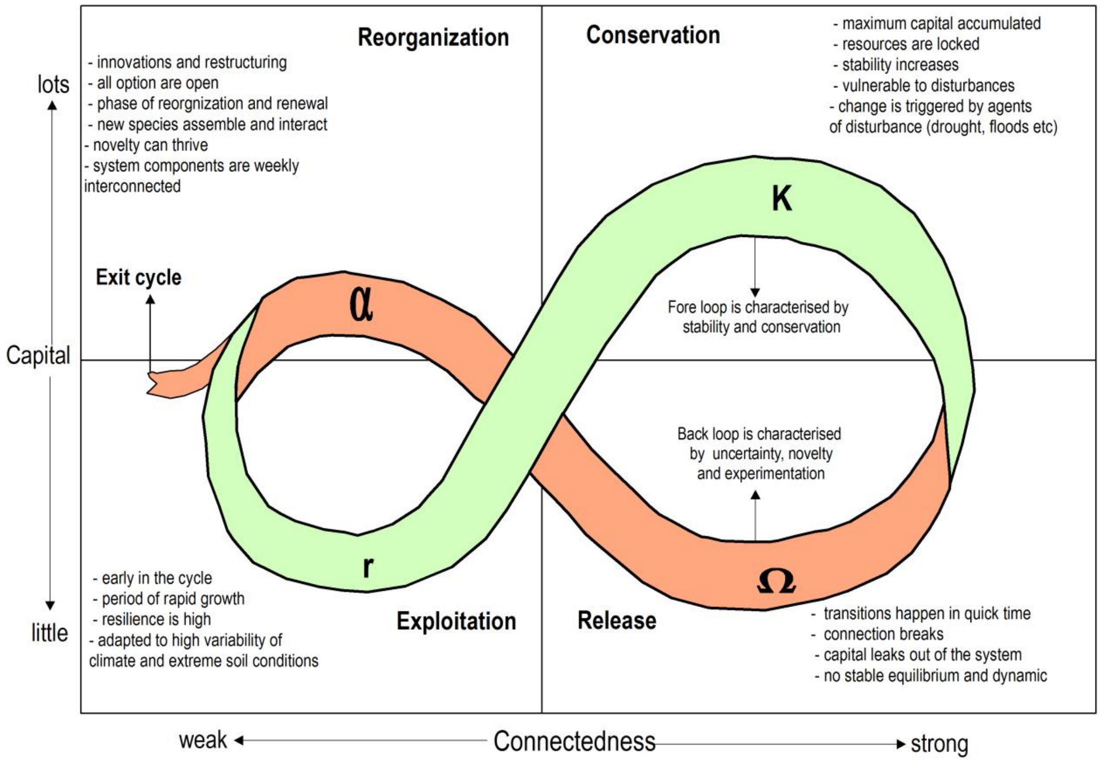


Figure 2.1 Adaptive cycle of change, indicating transitions among four phases: exploitation or growth (r phase) to conservation (K phase) to release (Ω omega phase) to renewal (α alpha phase). The cycle reflects changes in connectedness and capital, where the X- axis is the degree of connectedness among the controlling variables and the Y-axis is the capital that is inherent in the accumulated resources of biomass and nutrients. The exit from the cycle indicated at the left of the figure is the stage where the potential can leak away and where a change in threshold is most likely (adapted and modified from Holling 1986).

During the transition from reorganization to exploitation the system may reorganize into the same state or move into a new state via the exit cycle (Figure 2.1). The exit cycle is a stage where potential can leak away and may flip into a less productive and less organised system (Holling and Gunderson 2002). If the system does not flip into a new state or regime, then it moves back into the exploitation phase where a new cycle begins. The adaptive cycle has two opposing modes: a fore loop and a back loop (Holling and Gunderson 2002). The fore loop (exploitation to conservation) is a slow incremental phase of growth and accumulation, where resilience of the system to further disturbance is low because connectedness of elements within the system is high and predictable. The back loop (release to reorganization) is a rapid phase of reorganization and renewal, where resilience is high and connectedness is low (Holling and Gunderson 2002). Adaptive cycles thus provide a way of understanding change in complex systems and the relationship between change and resilience (Holling 1986, Gunderson *et al*. 2010, Jax 2010, Walker and Salt 2012).

Arising from its utility as a model to describe change, resilience and the associated concept of adaptive cycles have been applied in studies of socio-ecological systems, including rangelands, lakes and floodplain wetlands. An adaptive cycle was used to understand the switch from clear to turbid conditions in a shallow lake (Scheffer and Carpenter, 2003); a shift in grass to woody or shrub in rangelands (Wolf *et al*. 2007); benthic vegetaion to blue-green algae in a shallow lake systems (Scheffer 1997);and coral dominated reefs to algae dominated reefs (Hughes 1994). Likewise, the shift has also been observed in semi-arid floodplain where Walker and Salt (2012) reported that the river red gum/ box woodlands of the Australian Murray River floodplain have passed a threshold and are now dying due to a combination of over extraction of water for irrigated crops combined with change in climate. Similarly Whalley *et al*. (2011) found that the Gwydir Wetlands and Macquarie Marshes in northern NSW, Australia, have also crossed a threshold with the invasion of lippia (*Phyla canecens (Kunth) Greene*) an exotic weed forming a fifth phase of an adaptive cycle. Likewise, the Lower Goulburn-Broken Catchment in Murray Darling Basin, Australia has undergone a shift to a different state due to widespread clearing of native vegetation and high levels of water use for irrigation (Anderies 2005, Walker and Salt 2006). Release and reorganization in a socio ecological system has also been observed in a case study from Australia and Zimbabwe (Abel *et al*. 2006). Dearing (2008) also studied changes in the Erhai lake landscape in Yunnan, southwest China and found the possibility of state change in the landscape. Thus, there is a wide breadth of studies demonstrating the aspect of resilience theory related to threshold change between states in systems. Most of the past studies mostly focus on change in state in the socio-ecological context, few of the studies have tried to understand the over time change in vegetation productivity at different spatial and temporal scales using the adaptive cycle framework and how change happens around the adaptive cycle is a question which this study tries to understand, since the adaptive cycle is a model to understand change.

However, despite the adaptive cycle concept having been introduced nearly 30 years ago, there remains a relative paucity of empirical observations on this important component of resilience theory (Walker and Meyers 2004, Walker and Salt 2012). Adaptive cycles of release and renewal have been suggested to occur in economic systems, organizations, ecosystems and social systems (Allison and Hobbs 2004, Dearing 2008, Burkhard *et al*. 2011, Walker and Salt 2012), although these are rearely supported by emperical evidence. Because of human induced changes and regulation in the riverine floodplain there is evidence of change in vegetation conditions (Kingsford 2000, Bunn and Arthington 2002), which has led us to understand their response to spatio-temporal variability. Despite the potential for adaptive cycles to decipher complexity in the response of floodplain ecosystems to water availability, there has been limited application of this concept in floodplains (but see Colloff and Baldwin 2010 and Whalley *et al*. 2011 for exceptions).

2.2.2 Cross scale interaction (panarchy) or hierarchy in understanding change in ecosystems

A panarchy is a nested set of adaptive cycles operating at distinct ranges of scale. The concept of panarchy provides a framework for characterising complex ecosystem dynamics across scales of space and time (Gunderson and Holling 2002). Panarchy is the interaction between the large and small scale events affecting the resilience of a system at a particular focal scale (Walker *et al*. 2004, Whalley *et al*. 2011). Scale is very important in understanding the resilience of a system, since a self-organizing system operates over a range of different space and time scales (Walker and Salt 2006 and 2012). What happens at one scale can have a profound influence on the other scales of observation. The linkage across scales (panarchy) plays a major role in determining how the system at another scale is behaving. To understand the process of interest we should understand the hierarchal influences from the scale above and below (Allen and Starr 1982, O'Neill *et al*. 1989). Ignoring cross scale effects is of the most common reason for failure in natural resource management (Walker and Salt 2012). Thus, the notion of change in ecosystems should take into account of hierarchy theory (for e.g. see Allen and Starr 1982).

Hierarchy theory is a theory of complex systems derived from general systems theory and has been applied in ecology to understand ecological phenomena at a range of spatial and temporal scales (O'Neill *et al*. 1989, Bergkamp 1995, Wu and Loucks 1995). Hierarchy theory provides a framework for integrating pattern and process and the influence of pattern and process across different levels of organization. Hierarchy theory is a theory of scaled systems whereby all biological systems, ranging from a single cell to the total biosphere, are complex nonlinear systems (Allen and Starr 1982, O'Neill. 1988). A central tenet of hierarchy theory is that complex systems can be decomposed into a series of nested holons or levels of organisation (Wu 1999). Identifying pattern and processes operating at each level of organisation provides a better understanding of cross-scale interactions of pattern and processes operating within a system as a whole (Wu 1999). In hierarchy theory, subsystems are comprised of discrete units called ‘holons’. A holon at one level is composed of components of lower level holons, as well as components of higher level holons (Parsons and Thoms 2007). According to (Wu 1999) holons have been adopted because they convey the idea that subsystems at each level within a hierarchy are “Janus faced”: they act as whole when facing downward and as a part when facing upwards. Hierarchical levels are separated, fundamentally by characteristically different process rates - that is behaviour frequencies, relaxation time, and response times (Wu 1999). Higher levels of organization in a hierarchical system are characterised by low frequency events whereas lower levels are characterized by high frequency events. The higher level exerts constraint (e.g. boundary condition) to the lower level, whereas lower levels provide initiating conditions to the upper level (Wu and David 2002).

In landscape ecology the use of hierarchy theory allows patterns and processes across different spatio-temporal levels to be studied simultaneously. Taking into consideration complexity as an intrinsic attribute of a landscape, hierarchy explains how the different components, localized at a certain level are in contact with the other components, at a different scale. Hierarchy theory therefore considers a system as components of the larger system which in turn is composed of subsystems (Figure 2.2). Moving from one level to another level across subsystems, the character of the phenomena changes (Farina 2006). Landscape classification is one example of how a hierarchical framework can be applied to decompose systems into process-based levels. In a floodplain landscape, the hierarchy may be composed of the basin, functional process zone, reach, functional set, functional unit, through to the lowest holon of the hierarchy represented by a single mesohabitat (Figure 2.2). Hierarchy theory suggests that when one studies a phenomena at a particular hierarchical level (focal level or level 0), the mechanistic understanding comes from the next lower level (level- 1) whereas the significance of that phenomena can only be revealed at the next higher level (level +1) (Steinhardt 2003). These three levels usually are necessary and adequate for understanding most of the behaviour of ecological systems (O’Neill *et al.* 1989). Identifying the combined top-down constraints and bottom-up influences allows feedbacks between different levels of organisation to be identified (Poole 2002). Understanding hierarchical cross scale interactions is particularly valuable in interdisciplinary studies, because it identifies the appropriate scale of observation within each discipline. Floodplain or riverine landscapes are comprised of multiple hierarchies that interact with each other (Parsons and Thoms 2007). By linking, geomorphological, hydrological and ecological hierarchies (Figure

2.3) we can place hierarchy in to an applied context to view the complex riverine ecosystem from truly multidisciplinary perspective (Dollar *et al.* 2007, Thorp *et al.* 2008).

Hierarchy therefore provides a sound framework for dealing with patterns at multiple scales, as well as identifying particular frequencies and process rates associated with the holons. However, hierarchy is yet to be effectively applied in understanding floodplain vegetation patterns at the riverine landscape scale (but see van Coller *et al*. 2000, Gillson 2004, Shilpakar 2013). Much of the current knowledge of floodplain vegetation dynamics comes from small-scale studies, based on information collected at sites, transects or plots. Gillson (2004) applied hierarchy theory in an African savannah and showed different patterns of vegetation change are different at different scales of observation. Similarly Wiegand *et al*. (2006) studied the tree - grass coexistence in savannas using the hierarchical approach. Parsons *et al*. (2005) studied the effect of extreme floods in southern African and found a dynamic vegetation mosaic, following an extreme flood in 2002. Thus, further empirical studies are required to determine how aspects of hierarchy theory, particularly top down constraints and bottom up influences affects the dynamic of floodplain vegetation in a semi-arid floodplain.

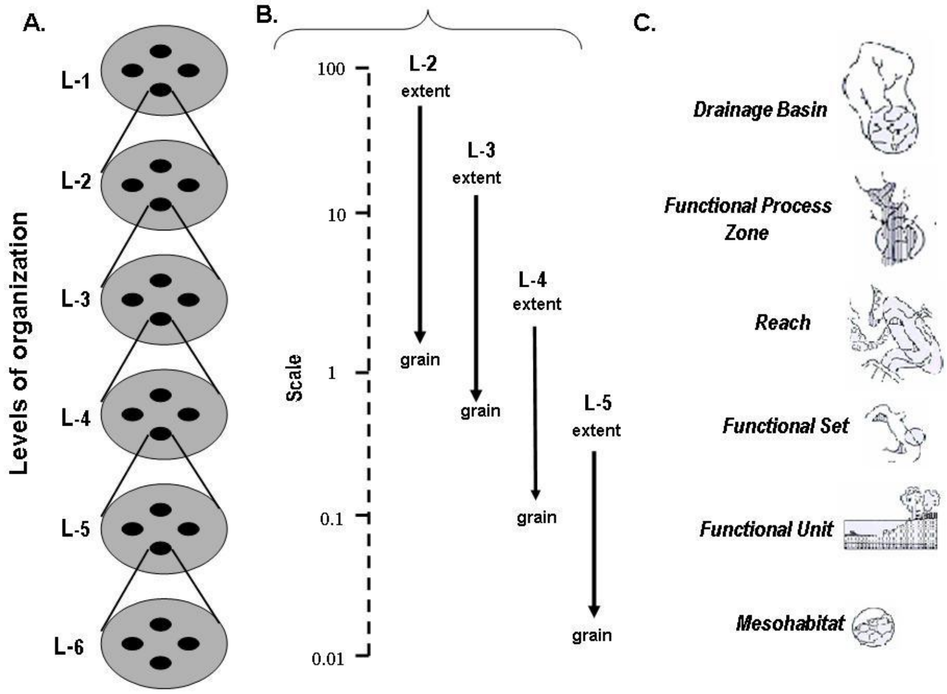


Figure 2.2 Hierarchical organisation of hydrological and geomorphological patches within the riverine landscape (Taken from Thorp *et al*. 2008). A. Nested hierarchy and level of organization, patches at one scale are nested within the level of organization above. B. The spatial scale associated with a hierarchically organised system. C. Hierarchical level of organisation and scale of geomorphological and hydrological patches within the riverine landscape.

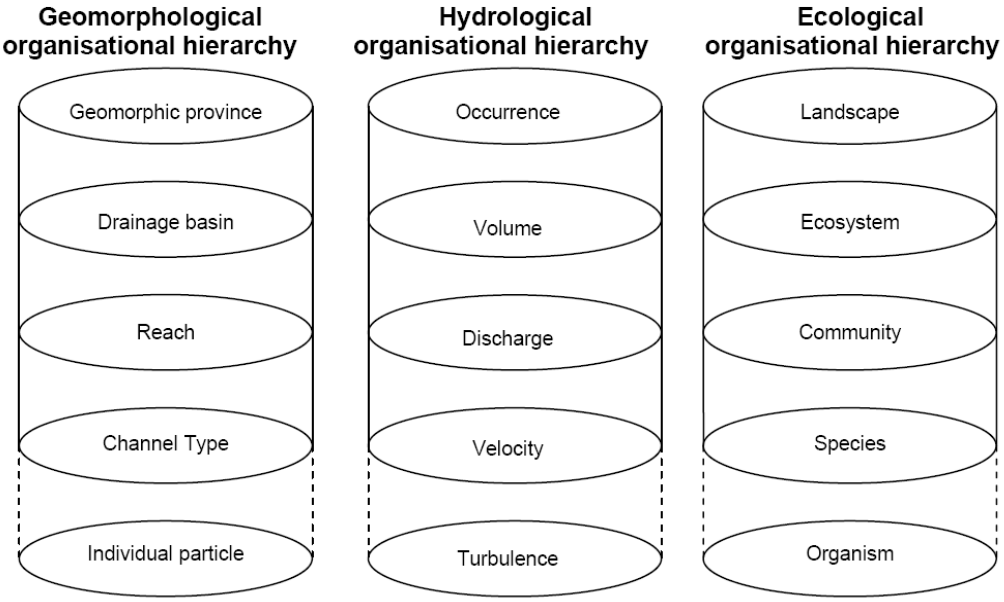


Figure 2.3 Hierarchical levels of organization in geomorphology, hydrology and ecology in a riverine system (taken from Dollar *et al*. 2007).

2.2.3 Floodplain ecosystems and resilience

Floodplain ecosystems are resilient systems to natural disturbances such as variability in flooding and drying, (Capon *et al*. 2009, Colloff and Baldwin 2010). The high biodiversity of floodplain ecosystems is maintained, in part, by variation in hydrological regimes and highly productive soils which in turn, influences the abundance, spatial organisation and resilience of floodplain plant and animal species over time (Whited *et al*. 2007). Flooding connects the floodplain with the river channel and when the floodplain is inundated a variety of physical and chemical changes occur. Flooding can be beneficial as well as a potential stress depending on the duration, extent and depth of inundation (Brock and Casanova 1997). Some floods bring more nutrients and moisture which are good for the overall growth of plants, whereas some floods are destructive which affects plant growth (Kozlowski 1984). The frequency and timing of floods can also change spatial patterns of plant community composition and structure (Brock *et al*. 2006). The capacity to shift between flooding and drying phases in response to inundation is an inherent character of floodplain systems (Bunn *et al*. 2006). On the other hand duration and intensity of drought may also affect floodplain vegetation community distribution, abundance and composition. Vegetation growth, photosynthesis and stomatal aperture may be limited under drought conditions (Xu *et al*. 2010). Vegetation that does not have physiological mechanisms to withstand drought conditions will not survive extended periods of drought (Xu *et al*. 2010). However, the response of vegetation mostly depends on plant adaptations. Some vegetation is not able to cope with irregular disturbances whereas others maintain the same function and structure after drought (Lichtenthaler 1996).

Despite the widespread acceptance of the theory of socio-ecological resilience (Walker and Salt 2012), very few studies have studied the resilience of floodplain ecosystems (Baldwin *et al*. 2013, Colloff and Baldwin 2010, Whalley *et al*. 2011). Colloff and Baldwin (2010) were the first to propose a conceptual model of resilience of a semi-arid floodplain and proposed single state ecosystems as having two alternating phases, a dry and wet state, driven by periodic droughts and floods. However, emphasis on floodplain ecosystems as consisting of two states does not account for processes that may occur in the transitions between the dry and wet states. The concept of adaptive cycles suggests that change in semi-arid floodplain ecosystems may be more complex than the two-state boom-bust model, and may provide a framework for further understanding of change in semi-arid floodplain ecosystems in response to wetting and drying. Adaptive cycles make us more cognizant of the importance of transitions, dominance of the different phases, and frequency of the individual transitions.

2.3. The role of disturbance in floodplain change

Understanding how communities change over time and how they respond to perturbation are two overarching questions that have occupied ecological research since Clements (1916) theory of succession. Change is a dynamic and continuous process that occurs over time and plays a prominent role in ecosystem functioning. Change is also the main driver that alters ecosystem structure, the physical environment and the availability of resources (Pickett and White 1985). Disturbance is a central concept in the field of ecology and can be natural or anthropogenic (Pickett and White 1985, White and Pickett 1985). Increasing anthropogenic disturbance leads to habitat fragmentation, and is a major threat to biological diversity. Disturbance is a key component for determining ecosystem dynamics and in understanding the effects of change in an ecosystem. Every landscape is shaped, maintained and or changed by disturbance. For example; disturbances such as fires, droughts and large floods will have a strong influence on the structure and function of ecosystems (Turner *et al*. 2001). Disturbance is a phenomenon of any system, at a range of scales, and alters resource availability and the structure of the system (Farina 1998, Lake 2000, Allan 2004, Turner 2005). Disturbance may shape long-term fluctuations in the structure and function of ecosystems and therefore influence ecosystem resilience (Chapin *et al*. 2009). Disturbance may cause an ecosystem property to cross a threshold, as for example clear water to turbid water transition (Carpenter 2003), grass to woodland transition (Walker *et al*. 2004, Wolf *et al*. 2007) or invasion of exotic species (Whalley *et al*. 2011). However, the response to disturbances may depend on the adaptive capacity of ecosystems. Some ecosystems are not able to cope with irregular disturbances whereas others maintain the same function and structure after the disturbances (Lichtenthaler 1996). Disturbance such as drought, fire, floods or diseases may shape the long-term fluctuations in the structure and function of an ecosystem and therefore their resilience and vulnerability to change (Chapin *et al*. 2009).

2.3.1 Disturbance in floodplain landscapes

All natural and anthropogenic disturbances impinge upon the floodplain directly or indirectly. Hydrological variability is a key disturbance driver that affects the ecological integrity of floodplain landscapes (Naiman *et al*. 2005). Flow regulation alters sediment transport and reduces the magnitude and frequency of flow (Naiman *et al*. 2005), and ultimately results in lower water tables, reduced lateral connectivity and modification of successional processes (Ward *et al*. 1999). Reduced flooding has known consequences for the ecology of dry land rivers, for example refugia loss, aquatic ecosystems converted into terrestrial systems and decline in biodiversity in water bodies (Bunn *et al*. 2006, Sheldon and Thoms 2006).

Disturbances caused by variation in water movement and flow volume exert a major influence on ecological structure and function in riverine ecosystems, across a range of scales from local to regional. The character of disturbance regimes especially the frequency and intensity of flow-mediated disturbances are thought to be a major regulating influence on species richness at the landscape level and may generate pools of potential colonists for the various types of habitat patches (Lake 2002). At the local scale there will be a strong interaction such as competition for resources, and this may regulate local diversity (Lake 2000). The biodiversity of flood plain ecosystems is relatively high compared to adjacent terrestrial environments because their periodic inundation provides renewal of resources (Lynch and Whigham 1984) that are sensitive to landscape change and disturbance. Hydrological connections also facilitate the exchange of carbon, nutrients and the movement of organisms and propagules between various parts of the floodplain-river ecosystem and create a dynamic mosaic of inundated-patches during the expansion and contraction of floodwaters (Thoms 2003, Murray *et al*. 2006).

Flow mediated disturbance also plays a key role in maintaining the spatial heterogeneity of vegetation communities in a floodplain landscape (Malanson 1995). Ecological fragmentation has occurred on many floodplains because of a decrease in lateral connection between the river channel and floodplain (Thoms 2003) due to human activities. Land and water resource development activities have changed lateral connectivity in two ways. Firstly, by altering the natural hydrological pattern of floodplain surface inundation and secondly, by reducing the reactive floodplain surface by the construction of dam, levees, dykes and other structural changes in the floodplain (Kingsford 2000, Nilsson *et al*. 2005). A change in ecological status of floodplains is directly linked to hydrological change. Especially in dry land areas, even a small decrease in flood volume can result in large reductions in area flooded (Taylor *et al*. 1996). Flooding renews nutrients, increases sediment diversity and allows new patches to emerge for colonisation (Ward 1998). Flow controls the structure and availability of habitat and mediates the exchange of organisms, nutrients and energy along the four dimensions of river systems – longitudinal, lateral, vertical and through time (Vannote *et al*. 1980, Junk *et al*. 1989, Ward 1989). Alteration of flow for irrigation and water resource development changes the natural character of fragmentation in the floodplain ecosystem and this can lead to overall declines in productivity (Thoms *et al*. 2005). Change in land use for agricultural intensification increases salinity which leads to overall reduction in diversity of both aquatic and terrestrial ecosystem (Brock *et al*. 2005). Flood duration and period is very much critical for vegetation growth; inundation will increase floodplain productivity (Parsons and Thoms 2013). On the other hand flooding can also be a stressor. For example, if soils are inundated for long enough to develop anoxic conditions, this will impact on the growth of vegetation (Sparks and Spink 1998, Baldwin and Mitchell 2000).

Over the last fifty years anthropogenic disturbances associated with land and water resource development have changed ecosystem structure and function (MEA 2005). Most dams on semi-arid rivers are built to divert water for human use, for example, water diverted to Namibia from the upstream portion of the Okavango River (Ramberg 1997), water diverted from the Macquarie Marshes in Australia, or water diverted from the Aral Sea in Central Asia (Lemly *et al*. 2000). In Australia, about fifty percent of the natural flow of the Murray River is diverted for agricultural use (Maheshwari *et al*. 1995).

Since European settlement in Australia the characteristics of floodplains have been altered by large-scale development. This resulted mainly from extensive water resource development reducing the connectivity between river channels and their adjacent floodplains (Thoms 2003). In the Murray Darling Basin, this has had a significant effect on the rivers and wetlands within the Murray system (Reid and Brooks 2000). Eighty seven percent of divertible water resources are already diverted, leaving almost no water for floodplains (Kingsford 2000). Reduction in the frequency and extent of flooding has reduced wetland size. Floodplain development has contributed to the isolation of the floodplain and resulted in significant decline of biodiversity and ecological processes (Kingsford 1999, 2000). Future global climate change will undoubtedly have a strong effect on the ecological structure and functioning of riverine ecosystems (Gibson *et al*. 2005). Major impacts of global warming on riverine systems especially in arid lands are likely to be experienced through changes in the frequency of extreme events such as floods and droughts (Lake 2000).

2.3.2 The boom and bust model of hydro-ecological change in floodplains

The boom (wet) and bust (dry) model of floodplain ecosystem productivity is generally applied in large semi-arid floodplains (Walker *et al*. 1995, Bunn *et al*. 2006, Sternberg *et al*. 2012), which have highly variable and unpredictable rainfall. The boom and bust brought about by hydrological variability is a major feature of semi-arid river systems (Kingsford 1999, Thoms and Sheldon 2000, Sheldon *et al*. 2010,) and plays a major role in the integrity of floodplain ecosystems (Kingsford 2000, Leigh *et al*. 2010). During extended periods of limited water availability (the ‘bust’ period) that may last for years, floodplain primary and secondary productivity is low (Arthington *et al*. 2010, Parsons and Thoms 2013). On the other hand, flooding generates a boom period that stimulates a rapid increase in floodplain productivity that may last for months across the floodplain. Increased vegetation growth in response to flooding is one of the most important processes controlling the carbon and nutrient dynamics on floodplains and in the adjacent terrestrial and riverine ecosystem (Sims and Thoms 2002). Flooding stimulates water bird (Kingsford *et al*. 1999, Roshier *et al*. 2002) and fish breeding (Puckridge *et al*. 2000, Balcombe *et al*. 2007, Balcombe and Arthington 2009), and increases vegetation productivity (Capon 2003, Westbrooke *et al*. 2005, Reid *et al*. 2011, Sims and Colloff 2012, Parsons and Thoms 2013) and soil nutrients (Junk *et al*. 1989, Ogden and Thoms 2002). Semi-arid floodplain ecosystems are therefore perceived to change between the dry or the bust state of limited water availability and a wet or boom state of abundant water availability or productivity. However, some challenges still remain surrounding our understanding of the complexity of response in a dry and wet state, since the boom and bust model of change does not account for the processes that occur in the transitions between wet and dry states. Sternberg *et al*. (2012) also reported the challenges in understanding the ecological response of extreme fluctuations in wet and dry conditions.

2.3.3 Floodplain vegetation dynamics

Floodplain vegetation is one of the most important components of floodplain ecosystems. Semi-arid floodplain plant communities are ecologically significant and support a diverse local and regional fauna (MEA 2005, Tockner *et al*. 2008). Floodplain vegetation is dynamic and flooding is a key driver that controls vegetation distribution over-time. Semi-arid floodplain vegetation communities exhibit high spatial heterogeneity and are temporally dynamic in response to changing flow conditions (Casanova and Brock 2000, Sims and Thoms 2002, Capon 2005). The dynamics of vegetation growth over time are influenced by the factors operating at the catchment, landscape and patch scale, but most vegetation cover types have a distinctive growth dynamic that is related to their composition and location together with landscape structure (Ludwig *et al*. 2005). At longer timescales (decades to centuries) regular floods influence the distribution of vegetation communities in a landscape, whereas at shorter timescales (seasons to years) wetting increases plant productivity and contributes to community composition changes in the long term (Reid *et al*. 2011). Drying events can generate new patches at different spatial scales and patch characteristics, such as species composition change with time after disturbances (Lake 2000). Changes in the flood pulse through water extraction can be expected to result in changes in vegetation composition and structure. These disturbances ultimately have a dramatic effect on overall ecosystem functioning and eventual loss of biodiversity (Capon 2003). Flood frequency is a major factor that drives variability in plant distribution. Areas that are inundated frequently exhibit similarities in plant types, whereas areas less frequently inundated show variability in plant distribution (Capon 2005). According to Mitsch and Gosselink (2000) species diversity is highest in regularly moist soils and lowest in continuously flooded marshes.

Understanding the dynamics of floodplain vegetation in response to wetting and drying is important to build our knowledge of the integrity of floodplain landscapes. Early research by Malanson (1995) conceptualised riparian landscapes as landscape corridors, controlled by the spatial dynamics of channels, flooding and soil moisture. However, much of the current knowledge of floodplain vegetation dynamics comes from small-scale studies, based on information collected at sites, transects or in plots. Most research on spatial patterns of vegetation distribution has adopted a gradient approach (Whittaker 1967, Austin and Gaywood 1994) to effectively describe the variability in plant distribution pattern. According to van Coller *et al*. (2000) a gradient approach adequately characterizes floodplain vegetation pattern and understanding of the influences of processes. But when we look at the complex floodplain vegetation landscape, a gradient approach does not deal effectively with the complexity of the patch mosaic structure arising from dynamic hydrological processes because vegetation distribution patterns are patchy and this patchiness has a nested hierarchical structure (van Coller *et al*. 2000, Gillson 2004, Parsons *et al*. 2005).

2.3.4 Floodplain vegetation resilience

Floodplain ecosystems are resilient systems (Capon *et al*. 2009, Colloff and Baldwin 2010). Variability in flooding and drying is a significant driver of floodplain vegetation resilience (Colloff and Baldwin 2010). Flooding connects the floodplain with the river channel and when the floodplain is inundated a variety of physical and chemical changes occur in vegetation communities. Some floods bring more nutrients and moisture which are good for the overall growth of the plant whereas some floods are destructive which effects plant growth. According to Junk *et al*. (1989) vegetation responds to characteristics of the flood pulse (timing, duration and the rate of rise and fall). However, the response of vegetation will mostly depend on plant adaptations. Some vegetation will not be able to cope with disturbance whereas some maintain the same function and structure after disturbance. Stressed vegetation communities may have less biodiversity, reduced primary and secondary production and lowered resilience. Due to multiple stressors some vegetation may suddenly shift from one stable domain to another domain, in this process the original native species are replaced by exotic species (Rapport and Whitford 1999). Rapport and Whitford (1999) found that stressed or damaged systems become more vulnerable to invasion from opportunistic species; disturbances to soil and sediments, and are severely limited in re-establishing organised biotic communities as they depend on complex structures and on stable substrates, and finally disruption in organic matter changes the entire character of ecosystem. Colloff and Baldwin (2010) framed semi-arid floodplain resilience as a single state ecosystem having two alternating phases: a dry and wet state, driven by periodic droughts and floods. However, the Colloff and Baldwin (2010) wet and dry model does not address the potentially important processes and patterns of floodplain vegetation that may arises through these transitions. The Adaptive cycle model suggests that change in semi-arid floodplains may be more complex than having alternating wet and dry phases. This lead me to think whether floodplain vegetation still maintains the same structure and function after undergoing a wet and dry phase. The other important feature of adaptive cycle is the change in state, and whether floodplain vegetation has the ability to stay in the same state is an important question. Thus, this PhD research tries to understand floodplain vegetation resilience.

2.4. The use of satellite remote sensing and Geographical Information Systems in understanding spatial and temporal change

Over the last forty years, a large number of space-borne and airborne sensors have been employed to gather information regarding the earth's surface and environment and their change. Many studies have recognised the potential of remote sensing (RS) and Geographic Information Systems (GIS) for analysing landscape pattern, gradients and trajectories of landscape pattern and process (Field *et al*. 1995, Varshney and Arora 2004, Farina 2006, Jensen 2007, Campbell and Wynne 2011). Remote sensing and GIS have the capability to manage, retrieve and combine large amounts of spatio-temporal data. Therefore, remote sensing methods and GIS based models are indispensable instruments in landscape-scale studies (Mertes 2002, Farina 2006), and have also facilitated research in the role of landscape heterogeneity in determining vegetation community and ecosystem dynamics (Walsh and Davis 1994). Monitoring by ground observations is impractical over large areas because it is time consuming, and often very expensive. Remote sensing potentially allows for more cost effective and regular monitoring of vegetation cover changes over large areas (Lillesand and Kiefer 1994). No other survey method can operationally provide a standardized survey of the landscape with which to analyse landscape-level pattern and change (Burnett and Blaschke 2003, Steinhardt 2003).

Remote sensing is the art of deriving information about the Earth's land and water surface from a distance, using electromagnetic radiation in one or more regions of the electromagnetic spectrum reflected from the earth surface (Steinhardt 2003, Jensen 2005). The history of remote sensing began with the invention of aerial photography and has been widely used in mapping the Earth's surface (Plieninger 2006). The advent of digital remote sensing technology expanded choices for monitoring vegetation conditions on the Earth's surface. Multispectral scanning systems (MSS) and hyper spectral remote sensors, introduced back in the 1970’s and 80’s, have brought revolution in the application of remote sensing for monitoring Earth’s surface processes and dynamics and continue to be the backbone of optical data acquisition systems (Varshney and Arora 2004, Bhatta 2008). Multi-spectral remote sensing is defined as the collection of reflected, emitted energy from an object in multiple bands (regions) of the electromagnetic spectrum (Turner *et al.* 2001). In contrast, hyper spectral remote sensors collect information simultaneously in dozens or hundreds of narrow bands as little as 0.01 μm in width. In earth observing programs, different commercial and research oriented sensors were launched at a range of spatial, spectral and temporal resolutions. The key characteristics of remote sensing data are that they range from sub meter to kilometres spatially and have a temporal resolution ranging from 30 minutes to days, weeks and months.

Different sensors have different characteristics and the selection of appropriate sensors is important. Evaluating over time vegetation response requires an understanding of the differences between the available sensors. Many studies have used different sensors in monitoring vegetation conditions, The most widely used sensors include Advanced Very High Resolution Radiometer (AVHRR), Moderate Resolution Imaging Spectroradiometer (MODIS), Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM+), SPOT (Satellite Pour l'Observation de la Terre), Indian Remote Sensing (IRS), IKONOS and Quick Bird (Xie *et al.* 2008). Among these sensors AVHRR and MODIS, are coarse resolution, ranging from 250 m to 1 km^2 in spatial resolution, with a temporal resolution of 1 – 2 days. These sensors have been used for global scale mapping such as Global Land Cover 2000 and MODIS land cover based on monthly composites from Terra MODIS (Munyati and Mboweni 2012). Besides this coarse resolution satellite imagery at the global and continental scales, there are numerous other medium to high spatial resolutions sensors that have been monitoring earth surface vegetation at the regional, landscape and local scale. Among these Landsat MSS provides regional observation at 80 m spatial resolution with four broad wavelength regions, two in visible (green and red) and two in the near infrared (NIR) region respectively. This was followed by the launch of Landsat 4-5 TM and Landsat ETM+ which provided additional measurement at a spatial resolution of 30 m together with the provision of a 15 m panchromatic band on the Landsat ETM+. The SPOT series of sensors use a spatial resolution of 20 m in three visible and NIR channels. The launch of SPOT-1 to 5 between years 1986 - 2002 introduced a new era in fine spatial resolution ranging from global scale 1 km^2 SPOT imagery to 2.5 m local scale imagery with a temporal resolution of 1 day.

This was followed by the IRS that complemented the Landsat and SPOT sensors with a spatial resolution between 23.5 – 36.35 m and a 6 m panchromatic band (Varshney and Arora 2004). Together with the above sensors other high resolution commercial sensors were launched such as IKONOS and Quick Bird. IKONOS has a 1 m panchromatic band and four multispectral visible and near infrared (VNIR) bands at a spatial resolution of 4 m. Likewise Quick Bird-2 has a spatial resolution of 0.6 m in its panchromatic bands and four VNIR bands at 2.4 m spatial resolution. However, the problem of these commercial satellite data is that imagery is of high cost and is not archived at regular intervals over time; this hinders the application of these high resolution satellite imagery.

With regards to coarse resolution imagery such as MODIS and AVHRR, recent studies suggest that vegetation monitoring with coarse resolution images especially in arid and semi-arid regions may only be indicative and need to consider the medium to higher resolution imagery not recommended for local and regional scale studies (Xie *et al*. 2008, Munyati and Mboweni 2012). The medium spatial resolution imagery captured by sensors such as Landsat TM (28.5 m), SPOT (20 m) and IRS-1C LISS III (23.5 m) can be cost effective and an ideal choice for examining the spatio-temporal pattern of vegetation response at the landscape scale. Among these medium resolution imagery, Landsat has been intensively used in vegetation monitoring at the landscape scale, because of its good spectral and radiometric qualities. Landsat imagery is well-suited for ecological characterization (Wulder *et al*. 2008, Rocchini *et al*. 2010). The other advantages of using Landsat imageries is that it is comparatively cheaper and easy to acquire and recent changes in Landsat data sharing policy by the USGS make this imagery free and easy to obtain.

Many studies have successfully used Landsat imagery to monitor change and elucidate pattern and processe in terrestrial as well as floodplain landscapes. Rocchini *et al*. (2010) predicted the vegetation species richness in a wetland using the high resolution Quick Bird multispectral images and medium resolution Landsat images and found similar results between the high and medium resolution images. Likewise Nagendra *et al*. (2010) examined vegetation diversity in dry tropical Indian forests using multi spectral IKONOS and Landsat images and found that Landsat imagery performed better than the IKONOS across a range of vegetation diversity measures. Landsat data have also been used successfully in change monitoring of Australian rangeland vegetation (Pickup *et al*. 1993, Sinha and Kumar 2013), landuse land cover change analysis in the Brahmaputra River Basin (Thapa et al. 2015a) and in monitoring floodplain vegetation response to wetting and drying (Sims and Thoms 2002, Thomas *et al*. 2010, Parsons and Thoms 2013).

2.4.1 NDVI as a surrogate of vegetation productivity

Vegetation growth or productivity can be examined using remote sensing by extracting spectral radiances from a simple ratio of near infrared and visible wavelength. The most common transformation procedure is to compute a vegetation index (O'Neill 1996). Vegetation indices are used to measure biomass or vegetative vigour based upon digital spectral brightness values. Green vegetation often displays low reflectance and transmittance in the visible regions (red, green and blue) of the spectrum, due to high absorptance by photosynthetic pigments. In contrast, reflectance and transmittance are both strong in the near infrared regions NIR (Varshney and Arora, 2004). Healthy vegetation commonly has high reflectance in the near infrared regions (Rouse *et al*. 1973, Tucker *et al*. 1986, Gamon *et al*. 2013). When the vegetation is affected by disturbances such as floods or drought, the leaves of healthy vegetation come under water stress or become diseased, they change their colour and become more yellow. Under these conditions, reflectance of vegetation is significantly lower in the near infrared range (Prasad and Badrinath 2004).

The Normalized Difference Vegetation Index (NDVI) developed by Rouse *et al*. (1973) is one of the most common vegetation indices used to determine vegetation greenness. The NDVI is based on the red and near infrared reflectance properties and is strongly correlated with photosynthetic activity (Tucker *et al*. 1985, Tucker *et al*.1986, Wang *et al*. 2004, Xu *et al*. 2012, Gamon *et al*. 2013,). The NDVI is calculated ($\rho NIR - \rho RED / \rho NIR + \rho RED$) as the normalized differences of the spectral reflectance of NIR and visible (Red). In the past three decades NDVI has been extensively used as an indicator of vegetation greenness or vigour and has shown a strong correlation with vegetation primary productivity by validating NDVI with field observation.The NDVI offers valuable information on the dynamics of changes in vegetation given that time series images are analysed (Xie *et al*. 2008). NDVI has been used in a variety of environments globally in assessing vegetation greenness or productivity. Not only in terrestrial environments with dense vegetation conditions (Wang *et al*. 2004, Hmimina *et al*. 2013), NDVI has also been used for vegetation monitoring in sparsely vegetated areas such as in arid and semi-arid regions (reviewed by Pettorelli *et al*. 2005). It has also been used for the assessment of ecological response to environmental change (Pettorelli *et al*. 2005); biodiversity assessment (Bawa *et al*. 2002); land use change

(Fuller 1998, Jordan *et al.* 2012); drought monitoring (Pennington and Collins 2007, Rulinda *et al*. 2012, Xu *et al*. 2012) and for examining greening and browning trends in vegetation (de Jong *et al*. 2011, Baird *et al*. 2012, Munyati and Mboweni 2012). Associations of NDVI to rainfall, temperature, drought and fire in arid and semi-arid regions have been a subject of considerable research and these factors have significant correlations with NDVI (Di *et al.* 1994, Nightingale and Phinn 2003, Al-Bakri and Suleiman 2004). However these studies are restricted to climatic factors such as rainfall and temperature.

There has been little testing of the association of NDVI to flooding and drying conditions and less is known about the associations of NDVI to flooding and drying conditions. However, a few studies have examined NDVI to monitor vegetation greenness or productivity under different environmental conditions such as flooding and drying (e.g. Sims and Thoms 2002, Sims and Colloff 2012, Wen *et al*. 2012, Parsons and Thoms 2013). These studies have either used very coarse resolution NDVI images such as MODIS, or AVHRR 250m to 500m which are less suitable in semi-arid lands where vegetation communities are often fragmented (Munyati and Mboweni 2012) Other studies have used medium resolution NDVI images taking one or two snapshots but not considering the temporal variation in NDVI in different resource states (Parsons and Thoms 2013). Wen *et al*. (2012) examined long-term variation in mean NDVI of 10 floodplain wetlands and the association of local climate and hydrology using 250m MODIS NDVI, and found that rainfall, temperature and inflow has a significant association with mean NDVI and that NDVI values varied with vegetation type. Their long term modelling shows rainfall has a close relationship with mean NDVI and inflows are primarily responsible for producing heterogeneity in wetland vegetation. In a similar study, Sims and Colloff (2012) examined the time-series MODIS NDVI (500m) to compare vegetation growth response in an unregulated floodplain wetland and its terrestrial buffer and found higher NDVI values in the wetland area than in the nearby terrestrial areas. Even studies of floodplain vegetation greenness or productivity using medium resolution NDVI from Landsat imageries are restricted to only a few flood or dry images. For example Sims and Thoms (2002) used 13 images from 1989 – 1999 to examine vegetation response to inundation by calculating NDVI in each average recurrence interval (ARI) of inundation and found that different ARIs produced different values of NDVI. Likewise Parsons and Thoms (2013) examined patterns of vegetation greenness in three resource states (flood, rain and dry) using two Landsat derived NDVI images from the 1980 and 1990 and found higher greenness (NDVI) in the flood state than the rain state.

Although vegetation indices such as NDVI have been shown to be powerful tools for studying vegetation biomass or vigour, they must be used with care if the values are to be rigorously interpreted. The spectral values of these ratios can be influenced by many factors external to the plant leaf, including viewing angle and soil background, because atmospheric effects typically influence some bands more than the others, resulting in greatly altered values of the ratio from its true value (Campbell 2007). Spectral and spatial variation in the brightness of the soil background can also introduce significant errors in floodplain vegetation mapping. The spectral signature of stressed plants appears altered from those of healthy plants (Huete 1988, O'Neill 1996).

Chapter 3 Study area and general methods

3.1. Study area

3.1.1 The Lower Balonne floodplain

The Condamine-Balonne River located in the northern part of the Murray-Darling Basin, Australia, has a catchment area of 162,641 km² (Figure 3.1). Like many Australian inland rivers systems the Condamine-Balonne River originates in well-watered headwaters of the eastern highlands and flows for most of their length across a dry landscape (Thoms and Sheldon 2000). The Condamine Balonne River has a single channel for most of its length (Figure 3.1) but downstream of St. George, it bifurcates into five distinct anabranching channels (Figure 3.1), which have developed on the surface of a large alluvial fan complex known locally as the Lower Balonne floodplain (CSIRO, 2008). The contemporary Lower Balonne has a geomorphologically complex surface, with a relatively low bed gradient (0.0002 to 0.0003),a highly sinuous channel (1.9 to 2.5), and decreasing bankfull cross sectional areas with distance downstream (Thoms 2003).

The Lower Balonne floodplain covers an area of 19,800 km^2 and is located in one climatic zone as hot with minimal rainfall according to the Köppen Climate Classification scheme. The climate of the Lower Balonne floodplain is hot and dry. Annual evaporation exceeds 1900 mm, and is well in excess of annual precipitation. The long term average annual rainfall (1887 – 2013) is 460.6 mm at Lightning Ridge (Thoms and Parsons 2011). Most rainfall occurs in the summer months (November – April) associated with monsoonal weather patterns across Northern Australia. Maximum summer temperature often exceeds 50° C and the minimum winter temperature is around 20° C. Average maximum January temperature between 1997 – 2013 is 36° C and average maximum July temperature is 19° C at Lightning Ridge (Bureau of Meteorology, Australia, 2011). Both mean annual temperature and mean annual precipitation vary greatly between years.

Discharges of the five channels in the Lower Balonne differ substantially and are highly variable over time with coefficients of variation, of annual flow ranging from 103 to 200 % (Thoms 2003). The Culgoa and Narran Rivers convey over 63 percent of the long term mean annual flow. The long-term (1966 – 2013) median annual discharge of the Culgoa River at Brenda is 206,732 ML with an average daily discharge of 1,219 MLD, while the average daily discharge for the Narran River is 413 MLD. By comparison the median annual discharge of the Bokhara River is 27,292 ML with an average daily discharge of 193 MLD (Parsons and Thoms 2013, NSW Office of Water 2013).

The hydrological regime of rivers within the Lower Balonne has significantly altered since the 1960s because of substantial water resource development activities. There are four public water storage dams in the Condamine Balonne catchment: Leslie Dam (106 GL), Chinchilla Weir (10 GL), Beardmore Dam (82 GL) and the Jack Taylor Weir (10 GL) and numerous off-stream privately owned water storages with a combined volume of 1,582 GL (CSIRO 2008). Land and water resource development activities have resulted in a marked decline in the magnitude of smaller flood events in the Condamine Balonne floodplain (Sheldon and Thoms 2006) with a decrease in annual flood volume by 22 percent (CSIRO 2008). Considerable water resource development in the Condamine-Balonne catchment affects the flows in the Lower Balonne including to the Narran floodplain and has caused approximately a 58 percent reduction in the mean annual flows at St. George with effects on Narran floodplain ecosystems (Thoms, 2003).

Alluvial sediments are the dominant geology of the Lower Balonne floodplain which contrasts to the complex geologies of the headwater regions (Galloway *et al*. 1974). The soil of the Lower Balonne floodplain comprises mostly red earths, hard setting red-brown earths and red, grey, brown and black self-mulching clays, with significant areas of cracking and non-cracking clays (NFRPC 2004). Land use within the Lower Balonne floodplain is dominated by irrigated semi-arid crops along with areas of opal mining and cattle farming (Reid *et al*. 2011). There are also two significant conservation reserves within the Lower Balonne floodplain, the Culgoa National Park gazetted in 1996 (16,616 ha) and the Narran Lakes Nature Reserve dedicated in 1988 (550 ha). The dominant vegetation community of the Lowe Balonne floodplain is grassland, which covers 40 percent of the total floodplain area (NFRPC 2004, Parsons and Thoms 2013). This is followed by a range of woodland community types that cover 28 percent of the floodplain area, including coolibah (*Eucalyptus coolabah*), river red gum (*Eucalyptus camaldulensis*), black box (*Eucalyptus largiflorens*), poplar box (*Eucalyptus populnea*), leopardwood (*Flindersia maculosa*), gidgee (*Acacia cambagei*), mulga (*Acacia brachystachya*), myall (*Acacia pendula*), rosewood (*Alectryon oleifolius*), yarran (*Acacia homalophylla*), Ironwood (*Acacia excelsa.*), whitewood (*Atalaya hemiglauca*) and wilga (*Geijera parviflora*). The third dominant vegetation community in the LowerBalonne floodplain is shrubland, occupying 9 percent of the floodplain area. Shrubland consists mostly of lignum (*Duma florulenta*), ruby saltbush (*Enchylanea tomentosa*), copperburrs (*Sclerolaena spp.*), river cooba (*Acacia stenophylla*), warrior bush (*Apophyllum* *anomalum*), cottonbush (*Maireana aphyllus*), nepine (*Capparis lasiantha*), eurah (*Eremophila bignoniiflora*) and budda (*E.mitchellii*), but may be interspersed by small trees. Crops and annual pastures, water bodies and barren ground cover 11 percent of the floodplain area. The remainder of the area is covered by various other vegetation community types consisting of different tree and shrub associations (NFRPC 2004).

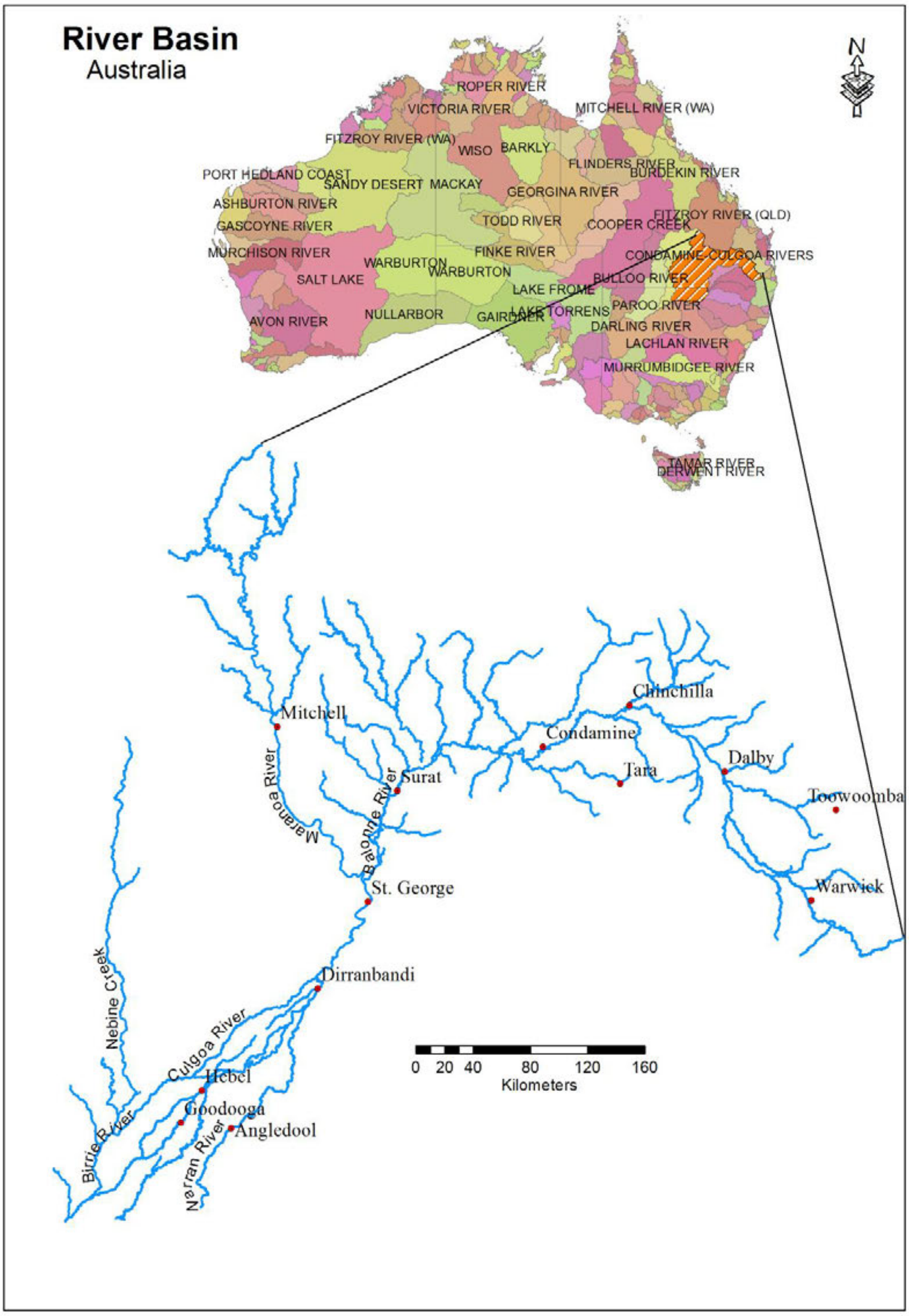


Figure 3.1 Location of the Condamine Balonne River Catchment within Australia (top) and the main river network within the catchment (bottom).

3.1.2 The Narran floodplain

Situated within the Lower Balonne floodplain, the Narran floodplain is a terminal wetland complex, located in the eastern most channel system of the Lower Balonne distributary river network (Figure 3.2). The Narran floodplain extends between 29º 40’ – 29º 57’ S and 147º 16’ – 147 º 30’E and covers an area of 296 km^2 (Figure 3.2). The Northern section of the Narran floodplain has regional, national and international importance as a Ramsar Convention site designated in June 1999. Part of the Narran floodplain has been managed as a Nature Reserve (5,500 ha) by the New South Wales National Parks and Wildlife Service since 1988. The local catchment area of the Narran floodplain is relatively small, with an approximate area of 50 km^2 (Rayburg and Thoms 2009). The Narran floodplain complex is an important breeding habitat for colonial waterbirds and has been identified as one of the nine significant waterbird refugia in semi-arid and arid New South Wales, Australia (Kingsford 2000, Rayburg and Thoms 2009). The climate of the Narran floodplain is semi-arid with a mean annual rainfall of 488 mm (1940 – 2009) and a mean annual evaporation of 2,250 mm y^{-1}. Rainfall is highly variable over time (Figure 3.3) with annual rainfall ranging from 144 mm (2002) to 957 mm (1950).

The Narran floodplain ecosystem is geomorphologically complex, within an overall setting of low gradient undulating plains. The Narran floodplain is comprised of several relatively distinct water bodies including Clear Lake, Back Lake and Long Arm Lake in the north and Narran Lake in the south (Figure 3.2), both with extensive floodplain channels. The Narran floodplain comprises eight geomorphic regions: The Narran Lake, Northern lake, Red soil, Southern floodplain, Central Eastern floodplain, Central Western floodplain, North Eastern floodplain and North Western floodplain (Rayburg *et al.* 2006) and several deep areas with complex interconnecting channel networks of approximately 800 km within the floodplain.

The geology of the Narran floodplain consists of Quaternary sediments, composed of moderately to highly weathered sedimentary rocks (Galloway *et al.* 1974). Soil consists of hard setting red-brown earth (red and brown Chromosols), pellitised clays (Lunettes), deep grey (Grey Vertosols), brown (Brown Vertosols) and black self -mulching, cracking and non-cracking clays (NFRPC, 2004). Higher elevated areas of the Narran floodplain include hard and soft red earth, gilgai clays and sandy rises (NFRPC, 2004).

The Narran River is one of the five distributary channels in the Lower Balonne floodplain, and is the only river flowing into the Narran floodplain complex (Figure 3.2). The discharge of the Narran River at Wilby Wilby, immediately upstream of the floodplain complex is highly variable over time (Rayburg and Thoms 2009). The long term average daily flow (1966 – 2013) is 413 MLD with a mean annual discharge in the Narran River of 128,717 ML; however, the mean annual discharge from 2000 to 2009 in the Narran River was only17,671 ML, while the overall the long term annual flow ranges between 100 – 150,000 The Narran River, remains dry approximately 60 percent of time (Thoms 2003,James *et al*. 2007, CSIRO 2008). Discharges of 13,000 MLD or greater initiate overbank flow and inundation of the Narran floodplain (Rayburg and Thoms 2009) The highest flood recorded in the Narran River was in 1983 (Figure 3.4), where discharge exceeded 560,000 ML. The high year to year variability of discharge in the Narran River (Figure 3.4) ensures that the Narran floodplain experiences a complex pattern of wetting and drying (Thoms 2003, Murray *et al*. 2006). Over the last 33 years Narran Lake was inundated for 23 times and Clear Lake was inundated 16 times (Murray *et al*. 2006). The complex response to the expansion and contraction of floodwater across the Narran floodplain produces a dynamic mosaic of inundated patches (Murray *et al*. 2006).

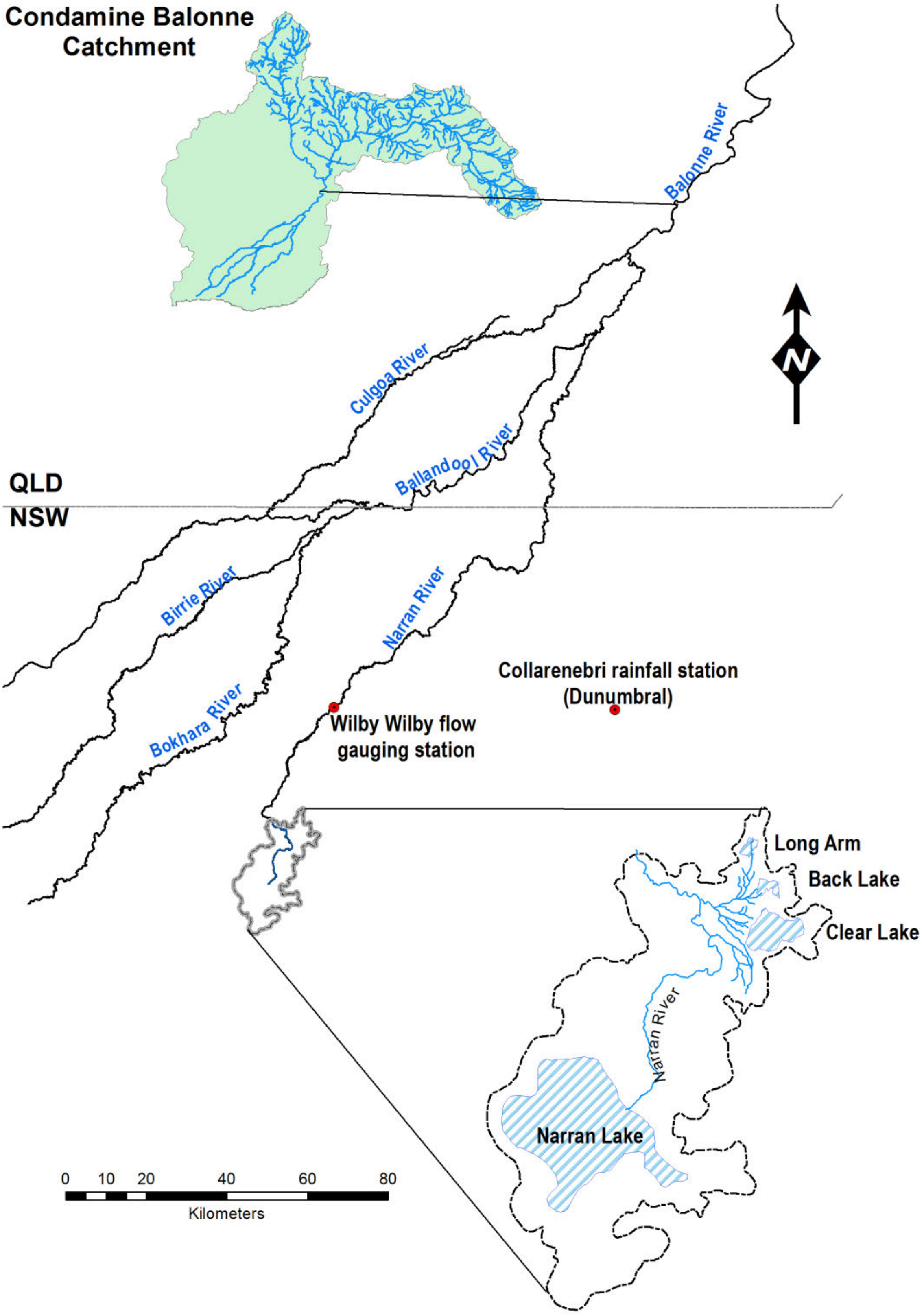


Figure 3.2 The Narran floodplain and its location within the Lower Balonne floodplain.

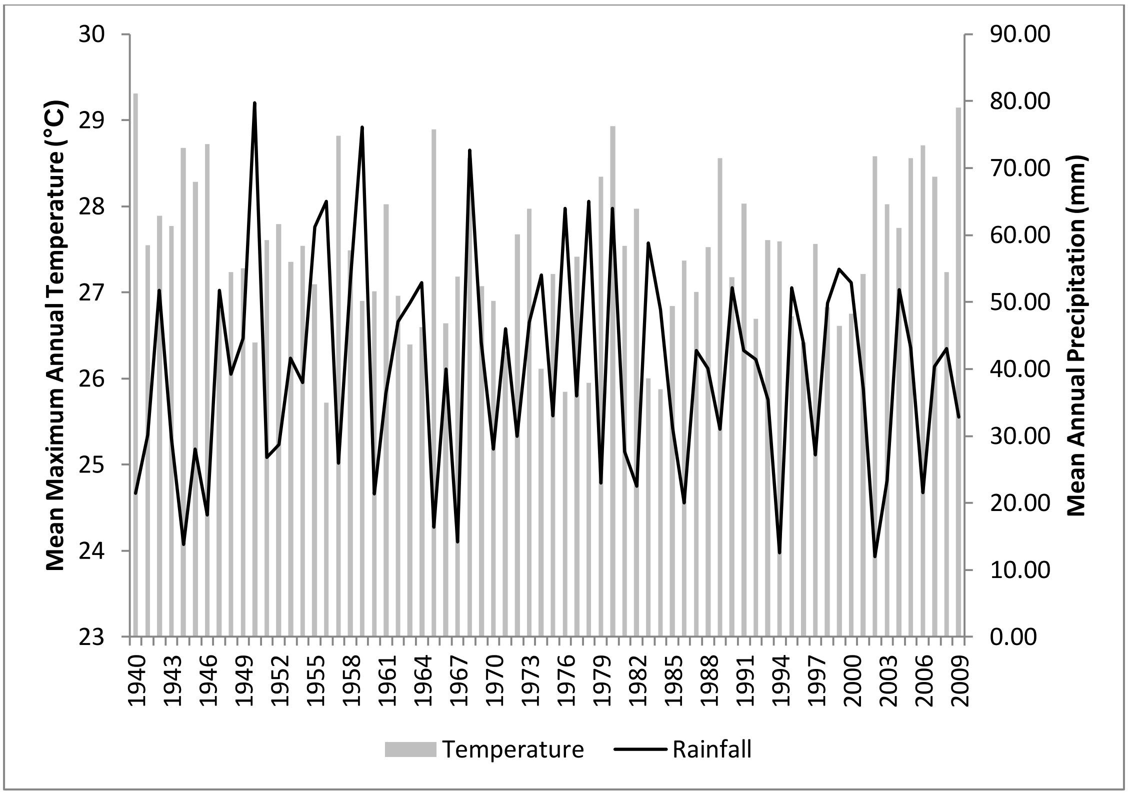


Figure 3.3 Long term variation in temperature and precipitation in the Narran floodplain at the Collarenebri (Danumbral 48038) station between 1940 and 2009.

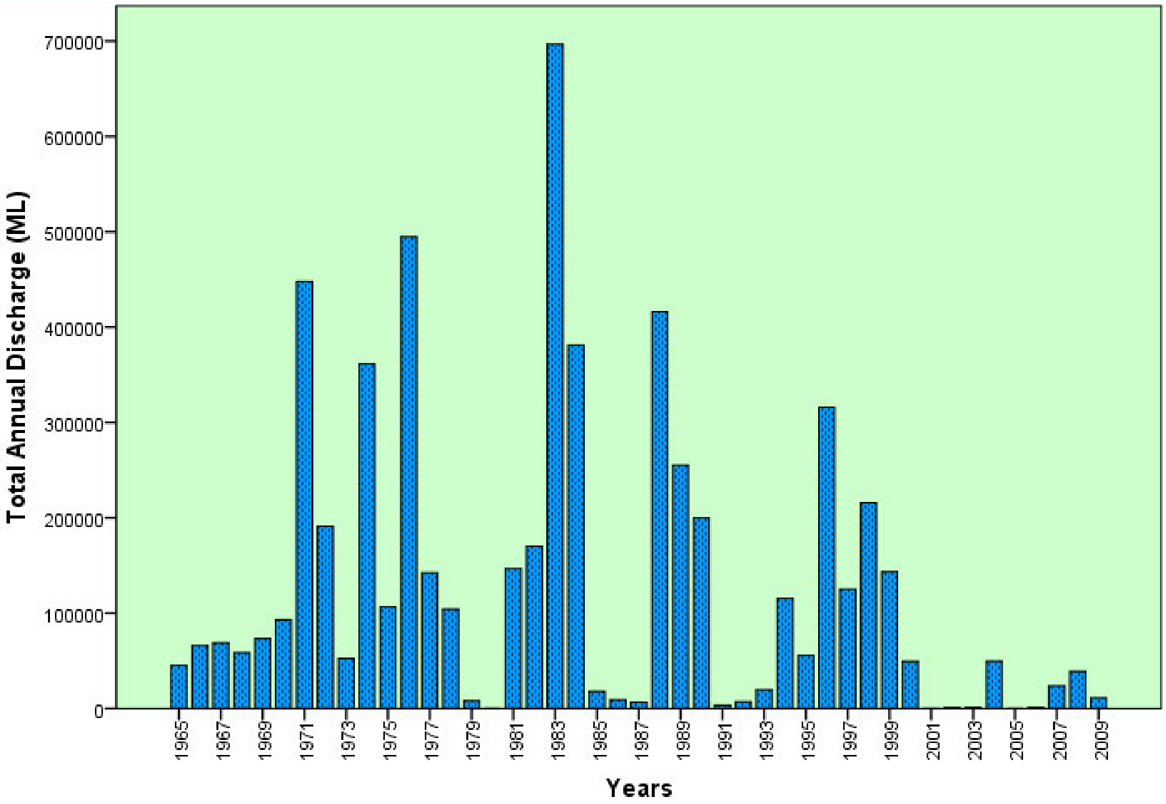


Figure 3.4 Annual discharge of the Narran River at the Wilby Wilby gauging station between 1965 and 2009.

Ground water can be an important source of soil moisture for floodplain vegetation, especially in semi-arid floodplains. Groundwater can be particularly important for trees whose deep roots can enable them to access groundwater for growth and maintenance when surface water is lacking (Roberts and Marston 2011). The importance of groundwater for floodplain vegetation in Narran is not well known. Fitzpatrick *et al*. (2005) reported that the ground water level of the Lower Balonne floodplain is on average approximately 100 metres deep, which is beyond the reach of vegetation roots. However, there may be small areas of relatively shallow groundwater, where taproot systems of deep-rooted trees may be able to access ground water.

The Narran floodplain has been used for cropping and grazing of sheep and cattle, but was gazetted as National Park in 1988 and listed as a Ramsar wetland of international importance in 1999. The northern portion of the floodplain close to the northern lakes is a nature reserve and Ramsar site (550 ha). The southern part of the Narran floodplain, near the main Narran Lake (Figure 3.2 and 3.5) is mainly used for semi-arid cropping and grazing of sheep and cattle.

The Narran floodplain contains five dominant vegetation community and land cover types (NFRPC 2004). Lignum (*Duma florulenta*) shrubland, a common Australian floodplain species, occupies 11,262 ha (38%) of the floodplain area and is mostly concentrated in the north western and the central part of the Narran floodplain and along the main Narran River (Figure 3.5). Lignum shrubland provides breeding habitat for many colonially nesting water birds in the Narran floodplain during wet periods. Colonies consist of the straw-necked ibis (*Threskiornis spinicollis*), glossy ibis (*Plegadis falcinellus*), Australian white ibis (*T.molucca*), magpie goose (*Anseranas semipalmata*) and the Australian pelican (*Pelicanus conspicilatus*) following flooding events (Brandis *et al*. 2011). Lignum shrubland may also feature a very sparse overstorey of woodland species such as coolibah (*Eucalyptus coolabah*), river red gum (*Eucalyptus camaldulensis*), black box (*Eucalyptus largiflorens*), poplar box (*Eucalyptus populnea*), leopardwood (*Flindersia maculosa*), gidgee (*Acacia cambagei*), white cypress pine (*Callitris glaucophyll),* and shrub/tree species such as river cooba (*Acacia stenophylla*) and eurah (*Eremophila bignoniiflora*).

The second dominant vegetation community of the Narran floodplain is grassland that covers 4,208 ha (14%) of the floodplain area. Grassland consists of Mitchell grass (*Astrebla* spp.), neverfail (*Eragrostis setifolia*) and box grass (*Paspalidium constrictum*) interspersed among clumps of trees and shrubs. The grasslands are mostly found in the south eastern and central western part of the floodplain (Figure 3.5). The third dominant vegetation community type in the Narran floodplain is a range of riparian and mixed woodland, that covers 3,925 ha (13%)

of the total floodplain area. This community is mostly found in the north eastern and north western part of the floodplain landscape and is mostly dominated by coolibah, river red gum, and black box with small clumps of trees/shrub river cooba, eurah and mulga (*Acacia brachystachya*). A range of mixed woodland communities consist of poplar box (*Eucalyptus populnea*), wilga (*Geijera parviflora)*, belah (*Casuarina cristata*), gidgee (*Acacia cacicola*), white wood (*Atalaya hemiglauca*), white cypress pine (*Callitris glaucophyll) and* leopardwood (*Flindersia maculosa*) together with scatted clumps of shrubs/trees (Figure 3.5). Crops and annual pastures cover 4,754 ha (16%) and the remaining 5,173 ha (18%) of the Narran floodplain is covered by lakes and barren ground.

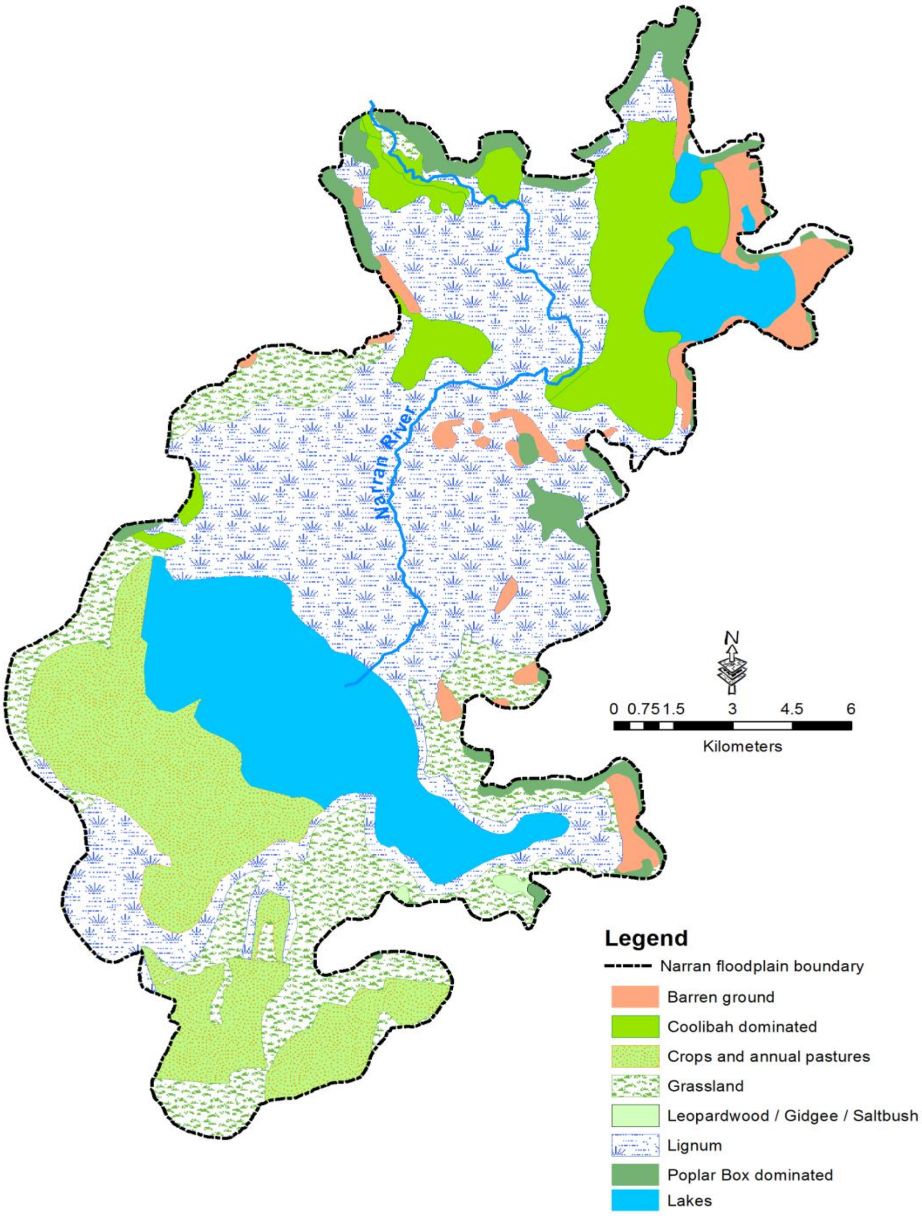


Figure 3.5 Distribution of vegetation community and land cover types within the Narran floodplain landscape. The vegetation map obtained for this study was produced for the region by the Northern Floodplain Regional Planning Committee (NFRPC 2004) and was verified and modified with the vegetation ground truth data collected in 2007 by the Narran ecosystem project (Thoms *et al*. 2007).

3.1.3 Wetting and drying of the Narran floodplain

The high variability of flows in the Narran River ensures that the Narran floodplain experiences complex floodplain inundation with periodic wet and dry cycles (Figure 3.6). Inundation of the floodplain has an average recurrence interval of 1.5 years, with flows above 13,000 MLD in the Narran River initiating overbank flows and a sequence of filling of the Narran Lakes. The filling of the lakes starts with the Clear Lake (5.86 ha) followed by Back Lake (97 ha), Long Arm Lake (72 ha) and finally the main Narran Lakes (Figure 3.2). Clear Lake, Back Lake and the Long Arm Lake can hold approximately 17,500 ML of water and may retain water for 3 – 9 months (Rayburg and Thoms 2009). In comparison Narran Lake (5,195 ha) in the south has a capacity of 122,500 ML and can retain water retain water up to 12-18 months following a flood event, but is dry 60 % of the time (Rayburg and Thoms 2009). The spatial pattern of floodplain inundation across the Narran floodplain is spatially complex irrespective of the size of the flood event (Murray *et al*. 2006). As a result, the expansion and contraction of floodwater across the Narran floodplain results in a dynamic mosaic of wetting and drying across the floodplain surface (Murray *et al*. 2006).

The hydrology of the Narran floodplain has been severely impacted by upstream water resource development. Water diversion for large scale irrigation after 1985 has altered catchment hydrology and there has been a significant increase in the frequency and duration of dry periods, which has led to reducing median annual flows and frequency of floodplain inundation (Thoms and Sheldon 2002, Thoms and Parsons 2003). Overall, water resource development has caused an estimated 58% reduction in average annual flows to the Narran floodplain (CSIRO 2008). These activities have reduced the frequency, duration and size of flood events in the system. In particular, moderate-sized floods in the Narran floodplain have declined, particularly since 1992 (Thoms *et al*. 2007).

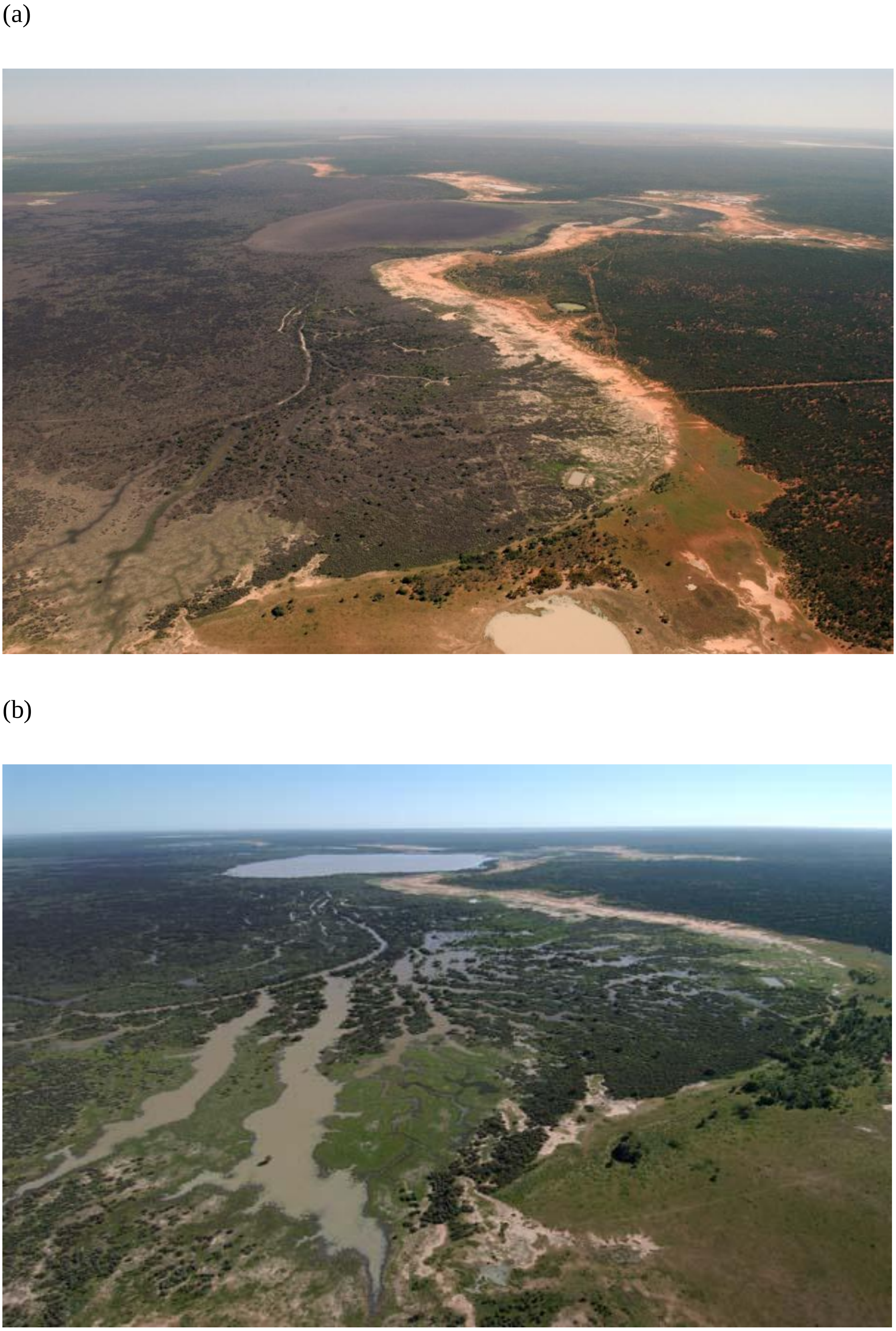


Figure 3.6 The Narran floodplain in a dry state (a) and wet state (b). Photos: Martin C. Thoms.

3.2. General methods

3.2.1 Identifying wet and dry resource states and selection of satellite images

Remotely sensed Landsat TM/ETM+ satellite images were used to track the productivity of vegetation within the Narran floodplain through a dry resource state (DRS) and a wet resource state (WRS). A three step process was used to obtain satellite images for analysis of vegetation productivity. First, the DRS and WRS were defined. A DRS is a period of no flow or flow below the long term average, combined with below average rainfall. In a DRS there is no moisture subsidy to the floodplain through flooding or rainfall. A WRS was defined as above average flow in the Narran River. An above average flow of 13,000 MLD or greater will initiate the inundation of the Narran floodplain (Rayburg and Thoms 2009).

Second, we searched hydrology and rainfall records for conditions matching our definition of dry and wet resource states. Daily Narran River flow data (January 1980 – December 2009) were acquired from the Department of Primary Industries Office of Water Information (NSW) for Wilby Wilby (Gauge 422016). Daily rainfall data for the same period were obtained from the Australian Bureau of Meteorology at Collarenebri (Station 048038). Monthly discharge and rainfall means were calculated and each month in the record was then delineated as being above or below average or as having no flow or rainfall. Periods fitting the DRS and WRS definitions were then identified in the hydrological and rainfall record.

Third, we examined the quality and availability of monthly Landsat satellite imagery corresponding to the DRS and WRS periods using the Geoscience Australia ACRES (www.acres.ga.gov.au) and the US Geological Survey GLOVIS (www.glvovis.usgs.gov) catalogues. The Narran floodplain is covered by one Landsat scene (Path 92, Row 81). In selecting images care was taken to select high quality images with no or minimum cloud cover. From the pool of high-quality satellite images we randomly selected the years 1987, 1993, 2002, and 2007 for the DRS and 1988, 1994, 2004 and 2008 for the WRS (Table 3. 1). A sequence of images taken at approximately monthly intervals was retrieved in each of these years.

3.2.2 Satellite data pre-processing

Seventy five monthly multispectral Landsat TM and ETM+ satellite images over four DRS events and four WRS events were used to examine vegetation productivity response in the

Narran floodplain (Table 3.1). Since the 1970 many research studies have recognised the potential of Landsat TM and ETM+ images for investigating spatio-temporal patterns on the Earth's surface because they are archived, cost effective and easy to acquire. Landsat images of 30 metres spatial resolution have the multi-spectral sensor capability to monitor change in ecosystems (Lillesand and Kiefer 1994, Lillesand and Kiefer 2000, Song *et al.* 2001, Pettorelli *et al.* 2005, Farina 2006, Jensen 2007, Wulder *et al.* 2008, Chander *et al.* 2009) and are ideal for landscape-scale studies (Mertes 2002, Pettorelli *et al.* 2005). Landsat data have been used successfully in change monitoring (Pickup *et al.* 1993, Sinha and Kumar 2013), to examine floodplain vegetation response to wetting and drying (Sims and Thoms 2002, Thomas *et al.* 2010, Parsons and Thoms 2013) and to determine the inundation pattern of Australian floodplains (Frazier and Page 2000, Overton 2005, Rayburg and Thoms 2009, Thomas *et al.* 2010).

The selected time-series sequence of 75 DRS and WRS Landsat images (Table 3.1) were already ortho-rectified, so no further geometric referencing was required. All the obtained images were resampled to 25 metres resolution and reprojected to the Geodetic Datum of Australia 1994 (GDA), Universal Transverse Mercator (UTM) zone 55S, since the images were obtained from two sources (Geoscience Australia and USGS). Among the 75 selected images, some of them had small patches of clouds; however, this did not affect the image quality so no further pre-processing was performed in these images.

The purpose of image pre-processing is to minimize the effects of atmospheric attenuation and scattering and to make all the images compatible spatially and spectrally to allow for the multi-temporal analysis of vegetation productivity response in wet and dry events. Thus the row Landsat TM/ETM+ images were converted to a measure of reflectance. This process included a radiometric calibration for each of the bands of the acquired images (Chander *et al.* 2009). For any change detection analysis, image pre-processing is a fundamental requirement for data analysis prior to performing pre-processing such as geometric correction, radiometric calibration and sensor calibration (Song *et al.* 2001, Chander *et al.* 2009).

Prior to radiometric and atmospheric calibration all 75 images were aligned to a correct geographic space using the ERDAS 2013 Autosync module (Figure 3.7). This process mainly performs image edge matching and geographic referencing with maximum registration accuracy. Image to image registration refers to aligning two or more images to map

Table 3.1 Satellite images comprising the dry and wet resource state of four events, with corresponding hydrology, rainfall and temperature conditions. A period refers to the comparison of two images, where the comparison of image 1 and 2 becomes period 1. Hydrology data were obtained from Department of Primary Industries (NSW) Office of Water Information and climatic data were acquired from Australian Bureau of Meteorology.

Date of image	Image number	Period	Dry or Wet images	Events	Total flow (MLD)	Total monthly rainfall (mm)	Mean monthly maximum temperature (°C)
27-05-1987	1		Dry	1	0	82	22
31-08-1987	2	1	Dry	1	2924	60	20
09-10-1987	3	2	Dry	1	0	42	27
21-12-1987	4	3	Dry	1	3862	75	35
06-01-1988	5		Wet	1	1156	32	37
07-02-1988	6	4	Wet	1	3712	31	32
23-02-1988	7	5	Wet	1	3712	31	32
26-03-1988	8	6	Wet	1	65717	50	31
13-05-1988	9	7	Wet	1	135747	19	22
29-05-1988	10	8	Wet	1	135747	19	22
16-07-1988	11	9	Wet	1	54725	92	19
04-10-1988	12	10	Wet	1	1608	1	32
20-10-1988	13	11	Wet	1	0	1	32
21-11-1988	14	12	Wet	1	0	21	31
23-12-1988	15	13	Wet	1	0	24	35
08-01-1989	16	14	Wet	1	0	3	34
09-02-1989	17	15	Wet	1	0	2	35
14-04-1989	18	16	Wet	1	30648	60	26
08-03-1993	19		Dry	2	0	77	38
09-04-1993	20	17	Dry	2	169	0	30
25-04-1993	21	18	Dry	2	169	0	30
11-05-1993	22	19	Dry	2	0	24	24
12-06-1993	23	20	Dry	2	0	20	18
28-06-1993	24	21	Dry	2	0	20	18
14-07-1993	25	22	Dry	2	0	69	19
03-11-1993	26	23	Dry	2	0	3	38
07-02-1994	27		Wet	2	6335	13	32
23-02-1994	28	24	Wet	2	18315	13	32
28-04-1994	29	25	Wet	2	0	0	27
14-05-1994	30	26	Wet	2	0	0	23
15-06-1994	31	27	Wet	2	0	0	20
01-07-1994	32	28	Wet	2	0	0	19
17-07-1994	33	29	Wet	2	0	0	19
02-08-1994	34	30	Wet	2	0	0	21
03-09-1994	35	61	Wet	2	0	0	24
19-09-1994	36	32	Wet	2	0	0	24
21-10-1994	37	33	Wet	2	0	12	29

Table 3.1 (cont.)

Date of image	Image number	Period	Dry or Wet images	Events	Total flow (MLD)	Total monthly rainfall (mm)	Mean monthly maximum temperature (°C)
22-11-1994	38	34	Wet	2	0	85	31
20-01-2002	39		Dry	3	0	0	37
05-02-2002	40	35	Dry	3	0	30	34
09-03-2002	41	36	Dry	3	0	4	33
10-04-2002	42	37	Dry	3	0	34	30
28-05-2002	43	38	Dry	3	997	0	23
29-06-2002	44	39	Dry	3	6	17	20
15-07-2002	45	40	Dry	3	0	0	20
16-08-2002	46	41	Dry	3	0	12	23
17-09-2002	47	42	Dry	3	0	19	26
19-10-2002	48	43	Dry	3	0	7	31
04-11-2002	49	44	Dry	3	0	6	37
06-12-2002	50	45	Dry	3	0	15	36
18-01-2004	51		Wet	3	8679	104	36
03-02-2004	52	46	Wet	3	18199	26	36
19-02-2004	53	47	Wet	3	18199	123	36
23-04-2004	54	48	Wet	3	407	27	29
09-05-2004	55	49	Wet	3	0.44	25	22
10-06-2004	56	50	Wet	3	0	10	20
12-07-2004	57	51	Wet	3	0	31	18
14-09-2004	58	52	Wet	3	0	19	25
16-10-2004	59	53	Wet	3	0	15	30
17-11-2004	60	54	Wet	3	0	108	32
19-12-2004	61	55	Wet	3	1115	107	33
26-01-2007	62	56	Dry	4	0	33	37
27-02-2007	63	57	Dry	4	0	76	36
16-04-2007	64	58	Dry	4	0	30	29
02-05-2007	65	59	Dry	4	0	50	24
23-09-2007	66	0	Dry	4	8	27	59
13-01-2008	67		Wet	4	6607	63	33
14-02-2008	68	60	Wet	4	21164	65	31
17-03-2008	69	61	Wet	4	0	14	31
02-04-2008	70	62	Wet	4	10000	0	26
09-09-2008	71	63	Wet	4	0	68	25
25-09-2008	72	64	Wet	4	0	68	25
27-10-2008	73	65	Wet	4	0	57	30
11-11-2008	74	66	Wet	4	0	98	30
30-12-2008	75	67	Wet	4	0	32	35

registration to accurately position the image into a correct geographic reference image (Rozenstein and Karnieli 2011,Yuan *et al*. 2013).

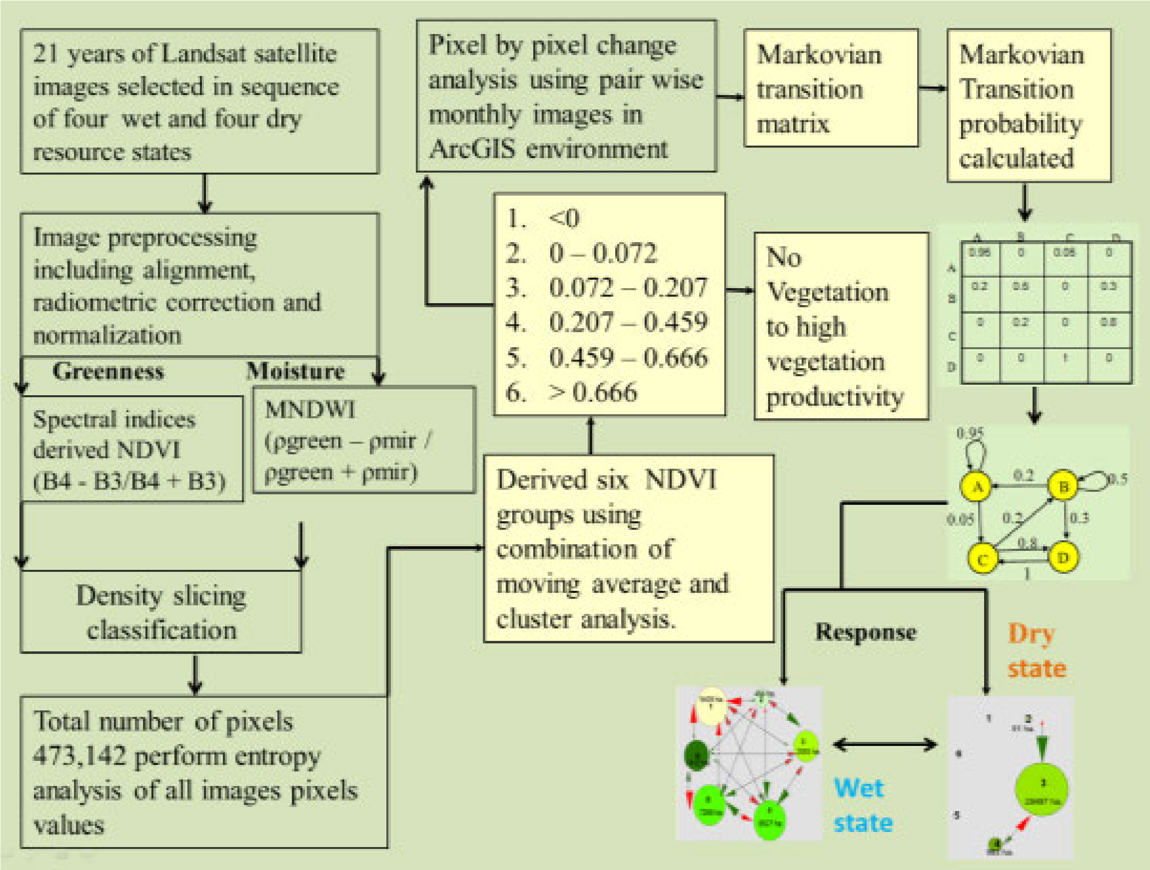


Figure 3.7 Flowchart showing the detail of the image pre-processing procedure adopted in this research to examine vegetation productivity and change response between images within the DRS and WRS.

Time-series images acquired on two different dates may show differences in brightness values due to changes in vegetation conditions. On the other hand, different atmospheric and land surface conditions, sun angle or phenological stages may also contribute to different brightness values in the image pixel and this may contribute to observed differences, which may have changed in the real surface of the earth (Myeong *et al*. 2006). To eliminate these effects, many studies have demonstrated the importance of normalizing radiometric values between two time period images (Lu *et al*. 2002). Performing image normalization or radiometric correction is an important step in multi temporal image analysis (Myeong *et al*. 2006). The six important reasons given by Lu *et al*. (2002) in support of radiometric and atmospheric correction are: I) time-series data analysis, II) across scene compression of spectral information, III) multi sensor data application, IV) vegetation productivity and other quantitative analysis, V) selected band application and VI) vegetation index calculations.

In this study all 75 aligned image Digital Numbers (DNs) were converted to radiometric reflectance using the methods suggested by Chander *et al*. (2009) following Equation 1 and 2.

Chander *et al*. (2009) suggested three advantages of using top of atmosphere (TOA) defined reflectance instead of at-sensor spectral radiance when comparing images from different dates and sensors. First, it removes the cosine effect at different solar zenith angles due to different time of data acquisition. Second, it adjusts the different values of the exo-atmospheric solar irradiance arising from spectral band differences. Third, it corrects for the variations in the earth-sun distance between different data acquisition dates.

$$\mathcal{L}\lambda = \mathrm{Q_{calmax}}\left(\frac{\mathcal{L}\mathrm{max}\lambda - \mathcal{L}\mathrm{min}\lambda}{\mathrm{Q_{calmax}} - \mathrm{Q_{calmin}}}\right)(\mathrm{Q_{cal}} - \mathrm{Q_{calmin}}) \qquad 1$$

Where $\mathcal{L}\lambda =$ Spectral radiance at the sensor in $[\mathrm{W/(m^2sr\ \mu m)}]$

$\mathrm{Q_{calmax}} =$ Maximum quatized calibrated pixel value in [DN] which is 255
$\mathrm{Q_{calmin}} =$ Minimum quantized calibrated pixel value in [DN] which is 0
$\mathrm{Q_{cal=}}$ Quantized calibrated pixel value in [DN]
$\mathcal{L}\mathrm{max}\lambda$ = Spectral at-sensor radiance that is scaled to $\mathrm{Q_{calmax}}$ $[\mathrm{W/m^2sr\ \mu m}]$
$\mathcal{L}min\lambda$ = Spectral at-sensor radiance that is scaled to Q_{calmin} $[\mathrm{W/m^2sr\ \mu m}]$

Radian corrected images were then converted to TOA reflectance values using Equation 2, suggested by Chander *et al*. (2009).

$$\rho\lambda = \left(\frac{\pi.\ L\lambda.\ d2}{ESUN\lambda.\ \cos\theta s}\right) \qquad 2.$$

Where $\rho\lambda =$ Unitless planetary TOA reflectance, $\pi =$ Unitless mathematical constant equation ~ 3.14159, $\mathcal{L}\lambda =$ Spectral radiance at the sensors aperture in $[\mathrm{W/m^2sr\ \mu m}]$, d = earth-sun distance in astronomical units based on the day of the year the image captured.

$\mathrm{ESUN}\lambda =$ Mean solar exo-atmospheric irradiances $[\mathrm{W/m^2sr\ \mu m}]$. The parameters in equation 1 and 2 are found in the header file or in (Chander *et al*. 2009) for Landsat data calibration.

A relative radiometric normalisation was performed so that images acquired on different dates could be radiometrically compared using dark and light targets. Regression models are usually used for image normalization in time-series image processing, where one date image acts as reference and other dates as the predicted image (Lu *et al*. 2002). A linear regression method was adopted for normalizing images on two different dates assuming the pixel values of image one to be a linear function of the image value on second image of the same location. The normalization process was carried out only for band 3 and band 4 of TM and ETM+

images, because these two bands were used to compute the Normalized Difference Vegetation Index (NDVI). The January band 3 image was normalized with the February band 3 image which is in turn normalized with the March band 3 image and the process was continued for all of the monthly images separately for DRS and WRS, based on the assumption that the pixel values of normalization targets are constant and any changes in the pixel values on the other image are due to atmospheric effects. For normalization some permanent features for both the dark and bright object were identified on the original images. The mean pixel values of the bright and dark features were extracted from two images and a linear regression model was computed to determine the correlation between the pixel values using Equation 3

$$\mathrm{DNy} = \mathrm{a} + \mathrm{b} * \mathrm{DNx} \qquad 3$$

Where DNy is the reference image (e.g. January band 3) and DNx is the predicted image (e.g. February band 3); ‘a’ is the intercept for the linear transformation; and ‘b’ is the slope for the linear transformation. The results obtained from here were used for computation of the regression equation using the above equation.

3.2.3 Floodplain surface area inundation mapping

The flood period (WRS) images were processed in ERDAS imagine software to delineate the expansion and contraction of flood waters across the floodplain. To map the inundation extent pixels representing water and non-water were identified by performing density slicing. Density slicing methods of inundation uses threshold reflectance values to classify inundated and non-inundated pixels as recommended by Overton (2005). In some images detecting inundated pixels that were covered by dense vegetation canopy is not possible using single band. For those images, we used a moisture related index such as the modified Normalised Difference Water Index Xu (2006) and unsupervised classification method to differentiate the inundated and non-inundated pixels. The Modified Normalized Difference Water Index (mNDWI) of Xu (2006) is calculated as shown in Equation 4.

$$mNDWI\ = \rho green - mir\ /\ \rho green + \rho mir \qquad (4)$$

Where, ρ represents the spectral reflectance values of spectral bands of Landsat TM/ETM+ images: green (band 2), mir (band 5), nir (band 4) and swir (band 7).

The results from these approaches were combined to estimate the extent of floodplain surface area inundation in the four WRS monthly images.

3.2.4 Calculation of the Normalized Vegetation Difference Index

The Normalized Difference Vegetation Index (NDVI) is based on the red and near infrared reflectance properties and is strongly correlated with photosynthetic activity and hence is a surrogate of vegetation productivity (Tucker *et al*. 1985, Tucker and Sellers 1986, Lillesand and Kiefer 2000, Wang *et al*. 2004, Farina 2006, Wen *et al*. 2012, Xu *et al*. 2012, Gamon *et al*. 2013). The Normalized Difference Vegetation Index (NDVI) was determined for each pixel in the 75 images. This provided 473,142 data points. The NDVI was calculated as the normalized differences of the spectral reflectance of NIR and visible (Red) bands as shown in Equation 5.

$$NDVI \ = \rho nir - \rho red \ / \ \rho nir + \rho red \qquad (5)$$

Where, ρ represent the spectral reflectance values of spectral bands of Landsat TM/ETM+ images: nir (band 4), red (band 3).

Entropy analysis, a non-parametric clustering technique, was performed on the 473,142 NDVI pixel values to determine the minimum number of NDVI groups accounting for the greatest variance in the data set. A moving window analysis was also undertaken to identify breaks in the distribution of NDVI values. Six NDVI groups emerged from both analyses which explained 83 percent of the variance in the NDVI data set, these being: NDVI Class 1 which had NDVI values of 0 and represents no vegetation greenness or vigour; NDVI Class 2 (0.0-0.072); NDVI Class 3 (0.073 – 0.207); NDVI Class 4 (0.208-0.459); NDVI Class 5 (0.460-0.666); and NDVI Class 6 (> 0.666). These six NDVI groups represent classes of increasing floodplain greenness or vegetation productivity. Each image was then reclassified according to the six NDVI classes and the area of each NDVI class in the 75 images calculated.

3.2.5 Analysis of change in vegetation productivity

The change in NDVI class between sequential monthly images for each DRS and WRS was determined on a pixel by pixel basis. The change data were then used to construct a first-order Markovian transition model for each DRS and WRS monthly sequence. Markovian transition probability models describe system changes through a finite set of states over fixed interval periods and have been successfully used to describe floodplain and riparian vegetation responses to various disturbances (Rogers and O'Keeffe 2003). In this study Markovian transition models depict changes between images in the various DRS and WRS sequences in terms of the surface area of the different NDVI class between consecutive images, across the DRS and WRS as well as the number of individual transitions between NDVI class, the direction and the probability of each transition (Figure 3.7). Each pixel was classified into a change class (C_{ij}) which represents a change from NDVI class *i* to NDVI class *j*. A total of 36 C_{ij} were possible among the six NDVI classes, including six constant classes, and 30 directional change classes. The total area of floodplain that increased or decreased in NDVI class between sequential images (termed a period) was calculated. First-order Markovian transition models (Weng 2002, Bolliger *et al*. 2009) were used to model the change of NDVI classes between sequential images. The Markovian transition model consists of the area of each NDVI change class (C_{ij}) present in each period and the probability (P_{ij}) of each C_{ij} occurring. The number of transitions and the direction (single or two-way) of transitions between NDVI classes were tallied from a pictorial representation of the Markovian transition model. Probability of change (P_{ij}) was calculated as the proportion of the total area of NDVI class *i* that transitioned to NDVI class *j*. The total area of floodplain whose NDVI class either increased or decreased between the images was then calculated for each DRS and WRS. The number of individual transitions between the six NDVI classes, the direction of change and the probability of change were also calculated. A period refers to the comparison of two images, where the comparison of image 1 and 2 becomes period 1.

Chapter 4 The response of dryland floodplain vegetation productivity to flooding and drying

Abstract

Dryland floodplains are characterized by highly variable flooding and drying. This variability plays a key role in the productivity of dryland floodplain vegetation. The Normalized Difference Vegetation Index, used as a surrogate for vegetation productivity, has been extensively used to examine floodplain vegetation productivity responses to flood inundation but generally focuses on inundation alone, or at a single scale thereby potentially omitting important elements of dryland variability. This study used fine resolution satellite imagery, through sequences of flood and dry resource states, at multiple scales of observation and with consideration of the relative influence of rainfall and flow to examine floodplain vegetation productivity in the dryland Narran floodplain, Australia. There were marked differences in floodplain vegetation productivity between wet and dry resource states. Overall, response patterns were complex and varied among vegetation communities and in different resource states in time. The findings suggest that vegetation productivity in the Narran floodplain does not correspond well with the boom and bust model of floodplain ecosystem productivity. Rather, understanding vegetation productivity in a highly variable floodplain requires an enhanced understanding of the nature of variability in space and time. Conceptual models that can better convey the complexity of vegetation productivity responses to floodplain wetting and drying are suggested.

Keywords: NDVI, hydrology, variability, complex response

4.1. Introduction

The importance of hydrological variability for sustaining riverine ecosystems is well-recognized (e.g. Poff and Ward 1989, Thoms 2006). Dryland rivers are characterized by high hydrological variability (McMahon 1979). Australia's dryland rivers have some of the most variable flow regimes in the world (Puckridge *et al*. 1998) and are characterized by long periods of low or no flow followed by periods of extreme flooding (Thoms 2006). Flow varies in duration, frequency, magnitude and timing over the time periods associated with a flow pulse, flow history and flow regime and flow is comparatively unpredictable in all time periods. Flow variability and unpredictability also translates to variability in floodplain inundation and influences the distribution and productivity of floodplain vegetation. Floods create an irregular mosaic of floodplain inundation in space and time in relation to the timing, magnitude and duration of overbank flows, and the interplay between flow and floodplain topography (Murray *et al.* 2006). Patterns of floodplain inundation in space and time influence the distribution of vegetation communities (Townsend 2001, Nakamura *et al.* 2007, Barrett *et al.* 2010, Reid *et al.* 2011) and the productivity of floodplain vegetation (Clowsen *et al.* 2001, Parsons and Thoms 2013).

The relationship between dryland floodplain inundation and vegetation productivity has typically been examined at small scales (sites or plots) and results up-scaled (e.g. Capon 2003, Reid *et al.* 2011). Rarely is the whole floodplain - which may be hundreds of square kilometres in area and contain a complex imprint of inundation variability - considered as a unit of study. Remote sensing provides a tool to examine floodplain vegetation productivity at large scales. The Normalized Difference Vegetation Index (Rouse *et al.* 1973) measures vegetation greenness and can be used as a surrogate for vegetation productivity (Lillesand and Kiefer 2000). Several studies have used the Normalized Difference Vegetation Index (NDVI) to examine floodplain vegetation productivity responses to flood inundation in Australian dryland floodplains. Flow was shown to be the primary driver of spatial variation in the NDVI across 10 semi-arid floodplain wetlands in the Macquarie Marshes, although rainfall and minimum temperature modified spatial variation in the NDVI, particularly among different vegetation communities (Wen *et al.* 2012). Sims and Colloff (2012) calculated that a single flood, which inundated more than 50% of a semi-arid floodplain along the Paroo River increased the NDVI by up to 19% above non-flood levels, and that these elevated values of the NDVI continued for up to 13 months following flood recession. Parsons and Thoms (2013) examined the NDVI in flood, rain and dry states in the Lower Balonne floodplain and found higher values of NDVI in the flood state, although trees situated in the riparian area also maintained high values of NDVI in the dry and rain states. Flooding was also shown to create a heterogeneous inundation mosaic in the lower Murrumbidgee River floodplain and this resulted in a non-uniform, spatially complex response in NDVI and vegetation biomass within the inundated mosaic (Shilpakar 2013). The united view emerging from these studies appears to be that flooding increases vegetation productivity in dryland floodplains, measured through the NDVI, but these productivity responses can be modified by rainfall, temperature, lack of surface water, the mosaic of floodplain inundation and vegetation community type.

Despite these successful uses of the NDVI to examine floodplain vegetation productivity in dryland floodplains, these studies have four limitations that may obscure signals of vegetation productivity response to hydrological variability. First, the resolution of satellite sensors and techniques used to compute NDVI varied from 250 m MODIS NDVI (Wen *et al*. 2012, Sims and Colloff 2012) to NDVI calculated using Landsat TM 5 or 7 bands and resampled to 25 m (Parsons and Thoms 2013, Shilpakar 2013). Coarser resolution MODIS NDVI images are unable to capture the detail of responses in semi-arid landscapes where vegetation communities are often spatially fragmented (Munyati and Mboweni 2012). Second, most of these studies focus on floodplain inundation only (Wen *et al*. 2012, Shilpakar 2013, Sims and Colloff 2012), omitting to examine NDVI during the characteristic and often long dry periods that occur between floods. As dryland floodplains have been conceptualized as boom-bust systems (Walker *et al.* 1995), vegetation productivity in both flood (the boom) and dry (the bust) states should be considered. Third, some studies examined the NDVI at one scale in the floodplain (Sims and Coloff 2013) while others examined vegetation response in the whole floodplain and in component vegetation types (Wen *et al.* 2012, Shilpakar 2013, Parsons and Thoms 2013) or in geomorphic units (Parsons and Thoms 2013). The interaction between pattern and process occurs at multiple scales and the interplay of flood inundation and vegetation response may therefore occur at different scales within the floodplain (Wiens 1989). Fourth, only Wen *et al*. (2012) considered the influence of rainfall and temperature on the NDVI of floodplain vegetation in concert with flooding. An integrated study using fine resolution satellite imagery, through sequences of flood and dry states, at multiple scales of observation and with consideration of the role of climatic variables is needed to better understand the responses of floodplain vegetation in highly variable dryland floodplains.

This study examines vegetation productivity in a dryland floodplain using a sequence of 75 high resolution remotely sensed images captured through a series of dry and wet resource states to determine if differences in NDVI are consistent between resource states at the entire Narran floodplain landscape scale and the vegetation community scale. It also seeks to identify what drives differences in NDVI at the landscape scale and between vegetation communities in terms of climate and flow.

4.2. Methods

4.2.1 Study area

The Narran floodplain is a terminal floodplain wetland complex located in the lower Condamine Balonne Catchment, in the northern Murray Darling Basin, Australia (Figure 1). The floodplain covers an area of 296 km^2 and its landscape is geomorphologically complex, with four major lakes, distributary channel networks and dissected floodplain surfaces. Quaternary alluvial sediments, the dominant geology of the region, are composed of moderately to highly weathered sedimentary rocks. The main soil types are hard setting red-brown earth (*red and brown Chromosols*), pellitised clays (*Lunettes*) along with deep grey (*Grey Vertosols*), brown (*Brown Vertosols*) and black self-mulching, cracking clays. The climate of the Narran floodplain is semi-arid with an average long-term (1940 – 2009) annual rainfall of 448 mm at Collarenebri (Station 048038) and an average annual evaporation of 2,250 mm. Rainfall is also highly variable over time, with annual rainfall ranging between 144 mm (2002) and 957 mm (1950). Thus, this ecosystem experiences significant periods of moisture deficit. Most rainfall in the Condamine-Balonne River catchment occurs in the well-watered uplands in the summer months (November – February) associated with tropical monsoonal activity. As a consequence, flows to the Narran floodplain are also highly variable. The long term mean annual discharge (1965 – 2009) of the Narran River at Wilby Wilby, just upstream of the Narran floodplain, is 128,717 ML with a range of 690,000 ML to 1,003 ML and a coefficient of variation of 307 percent. Average mean summer and winter temperatures for the region are 36° C and 19° C respectively.

Flows in excess of 13,000 MLD in the Narran River at Wilby Wilby result in inundation of the Narran floodplain. The Northern floodplain inundates first and fills in sequence through Clear Lake, Back Lake and Long Arm (Figure 4,1). Water continues along the main Narran River or flows overland to Narran Lake, in the southern part of the floodplain (Figure 4.1). These floodplain lakes can retain water for approximately 12-15 months following inflows to the system. However, given the highly variable and unpredictable nature of the flow regime of the Narran River there are periodic dry and flood (wet) states in the Narran floodplain (Murray *et al*. 2006). The Narran floodplain remains dry approximately 60% of the time (Rayburg and Thoms 2009). The drying and wetting of the Narran floodplain has been significantly impacted by water resource development in the upper catchment (Thoms 2003). Water extraction has reduced the median annual flow in the Narran River by approximately

30%, significantly reducing moderate-sized floods to the Narran floodplain (Thoms 2003).

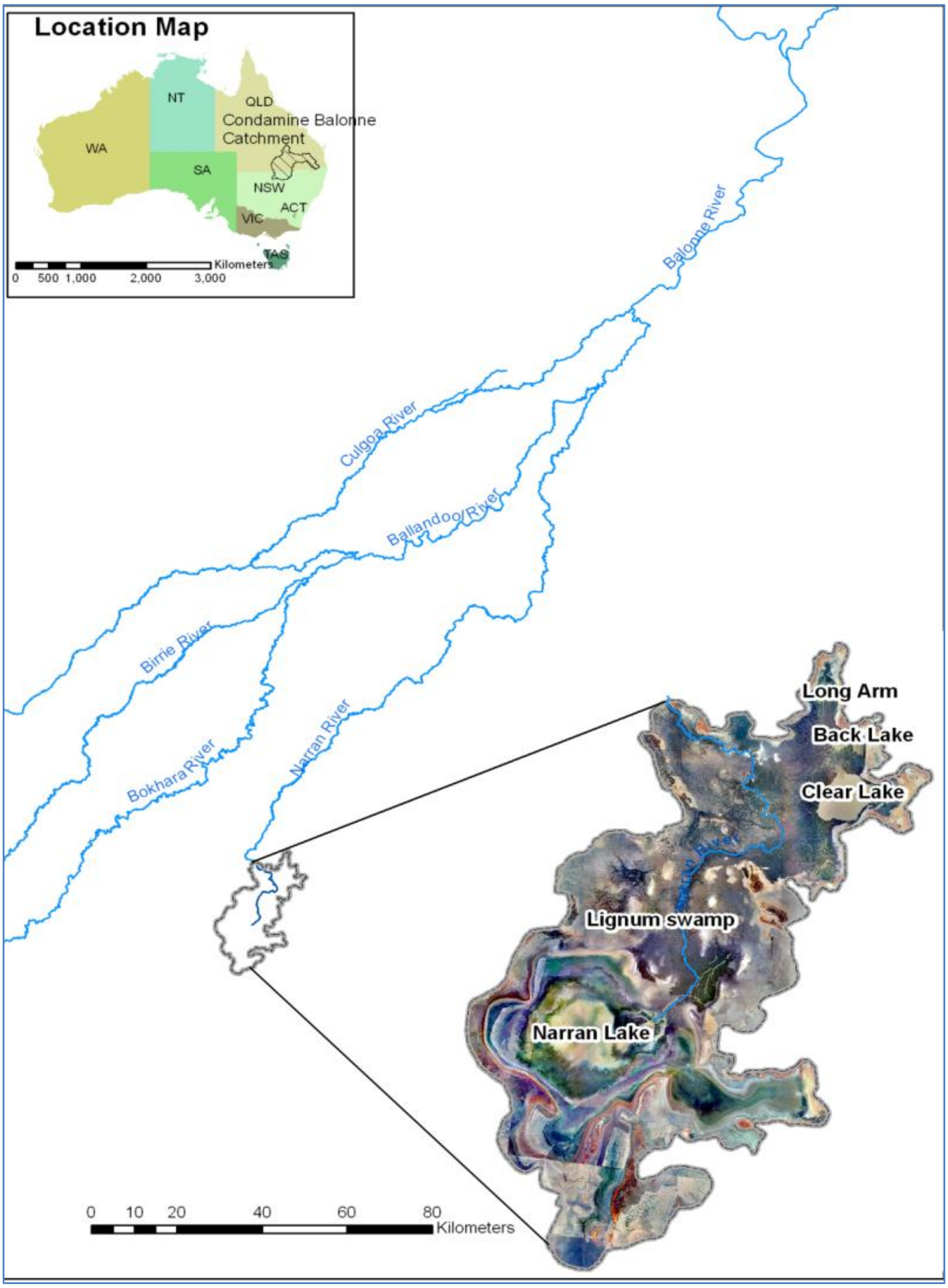


Figure 4.1 The location of the Narran floodplain.

The Narran floodplain was gazetted as a National Park in 1988 and listed as a Ramsar wetland of international importance in 1999. The floodplain serves as a critical habitat for colonial water birds and has been identified as one of nine significant refugia for biological diversity in semi-arid areas of NSW (Kingsford 2000).The Narran floodplain contains several vegetation communities but is dominated by four major vegetation community types (Figure 4.2). Extensive areas of the floodplain are dominated by the perennial shrub lignum (*Duma florulenta*). Lignum shrubland occupies 11,242 ha (38%) of the floodplain area and can also feature a very sparse overstorey of woodland species such as coolibah (*Eucalyptus coolabah*), river red gum (*Eucalyptus camaldulensis*), black box (*Eucalyptus largiflorens*), poplar box (*Eucalyptus populnea*), leopardwood (*Flindersia maculosa*), gidgee (*Acacia cambagei*), white cypress pine (*Callitris glaucophyll),* and smaller shrub/tree species such as river cooba (*Acacia stenophylla*) and eurah (*Eremophila bignoniiflora*). Grassland covers 4,163 ha (14%) of the floodplain area. Grassland consists of Mitchell grass (*Astrebla spp*), neverfail (*Eragrostis setifolia*), box grass (*Paspalidium constrictum*), kangaroo grass (*Themeda triandra*) and Warrego summer grass (*Paspalidium jubiflorum*) interspersed among clumps of trees and shrubs. The third major vegetation community type is a complex of riparian and mixed woodlands that cover 2,616 ha (9%) of the floodplain area. This vegetation community complex (hereafter referred to as Coolibah) is dominated by Coolibah woodland, but other tree species such as belah (*Casuarina cristata*), gidgee, leopardwood, mulga (*Acacia aneura*), black box, river red gum, poplar box, and whitewood (*Atalaya hemiglauca*) are also interspersed through the Coolibah woodland. Common shrubs within Coolibah woodland include lignum, eurah, river cooba, budda (*Eremophila duttonii*), spiny saltbush (*Rhagodia spinescens*) and wild orange (*Capparis mitchellii*). Poplar Box woodland covers 1,218 ha (4%) of the floodplain area. This vegetation community is dominated by poplar box but other tree species such as coolibah, leopardwood, mulga, belah, whitewood, wilga (*Geijera parviflora),* mulga and white cypress pine also occur within the community (NFRPC 2004).

4.2.2 Selection of satellite imagery

Remotely sensed satellite images were used to determine the productivity of vegetation within a dry resource state (DRS) and wet (flood) resource state (WRS) within the Narran floodplain. A three-step process was used to obtain satellite images for analysis of vegetation productivity. First, the DRS and WRS were defined. A DRS is a period of no flow or flow below the 95th percentile of the long term flow duration curve, combined with below average rainfall. In the DRS it is assumed there is no moisture subsidy to the floodplain through flooding or rainfall. There is no groundwater influence in the Narran floodplain as regional groundwater levels are more than 100 m below the floodplain surface (Fitzpatrick *et al.* 2005). The WRS was defined as flow periods above 13,000 MLD in the Narran River at Wilby Wilby; that flow required to initiate floodplain inundation (Rayburg and Thoms 2009).

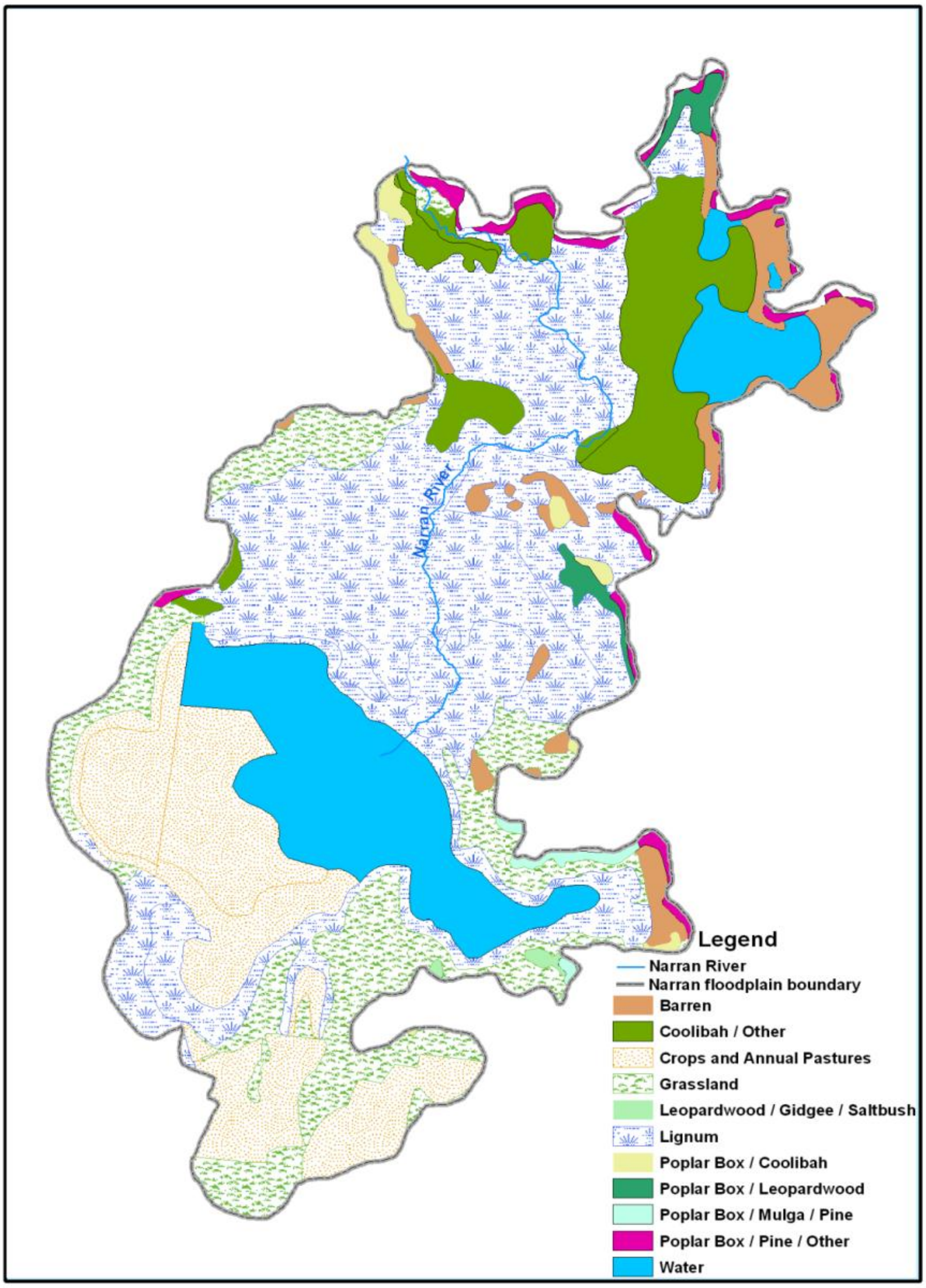


Figure 4.2 The distribution of major vegetation communities and general land cover types in the Narran Floodplain. Modified from NFRPC (2004).

Second, flow and rainfall records were searched for conditions matching the definition of dry and wet resource states. Daily Narran River flow data (January 1980 – December 2009) were acquired at Wilby Wilby (Gauge 422016). Daily rainfall data were obtained for the same period. Monthly discharge and rainfall means were calculated and each month in the record was then delineated as being above or below average or as having no flow or rainfall. Periods fitting the DRS and WRS definitions were then identified in the flow and rainfall record.

Third, the availability and quality of monthly Landsat 5 and 7 TM and ETM + satellite imagery corresponding to the DRS and WRS periods was examined using the Geoscience Australia ACRES and the US Geological Survey catalogues. The Narran floodplain is covered by one Landsat scene (Path 92, Row 81). In selecting images, care was taken to select high quality images with no or minimum cloud cover. From the pool of high-quality satellite images sequences of images taken at approximately monthly images were selected in four replicate DRS (1987, 1993, 2002, 2007) and WRS (1988, 1994, 2004, 2008). The DRS sequence was stopped when rain occurred, and the WRS sequence was stopped when floodwater completely contracted and dry images started. For each DRS there was approximately six months of prior dry. A total of 75 images were selected for this study.

4.2.3 Calculation of NDVI

Images were cropped to a standard (296 km^2) floodplain area denoted by the boundary of floodplain soils. Images were re-sampled to a 25 metre resolution and re-projected to the Geodetic Datum of Australia 1994 Universal Transverse Mercator zone 55S. The aligned image digital numbers were converted to top of atmosphere reflectance using the methods of Chander *et al*. (2009). A relative radiometric normalisation was performed using dark and light targets to make images acquired on different dates comparable. The Normalized Difference Vegetation Index (NDVI) was calculated for each pixel in each image as NDVI = $\rho nir - \rho red / \rho nir + \rho red$, where ρ is the spectral reflectance values of spectral bands nir (band 4) and red (band 3) of Landsat TM/ETM+ images. The NDVI was calculated in the whole floodplain (landscape scale) and the four major vegetation communities (Coolibah, Grassland, Lignum and Poplar Box) within the floodplain (vegetation community scale). The area of the four vegetation communities was extracted from published 1:50,000 maps of vegetation communities (NFRPC 2004).

4.2.4 Statistical analysis

Statistical analyses were performed on 473,142 NDVI values extracted from each image, at the landscape scale and the vegetation community scale. Analysis of Variance and a Wilcoxon-signed rank test was used to test differences in median NDVI values between the DRS and WRS, the years comprising each DRS and WRS, and vegetation communities. Post-hoc Tukey's multiple comparison tests were used to examine differences among resource states as well as among years comprising each DRS and WRS, vegetation communities and year by vegetation community.

Relationships between NDVI, the images within each resource state, monthly precipitation and discharge were examined using generalised estimating equation (GEE) models, at the vegetation community scale. Generalised estimating equation models are a semi-parametric regression technique that estimates the average response of a population rather than the regression parameters that would enable prediction of the effect of changing one or more covariates on a given individual (Loader 1999). Outputs from GEE models include a measure of the significance and strength of relationships. Generalised estimating equation models for the Narran floodplain considered trends in NDVI through the resource states by using the eight individual monthly sequences of NDVI data, termed year in this analysis, and their relation to monthly precipitation and discharge. Initially, scatter plots for each vegetation community were produced from the GEE modelling, to place a median NDVI value with a covariate response variable. Logistic regression was then used to estimate the potential trends and its uncertainty of the monthly sequences of NDVI. The use of GEE models allow for formal statistical testing in a manner which accounts for the fact that the observations within a vegetation community were both correlated and ordered across time. To ensure the parametric assumptions of the GEE were met, distributions of the median NDVI values for each community were constructed. These histograms, coupled with kernel density estimates and Shapiro-Wilk tests were used to assess the community-level median NDVI values for normality. Evidence of non-normality of median NVDI values of at least three out of the four communities was detected (as indicated by the magnitude of the W-statistics and multiple comparison corrected p-value of the Shapiro-Wilks tests). This evidence of non-normality necessitated the use of bootstrap methods in order to estimate the 95 % confidence interval with respect to each of the vegetation communities. The presence of correlations among the NDVI values along the monthly sequences required a fixed block-bootstrapping method being applied to estimate these confidence intervals. Similarly, the lack of normality of the community-level median NDVI necessitated the use of a logistic regression to perform the statistical tests which indicate which model terms (resource state, precipitation, discharge, community, and their interactions) are significant.

4.3. Results

4.3.1 Distribution of major vegetation communities

The major vegetation communities are not uniformly distributed in the Narran floodplain (Figure 4.2). Lignum communities dominate the central and southern regions of the floodplain and are present as continuous patches in both regions. The remaining three Coolibah, Grassland and Poplar Box vegetation communities are present as more numerous but smaller patches in the floodplain (Figure 4.2). The Grassland community is located throughout the entire floodplain whereas Coolibah and Poplar Box communities are located in the northern regions of the floodplain only (Figure 4.2). Although most of the individual patches of these vegetation communities are relatively small, there is one relatively large patch of Poplar Box located on the western margins of Clear and Back Lakes (Figure 4.2). Overall, the spatial distribution of the major vegetation communities has a mosaic pattern, but this is not related to any systematic variations in moisture or soil nutrient conditions in the Narran floodplain (Rayburg *et al*. 2006).

4.3.2 Differences in NDVI between wet and dry resource states at the landscape scale

A wide range of NDVI values (0.001 to 0.85) was recorded in the 75 Narran floodplain images. Despite this overall range there was a significant difference in NDVI between the DRS and WRS (ANOVA: $F = 5.48$, $P < 0.05$). NDVI values in the WRS were on average 0.10 higher than in the DRS (Figure 4.3a). There was also a significant difference in NDVI between the individual DRS and WRS (ANOVA: $F = 8.491$, $P < 0.05$ – DRS; ANOVA: $F = 12.321$, $P<0.05$ - WRS). For the WRS, median NDVI was largest in 1988 followed by 2008, 1994 and 2004 (Figure 4.3b). By comparison, median NDVI was largest in 1987, followed by 1993, 2007 and 2002 (Figure 4.3b). Sixty eight percent (19 of the 28) of multiple pair-wise comparisons between individual DRS and WRS were significantly different (Table 4.1). All WRS were significantly different to each another but only 50 percent of DRS were significantly different to each other (Table 4.1). The 1988 WRS and 2008 WRS were generally consistently different to all other resource states, whereas the 2007 DRS was generally not significantly different to other resource states (Table 4.1). Overall, NDVI values were higher in the WRS compared to those in the DRS but this was not consistent for all resource states. Thus, vegetation productivity in the Narran floodplain in wet and dry resource states was highly variable.

Table 4.1Pair-wise comparisons of NDVI in different Dry and Wet resource states for the Narran floodplain. D = dry resource state and W = wet resource state; * = significant difference ($p < 0.05$) and NS = not significant.

	D 1987	W 1988	D 1993	W 1994	D 2002	W 2004	D 2007	W 2008
D 1987								
W 1988	*							
D 1993	*	*						
W 1994	NS	*	NS					
D 2002	*	*	*	*				
W 2004	*	*	NS	*	NS			
D 2007	NS	*	NS	*	NS	NS		
W 2008	NS	*	*	*	*	*	*	

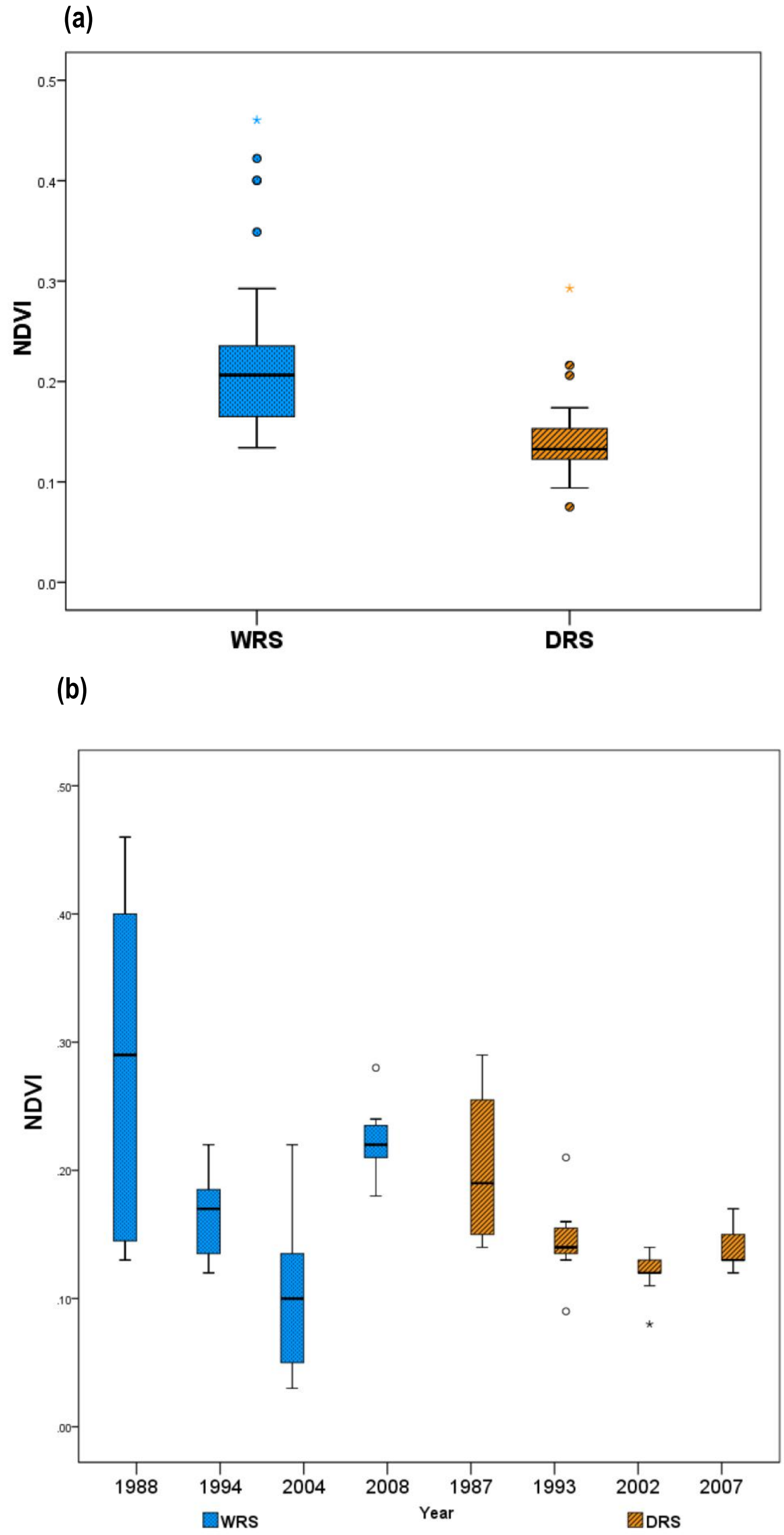


Figure 4.3 NDVI for the Narran floodplain in different resource states. A) Combined values for all dry (DRS) and wet (WRS) resource states; and, B). Individual resource states. Box and whisker plot provide the median (solid line within the box), the 25th and 75th percentile (outer edges of the box) and 5th and 95th percentiles (end of each line) as well as main outliers.

4.3.3 Differences in NDVI between wet and dry resource states at the vegetation community scale

There was a significant difference in NDVI between the eight vegetation community-resource state combinations (ANOVA: F = 6.927, P <0.05). In the WRS, Coolibah recorded the highest median NDVI followed by Poplar Box, Lignum and Grassland (Figure 4.4a). By comparison, NDVI in the DRS was lower overall but followed the same order in terms of vegetation community (Figure 4.4a). Multiple pair-wise comparisons highlighted differences among the eight vegetation community-resource state combinations (Table 4.2). Overall, only 50 percent of the 28 multiple pair-wise comparisons were statistically different (Table 4.2). Vegetation communities in a DRS were mostly different to each other with 83 percent of the within-DRS pair-wise comparisons being significantly different, whereas only 50 percent of the vegetation communities within a WRS were significantly different (Table 4.2). Of these, only Coolibah in a WRS was significantly different to all the other vegetation community-resource state combinations (Table 4.2) while Grassland and Lignum were not significantly different to other vegetation community resource state combinations, although Coolibah in a WRS was an exception (Table 4.2). By comparison, only 43 percent of the possible pair-wise comparisons between vegetation community and resource state (DRS vs WRS) were significantly different (Table 4.2). Overall, no consistent differences in NDVI were recorded among the eight vegetation community-resource state combinations.

Table 4.2 Pair-wise comparisons of NDVI for Coolibah, Poplar Box, Lignum and Grassland vegetation communities in different resource states. D = dry resource state and W = wet resource state; * = significant difference (p < 0.05)and NS = not significant.

	D Coolibah	W Coolibah	D Poplar Box	W Poplar Box	D Lignum	W Lignum	D Grass	W Grass
D – Coolibah								
W – Coolibah	*							
D – Poplar Box	*	*						
W – Poplar Box	NS	*	NS					
D – Lignum	*	*	*	*				
W – Lignum	NS	*	NS	NS	NS			
D – Grass	*	*	*	*	NS	NS		
W – Grass	NS	*	NS	NS	NS	NS	NS	

Further, variability in NDVI was also recorded in the 32 vegetation community individual resource state combinations (i.e. four vegetation communities and the eight monthly sequences that comprise each resource state) (Figure 4.4b). There was a significant difference in NDVI between the 32 vegetation community-resource state combinations (ANOVA: F = 12.21, P <0.05) and the multiple pair-wise comparisons showed significant differences in NDVI within both the vegetation community DRS and WRS combinations as well as between the vegetation community DRS and WRS combinations. Overall, 73 percent of the 32 vegetation community-individual resource state combinations were significantly different. Most of these occurred within the WRS (91 percent) and there were differences within the DRS (55 percent). No consistent patterns in the number of significant differences were recorded for vegetation community or individual resource state (year) for the vegetation community resource state combinations. Enhanced variability in NDVI exists at the community scale both between and within the different vegetation community-resource state combinations.

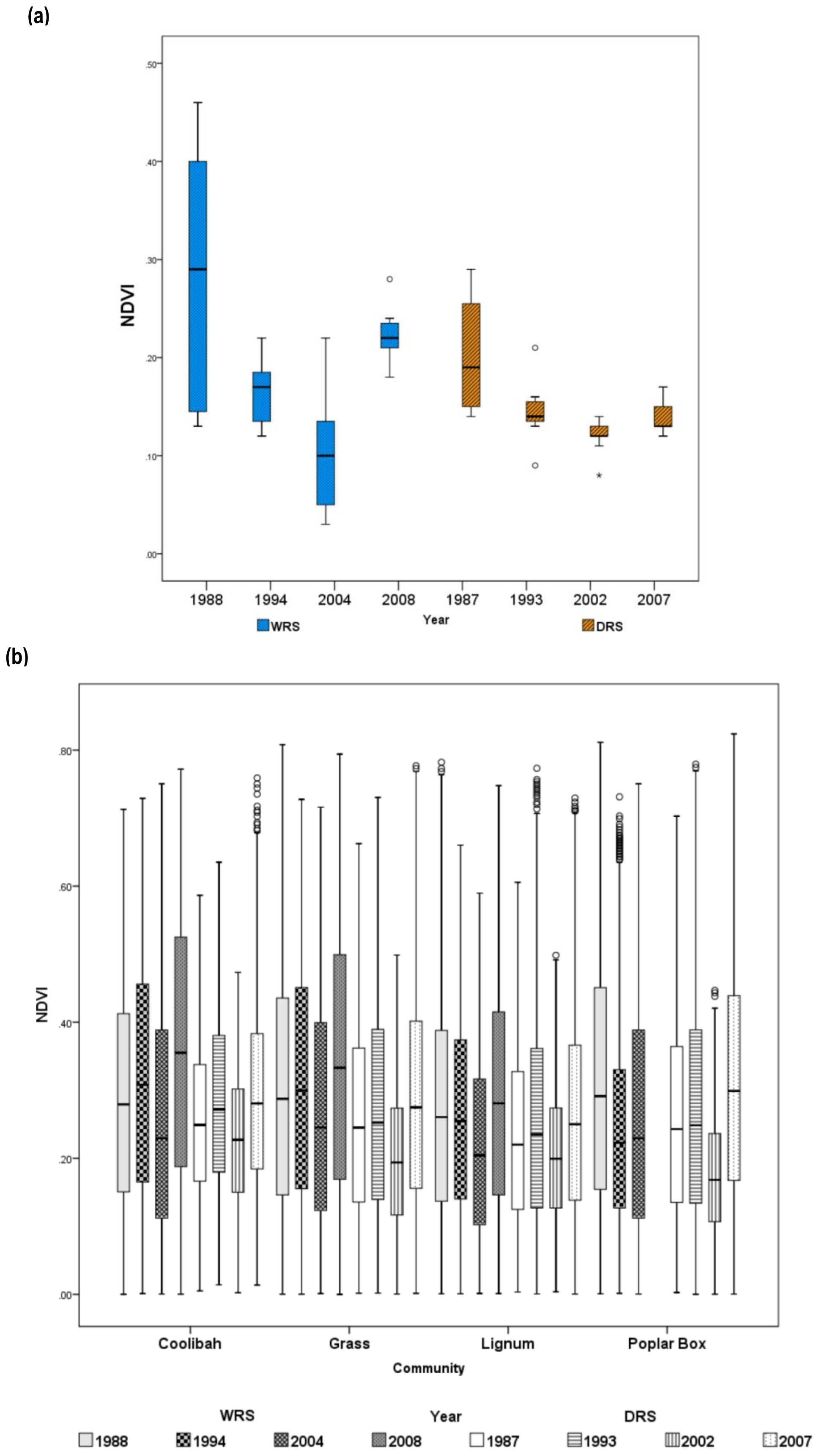


Figure 4.4 NDVI for the four major vegetation communities in the Narran floodplain. a). Vegetation communities in the wet (WRS) and dry (DRS) resource states; and, b). Vegetation communities in the individual resource states. Box and whisker plots provide the median (solid line within the box), the 25th and 75th percentile (outer edges of the box) and 5th and 95th percentiles (end of each line) as well as main outliers.

4.3.4 Climatic drivers of NDVI

First order auto-regressive structures capture the dependence of NDVI with year as well as the covariates of monthly precipitation, monthly discharge and their interactions. The Wald test statistic describes the strength of the dependence and the significance level between the NDVI values and each of the covariates and their interactions. There was a significant dependence of NDVI on all covariates and some of their interactions, with the exception of the interaction between resource state and precipitation (Table 4.3). The relationship between NDVI and the covariates of the resource state and monthly precipitation, while significant, were not as strong as that for monthly discharge; as indicated by Wald values of 6.49, 6.02 and 142.68 respectively (Table 4.3). The combination of the monthly sequence and monthly discharge increased the strength of the NDVI dependency considerably (Wald = 155.77). However the strongest dependency relationship was shown for the interaction of resource state, precipitation and discharge; precipitation and discharge combination were highly significant (Wald = 833; p <0.05).

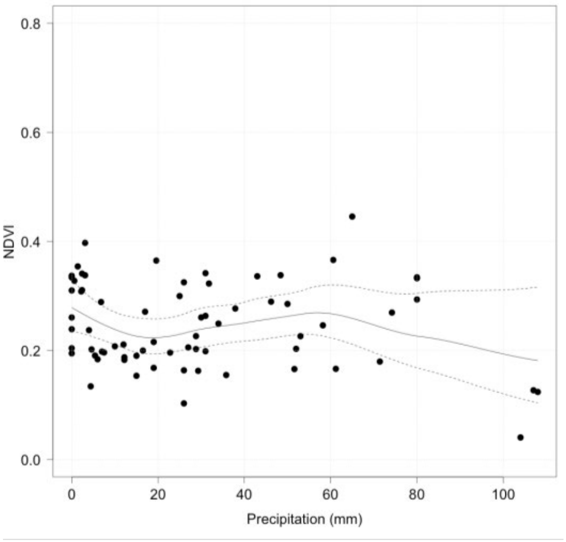
Table 4.3. Associations between resource state, monthly precipitation, monthly discharge and NDVI values in the Narran floodplain. Results were generated from a Generalised Estimating Equation Model where * = a significant association (p < 0.05) and NS = not-significant.

Covariates	Estimate	Std Error	Wald	*p*-value
Resource State	-1.73e-2	6.80e-3	6.49	0.011 *
Precipitation	-3.60e-3	1.47e-3	6.02	0.014 *
Discharge	-7.99e-6	6.69e-7	142.68	0.001 *
Resource State/Precipitation	8.60e-5	9.24e-5	0.87	0.352 NS
Resource State / Discharge	1.51e-6	1.21e-7	155.77	0.001 *
Precipitation/Discharge	3.56e-7	4.65e-8	58.76	0.001 *
Resource State/ Precipitation/Discharge	-4.55e-8	1.58e-9	833.32	0.001 *

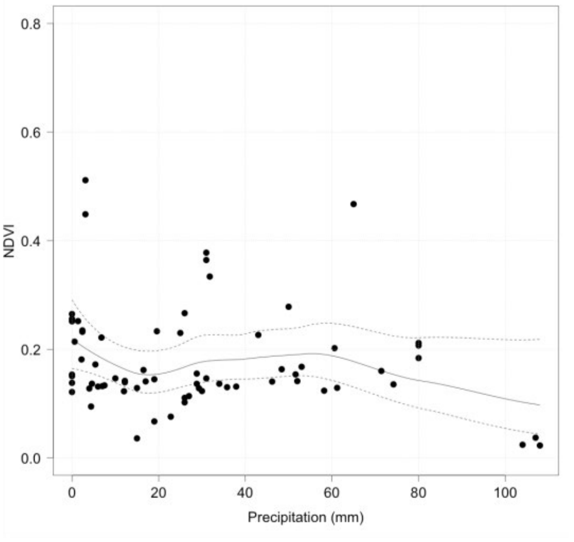
Logistic regression models, used to model NDVI trends with respect to selected covariates, displayed different non-linear responses of NDVI to monthly precipitation (Figure 4.5) and monthly discharge (Figure 4.6). The NDVI of all vegetation communities changed with increasing monthly precipitation in a similar manner. On average, NDVI values declined with an increase in monthly precipitation from zero to approximately 20 mm of precipitation. Thereafter, NDVI values increased with increasing monthly precipitation until approximately 60 mm of precipitation at which point NDVI then decreased with increasing monthly precipitation (Figure 4.5). This non-linear response with abrupt changes in the slope of the

NDVI precipitation relationship contrasts with that displayed in the relationship of NDVI to monthly discharge (Figure 4.6).

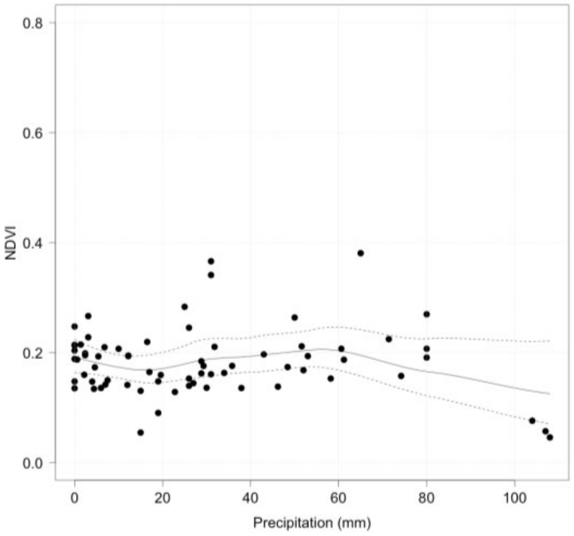
a



b



c



d

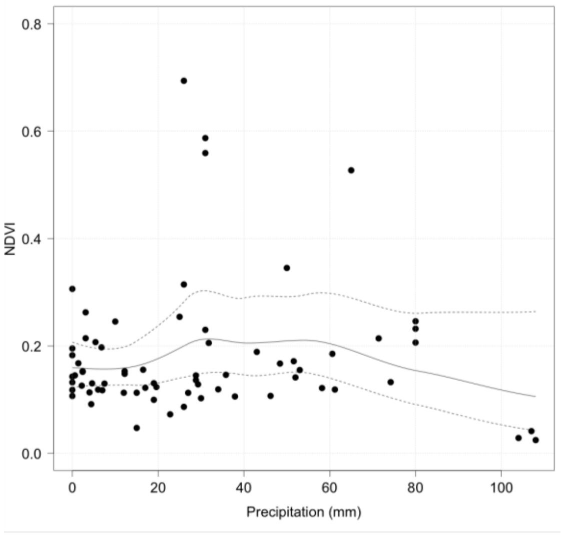


Figure 4.5 The effect of monthly precipitation on NDVI of the major vegetation communities in the Narran floodplain; (a) Coolibah, (b) Lignum, (c) Poplar Box, and (d) Grass. Solid lines are the local regression lines while dashed lines are the 5th and 95th confidence intervals.

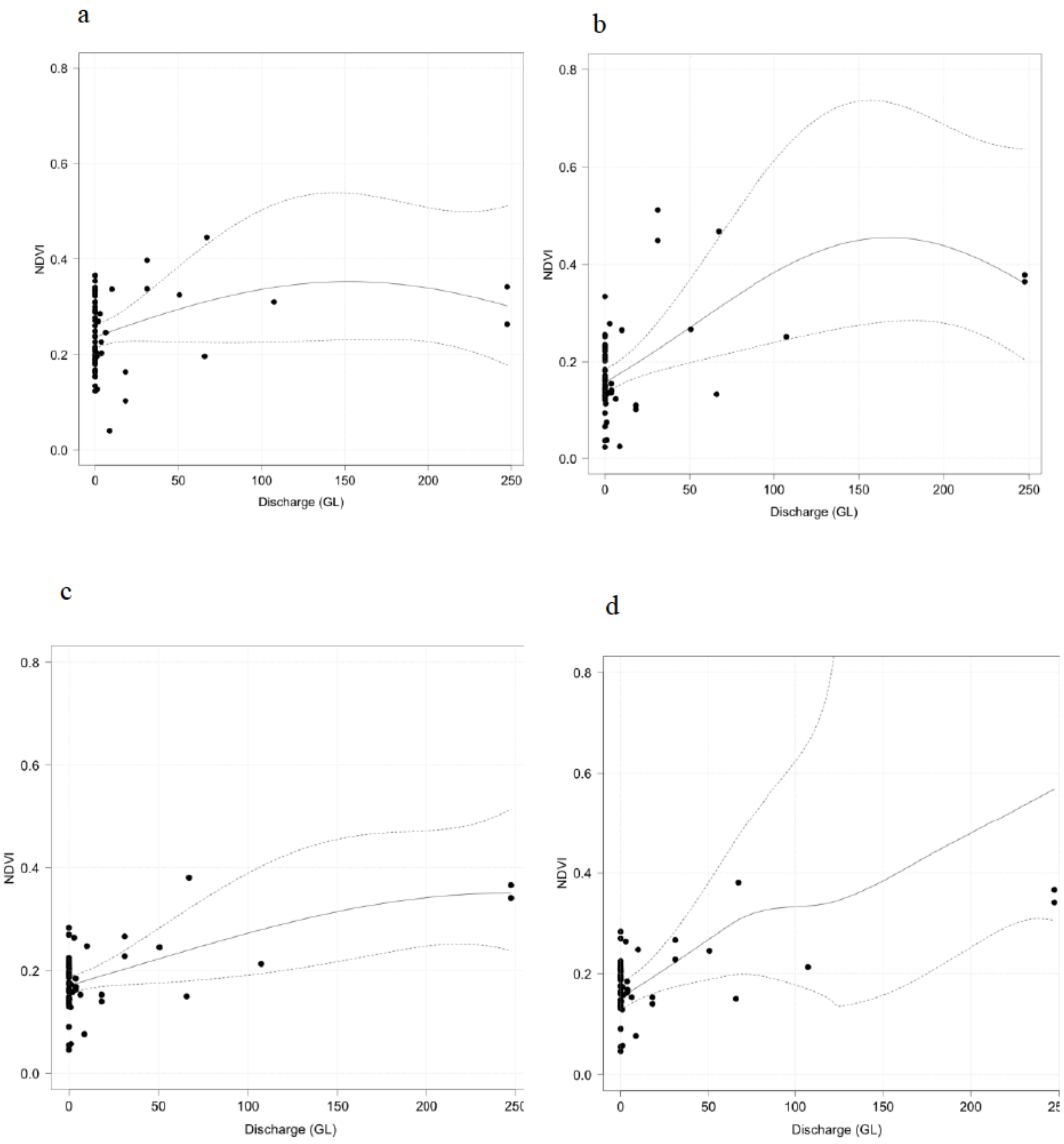


Figure 4.6 The effect of monthly discharge (GL) on NDVI of the major vegetation communities in the Narran floodplain; (a) Coolibah, (b) Lignum, (c) Poplar Box, and (d) Grass. Solid lines are the local regression lines while dashed lines are the 5th and 95th confidence intervals.

The combined effect of monthly precipitation and monthly discharge and NDVI values all display curve-linear relationships (Figure 4.7), which differ slightly in character. Overall, the Grassland and Lignum vegetation communities had a greater response of NDVI to the addition of water than the Coolibah and Poplar Box communities (Figure 4.7b and 4.7d). The NDVI isolines range from 0.2 to 0.9 for both Lignum and Grassland compared to 0.15 to 0.65

for Coolibah and 0.2 to 0.8 for Poplar Box (Figure 4.7). The models also show that monthly discharge has a greater influence on NDVI than monthly precipitation for all four vegetation communities. For example, with a monthly precipitation of 60 mm in the Narran floodplain, NDVI values for Grassland were modelled to increase from 0.2 to 0.9 with an increase in monthly discharge from 50 GL to 175 GL. In contrast, at a monthly discharge of 100 GL there is no increase in NDVI after a monthly precipitation of 50 mm (Figure 4.7).

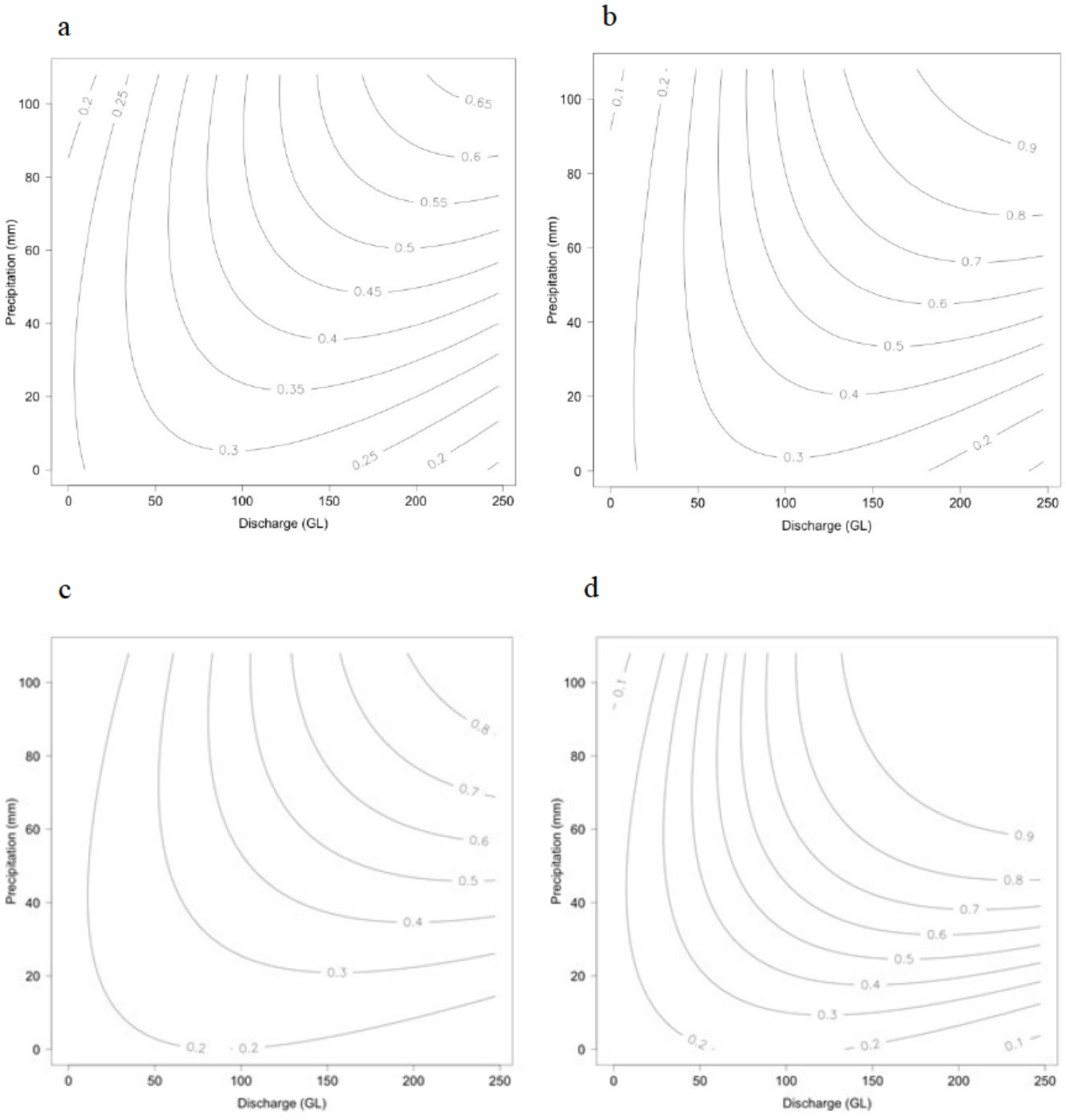


Figure 4.7 Combined effect of monthly discharge (GL) and monthly precipitation (mm) on NDVI of the major vegetation communities in the Narran floodplain. (a) Coolibah, (b) Lignum, (c) Poplar Box, and (d) Grassland. Contour lines are median NDVI values.

4.4. Discussion

Water is the driver of life in dryland floodplains. Yet the supply of water to the floodplain is highly variable in space and time, leaving a heterogeneous imprint of inundation frequencies that can often be distinctly associated with ecological patterns (Hughes 1997, Capon 2003, Rayburg and Thoms 2009). Ecological responses to the variability of water in the floodplain are often viewed using a two-state boom and bust model, in which the boom is characterised by an inundated floodplain and the bust is characterised by a dry floodplain in moisture deficit (Walker *et al*. 1995). The boom stimulates great primary and secondary ecological production (e.g. Roshier *et al*. 2002). The bust brings contraction of the ecosystem into refugia and a reduction in primary and secondary production (e.g. Arthington *et al.* 2005). While understanding of the way that water drives primary and secondary production in flood (boom) events is important for ecosystem management (Bunn *et al*. 2006, Leigh *et al*. 2010), the dry (bust) periods between floods are not as well understood. This study considered both parts of the boom-bust model and examined vegetation productivity in multiple wet and dry resource states in the Narran floodplain. The results demonstrated that there is a marked difference in floodplain vegetation productivity between wet and dry resource states. However, the addition of scale, climate and high resolution Landsat imagery as elements of an integrated study also revealed the complexity of vegetation productivity in the wet and dry resource states. Hydrology drives vegetation productivity overall, but productivity varied among vegetation communities, and in different resource states in time. Like the hydrological variability that is characteristic of dryland floodplains, the association between floodplain state as wet or dry and floodplain vegetation productivity is also variable in space and time.

Previous studies using NDVI to examine dryland floodplain vegetation productivity in Australia have generally focused on the wet resource state (Sims and Colloff 2012, Shilpakar 2013, Wen *et al*. 2013). This is not unexpected because water is the overriding determinant of dryland biological production (Noy-Meir 1973). Many studies in dryland ecosystems report increased vegetation productivity with increased water availability (Nightingale and Phinn 2003, Al-Bakri and Suleiman 2004). Water stimulates dryland vegetation productivity through physiological mechanisms that enhance photosynthetic activity and biomass production (Warwick and Brock 2003, Xu *et al.* 2010). Vegetation that does not have physiological mechanisms to withstand drought has lower growth and productivity, and may not survive extended periods of drought (Xu *et al.* 2010). This study considered the wet and dry resource states concurrently and found congruence with the expectation of higher floodplain vegetation productivity in the wet resource state. However, the study also demonstrated that floodplain vegetation productivity continues in the dry resource state, albeit at lower intensity and at different levels in different vegetation communities. Thus, the dry resource state is not a state of inactive vegetation production in the Narran floodplain. The factors influencing the continuation of vegetation productivity in the dry resource state of no surface water availability may include local soil water storage in the mulched clay floodplain soil, adaptations of floodplain tree species such as Coolibah to moderate stomatal apertures to avoid plant water loss, and dormancy strategies (James *et al*. 2015).

Scale is a window through which ecosystems can be viewed (Wiens 1989). However, what is seen at any particular scale is related to the size of the window through which the system is viewed (Wiens 1989) and to the way that the scales of observation used relate to the hierarchical organization of processes operating within the system (Dollar *et al*. 2007). Without consideration of multiple scales, incorrect interpretations of system behaviour can be made because the process under consideration is not captured by the scale of observation(s) used (Parsons and Thoms 2007). This study examined vegetation productivity at two scales: the whole floodplain and vegetation communities. The results showed that vegetation productivity responses were different at each scale (cf. Figures 4.3 and 4.4). Vegetation productivity in the whole floodplain, for the most part, differed between the WRS and DRS, and differed for some vegetation communities. For example, Coolibah displayed consistent differences in NDVI between and within resource states. At the landscape scale all WRS were different to one another and to most DRS, but only 50 percent of the DRS were different to one another. However, vegetation productivity at the vegetation community scale displayed marked but inconsistent patterns of variation between and within vegetation communities and individual resource states. Thus, multi-scaled study of floodplain vegetation productivity is needed to understand the complexity of vegetation productivity responses to hydrological variability in dryland floodplains.

The differences in vegetation productivity among vegetation communities reflect different vegetation life-form responses to hydrological variability. The highest and lowest median NDVI was found in Coolibah and Grassland communities, while Lignum and Poplar Box tree communities showed mid-range median NDVI. However, with the availability of water in the Narran floodplain Grassland and Lignum NDVI had a greater overall response. Dryland grassland and shrub species may persist in reserve form during dry periods and growth is stimulated by the availability of water (Noy-Meir 1973). Dryland trees may persist through dry periods because of the ability to access limited water in the vadose zone (Engel *et al.* 2005). Parsons and Thoms (2013) used NDVI to examine vegetation productivity in the Lower Balonne floodplain and showed that corridors of trees along main water courses maintain most of the overall floodplain productivity in dry periods. During floods, grasses and lignum shrubland contribute the most productivity and trees decrease in productivity. In the Narran floodplain, it is likely that the higher productivity observed in trees (Coolibah and Poplar Box) in the DRS is a function of the proximity of trees to permanent water courses or their position in relation to micro-habitats at different elevations within the floodplain that may retain water for longer periods than the surrounding floodplain. Localized rainfall may also influence the productivity of Poplar Box in the DRS. The lower productivity of Grassland and Lignum in the DRS is likely a function of grasses and shrubs going into reserve form. In contrast, the high productivity observed in Grassland and Lignum in the WRS might be related to utilization of available resources quickly, while the lower productivity observed in tree communities could be related to soil saturation and delayed responses to water availability.

Flow was the main influence on vegetation productivity in the Narran floodplain as shown by marked increases in NDVI with flooding relative to that observed with precipitation. There was also strong inter- and intra-annual variability among and within years, driven by variation in hydro-meteorological conditions. The highest NDVI values were observed in the largest wet event (1988) and the lowest NDVI values in the driest year (2002). Rainfall can contribute to the productivity of dryland floodplain systems (Parsons and Thoms 2013) and Baldwin *et al.* (2013) reported that approximately 40-45 mm of rainfall was required to increase soil moisture at 30 cm in the floodplain of the lower Murrumbidgee River, Australia. The present study showed that monthly precipitation contributed to some of the observed vegetation productivity. However, monthly precipitation was not important until associated with approximately 150 GL of monthly discharge in the Narran floodplain, where this combination of rainfall and discharge generated much higher NDVI values in the Narran floodplain. This result concurs with the field based study conducted in the Narran floodplain which showed that the combination of discharge with rainfall substantially increased floodplain biomass productivity Reid *et al.* (2011). Thus, flooding is a key driver of vegetation productivity in the Narran floodplain, but can vary between multiple events in concert with rainfall.

Differences in vegetation productivity between the WRS and DRS and among vegetation communities suggest that vegetation productivity in the Narran floodplain is complex and may not correspond well with the boom-bust model typically used to characterize the relationship between hydrological variability and ecological response. Rather this study observed that a variable structural driver (hydrology) results in a complex and multi-scaled functional response (productivity). Acknowledgement of the heterogeneity and variability of moisture supply and the functional responses of vegetation are well known in rangeland and desert ecosystems (Ludwig *et al*. 1997) and appears to also be an important consideration in dryland floodplains. Systems characterized by high variability and heterogeneity, and complex multi-scaled processes, require investigation techniques that go beyond reductionist models that use falsification to determine linear relationships between driving factors and ecological responses. Explanation of patterns and their causal processes are both required to decipher ecosystems (Pickett *et al*. 1994) and understanding vegetation productivity in highly variable floodplains requires an enhanced understanding of the nature of that variability in space and time to then construct and or improve conceptual models about the function of vegetation in these landscapes.

Application of alternative models for examining ecosystem responses in variable environments may provide new insights into dryland floodplains. One such alternative is a state and transition model (Westoby *et al*. 1989) that describes vegetation dynamics in a non-linear framework as an alternative to the common linear continuum process incorporated in quantitative climax vegetation models. A state is defined as an alternative, persistent vegetation community that is not reversible in the linear successional framework. However, there is still much debate about the use of state transition models and their relevance to rangeland management (Briske *et al*. 2003). Another model is adaptive cycles, which describe processes of change in complex systems. Adaptive cycles are a key component of resilience theory, and describe change as a cyclic process with four phases: exploitation, conservation, release and reorganization (Holling and Gunderson 2002). The adaptive cycle model may be an alternative model that can be used to better understand the variability of floodplain vegetation productivity response to wetting and drying in the Narran floodplain. Further an adaptive cycle model can explain the transitions that may occur between wet and dry resource states. Thus, while the simpler boom bust model may capture the role of flooding as a key signal for vegetation productivity, the adaptive cycle model examines transitions between wet and dry resource states and the relationship of the overall cycle to hydrological variability.

Viewing dryland floodplains as more complex than a simple boom bust system is imperative given the increasing anthropogenic pressures on floodplains. Land and water resource development (Thoms 2003) and climate change (CSIRO 2008) will have marked impacts on the variability of floods and dry periods in dryland regions. Change in hydrological variability is predicted to increase periods of drying resulting in prolonged dessication (Capon *et al*. 2013) with corresponding reductions in floodplain vegetation productivity. The Narran floodplain landscape is already under pressure from land and water resource development activities, and this has reduced the flows of the Narran River by 30% (Thoms 2003). An integrated understanding of the complex and multi-scaled patterns of floodplain vegetation productivity in wet and dry resource states will help to better manage dryland floodplain ecosystems, and to make predictions about their future dynamics under scenarios of changing hydrological variability.

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Chapter 5 An adaptive cycle hypothesis of semi-arid floodplain vegetation productivity in dry and wet resource states

Abstract

Spatial and temporal variability in flooding plays a significant role in the productivity of semi-arid floodplain ecosystems. Floodplains may be perceived as boom–bust systems, but this model does not account for transitions that may occur between wet and dry floodplain states. This study used the concept of adaptive cycles to examine how floodplain vegetation productivity changes in response to wetting and drying. Floodplain vegetation productivity was tracked through a wet and dry state using the normalized difference vegetation index (NDVI). Floodplain inundation revealed complex vegetation productivity responses to resource availability. There was low NDVI in the dry phase, whereas vegetation vigour increased and decreased through the wetting, wet and drying phases. There was a marked difference in NDVI class area, number of transitions, direction of transitions, probability of transitions and NDVI class diversity between the dry phase and the combined wetting, wet and drying phases of floodplain inundation. The distribution of transition probabilities was platykurtic in the dry phase and bimodal during the wetting, wet and drying phases. Overall, anti-clockwise hysteresis was the dominant direction of hysteresis. All vegetation productivity measures demonstrated a switch in direction during the wet phase. The hysteresis observed in this study indicates the cyclic nature of vegetation response to floodplain inundation through dry, wetting, wet and drying phases. We propose that vegetation productivity response follows an adaptive cycle and that this is an appropriate model for understanding the complexity of semi-arid floodplain vegetation response to wetting and drying.

Key words: resilience; complex response; floodplain ecosystems; adaptive cycle; NDVI

5.1. Introduction

Semi-arid floodplains are characterized by variable productivity, driven by spatial and temporal variability in flood inundation (Walker *et al*. 1995, Bunn *et al*. 2006). During extended periods of limited water availability that may last for years, floodplain primary and secondary productivity is relatively low (Arthington *et al*. 2010, Parsons and Thoms 2013). In contrast, flooding stimulates a rapid increase in floodplain productivity that may be maintained for months (Thoms 2003, Bunn *et al*. 2006, Leigh *et al*. 2010). Flooding stimulates water bird migration and breeding (Kingsford 1999, Roshier *et al*. 2002), fish breeding (Puckridge *et al*. 2000, Balcombe *et al*. 2007, Balcombe and Arthington 2009), increases vegetation productivity (Sims and Thoms 2002, Capon 2003, Westbrooke *et al*. 2005, Reid *et al*. 2011) and the availability of soil nutrients (Baldwin and Mitchell 2000, Thoms 2003, Baldwin *et al*. 2013). Semi-arid floodplain ecosystems are therefore perceived to change between two states: a dry 'bust' state of limited water availability and a wet 'boom' state of abundant water availability and productivity (Walker *et al*. 1995).

Ecosystems respond in a complex manner to the availability of resources (Schwinning and Sala 2004, Smith *et al*. 2009) and may show multiple stable states, non-linearity and self-organization (Holling 1973, Holling and Gunderson 2002, Folke *et al*. 2010). Emphasis on floodplain productivity as consisting of two states may not account for the potential complexity in response to water availability. Examining semi-arid floodplains through an adaptive cycle lens may help to better understand the complexity of floodplain productivity response to the intermittent availability of water. Derived from complex adaptive systems theory, the concept of adaptive cycles provides a framework to understand the dynamics of change in complex systems (Holling and Gunderson 2002). Adaptive cycles describe change as a cyclic process with four phases: exploitation, conservation, release and reorganization (Holling and Gunderson 2002). In the exploitation phase, the system is engaged in rapid growth to exploit available resources (Walker and Salt 2006). Through the conservation phase, biomass gradually builds with energy and materials accumulating in the system. The release phase is triggered by an internal or external disturbance. In the release phase the biomass, energy and materials stored in the system are released, providing a template for the reorganization phase. In the reorganization phase the ecosystem reorganizes into the same state or into a new configuration via an exit cycle (Walker and Salt 2012). The cyclic movement of an ecosystem through the adaptive loop is linked to resilience, where a resilient system has the structural and functional diversity to move through cycles of release and reorganization without transforming to an alternative state (Holling and Gunderson 2002). Despite the potential for adaptive cycles to decipher complexity in the response of floodplain ecosystems to water availability, there has been limited application of this concept in floodplains (but see Colloff and Baldwin (2010) and Whalley *et al.* (2011) for exceptions). The aim of this study is to examine how semi-arid floodplain vegetation productivity changes in response to floodplain inundation and drying, and to evaluate whether observed responses correspond to an adaptive cycle.

5.2. Study area

The Narran floodplain is a terminal floodplain wetland complex in the Condamine-Balonne River catchment, Australia (Figure 5.1). The Narran floodplain covers 296 km² (29,600 ha) and is geomorphologically complex, with numerous lakes, channel networks and dissected floodplain surfaces (Figure 5.1). The climate of the Narran floodplain is semi-arid with average maximum summer and winter temperatures of 36° C and 19° C respectively. Mean annual rainfall is 448 mm at Collarenebri (1940 – 2009) while mean annual evaporation is 2,250 mm. Rainfall is highly variable with annual rainfall ranging from 144 mm (2002) to 957 mm (1950). Most rainfall in the Condamine-Balonne River catchment occurs in the well-watered uplands in the summer months (November – February) associated with tropical monsoonal activity.

Water is delivered to the Narran floodplain along the Narran River (Figure 5.1). The long term mean annual discharge (1965 – 2009) of the Narran River at Wilby Wilby, just upstream of the Narran floodplain is 128,717 ML with a range of 690,000 ML to 1003 ML. There are periodic dry and wet resource states in the Narran floodplain arising from this flow variability in Narran River hydrology (Murray *et al.* 2006). Flows in excess of 13,000 Megalitres per day (MLD) in the Narran River at the Wilby Wilby gauge result in the initial wetting of the northern floodplain surface. The Northern floodplain fills in sequence through Clear Lake, Back Lake and Long Arm (Figure 5.1). Water continues along the main Narran River or flows overland to Narran Lake (Figure 5.1), which can retain water for around 12-15 months. The Narran floodplain remains dry approximately 60% of the time (Rayburg and Thoms, 2009). However, the drying and wetting of the Narran floodplain has been severely impacted by water resource development in the upper catchment. Water extraction has reduced the median annual flow in the Narran River by approximately 30% (Rayburg *et al*. 2006), significantly reducing moderate-sized floods to the Narran floodplain (Thoms *et al*. 2007).

The Narran floodplain was gazetted as a National Park in 1988 and listed as a Ramsar wetland of international importance in 1999. Floodplain vegetation cover is dominated by the perennial shrub lignum (*Duma florulenta*). There is an overstorey of riparian woodland along main watercourses including river red gum (*Eucalyptus camaldulensis*), coolibah (*Eucalyptus coolabah*) and black box (*Eucalyptus largiflorens*). A range of woodland communities found in the Narran floodplain includes poplar box (*Eucalyptus populnea*), whitewood (*Atalaya hemiglauca*), belah (*Casuarina cristata*), gidgee (*Acacia calcicola*), wilga (*Geijera parviflora*), black box (*Eucalyptus largiflorens*) and whitewood (*Atalaya hemiglauca*). Lignum shrubland and tree communities cover approximately 151 km^2 (51 %) of the Narran floodplain. Grassland covers approximately 42 km^2 (14 %) and consists of Mitchell grass (*Astrebla* spp.*)*, neverfail (*Eragrostis setifolia*) and box grass (*Paspalidium constrictum*) interspersed among clumps of trees and shrubs. There is minor crop and pasture cover (48 km^2 - 16%) and the remaining areas are lakes and barren ground cover (55 km^2 - 19%).

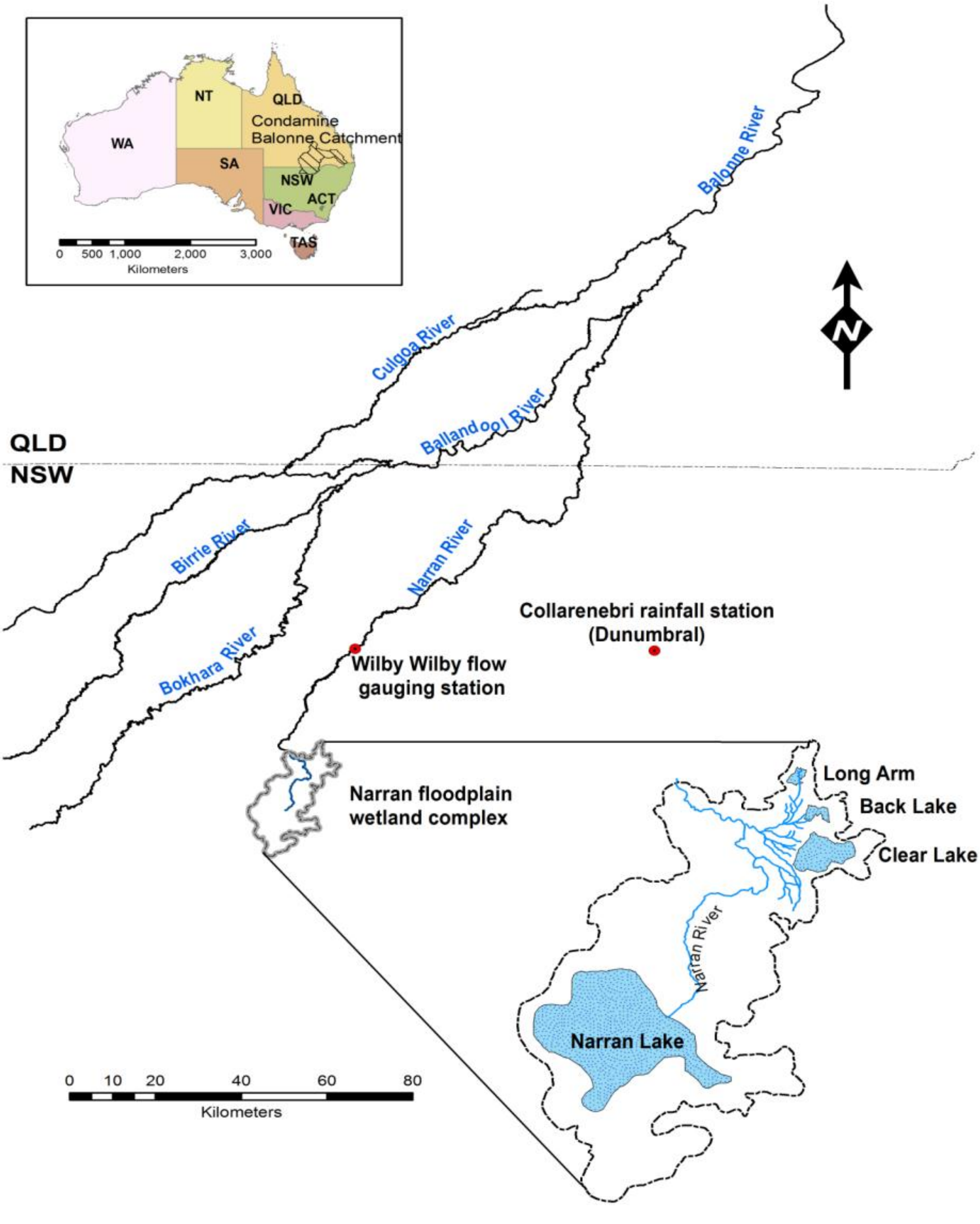

Figure 5.1. Location of the Narran floodplain within the lower reaches of the Condamine-Balonne River catchment.

5.3. Methods

5.3.1 Satellite image selection

We used remotely sensed satellite images to track the productivity of vegetation through a dry resource state (DRS) and a wet resource state (WRS) within the Narran floodplain. A three-step process was used to obtain satellite images for analysis of vegetation productivity. First, DRS and WRS were defined. A DRS is a period of no flow or flow below the long-term 95th percentile flow, combined with below average rainfall. In a DRS, there is no moisture subsidy to the floodplain through flooding or rainfall. There is no groundwater influence as regional groundwater levels are more than 100 m below the floodplain surface (Fitzpatrick *et al*. 2005). A WRS was defined as flow periods above 13,000 MLD in the Narran River at Wilby Wilby; that flow required to initiate floodplain inundation (Rayburg andThoms 2009).

Second, we searched flow and rainfall records for conditions matching our definition of dry and wet resource states. Daily Narran River flow data (January 1980 – December 2009) were acquired at Wilby Wilby gauge. Daily rainfall data for the same period were obtained for the area. Monthly discharge and rainfall means were calculated and each month in the record was then delineated as being above or below average or as having no flow or rainfall. Periods fitting the DRS and WRS definitions were then identified in the flow and rainfall record.

Third, we examined the availability of monthly Landsat imagery corresponding to the DRS and WRS periods using the Geoscience Australia ACRES and USGS catalogues. The Narran floodplain is encompassed in one Landsat scene (Path 92, Row 81). Care was taken to select high quality images with no or minimum cloud cover. From the pool of high-quality satellite images we randomly selected 2002 as the DRS and 2004 as the WRS. A total of 23 images, at approximately monthly intervals were selected for this study.

The WRS images were also processed in ERDAS imagine software to delineate the expansion and contraction of floodwaters across the floodplain. To map the extent of inundation, pixels representing water and non-water were identified by performing density slicing, which used threshold reflectance values recommended by Overton (2005). In a number of images the detection of inundated pixels was not possible using a single band because of the presence of a dense vegetation canopy. For those images we used the moisture related index (Normalised Difference Water Index) of Xu (2006) and an unsupervised classification method to differentiate the inundated and non-inundated pixels. Both methods have been successfully used to map inundation across Australian floodplains using Landsat satellite imagery (Frazier and Page 2000, Shaikh *et al.* 2001, Rayburg and Thoms 2009, Thomas *et al.* 2010). The results from both methods were then combined to map the expansion and contraction of floodwater across the Narran floodplain and to calculate the area of inundation in each image.

5.3.2 Calculation of the Normalized Difference Vegetation Index

Vegetation productivity was tracked through the DRS and WRS at approximately monthly intervals for approximately one year (Table 5.1). Images were re-sampled to 25-m resolution and re-projected to the Geodetic Datum of Australia 1994 Universal Transverse Mercator zone 55S, to ensure images from different sources (i.e. from the Geoscience Australia and USGS catalogues) were of the same resolution. The aligned image digital numbers were converted to top of atmosphere reflectance using the methods of Chander *et al.* (2009). A relative radiometric normalisation was performed using dark and light targets to make images acquired on different dates comparable (Myeong *et al.* 2006). The Normalized Difference Vegetation Index (NDVI) was calculated in each image as NDVI = $\rho nir - \rho red / \rho nir + \rho red$, where ρ is the spectral reflectance values of spectral bands nir (band 4) and red (band 3) of Landsat TM/ETM+ Images. The NDVI measures vegetation greenness and is a surrogate for vegetation productivity (Farina 2006, Lillesand and Kiefer 2000, Wen *et al.* 2012). Entropy analysis, a non-parametric clustering technique, was performed on the 473,142 NDVI pixel values to determine the minimum number of NDVI groups accounting for the greatest variance in the data set. In addition, a moving window analysis was undertaken to identify breaks in the distribution of NDVI values, following the methods of Parsons and Thoms (2013). Six NDVI classes emerged from the range of NDVI values of < 0 to 0.792. Group 1 is no greenness (NDVI <0). Group 2 (NDVI 0-0.072), Group 3 (NDVI 0.072 – 0.207), Group 4 (NDVI 0.207-0.459), Group 5 NDVI (0.459-0.666) and Group 6 (NDVI > 0.666) represent a continuum of increasing vegetation greenness.

Table 5.1 Satellite images comprising the dry and wet resource states, with corresponding hydrology, rainfall and temperature conditions. A period refers to the comparison of two images, where the comparison of image 1 and 2 becomes period 1.

Date of image	Image number	Period	Total flow (ML)	Total monthly rainfall (mm)	Mean monthly maximum temperature (°C)
Dry resource state					
20-01-2002	1		0	0	37.0
05-02-2002	2	1	0	30.0	34.2
09-03-2002	3	2	0	4.0	33.3
10-04-2002	4	3	0	34.0	29.8
28-05-2002	5	4	997	0	23.3
29-06-2002	6	5	6	17	20.0
15-07-2002	7	6	0	0	20.4
16-08-2002	8	7	0	12.0	22.5
17-09-2002	9	8	0	19.0	26.2
19-10-2002	10	9	0	7.0	31.3
04-11-2002	11	10	0	6.0	36.7
06-12-2002	12	11	0	15.0	35.5
Wet resource state					
18-01-2004	13		8679	104.0	35.6
03-02-2004	14	12	18199	26.0	36.1
19-02-2004	15	13	18199	123.0	36.1
23-04-2004	16	14	407	27.0	29.1
09-05-2004	17	15	0.44	25.0	21.6
10-06-2004	18	16	0	10.0	19.7
12-07-2004	19	17	0	31.0	17.9
14-09-2004	20	18	0	19.0	24.9
16-10-2004	21	19	0	15.0	30.2
17-11-2004	22	20	0	108.0	32.0
19-12-2004	23	21	1115	107.0	33.1

5.3.3 Analysis of vegetation productivity

The area of floodplain in each NDVI class was calculated for each image in the DRS and WRS. NDVI Class 1 was excluded because this area has no greenness and corresponds to water bodies and bare land. To examine change in productivity, pair-wise transitions between NDVI classes in sequential monthly images were calculated on a pixel-by-pixel basis. Each pixel was classified into a change class (C_{ij}) which represents a change from NDVI class *i* to NDVI class *j*. A total of 36 C_{ij} were possible among the six NDVI classes, including six constant classes, and 30 directional change classes. The total area of floodplain that increased or decreased in NDVI class between sequential images (termed a period) was calculated. First-order Markovian transition models (Weng 2002, Bolliger *et al.* 2009) were used to model the area, number, direction and probability of change of NDVI classes between sequential images. The Markovian transition model consists of the area of each NDVI change class (C_{ij}) present in each period and the probability (P_{ij}) of each C_{ij} occurring. The number of transitions and the direction (single or two-way) of transitions between NDVI classes were tallied from a pictorial representation of the Markovian transition model. Probability of change (P_{ij}) was calculated as the proportions of the total area of NDVI class i that transitioned to NDVI class j.

The diversity of NDVI classes in each image was calculated using the Shannon-Wiener diversity index, as recommended by Magurran (1988) for large and continuous datasets. In calculating diversity, monthly images are considered as samples, NDVI classes as species, and NDVI area as abundance.

Change in vegetation productivity over time was examined in relation to floodplain inundation. Vegetation productivity measures from each image (NDVI class area, number of transitions, direction of transitions, probability of transitions and diversity of NDVI class area) were plotted against the corresponding area of floodplain inundation in order to explore the existence of hysteresis loops. The direction of the loop, location of change in loop direction and steepness of the loop were assessed from each plot. Hysteresis-driven systems will have multiple transitions over time, a bimodal distribution, and change in a loop pattern in response to driving parameters (Schröder *et al.* 2005).

5.4. Results

5.4.1 Floodplain inundation in the dry resource state and wet resource state

The availability of water as a resource differed markedly between the dry and wet floodplain states. Surface water was not visible on the floodplain during the DRS (Figure 5.2). Flow in the Narran River resulted in floodplain inundation of up to 35 km^2 during the WRS and corresponded to a pattern of expansion and contraction of floodwater (Figure 5.2). The initial rapid expansion of floodwaters across the floodplain (images 13 to 14) was followed by a phase of high floodplain inundation (images 15 to 18) (Figure 5.2). The phase between image 19 and 20 was associated with an initial rapid contraction of floodwaters and decrease in area of inundation, followed by gradual contraction of floodwater through images 20 to 23 (Figure 5.2). Thus, the WRS is not uniform but is made up of three distinct phases of inundation: wetting, wet and drying (Figure 5.2). The DRS is uniform and comprises a dry phase only. From here forward we report aspects of floodplain vegetation productivity in relation to these four phases.

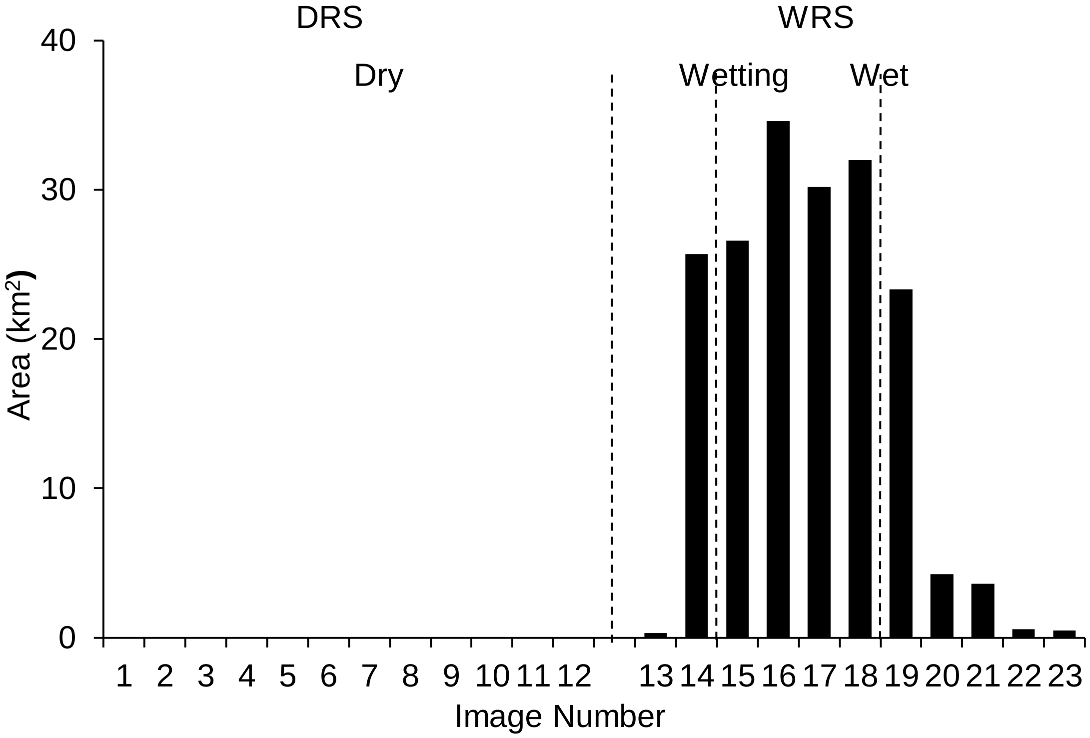

Figure 5.2 Area of floodplain inundation during the dry resource states (DRS) and wet resource states (WRS). The WRS is further divided into wetting, wet and drying phases. Image numbers are explained in Table 5.1

5.4.2 Vegetation productivity

The area of floodplain associated with vegetation vigour (i.e. NDVI Classes 2-6) was greater during the dry phase (mean area of NDVI Classes 2-6 across the dry phase = 98 km^2; range = 0.71 km^2 - 285 km^2) than the wetting, wet and drying phases combined (mean of NDVI Classes 2-6 across the wetting, wet and drying phases = 55 km^2; range = 0.004 km^2 - 171 km^2). However, the quality of vegetation vigour differed between phases. In the dry phase, NDVI Class 3 was consistently dominant in area (Figure 5.3). NDVI Classes 2, 3 and 4 were also present during the dry phase (Figure 5.3). In the wetting, wet and drying phases the dominant NDVI class was not consistent (Figure 5.3). In the first image of the wetting phase NDVI Class 2 was dominant but NDVI Class 3 was dominant in the remainder of the wetting phase (Figure 5.3). NDVI Classes 2, 3, 4 and 5 were present during the wetting phase (Figure 5.3). In first two images of the wet phase NDVI Class 3 was dominant but NDVI Class 4 dominated the third image and NDVI Class 3 dominated the fourth image (Figure 5.3). All NDVI classes were present during the wet phase (Figure 5.3). In the drying phase, images 19 and 20 were dominated by NDVI Class 3, then by NDVI Class 2 through the remainder of the drying phase (Figure 5.3). NDVI Classes 2, 3, 4 and 5 were present during the entire drying phase (Figure 5.3). Thus, the area of floodplain with vegetation vigour was higher in the dry phase than in the wetting, wet and drying phases. However, vegetation vigour was of higher quality in the wetting, wet and drying phases, with very high vegetation vigour (NDVI Class 6) only present during the wet phase.

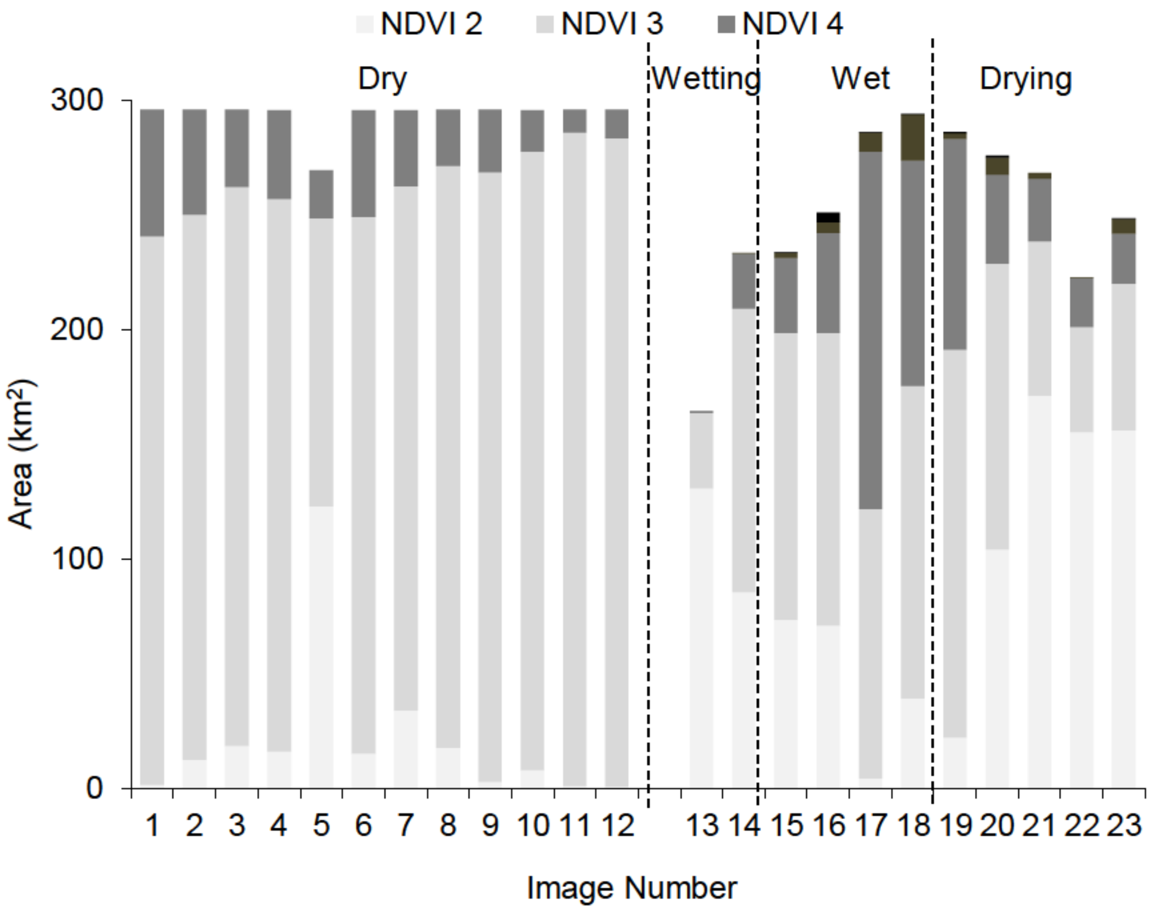

Figure 5.3. Area of NDVI Classes 2-6 in the Narran floodplain in the dry, wetting, wet and drying phases of inundation. NDVI Class 1 is not shown because it represents bare ground or water. Image numbers are explained in Table 5.1.

5.4.3 Vegetation productivity change

The area and broad direction of change (increase or decrease) between the six NDVI classes differed between the flood and dry phases. The area of floodplain that changed NDVI class between consecutive monthly images (henceforth called a period) was greater in the wetting, wet and drying phases than the dry phase (Figure 5.4). However, in all phases the area of change is made up of increases and decreases in NDVI class, indicating variability in vegetation productivity. In the wetting phase, an average 143 km^2 of floodplain area changed NDVI class each month and most of this change (82%) came from increasing NDVI class (Figure 5.4). In the wet phase, an average 151 km^2 changed NDVI class and most of this change (63%) came from increasing NDVI class (Figure 5.4). In the drying phase, an average 131 km^2 changed NDVI class and most of this change (74%) came from decreasing NDVI class (Figure 5.4). This contrasts with the dry phase, where an average of 53 km^2 changed NDVI class each month, about half (54%) of which was from decreasing NDVI class and about half (46%) from increasing NDVI class. However, the marked increase and decrease in

NDVI during periods 4 and 5 is an apparent anomaly, associated with a small pulse of water along the Narran River (Table 5.1).

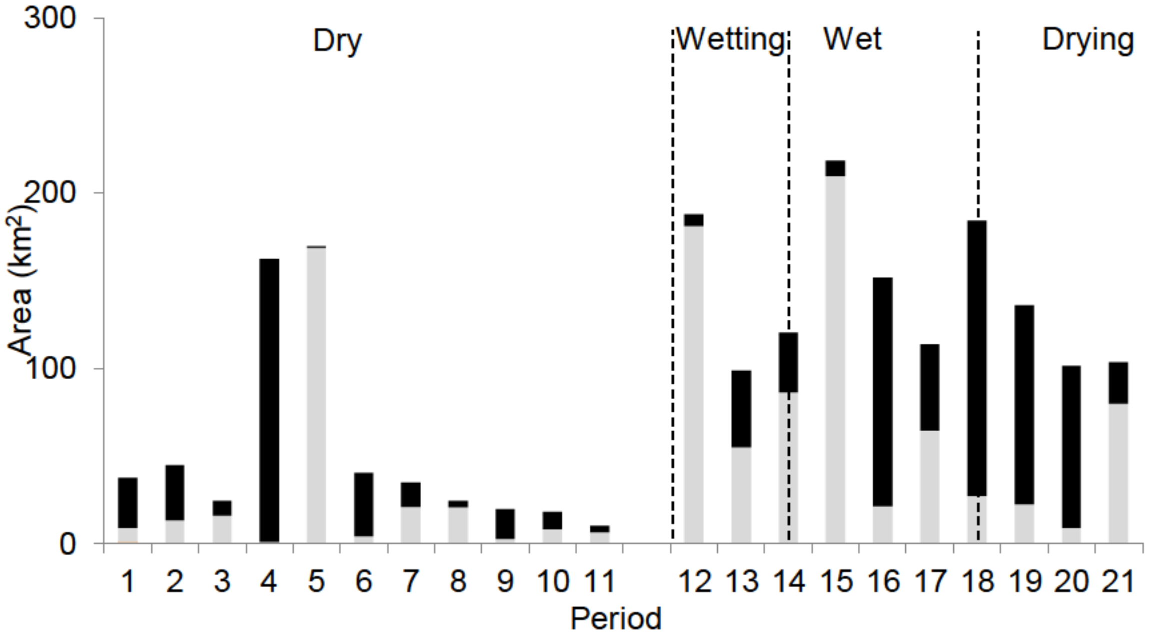

Figure 5.4 Area of floodplain change among six NDVI classes for the dry, wetting, wet and drying phases of inundation. Floodplain change is divided into the area that increased or decreased in NDVI class between consecutive images. Periods are explained in Table 5.1

The Markovian transition models demonstrate marked complexity in the area, number, direction and probability of transitions between NDVI classes in the flood and dry phases. The area of an NDVI class was more stable in the dry phase than the wetting, wet and drying phases (Figure 5.5). Across all periods of the dry phase an average 242 km^2 of the 296 km^2 floodplain area was concentrated in NDVI Class 3 (Figure 5.5a). In contrast, in the wetting, wet and drying phases floodplain area was spread across all NDVI classes (Figure 5.5b). The number of transitions among NDVI classes differed markedly among the flood and dry phases. Overall, there were 81 transitions among NDVI classes in the dry phase (average: 7 transitions, range: 4 to 11 transitions; Figure 5.5a) and 225 transitions in the wetting, wet and drying phases combined (average: 22 transitions, range 16 to 27 transitions; Figure 5.5b), indicating that change among NDVI classes is greater when the floodplain is wet than when it is dry. Within a flood, the greatest number of transitions occurred in the wet phase (average: 25 transitions range 24 to 27 transitions; Figure 5.5b). The drying phase had a moderate number of transitions (average: 22 transitions, range 16 to 28 transitions; Figure 5.5b), and the wetting phase had a lower number of transitions (average: 19 transitions, range 16 to 21 transitions; Figure 5.5b). Of the 30 possible directional transitions 11 transitions occurred in the dry phase, 21 in the wetting phase, 28 in the wet phase and 23 in the drying phase. The wet phase had the most transitions, with 28 of the 30 directional transitions occurring during maximum inundation.

The direction of transitions between NDVI classes also differed among the four phases. Single and two-way transitions between the NDVI classes occurred in all phases, but the ratio of single to two-way transitions was higher in the dry phase than the wetting, wet and drying phases combined. The average ratio of single to two-way transitions was 1.25 in the dry phase compared to 0.33 for the wetting, wet and drying phases combined. Thus, the dry phase is dominated by single direction transitions among NDVI classes while the wetting, wet and drying phases are dominated by two-way transitions. In the dry phase, single direction transitions were largely to or from NDVI Classes 1, 2 and 3 (Figure 5.5a). In the wetting, wet and drying phases, transitions were two-way among all NDVI classes (Figure 5.5b). For example in period 18 of the wet phase, there were four or more changes from or to each NDVI class (Figure 5.5b).

The probability of transitions between NDVI classes also differed between the dry and flood phases. The distribution of transition probabilities in the dry phase was platykurtic (Figure 5.6). Change between NDVI classes was dominated by low (< 1 %) and high (>50 %) probability transitions (Figure 5.5a and Figure 5.6). In the combined wetting, wet and drying phases the distribution of transition probabilities was bimodal (Figure 5.6). There was a dominant peak at the <1 % probability class (Figure 5b and Figure 5.6) indicating that most of the transitions that occurred between NDVI classes in the wetting, wet and drying phases were low probability transitions. However, transitions were spread across all probabilities and a secondary peak occurred in the 20-50 % probability class (Figure 5.6).

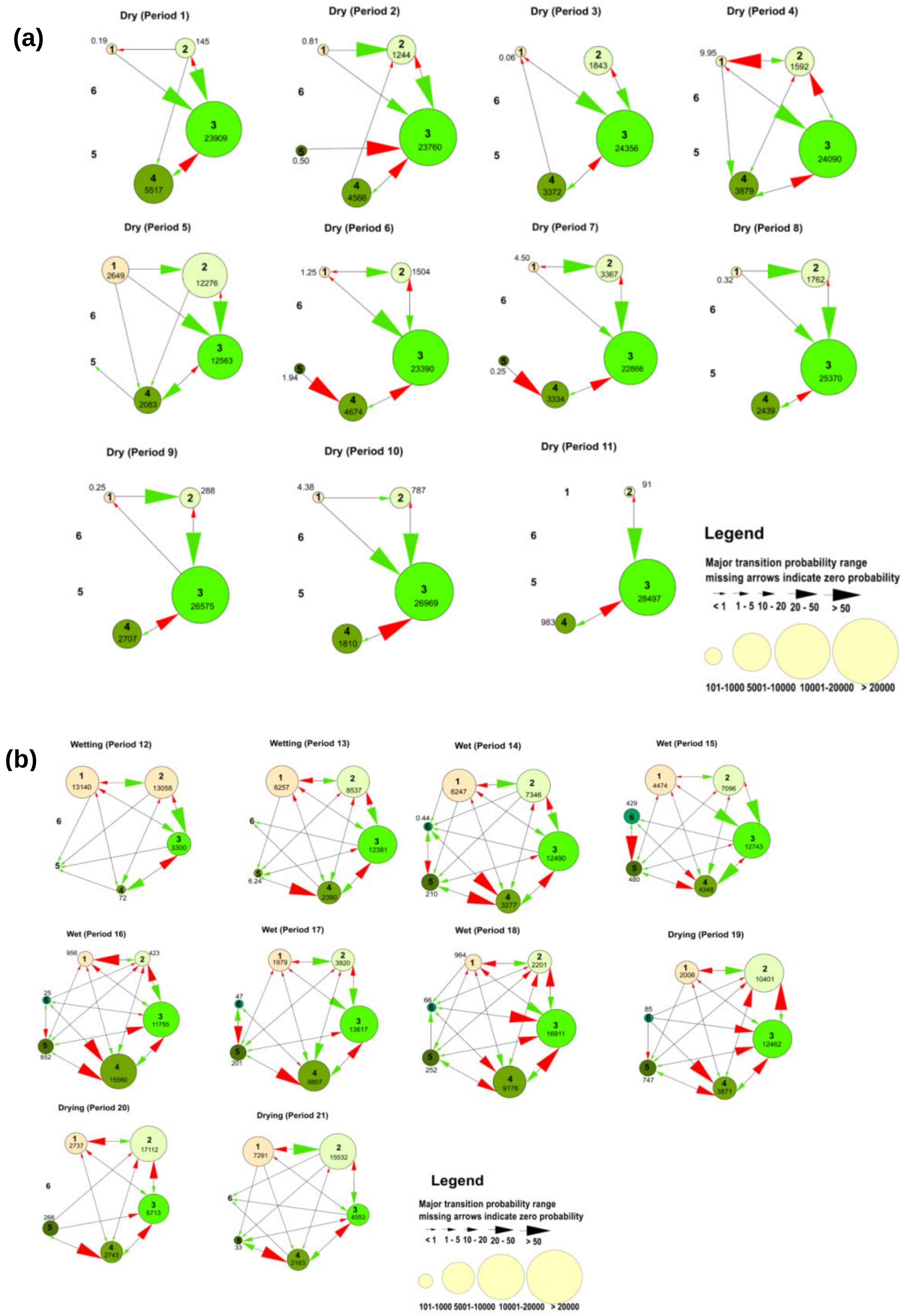

Figure 5.5 Markovian transition models of change between NDVI classes 1-6 in the dry (a) and wetting, wet and drying (b) phases of floodplain inundation. The area of floodplain in each NDVI class is shown by different sized circles, and labelled with area (ha). Arrows identify the changes between NDVI classes, where red arrows indicate decrease green arrows indicate increase in NDVI classes. The size of the arrowhead indicates the probability of change among NDVI classes. Periods are explained in Table 5.1.

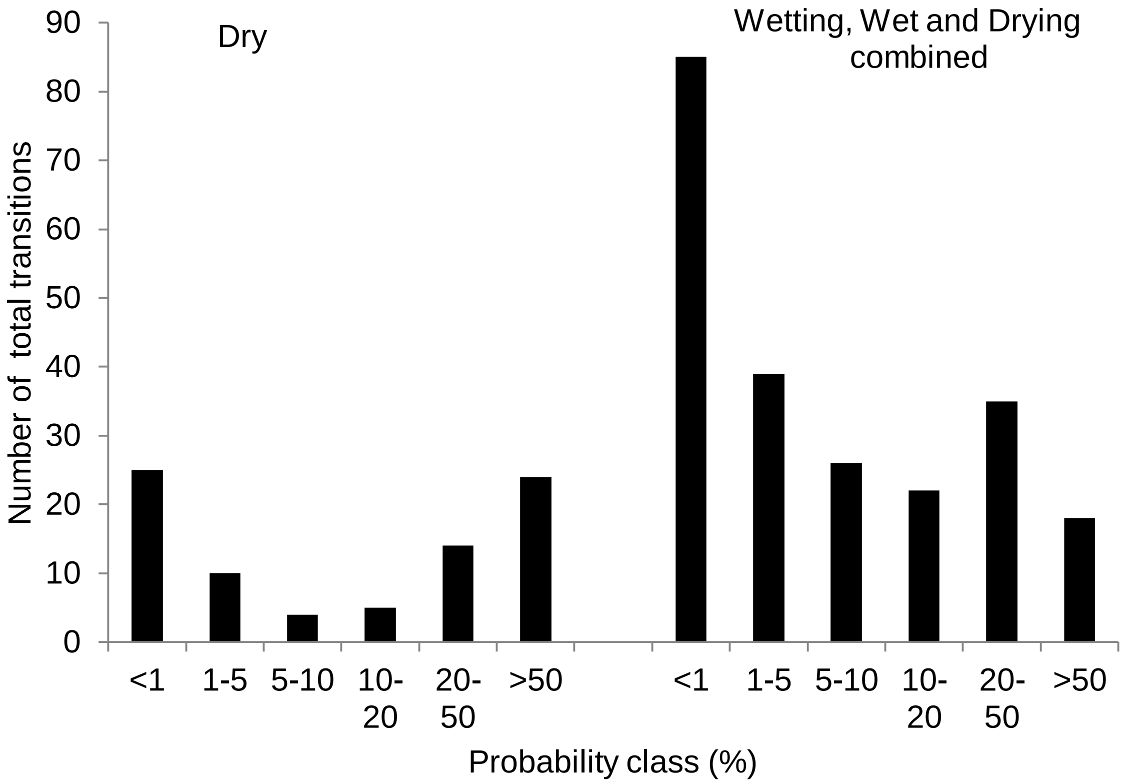

Figure 5.6 Distribution of the probability of transitions between all NDVI classes in the dry and combined wetting, wet and drying phases of flood inundation. Probability transitions were tallied from the Markovian transition models shown in Figure 5.5.

5.4.4 Diversity of vegetation productivity

The diversity of NDVI class area was generally higher in the wetting, wet and drying phases than the dry phase (Figure 5.7). The dynamism of transitions is expressed in the behavior of the Shannon-Wiener diversity index during each phase. In the dry phase, diversity was relatively stable (mean: 0.56; range 0.51-1.13) until image 7 when diversity declined markedly, reaching a minimum of 0.2 in image 11 (Figure 5.7). In contrast, diversity increased during the wetting phase, varying between 0.98 and 1.40 in the wet phase and then dropping slightly to average 1.16 through the drying phase (Figure 5.7).

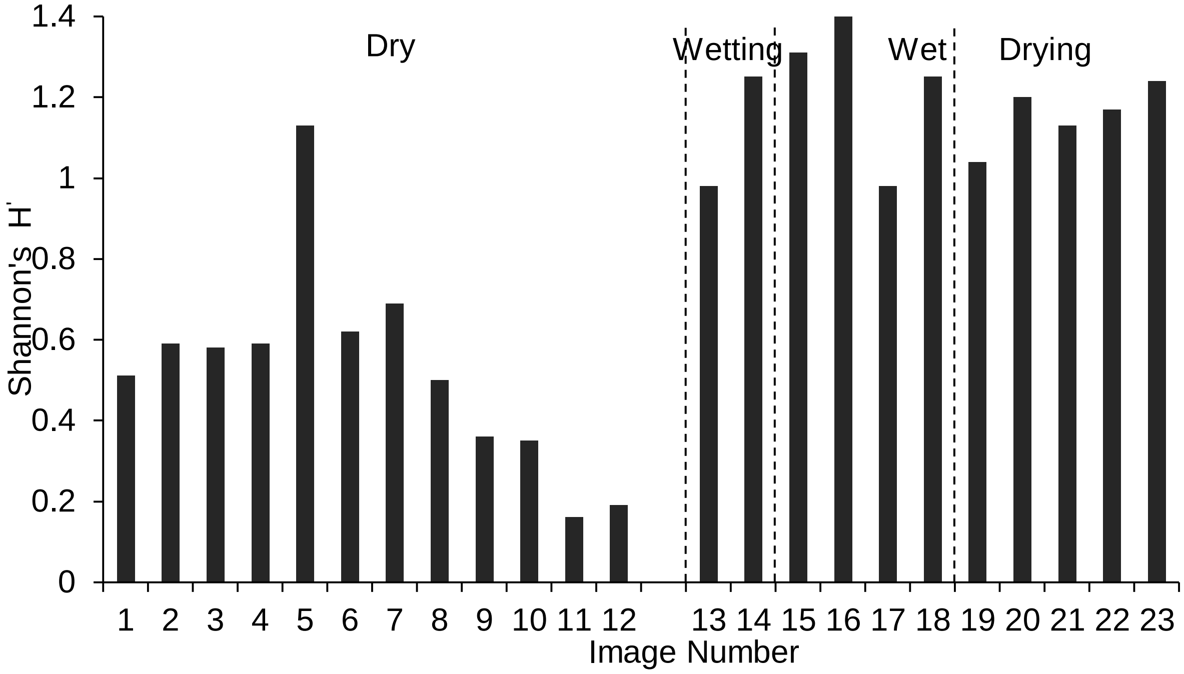

Figure 5.7 Shannon-Wiener Diversity Index of change in NDVI classes 2-6 for the dry, wetting, wet and drying phases. Images are explained in Table 5.1.**Figure 5.7. Shannon-Wiener Diversity Index of change in NDVI classes 2-6 for the dry, wetting, wet and drying phases. Images are explained in Table 5.1.**

5.4.5 Cyclic change of vegetation productivity in relation to floodplain inundation

A distinct loop is evident in all vegetation productivity measures in relation to the surface area of floodplain inundation (Figure 5.8; Table 5.2). Overall, anti-clockwise hysteresis was the dominant form of hysteresis, although several vegetation productivity measures (change in NDVI Class 2, single direction transitions, probability of transition 1-5 % and diversity) demonstrated clockwise hysteresis (Table 5.2). All vegetation productivity measures demonstrated a switch in direction during the wet phase: a switch of direction was not observed in any other phase (Table 5.2). The switch during the wet phase was flat for most vegetation productivity measures, but the higher NDVI classes (Class 4, 5 and 6), single direction of change and low probability of transition (<1%) had a steep switch (Table 5.2). This indicates that measures of vegetation productivity decline or increase sharply during the wet phase, corresponding to a switch of direction in the hysteretic loop.

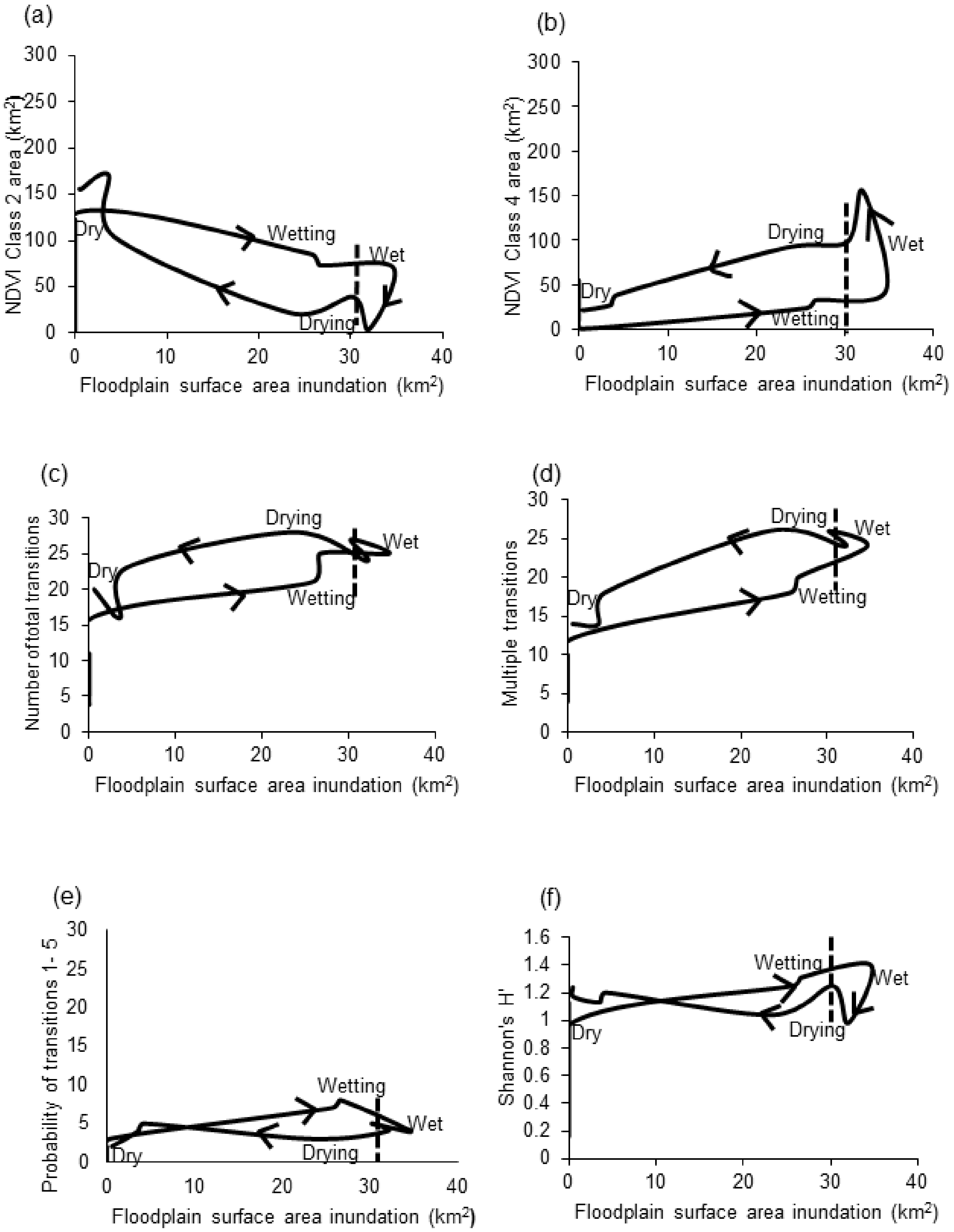

Figure 5.8 Cyclic change in (a) Normalized difference vegetation index (NDVI) Class 2 area, (b) NDVI Class 4 area, (c) total number of transitions, (d) two-way transitions, (e) transition probability 1-5 % and (f) diversity in relation to floodplain inundation. The dry, wetting, wet and drying phases correspond to the phases of floodplain inundation outlined in Figure 5.2.

Table 5.2 Pattern of cyclic change in vegetation productivity measures in response to floodplain inundation. NDVI = Normalised Difference Vegetation Index. For hysteresis direction AC = anti-clockwise and C = clockwise. Example hysteresis loops are given in Figure 5.8.

Response pattern	Vegetation productivity measure														
	Change in NDVI class area					Number of transitions	Direction of transition		Probability of transition						Diversity of change
	NDVI 2	NDVI 3	NDVI 4	NDVI 5	NDVI 6		Single	Multi	<1	1-5	5-10	10-20	20-50	>50	
Hysteresis direction	C	AC	AC	AC	AC	AC	C	AC	AC	C	AC	AC	AC	AC	C
Phase of switch	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet	Wet
Shape of switch	Flat	Flat	Steep	Steep	Steep	Flat	Flat	Steep	Steep	Flat	Flat	Flat	Flat	Flat	Flat

5.5. Discussion

5.5.1 Vegetation productivity responses to wetting and drying

Colloff and Baldwin (2010) framed semi-arid floodplain resilience as a single state characterised by alternate dry and wet conditions. Broadly, our results fit a two-state boom-bust model because of the marked differences in vegetation productivity between the dry and wet resource states. The availability of water on the Narran floodplain, as noted by the area of floodplain inundation, differed between the DRS and WRS. There were marked differences in NDVI class area, number of transitions, direction of transitions, probability of transitions and NDVI class diversity between the dry phase and the combined wetting, wet and drying phases of floodplain inundation. This is related to the presence of water as a primary driver of floodplain vegetation productivity, where the arrival of floodwater stimulates a boom in production (Bunn *et al*. 2006) and may trigger recruitment or seed production (Capon 2007). In contrast, the absence of water is associated with reduced vegetation production (Parsons and Thoms 2013) and plant dormancy (Xu *et al*. 2010).

Division of the imagery into dry, wetting, wet and drying phases of floodplain inundation revealed complexity in vegetation productivity responses to resource availability. Most of the Narran floodplain was associated with low vegetation vigour during the dry phase, but the area and quality of vegetation vigour increased through the wetting and wet phases and decreased through the drying phase (Figure 5.3). None of the phases were stable, and there was always change between NDVI classes within a phase, with the greatest change between NDVI classes occurring in the wet phase (Figure 5.5). The ratio of single to two-way transitions was higher in the dry than the wetting, wet and drying phases combined (Figure 5.6). The dry phase had a platykurtic distribution of transition probabilities whereas the wetting, wet and drying phases had a bimodal distribution (Figure 5.7). These complex responses of vegetation to water availability are not unexpected. In a semi-arid floodplain ecosystem, Wen *et al*. (2012) reported that the interplay of flood size and flow path created a complex inundation pattern over time that was associated with complexity in NDVI response. Likewise, Parsons and Thoms (2013) examined the NDVI of Australian floodplain vegetation in wet, dry and rain resource states and concluded that NDVI values were varied and the spatio-temporal response was complex. Vegetation productivity responses within and between phases of flood inundation in our study suggest that complexity is related to a cycle of floodplain wetting and drying with different components of vegetation productivity responding differently to the availability of water.

In addition to the complexity of vegetation productivity through the dry, wetting, wet and drying phases of floodplain inundation, a distinct hysteretic loop was shown in the relationship between floodplain inundation and productivity (Figure 5.8 and Table 5.2). Hysteresis loops track the path of change in a system in response to external conditions and whether the system returns to its initial state or changes state (Nikanorov and Sukhorukov 2008, Searle *et al.* 2009). Vegetation productivity in the Narran floodplain consistently demonstrated a switch of direction during the wet phase of inundation. Most productivity measures also showed anti-clockwise hysteresis, and a flat trajectory (Table 5.2). Hysteretic patterns have been observed in semi-arid grassland response to grazing (Searle *et al.* 2009). Floodplain research by Murray *et al.* (2006) and Shilpakar (2013) has also reported hysteretic relationships between surface inundation and vegetation patchiness. Hysteresis in vegetation communities occurs when the return path to an original state differs from that taken during the degradation pathway (Searle *et al.* 2009). The pattern of vegetation response to floodplain inundation observed in this study (Figure 5.8) indicates a hysteretic response of productivity to floodplain inundation through the dry, wetting, wet and drying phases.

We propose that this hysteretic pattern of vegetation productivity in response to floodplain inundation resembles an adaptive cycle. Thus, we derived a hypothesised adaptive cycle for the Narran floodplain where floodplain inundation drives vegetation responses through a cycle of exploitation, conservation, release and reorganization phases of an adaptive cycle (Figure 5.9). The adaptive cycle starts as floodwater inundates the floodplain in the wetting phase. The wetting phase corresponds to the exploitation part of the adaptive loop (Figure 5.9), where the area of vegetation productivity and its quality will increase because of the availability of water as an exploitable resource. Observed vegetation productivity responses during the wetting phase in the Narran floodplain were; a change in NDVI quality with NDVI moving from lower to higher classes; an increase in the number and direction of transitions between the different NDVI classes; and, an overall increase in the diversity of change in vegetation productivity (cf. Figures 5.3 and 5.5).

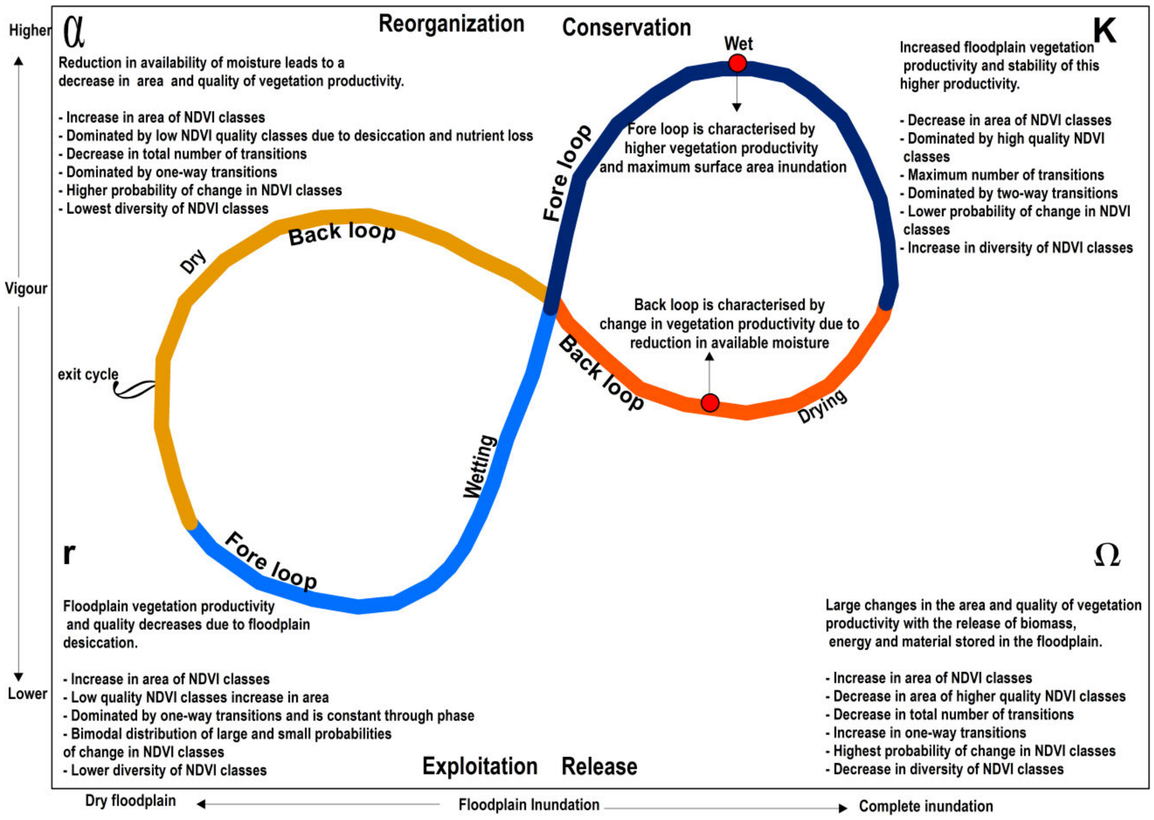

Figure 5.9 The hypothesised adaptive cycle model of the Narran floodplain based on hydrology and vegetation productivity.

The wet phase is the phase of maximum floodplain inundation and corresponds to the conservation phase of the adaptive loop (Figure 5.9). The conservation phase is a period of increased vegetation productivity and stability of this productivity. Through the conservation phase vegetation biomass builds to its maximum because of ample water availability. During the wet phase vegetation productivity in the Narran floodplain was observed to be lower in terms of the area of vegetation productivity but higher in quality with a greater number of two-way directional transitions between NDVI classes (Figures 5.3 and 5.5). The wet or conservation phase was associated with an increase in vegetation productivity but lower stability.

The contraction of floodwater triggers the drying phase and corresponds to the release phase of an adaptive cycle (Figure 5.9). The release phase is an expected period of enhanced change triggered by internal or external agents of disturbances such as drought, fire or disease (Holling and Gunderson 2002). This phase initiates when tightly bound resources in vegetation and soil are released from the conservation phase and become a source for reorganization and renewal (Holling and Gunderson 2002). During the drying phase in the Narran floodplain vegetation productivity was observed to decrease in area but the quality increased, as did the probability of change in vegetation productivity, the number of singular transitions and the overall diversity of NDVI class changes (Figures 5.3 and 5.5).

Further desiccation of the floodplain occurs with the draining of floodwaters until the floodplain reaches a dry phase; a phase of no surface water availability. The dry phase corresponds to the reorganization phase of the adaptive cycle. Reorganization is a critical phase of the adaptive cycle as it is during this phase that vegetation may reorganise into the same state as existed prior to the onset of wetting or the community may move to a new state in which case it is considered to have entered an “exit cycle” (Figure 5.9) (Holling and Gunderson 2002, Scheffer and Carpenter 2003). A decrease in the area of vegetation productivity and quality was expected in response to floodplain desiccation. However, during the dry phase in the Narran floodplain, the area of vegetation productivity increased but its quality declined. In addition decreases in two-way directions of change and diversity of change were observed (Figures 5.3 and 5.5) suggesting a period of stability (Figure 5.9).

The fore and back loops are key features of an adaptive cycle (Holling and Gunderson 2002). The fore loop involves the exploitation to conservation phase of the adaptive loop and is characterized by stability and conservation (Holling and Gunderson 2002, Walker and Salt 2006, Walker and Salt 2012). The back loop involves the release to reorganization phase and is characterized by uncertainty, novelty and experimentation (Holling and Gunderson 2002, Walker and Salt 2006, Walker and Salt 2012). In our adaptive cycle of the Narran floodplain the fore loop is the wetting and wet phases between the exploitation and conservation phases. The fore loop in the Narran floodplain is characterised by higher vegetation productivity because of the availability of surface water. The back loop is the drying and dry phase between the release and reorganization phases, characterised in the Narran floodplain by change in vegetation productivity because of the withdrawal of energy and material associated with inundation. This arrangement of flooding as the fore loop and drying as the back loop of the adaptive cycle contrasts with the relatively simple single state model proposed by Colloff and Baldwin (2010) with the floodplain switching between the release (wet) and conservation (dry) phases only. Our results suggest greater complexity in the cycle of floodplain wetting and drying. The model of Colloff and Baldwin (2010) is not based on data but relies on their experience of floodplain soil carbon response in systems where the flow regime is highly regulated by dams and where floodplain inundation is more tightly coupled with managed flow releases. Riverine landscapes subject to highly variable and unpredictable flow regimes frequently display complex responses because of this variability cf. Thoms (2006). The Narran floodplain is a semi-arid system that experiences highly variable and unpredictable flow regimes (Thoms 2003); the ecosystem response to which resembles an adaptive cycle.

The other key feature of an adaptive cycle is the change in the stability, or crossing of a threshold, where the system will flip in to a different regime while transitioning between the reorganization and exploitation phase (Scheffer and Carpenter 2003). In our hypothesised floodplain adaptive cycle model we propose that such a flip may occur in the back loop transitioning between reorganization and exploitation phase or the dry phase of the floodplain adaptive cycle (Figure 5.9).

5.6. Conclusion

Despite the widespread acceptance of the theory of social-ecological resilience (Walker and Salt 2012), there remains a relative paucity of empirical observations on one important component of resilience theory: the movement of systems through an adaptive cycle. Adaptive cycles of release and renewal have been proposed in economic systems, organizations, ecosystems and social systems (Allison and Hobbs 2004, Burkhard *et al*. 2011, Dearing 2008,Walker and Salt 2012). Our data suggests that adaptive cycles occur in semi-arid floodplain ecosystems in response to floodplain inundation. Adaptive cycles are a useful concept for understanding the complexity of semi-arid floodplain ecosystem responses to inundation. Maintaining the natural variability of floodplain inundation is a key ecological management issue because variability in the wetting and drying of semi-arid floodplains maintains their resilience (Colloff and Baldwin 2010, Baldwin *et al*. 2013). However, change in climate and land and water resource development activities has reduced the natural variability of floodplain inundation and may worsen in the future (Thoms and Sheldon 2000, Erwin 2009). Adaptive cycles make us more cognizant of the importance of transitions, dominance of the different phases, and the frequency of the individual transitions driving ecosystem change. Knowledge of the phases of vegetation response around an adaptive cycle will enable better management of floodplains because management activities can be tailored to specific phases or used to push vegetation through different phases (Colloff and Baldwin 2010, Walker and Salt 2012).

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	Author's Name (please print clearly)	% of contribution
Candidate	Rajesh Thapa	80 %
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29/06/2015

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Chapter 6 Adaptive cycles of floodplain vegetation response to flooding and drying

Abstract

Flooding is a key driver of floodplain vegetation productivity. Adaptive cycles provide a model for examining the productivity of semi-arid floodplain vegetation in response to hydrology. We examined the response of vegetation productivity (measured as NDVI) through a hypothesized adaptive cycle to determine if the cycle repeats over time and how it is affected by different sized flood events. The area of floodplain inundation was associated with an adaptive cycle that repeated in four flood events through phases of wetting (exploitation phase), wet (conservation phase), drying (release phase) and dry (reorganisation phase). Vegetation productivity responses corresponded to these phases. The area and quality of floodplain vegetation productivity followed the hypothesised pattern of higher quality vegetation vigour in the wetting and wet phases, lower vigour in the drying phase and lowest vigour in the dry phase. There were more transitions between NDVI classes in the wet phase, which was dominated by two-way transitions. Overall, the wetting, wet and drying phases were dominated by smaller probability class changes, whereas in the dry phase higher probability class changes were more prominent. Although the four flood events exhibited an adaptive cycle the duration of the adaptive cycle phases, and the nature of vegetation productivity response, differed with the character of the flood event. Vegetation response in two of the adaptive cycle phases - the release and reorganisation phases - were as hypothesised, but in the exploitation and conservation phases changes in vegetation productivity were more dynamic. The character of vegetation response through the adaptive cycle also indicates that semi-arid floodplain vegetation productivity is more vulnerable to changing state during the conservation and release phases and not during the exploitation and reorganisation phases as resilience theory suggests. Overall, the adaptive cycle represents a new model to improve our understanding of the complexity of change in semi-arid floodplain vegetation productivity through cycles of flooding and drying.

Keywords: NDVI, floodplains, resilience, adaptive cycles, riparian vegetation

6.1. Introduction

Ecosystems are complex adaptive systems characterized by multiple stable states, nonlinear dynamics, fast and slow drivers and self-emergence (Holling 1973, Holling and Gunderson 2002, Folke *et al*. 2010). These characteristics influence structure and function and as a result, change is a fundamental feature of ecosystems (Chapin *et al*. 2012). Resilience theory proposes that change in ecosystems can be viewed as an adaptive cycle with four phases - exploitation, conservation, release and reorganisation - that occur in sequence as a result of external influences and internal system dynamics (Holling and Gunderson 2002). The exploitation phase (r phase) occurs early in the adaptive cycle and follows a previous disturbance. In this phase, elements of the system are engaged in rapid growth to exploit available resources (Walker and Salt 2006). Through the conservation phase (K phase) biomass gradually builds and energy and materials accumulate in the system (Holling and Gunderson 2002). The release phase (Ω phase) is triggered by internal or external disturbances (Holling and Gunderson 2002). In the release phase, biomass, energy and materials stored in the system are released, becoming available as the template for the reorganization phase. In the reorganization phase (α phase) the system reorganizes into the same state or may become vulnerable to flipping into a new state, which is likely to be organized differently and less productive (Holling and Gunderson 2002). If the system does not flip into a new state it moves back into the exploitation phase where a new cycle begins.

Semi-arid floodplains are ecosystems characterised by long periods of no or limited surface water interspersed by periods of floodplain inundation (Thoms 2003). Flooding is a primary driver of floodplain productivity that can stimulate a rapid increase in vegetation productivity that may be maintained for months across large areas of floodplain (Capon 2003, Reid *et al*. 2011, Parsons and Thoms 2013). The productivity of floodplain vegetation in response to flooding has been hypothesised to be more complex than a simple boom-bust model and follow an adaptive cycle of exploitation, conservation, release and reorganisation (Thapa *et al*. 2015b). There are two interacting elements of this hypothesised floodplain adaptive cycle (Figure 6.1). The first describes the progression of flooding as the key driver of floodplain vegetation productivity through the adaptive cycle. The second describes the progression of vegetation productivity response to the driver through the phases of the adaptive cycle. Thus, the adaptive cycle hypothesis proposes that floodplain ecosystem change is characterized by the relationship between the availability of floodplain surface water and vegetation productivity.

The hypothesis of Thapa *et al*. (2015b) describes change in semi-arid floodplain vegetation productivity through an adaptive cycle with four phases: wetting, wet, drying and dry. The wetting and wet phases (exploitation to conservation), where the floodplain is wetting towards maximum inundation, is a period of enhanced vegetation productivity (Figure 6.1). With maximum inundation, vegetation productivity is expected to decrease in total area, but be higher in quality and stable in these aspects across the floodplain (Figure 6.1). During the drying phase (release), surface water inundation contracts and the floodplain commences drying (Figure 6.1). Vegetation productivity is expected to not only decrease in area and quality in this phase but also have a higher probability of change in the area and quality of vegetation productivity because of the release of biomass, energy and material stored in the floodplain (Figure 6.1). As the floodplain surface dries further, vegetation productivity moves into the dry phase (reorganization), with vegetation productivity expected to decline even further in area and quality (Figure 6.1). Some vegetation communities with access to remaining moisture may thrive in this phase, however, as the floodplain becomes desiccated during the dry phase, floodplain vegetation productivity is expected to be lower in area and quality and unstable. The highest likelihood of change to a new state should occur during the movement from the reorganization to the exploitation phase (Holling and Gunderson 2002). In the dry phase, floodplain vegetation may reorganise into the same state ready to begin a new cycle when flooding occurs or exit the cycle to flip into a different state (Figure 6.1). Overall, the fore loop of the adaptive cycle (exploitation to conservation) is characterised by higher vegetation productivity and the back loop (release to reorganization) is characterised by greater change in vegetation productivity because of the release of biomass and energy stored in the floodplain. In moving between the phases of the adaptive cycle the area of floodplain inundated varies from low to high (Figure 6.1, x axis), which corresponds to connectedness of the system through an adaptive cycle. Vigour varies from low to high (Figure 6.1, y axis), which relates to the potential of the system through an adaptive cycle. Systems with low potential and low connectedness will have higher resilience and vice versa (Holling and Gunderson 2002).

The hypothesis proposed by Thapa *et al*. (2015b) is derived from observations of floodplain vegetation productivity through only one cycle of flooding and drying. However, unanswered questions remain about the efficacy of adaptive cycles for characterizing floodplain vegetation productivity in response to different flooding and drying events. Floods, and therefore the character of floodplain inundation, differ in magnitude, timing, duration and spatial pattern of inundation (Murray *et al*. 2006, Thoms and Parsons 2011). As these factors influence vegetation productivity responses (Capon 2003, Parsons and Thoms 2013) the passage of vegetation productivity around an adaptive cycle in response to flooding and drying might not occur in all floods, making the application of adaptive cycles untenable. This study examines adaptive cycles of floodplain vegetation in response to four flood events to determine if an adaptive cycle repeats and how it is influenced by different-sized flood events.

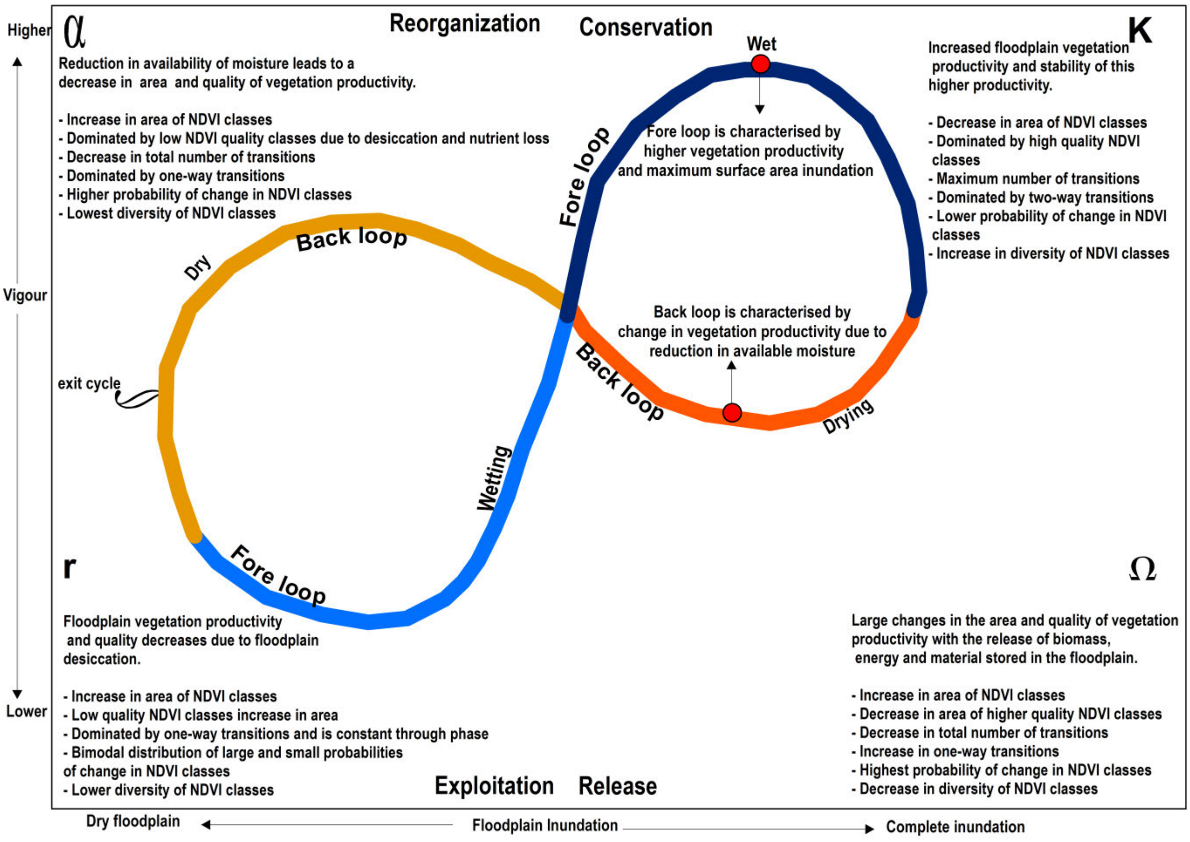

Figure 6.1 The hypothesised adaptive cycle model of vegetation productivity response to hydrology in semi-arid floodplains. The adaptive cycle starts as floodwater inundates the floodplain in the wetting (exploitation phase), the wet (conservation phase) is the phase of maximum inundation, the drying (release phase) starts with the contraction of floodwater, the dry (reorganisation phase) occurs with desiccation of floodplain. The adaptive cycle reflects changes in the two properties: i) floodplain connectedness, which ranges from a totally dry to complete inundation of the floodplain along the x-axis, and; ii) vegetation productivity, ranging from low to high vegetation vigour along the y-axis. Exit from the cycle occurs within left quadrant of the figure and represents the stage where there is potential for a change in state or a flip to a new state. After Thapa *et al*. (2015b).

6.2. Study area

The Narran floodplain is located in the Condamine-Balonne catchment, within the northern region of the Murray Darling Basin, Australia (Figure 6.2). The Condamine-Balonne River originates in well-watered uplands of the south-east Queensland highlands but flows for most part across a dry landscape (Thoms and Sheldon 2000). The river has a single channel for most of its length but bifurcates into five anabranching channels downstream of St. George, known locally as the Lower Balonne (Figure 6.2). These channels have relatively low gradients (0.0002 to 0.0003), are highly sinuous (1.9 to 2.5) and the bankfull cross-sectional area of each decreases with distance downstream (Thoms 2003). The Narran River, which flows along the eastern boundary of the Lower Balonne, terminates within the Narran Floodplain (Figure 6.2).

The Narran floodplain covers 296 km². It has regional, national and international importance as a Ramsar Convention site and 5.5 km² (2%) of the floodplain landscape is managed as National Park. The local drainage area of the Narran floodplain is small (50 km^2); therefore the Narran floodplain is not inundated as a result of local rainfall but from flows in the Narran River (Rayburg and Thoms 2009). Local rainfall is highly variable with annual rainfall ranging from 144 mm (2002) to 957 mm (1950) at Collarenebri, and occurs mainly in the summer months (November – February) associated with tropical monsoonal activity. With a mean annual evaporation of 2,250 mm the Narran floodplain landscape is dry most of the time. The Narran floodplain is geomorphologically complex with numerous lakes, channel networks and dissected floodplain surfaces (Rayburg and Thoms 2009).

The long-term (1965 – 2009) mean annual discharge of the Narran River at Wilby Wilby (Gauge 422016) is 128,717 ML, ranging from 1,003 ML to 690,000 ML. Flows exceeding 13,000 Megalitres per day (MLD) at Wilby Wilby result in overbank flows and inundation of the Narran floodplain (Rayburg and Thoms, 2009). These flows have an average recurrence interval of 1.5 years. The highly variable nature of flow in the Narran River results in infrequent periods of floodplain inundation (Murray *et al*. 2006). Inundation of the Narran floodplain is also spatially complex irrespective of the size of the flood event with the expansion and contraction of floodwaters across the floodplain resulting in a dynamic mosaic of inundated patches (Murray *et al*. 2006). The relationship between floodplain inundated area and the number of inundated wet patches displays an anticlockwise hysteresis; therefore significant fragmentation of floodwaters occurs during the contraction of floodwaters on the Narran floodplain (Murray *et al*. 2006).

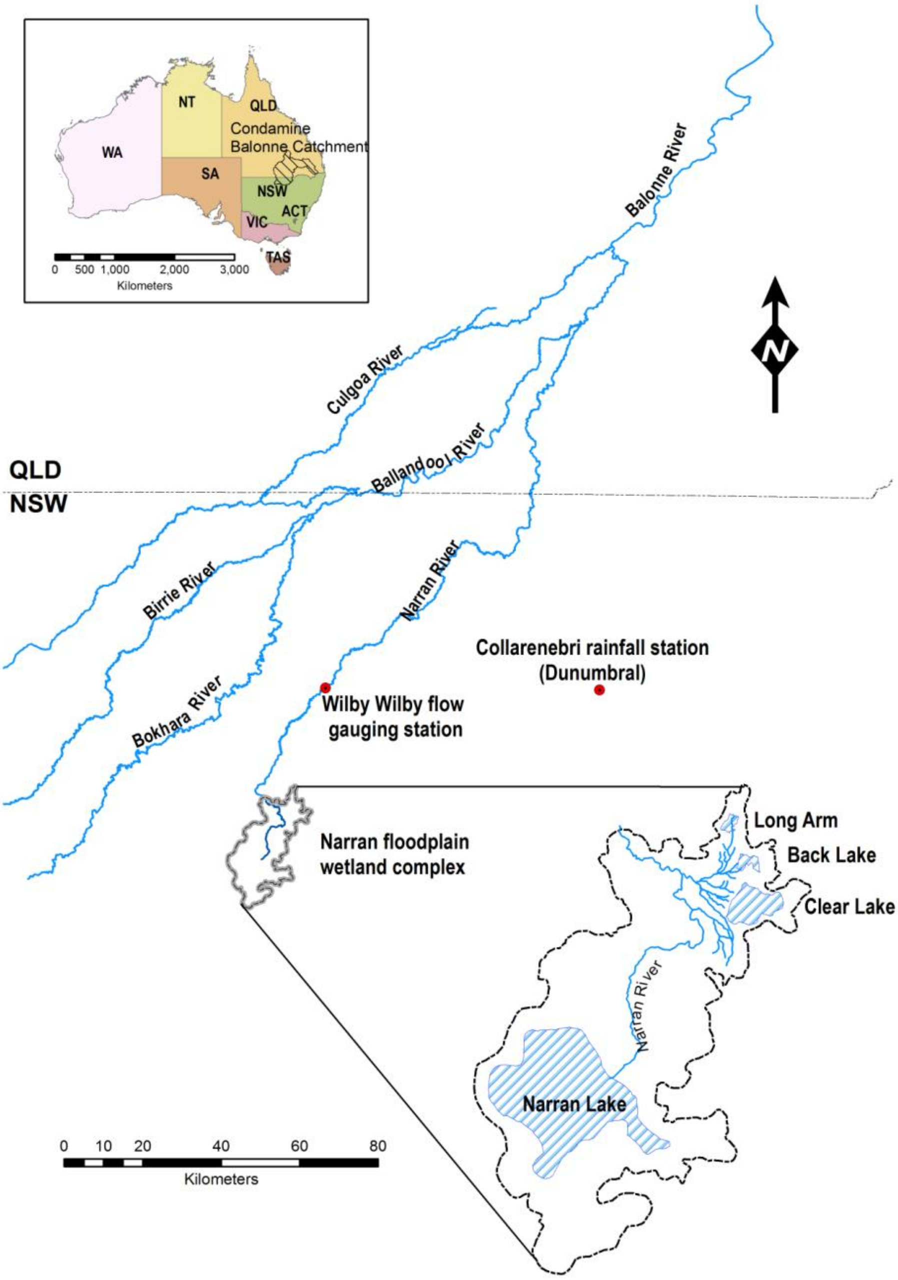

Figure 6.2 The Narran floodplain within the lower reaches of the Condamine Balonne Catchment, Australia.

The four main lakes of the Narran floodplain – Clear Lake, Back Lake, Long Arm and Narran Lake – (Figure 6.2) hold water for different periods of time. Narran Lake (51.95 km²) has a capacity of 122,500 ML and retains water up to 12-15 months following a flood event, but is dry 60% of the time (Rayburg and Thoms 2009). Clear Lake (5.86 km²), Back Lake (0.97

km²) and Long Arm (0.72 km²) have a combined capacity of 17,500 ML and retain water for 4-12 months (Thoms *et al*. 2007). The northern part of the floodplain fills in sequence through Clear Lake, Back Lake and Long Arm (Figure 6.2) and Narran Lake from flow in the Narran River (Rayburg and Thoms 2009). The wetting and drying of the Narran floodplain has been severely impacted by water resource development in the upper catchment. Water extraction has reduced the median annual flow in the Narran River by approximately 30% (Thoms 2003), significantly reducing moderate-sized floods on the Narran floodplain (Thoms *et al*. 2007).

Vegetation on the Narran floodplain is dominated by the perennial shrub lignum (*Duma florulenta*). Lignum shrubland is mostly found in the northern and central part of the floodplain along the Narran River. There is an overstorey of riparian woodland along main watercourses comprising river red gum (*Eucalyptus camaldulensis*), coolibah (*Eucalyptus coolabah*) and black box (*Eucalyptus largiflorens*). Other woodland species found in the Narran floodplain include poplar box (*Eucalyptus populnea*), whitewood (*Atalaya hemiglauca*), belah (*Casuarina cristata*), gidgee (*Acacia calcicola*), wilga (*Geijera parviflora*), black box (*Eucalyptus largiflorens*) and whitewood (*Atalaya hemiglauca*). Lignum shrubland and woodland communities cover approximately 151 km^2 (51 %) of the Narran floodplain. Grassland covers approximately 42 km^2 (14 %) and consists of Mitchell grass (*Astrebla* spp.), neverfail (*Eragrostis setifolia*) and box grass (*Paspalidium constrictum*) interspersed among clumps of trees and shrubs. Crops and pastures cover 48 km^2 (16%) and the remaining 55 km^2 (19%) is lake area and barren ground.

6.3. Methods

6.3.1 Satellite image selection

Remotely sensed satellite images were used to track the productivity of vegetation through periods of flooding and drying in the Narran floodplain. A three-step process was used to obtain satellite images for analysis of vegetation productivity. First, the conditions of dry and flood periods were defined. A dry period is a period of no flow or flow below the long-term 95th percentile flow, combined with below average rainfall. In a dry period there is no moisture subsidy to the floodplain through flooding or rainfall. Although groundwater can be an important source of moisture for floodplain vegetation in some contexts (Horner *et al*. 2009), groundwater in the Narran floodplain is approximately 100 m below the floodplain surface (Fitzpatrick *et al*. 2005). The flood period was defined as flow above 13,000 MLD in the Narran River (Wilby Wilby); the flow required to initiate floodplain inundation (Thapa *et al*. 2015b).

Second, discharge and rainfall records were searched for conditions matching the definition of dry and flood periods. Daily Narran River flow data (January 1980 – December 2009 at Wilby Wilby) were acquired from the NSW Department of Primary Industries. Daily rainfall data for the same period were obtained from the Australian Bureau of Meteorology (Station 048038 at Collarenebri). Monthly discharge and rainfall means were calculated and each month in the record was delineated as being above or below average or as having no flow or rainfall. Periods fitting the definitions of flood and dry were identified in the discharge and rainfall record.

Third, the quality and availability of Landsat satellite imagery corresponding to the dry and flood periods were examined using the Geoscience Australia Australian Centre for Remote Sensing (ACRES) and United States Geological Survey (USGS) catalogues. The Narran floodplain is encompassed in one Landsat scene (Path 92, Row 81). From the pool of high-quality satellite images the years 1987, 1993, 2002 and 2007 for the dry period and 1988, 1994, 2004 and 2008 for the flood period were randomly selected. In each year, a sequence of images was selected at approximately monthly intervals. Care was taken to select high quality images with no or minimum cloud cover. The dry period image sequence was stopped when rain occurred, and the flood period image sequence stopped when floodwater completely contracted and dry images started. The 75 dry and flood images were rearranged into four events. The details of images in each event are provided in Table 6.1.

Images were cropped to a standard floodplain area denoted by the boundary of floodplain soils (Rayburg *et al*. 2006). Images were re-sampled to 25 metre resolution and re-projected to the Geodetic Datum of Australia 1994 Universal Transverse Mercator zone 55S, to ensure compatibility of images from different sources (i.e. from ACRES and USGS). The aligned image digital numbers were converted to top of atmosphere reflectance using the methods of Chander *et al*. (2009). A relative radiometric normalisation was performed using dark and light targets to make images acquired on different dates comparable (Myeong *et al*. 2006).

Table .6.1 Satellite images for the four events, with corresponding hydrology, rainfall and temperature conditions. A period refers to the comparison of two images, where the comparison of Image 1 and 2 becomes Period 1. Hydrology data were obtained from the Department of Primary Industries (NSW) Office of Water Information and climatic data were acquired from the Australian Bureau of Meteorology.

Date of image	Image number	Period	Dry or Flood images	Events	Total flow (MLD)	Total monthly rainfall (mm)	Mean monthly maximum temperature (^{o}C)
27-05-1987	1		Dry	1	0	82	22
31-08-1987	2	1	Dry	1	2924	60	20
09-10-1987	3	2	Dry	1	0	42	27
21-12-1987	4	3	Dry	1	3862	75	35
06-01-1988	5		Flood	1	1156	32	37
07-02-1988	6	4	Flood	1	3712	31	32
23-02-1988	7	5	Flood	1	3712	31	32
26-03-1988	8	6	Flood	1	65717	50	31
13-05-1988	9	7	Flood	1	135747	19	22
29-05-1988	10	8	Flood	1	135747	19	22
16-07-1988	11	9	Flood	1	54725	92	19
04-10-1988	12	10	Flood	1	1608	1	32
20-10-1988	13	11	Flood	1	0	1	32
21-11-1988	14	12	Flood	1	0	21	31
23-12-1988	15	13	Flood	1	0	24	35
08-01-1989	16	14	Flood	1	0	3	34
09-02-1989	17	15	Flood	1	0	2	35
14-04-1989	18	16	Flood	1	30648	60	26
08-03-1993	19		Dry	2	0	77	38
09-04-1993	20	17	Dry	2	169	0	30
25-04-1993	21	18	Dry	2	169	0	30
11-05-1993	22	19	Dry	2	0	24	24
12-06-1993	23	20	Dry	2	0	20	18
28-06-1993	24	21	Dry	2	0	20	18
14-07-1993	25	22	Dry	2	0	69	19
03-11-1993	26	23	Dry	2	0	3	38
07-02-1994	27		Flood	2	6335	13	32
23-02-1994	28	24	Flood	2	18315	13	32
28-04-1994	29	25	Flood	2	0	0	27
14-05-1994	30	26	Flood	2	0	0	23
15-06-1994	31	27	Flood	2	0	0	20
01-07-1994	32	28	Flood	2	0	0	19
17-07-1994	33	29	Flood	2	0	0	19
02-08-1994	34	30	Flood	2	0	0	21
03-09-1994	35	61	Flood	2	0	0	24
19-09-1994	36	32	Flood	2	0	0	24

Table 6.1 (cont.)

Date of image	Image number	Period	Dry or Flood images	Events	Total flow (MLD)	Total monthly rainfall (mm)	Mean monthly maximum temperature (^{o}C)
21-10-1994	37	33	Flood	2	0	12	29
22-11-1994	38	34	Flood	2	0	85	31
20-01-2002	39		Dry	3	0	0	37
05-02-2002	40	35	Dry	3	0	30	34
09-03-2002	41	36	Dry	3	0	4	33
10-04-2002	42	37	Dry	3	0	34	30
28-05-2002	43	38	Dry	3	997	0	23
29-06-2002	44	39	Dry	3	6	17	20
15-07-2002	45	40	Dry	3	0	0	20
16-08-2002	46	41	Dry	3	0	12	23
17-09-2002	47	42	Dry	3	0	19	26
19-10-2002	48	43	Dry	3	0	7	31
04-11-2002	49	44	Dry	3	0	6	37
06-12-2002	50	45	Dry	3	0	15	36
18-01-2004	51		Flood	3	8679	104	36
03-02-2004	52	46	Flood	3	18199	26	36
19-02-2004	53	47	Flood	3	18199	123	36
23-04-2004	54	48	Flood	3	407	27	29
09-05-2004	55	49	Flood	3	0.44	25	22
10-06-2004	56	50	Flood	3	0	10	20
12-07-2004	57	51	Flood	3	0	31	18
14-09-2004	58	52	Flood	3	0	19	25
16-10-2004	59	53	Flood	3	0	15	30
17-11-2004	60	54	Flood	3	0	108	32
19-12-2004	61	55	Flood	3	1115	107	33
26-01-2007	62	56	Dry	4	0	33	37
27-02-2007	63	57	Dry	4	0	76	36
16-04-2007	64	58	Dry	4	0	30	29
02-05-2007	65	59	Dry	4	0	50	24
23-09-2007	66	0	Dry	4	8	27	59
13-01-2008	67		Flood	4	6607	63	33
14-02-2008	68	60	Flood	4	21164	65	31
17-03-2008	69	61	Flood	4	0	14	31
02-04-2008	70	62	Flood	4	10000	0	26
09-09-2008	71	63	Flood	4	0	68	25
25-09-2008	72	64	Flood	4	0	68	25
27-10-2008	73	65	Flood	4	0	57	30
11-11-2008	74	66	Flood	4	0	98	30
30-12-2008	75	67	Flood	4	0	32	35

6.3.2 Delineation of adaptive phases

The flood period images were processed in ERDAS imagine software to delineate the expansion and contraction of flood waters across the floodplain. To map inundation extent, density slicing was used to identify inundated (water) and non-inundated (non-water) pixels and their threshold reflectance values, as recommended by Overton (2005). In some images, detecting inundated pixels was not possible using a single band because of the presence of a dense vegetation canopy. For those images, the Normalised Difference Water Index (Xu 2006) and unsupervised classification were used to differentiate inundated and non-inundated pixels. These methods have been successfully used to map inundation across Australian floodplains using Landsat satellite imagery (Frazier and Page 2000, Shaikh 2001, Rayburg and Thoms 2009, Thomas *et al*. 2010). The results from both methods were combined to estimate the area of floodplain inundation.

Phases of the adaptive cycle were delineated from the area of floodplain inundation. The wetting phase is an initial rapid expansion of floodwater across the floodplain. The wet phase is a period of maximum inundation. The drying phase is associated with the contraction of floodwaters and the dry phase is associated with no surface water availability. Differences in the area of floodplain inundation among the adaptive phases were examined for each event using non-parametric Kruskal-Wallis one-way analysis of variance on ranks in Sigma Plot (Version 12). Differences in the area of floodplain inundation among the four events were also examined using this test.

6.3.3 Calculation of the Normalized Difference Vegetation Index

The Normalized Difference Vegetation Index (NDVI) is based on the red and near infrared band reflectance properties and is strongly correlated with photosynthetic activity. Hence, NDVI is a surrogate for vegetation productivity (Lillesand and Kiefer 2000, Farina 2006, Wen *et al*. 2012). The Normalized Difference Vegetation Index was calculated in each image as $\text{NDVI} = \rho\text{nir} - \rho\text{red} / \rho\text{nir} + \rho\text{red}$, where ρ is the spectral reflectance values of spectral bands nir (band 4) and red (band 3) of Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) images. Entropy analysis and moving window analysis were used to divide the NDVI values of all 473,142 pixels into classes, following the method of Parsons and Thoms (2013). Six NDVI classes emerged. Class 1 is no greenness ($\text{NDVI} < 0$).

Class 2 (NDVI 0-0.072), Class 3 (NDVI 0.072 – 0.207), Class 4 (NDVI 0.207-0.459), Class 5 NDVI (0.459-0.666) and Class 6 (NDVI > 0.666) represent a continuum of increasing vegetation productivity.

6.3.4 Analysis of vegetation productivity among adaptive cycle phases

Each image was allocated to the corresponding wetting, wet, drying or dry phase of the adaptive cycle. Four broad types of NDVI data were used to explore vegetation productivity through the dry, wetting, wet and drying phases: area and quality of NDVI; number and direction of NDVI class transitions; probability of NDVI class transitions; and, NDVI class diversity. The area of floodplain with active vegetation productivity (total area of NDVI Classes 2 – 6) was calculated for each image. Quality of vegetation productivity was calculated as the area of individual NDVI classes in each image, where low quality productivity is NDVI Class 2 and 3 (low greenness) and high quality productivity is NDVI Classes 4, 5 or 6 (higher greenness). NDVI Class 1 was excluded because this class has no greenness and corresponds to water bodies and barren ground.

Pair-wise transitions between NDVI classes were calculated on a pixel-by-pixel basis between sequential images. Each pixel was classified into a change class (C_{ij}) which represents a change from NDVI class i to NDVI class j. A total of 36 C_{ij} were possible among the six NDVI classes, comprising six constant classes and 30 directional change classes. First-order Markovian transition models (Weng 2002, Bolliger *et al*. 2007) were used to model the number and direction of NDVI class transitions and the probability of NDVI class transitions between sequential images (termed a period). The Markovian transition model consists of the area of each NDVI change classes (C_{ij}) present in each period and the probability (P_{ij}) of each C_{ij} occurring. Periods were allocated to the corresponding wetting, wet, drying or dry phase. The number of transitions and the direction of transitions (one-way or two-way) between NDVI classes were tallied from a pictorial representation of the Markovian transition model. Probability of change (P_{ij}) was calculated as the proportion (%) of the total number NDVI classes *i* that transitioned to NDVI Class j. The probabilities of transition were divided into six classes of transition probability: < 1, 1-5, 5-10, 10-20, 20-30 and > 50 %. The diversity of NDVI classes in each image was also calculated using the Shannon-Wiener diversity index (Magurran 1988). Monthly images are considered as samples, NDVI classes as species, and NDVI area as abundance.

Differences in the total area of NDVI, area of each NDVI class, total transitions, one-way transitions, two-way transitions, probability of transitions and diversity among adaptive phases were examined separately using a non-parametric Kruskal-Wallis one-way analysis of variance on ranks in Sigma Plot (Version 12). The same test was also used to examine differences in these variables among flood events. Multivariate analyses were used to examine differences among adaptive phases, using PRIMER_E and PERMANOVA+. Three types of data (area and quality, number and direction of transitions, probability of transitions) were analysed separately, but the four events were combined. Multi-dimensional scaling was performed using the Bray Curtis similarity coefficient. The relative dispersion of images within an adaptive phase was examined using the MVDISP routine (Warwick and Clarke 1993), where lower values indicate similarity of images from the same adaptive phase in multivariate space. The relative dispersion among adaptive phases was examined using the distance among centroids routine in PERMANOVA+, which calculates distances among group centroids (Anderson *et al*. 2008). Lower values indicate closer centroids and hence, greater similarity among adaptive phases.

6.4. Results

6.4.1 Floodplain inundation and adaptive cycle phases

The area of floodplain inundation corresponds to the dry, wetting, wet and drying phases of an adaptive cycle. The adaptive cycle commences with an initial rapid expansion of floodwaters across the floodplain in the wetting phase (Figure 6.3a). The wetting phase is followed by the wet phase during which inundation is at its maximum extent, remaining relatively stable within the phase (Figure 6.3a). The wet phase is followed by the drying phase during which the area of inundated floodplain contracts (Figure 6.3a). The dry phase follows the drying of the floodplain and remains in place until a flow event starts the next wetting phase. During the dry phase, surface water is absent from the floodplain (Figure 6.3a). There was a significant difference in the area of floodplain inundation among the wetting, wet, drying and dry phases in each event (Event 1 $H=15.793$, $p=0.001$; Event 2 $H=16.309$, $p=<0.001$; Event 3 $H=19.480$, $p=<0.001$; Event 4 $H=12.005$, $p=0.007$). Thus, the divisions among phases are repeated across the four events.

Although the four events exhibit an adaptive cycle, the duration of each phase and the area inundated differed between events. Event 1 was characterised by phases of relatively similar duration; where wetting took approximately three months, the wet phase occurred for four months while the drying phase occurred over four months (Figure 6.3a). In contrast, Events 2 and 3 were characterised by short wetting and drying phases of approximately two months and a long wet phase of six months (Figure 6.3a). Event 4 was very different from the other events and was characterised by a short wetting and wet phase of one month and an extended drying phase of over six months (Figure 6.3a). There was a significant difference in inundated area among the four flood events (H=8.507, p=0.037), related to flow in the Narran River. The largest area of floodplain inundation occurred in Event 1 (114 km^2) and was associated with inflows that peaked at 135,747 MLD in May 1988 (Figure 6.3a and b). The second largest floodplain inundation of 37 km^2 occurred in Event 2 and was associated with a peak flow of 88,974 MLD in March 1994. Floodplain inundation in Event 3 and Event 4 was associated with flows of 21,307 MLD and 21,164 MLD, resulting in inundation of 34 km^2 and 31 km^2 respectively (Figures. 5.3a and b). Overall, these differences largely reflect the hydrograph for each event, where larger floods are associated with some phases having a longer duration (Figure 6.3b). Despite differences in the area of floodplain inundation between events and the length of the wetting, wet and drying phases, there is consistently a wetting, wet, drying and dry phase. Thus, vegetation productivity can be further examined in relation to the adaptive cycle phases of floodplain inundation.

6.4.2 Area and quality of vegetation productivity through the adaptive cycle phases

The total area of NDVI followed the hypothesised pattern (Figure 6.1) of an increase in the dry and drying phases and decrease in the wetting and wet phases. In most events there was a significant difference in the total area of NDVI among the dry, wetting, wet and drying phases of the adaptive cycle (Table 6.2). The total area of NDVI was always highest in the dry phase than the other phases (Figure 6.4). Across all events the mean area of NDVI in the dry phase was 288 km^2 (range: 164 km^2 to 296 km^2). In comparison, the mean area of NDVI in the wetting phase was 255 km^2 (range: 202 km^2 to 293 km^2), the wet phase was 246 km^2 (range: 181 km^2 to 286 km^2) and the drying phase was 268 km^2 (range: 193 km^2 to 296 km^2).

As hypothesised in the adaptive cycle model (Figure 6.1) the highest quality NDVI (Class 6) occurred mostly in the wetting and wet adaptive phases (Figure 6.4). NDVI Class 6 did not occur in any dry phase across the four events (Figure 6.4) as hypothesised. In contrast to the model, higher quality NDVI did occur in the drying phase of Events 1 and 4, although the area of NDVI Class 6 was relatively low (Figure 6.4). This was presumably because of additional water being available in both events; Event 1 through the large magnitude of inflow and the contribution of managed environmental water in Event 4 (Table 6.1).

In most events there was a significant difference in NDVI quality (i.e. individual NDVI classes) between the wetting, wet, drying and dry adaptive phases (Table 6.2). During the dry phase, most of the floodplain was associated with NDVI Class 3 (Figure 6.4) with a mean floodplain area across all events of 232 km^2 (range: 32 km^2 to 285 km^2). The next largest class was NDVI Class 4 (mean area of 47 km^2; range: 0.7 to 244 km^2), followed by NDVI Class 2 (mean 14 km^2; range: 0.12 to 131 km^2) and NDVI Class 5 (mean 0.76 km^2; range: 0.01 to 19 km^2) (Figure 6.4). NDVI Class 3 was dominant in the wetting phase with a mean area of 136 km^2, while in the wet phase NDVI Classes 3 and 4 were dominant with a mean floodplain area of 101 km^2 and 102 km^2 respectively. In the wetting and wet phases all six NDVI classes were present. The drying phase was also dominated by NDVI Class 3 and 4, with mean areas of 119 km^2 and 94 km^2 respectively, and all NDVI classes were present in this phase. Thus, in the wetting, wet and drying phases the quality of NDVI was consistent in all events with an increase and decrease in quality as hypothesised in the model. However, the quality of NDVI was expected to decrease in the dry adaptive phase but this was not observed and it remained in Class 3 in this phase in all events (Figure 6.4).

Ordination revealed some separation of images among the four phases of the adaptive cycle based on area of the NDVI classes (Figure 6.5a). The dry images were clumped in multivariate space, whereas the wetting, wet and drying images were more dispersed (Table 6.2). The greatest distance among centroids was between the dry adaptive phase and the wetting, wet and drying adaptive phases (Table 6.3). The wetting, wet and drying phase centroids were relatively close to each other in multivariate space (Table 6.3).

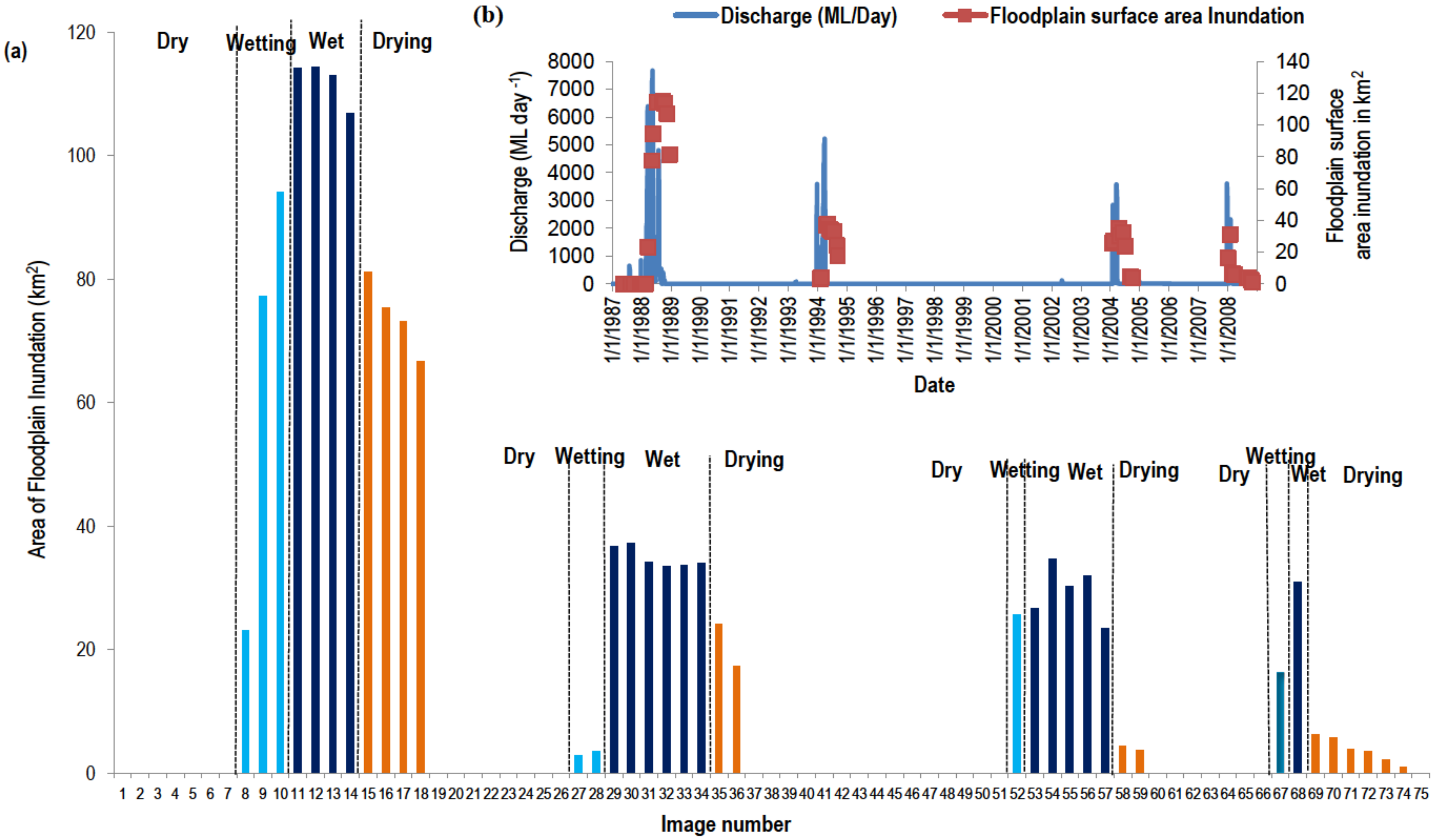

Figure 6.3 Surface area inundation of the Narran floodplain divided into corresponding dry, wetting, wet and drying phases of the adaptive cycle (a). Image numbers are explained in Table 3.1. Inset graph (b) shows the total discharge in (ML) in the Narran River and corresponding Narran floodplain surface area inundation.

Table 6.2 Differences in NDVI class area and quality, number and direction of NDVI class transitions, probability of NDVI class transitions and NDVI class diversity among adaptive cycle phases of four events. NS = not significant (p> 0.05).

Data type	P values			
	Event 1	Event 2	Event 3	Event 4
Area and quality				
Total area of active NDVI	0.002	0.016	0.003	NS
NDVI Class 2	0.002	NS	0.017	NS
NDVI Class 3	0.021	0.014	0.003	NS
NDVI Class 4	NS	0.031	0.044	0.004
NDVI Class 5	0.027	0.002	0.002	0.005
NDVI Class 6	NS	0.026	0.006	0.007
Number and direction of transitions				
One way transitions	NS	NS	NS	NS
Two-way transitions	0.004	0.010	<0.001	0.016
Total transitions	0.005	0.006	<0.001	0.004
Probability of transitions (%)				
Number of transition with probability < 1	0.020	NS	<0.001	NS
Number of transition with probability 1 to 5	0.007	0.009	<0.001	NS
Number of transition with probability 5 to 10	NS	NS	0.008	NS
Number of transition with probability 10 to 20	0.0045	0.043	0.004	NS
Number of transition with probability 20 to 50	0.041	NS	0.024	NS
Number of transition with probability > 50	NS	NS	NS	NS
Diversity of NDVI Class area				
Diversity of NDVI class area	0.004	0.005	0.004	NS

6.4.3 Number and direction of vegetation productivity transitions through the adaptive cycle phases

The observed pattern of the total number of NDVI class transitions followed the hypothesised adaptive cycle model. In all events there was a significant difference in the total number of transitions among the wetting, wet, drying and dry phases of the adaptive cycle (Table 6.2). In the dry phase 295 transitions occurred compared to 851 transitions (see appendix 2) in the combined wetting, wet and drying phases (Figure 6.6). There was a marked increase in the total number of transitions during the wet and wetting phases followed by a decrease during the drying phase, with the lowest number of transitions in the dry phase (Figure 6.6). The average number of transitions in the dry phase was 11 (range: 4 - 18). In comparison, the average number of transitions was greater in the wet phase (average: 25; range: 19 – 30) followed by the wetting and drying phases (average: 19; range: 16 – 22; average: 17; range: 15 – 26 respectively).

The observed pattern of the direction of transitions also followed the hypothesised adaptive cycle model. In all events there was a significant difference in the number of two-way transitions among the wetting, wet, drying and dry phases of the adaptive cycle (Table 6.2). However, in all events there was no significant difference in the number of one-way transitions among the phases in any of the events (Table 6.2). In all events, both one-way and two-way transitions occurred in the dry, wetting, wet and drying phases (Figure 6.7). The wet phase was more dynamic, with a higher frequency of one-way and two-way transitions, which was not hypothesised in the model. Overall, one-way transitions were more prevalent in the dry phase and two-way transitions in the wet phase (Figure 6.6). The ratio of one-way to two-way transitions in the dry phase was 0.42, significantly higher (Students t test: $p<0.001$) than the ratios of the other phases (0.27 for the wetting phase; 0.09 for the wet phase; and, 0.25 for the drying phase).

Ordination based on one-way and two-way transitions revealed little separation of the wetting, wet and drying phase images, but a separation of dry phase images (Figure 6.5b). The dry phase images are clumped in multivariate space, whereas the wetting, wet and drying phase images are more dispersed (Table 6.3). The greatest distance among centroids is between the dry phase and the wetting, wet and drying phases (Table 6.4). This suggests the wetting, wet and drying phases are more similar to each other than to the dry phase (Table 6.4).

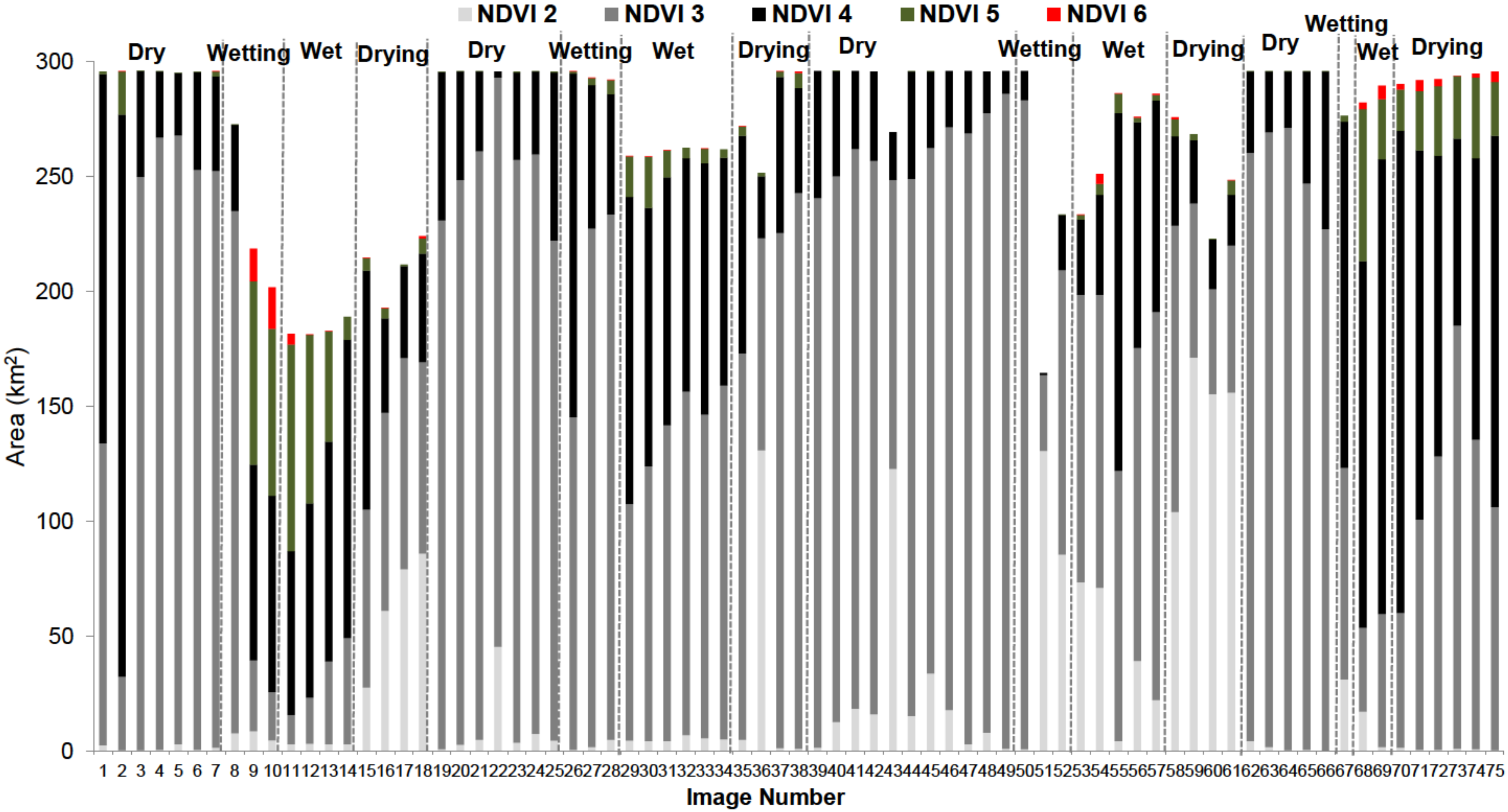

Figure 6.4 Area of NDVI Class 2 through 6 in the Narran floodplain during the dry, wetting, wet and drying phases of the adaptive cycle. NDVI Class 1 is not shown because it represents bare ground or water. Image numbers are explained in Table 6.1.

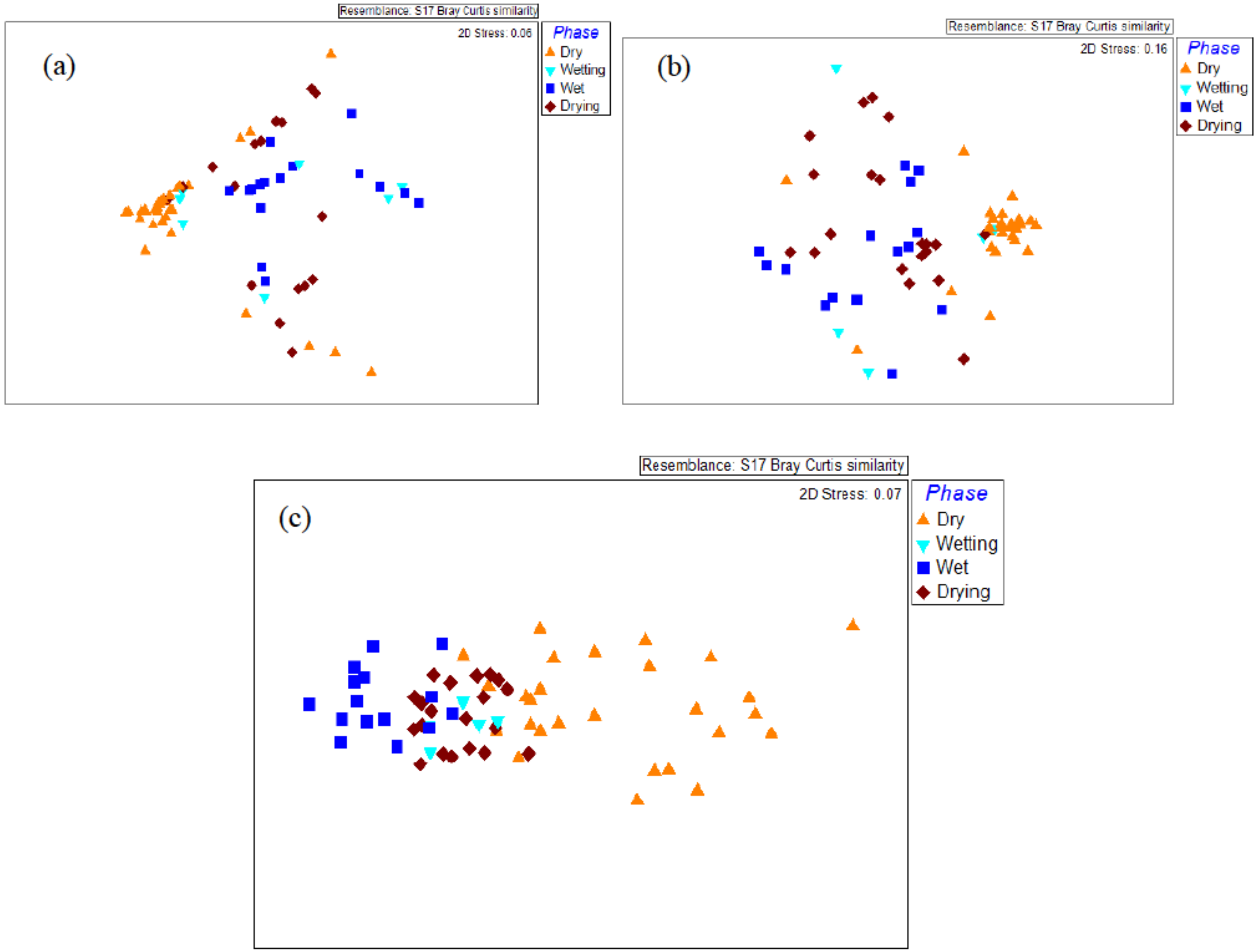

Figure 6.5 Non-metric multidimensional scaling (MDS) ordination comparing adaptive phases using (a) area and quality (b) number of transitions and (c) probability of transitions data.

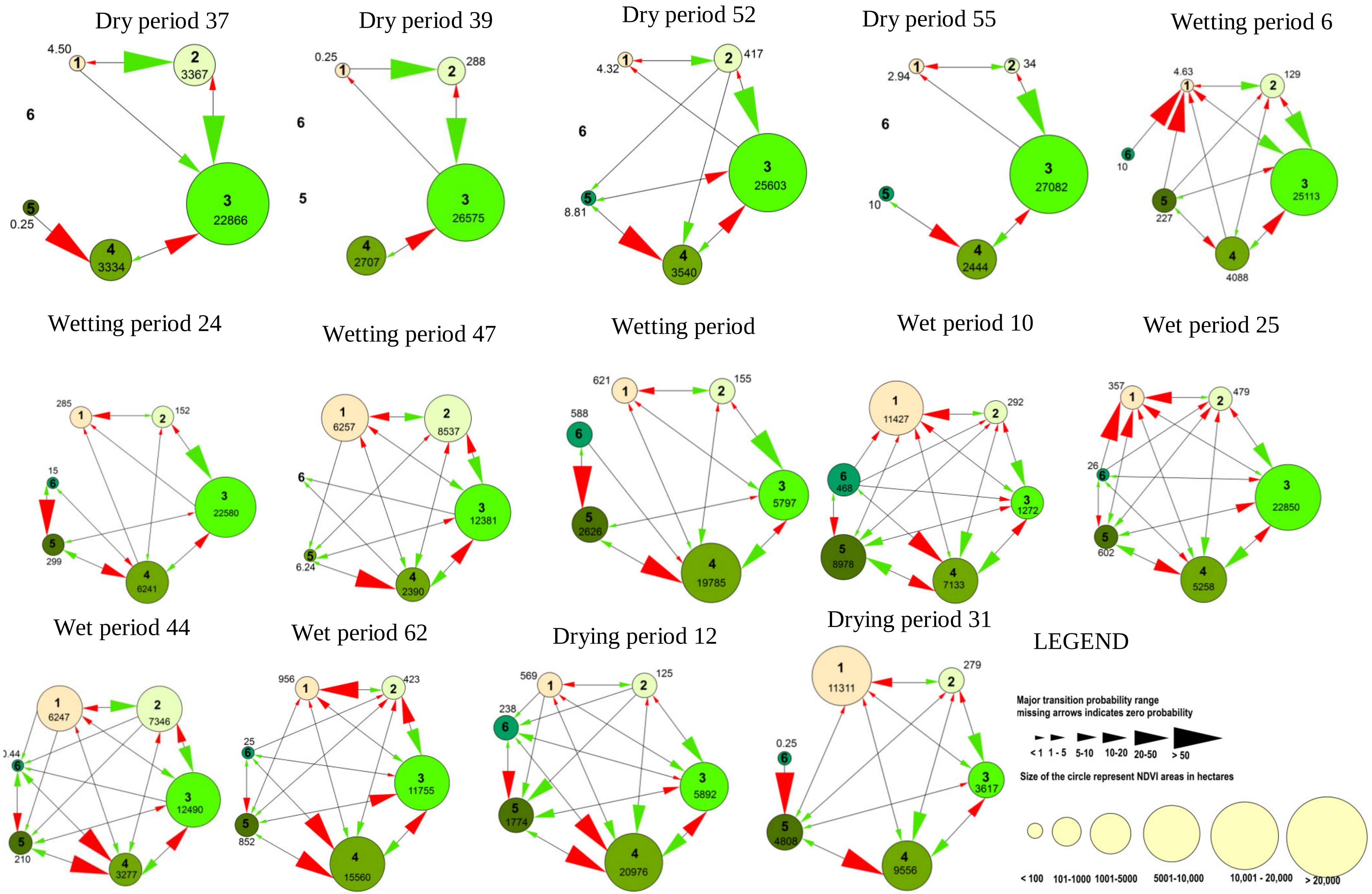

Figure 6.6 An example of Markovian transition models of change between NDVI Classes 1-6 in the dry, wetting, wet and drying phases of floodplain inundation. The area of floodplain in each NDVI class is shown by different sized circles, and labelled with area (ha). Arrows identify the changes between NDVI classes, where red arrows indicate decrease and the green arrows indicate increase in NDVI classes. The size of the arrowhead indicates the probability of change among NDVI classes. Periods are explained in Table 6.1.

6.4.4 Probability of NDVI class transitions through the adaptive cycle phases

Distributions of the probability of NDVI class transitions were bimodal for each flood event (Figure 6.8a) and each phase of the adaptive cycle (Figure 6.8b). All distributions had a primary mode at the < 1% probability class and a secondary mode occurring either at the 10-20 %, 20-50% or > 50% probability class. There were differences in the bimodality of the probability of NDVI class transitions between the dry, wetting, wet and drying phases (Figure 6.8b). In particular, the dry phase was characterised by a primary mode at < 1% and a secondary mode at the 20-50% and > 50% probability class (Figure 6.8b). Combined, the number of transitions in the 20-50% and > 50% probability classes was equivalent to that recorded in the < 1% probability class. Thus, the probability of NDVI class transitions in the dry phase is dominated by a higher frequency of both low and high probability transitions. This contrasts to the wetting phase, where the distribution of NDVI class transitions was weakly platykurtic in nature with a primary mode at < 1% and a weaker secondary mode at 10-20%; suggesting the probability of class transitions is dominated by lower probability transitions (Figure 6.8b). The distribution of the probability of NDVI class transitions in the wet and drying phases were similar to each other but different to the dry and wetting phases (Figure 6.8b). These distributions had a dominant primary mode at < 1% and a secondary mode at 20-50 %. These observed class transitions were as hypothesized for the wetting, wet and drying phases but not for the dry phase.

In contrast to the other types of data, ordination based on transition probability classes revealed dispersion of the dry phase images and clumping of the wetting, wet and drying phase images (Table 6.3 and Figure 6.5c). In addition, the greatest distance among centroids was between the dry phase and the wetting, wet and drying phases (Table 6.4). The wetting, wet and drying-phase centroids were closer to each other in multivariate space (Table 6.4), but the centroid distances between the drying and wetting phase were similar (Table 6.4).

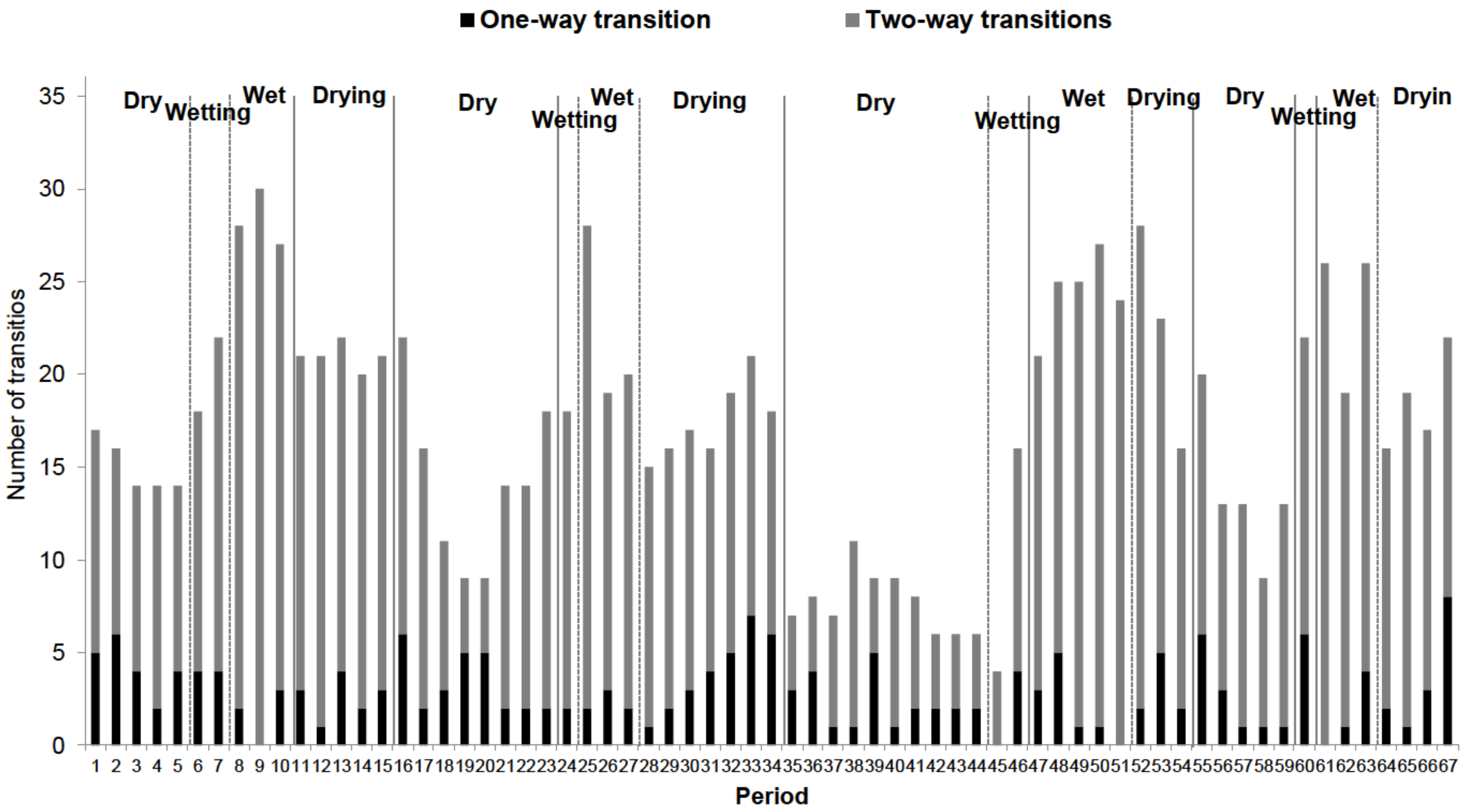

Figure 6.7 Total number transitions, one-way and two-way transitions between NDVI classes in the adaptive cycle phases. Periods are explained in Table 6.1.

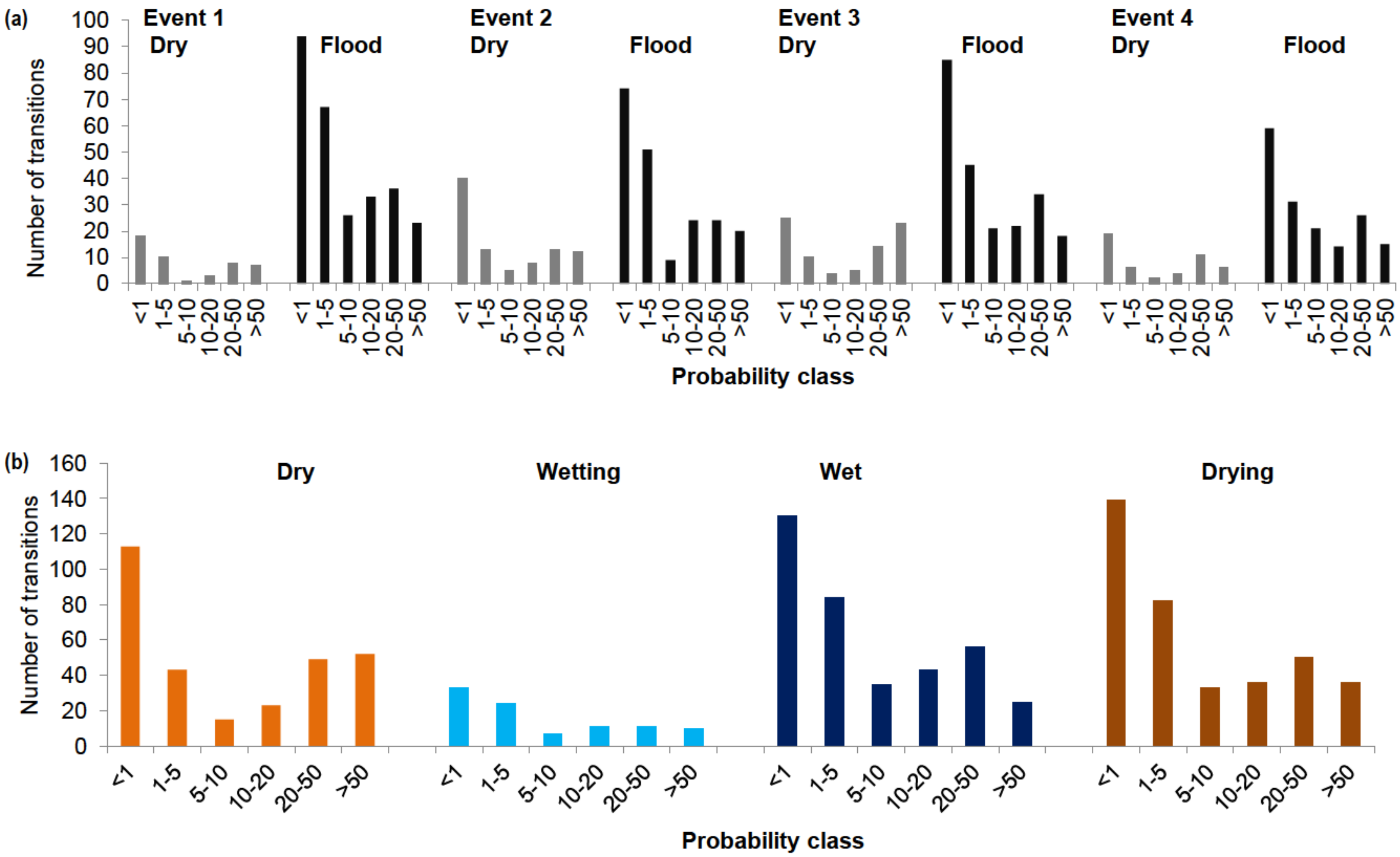

Figure 6.8 The distribution of probability transition classes in a) events divided into flood an dry components and b) the dry, wetting, wet and drying adaptive cycle phases.

Table 6.3 Multivariate dispersion index values of different adaptive cycle phases for NDVI class area and quality, number and direction of NDVI class transitions and probability of NDVI class transitions data.

Data type	Multivariate dispersion index			
	Dry	Wetting	Wet	Drying
Area and quality	0.89	1.34	1.29	1.29
Number and direction of transitions	0.75	1.63	1.29	1.28
Probability of transitions	1.28	0.38	0.72	0.67

Table 6.4 Matrices of group centroid distances between the adaptive cycle phases using NDVI class area and quality, number and direction of NDVI class transitions and probability of NDVI class transition data.

Data type	Group centroid distances			
	Dry	Wetting	Wet	Drying
Area and quality				
Dry	-			
Wetting	28.33	-		
Wet	39.70	12.52	-	
Drying	30.34	10.60	13.70	-
Number and direction of transitions				
Dry	-			
Wetting	37.76	-		
Wet	48.15	25.78	-	
Drying	40.82	23.32	13.42	-
Probability of transitions				
Dry	-			
Wetting	27.37	-		
Wet	39.59	15.96	-	
Drying	27.36	1.71	15.96	-

6.4.5 Diversity of vegetation productivity through the adaptive cycle phases

The diversity of NDVI classes among the wetting, wet, drying and dry phases followed the hypothesised adaptive cycle model. In all four events there was an increase in NDVI class diversity from the wetting to the wet phase followed by a decrease in the drying phase, with the lowest diversity occurring following the dry phase (Figure 6.9). In most events there was a significant difference in NDVI class diversity among the wetting, wet, drying and dry phases (Table 6.2). In the dry phase, diversity was relatively low, averaging 0.55 (range: 0. 16 to 1.24), while the wetting phase had an average diversity of 1.02 (range: 0.65 to 1.56). In comparison the wet phase had the highest average diversity of 1.21 (range: 0.98 to 1.40) and the drying phase had an average diversity of 1.08 (range: 0.57 to 1.45).

6.4.6 Vegetation productivity among flood events

Despite the occurrence of adaptive phases in all four events, the size of each flood had some effect on aspects of vegetation productivity in some of the adaptive cycle phases. There was a significant difference in total NDVI area and NDVI quality among events in the dry, wet and drying phases, but not in the wetting phase (Table 6.5). However, these differences among events did not apply to all NDVI quality classes (Table 6.5). Significant differences in the direction of NDVI class transitions occurred among events in the dry and drying phases but not in the wet phase (Table 6.4). In contrast, there were generally no significant differences in probability of NDVI class transitions among events in any of the phases (Table 6.5). Diversity only differed among events in the drying phase (Table 6.5). Thus a positive relationship between flood size and the area of floodplain vegetation productivity was observed in the Narran floodplain. However, all floods had a similar response in terms of the relative quality of NDVI and nature of changes in floodplain vegetation productivity through each of the adaptive cycle phases.

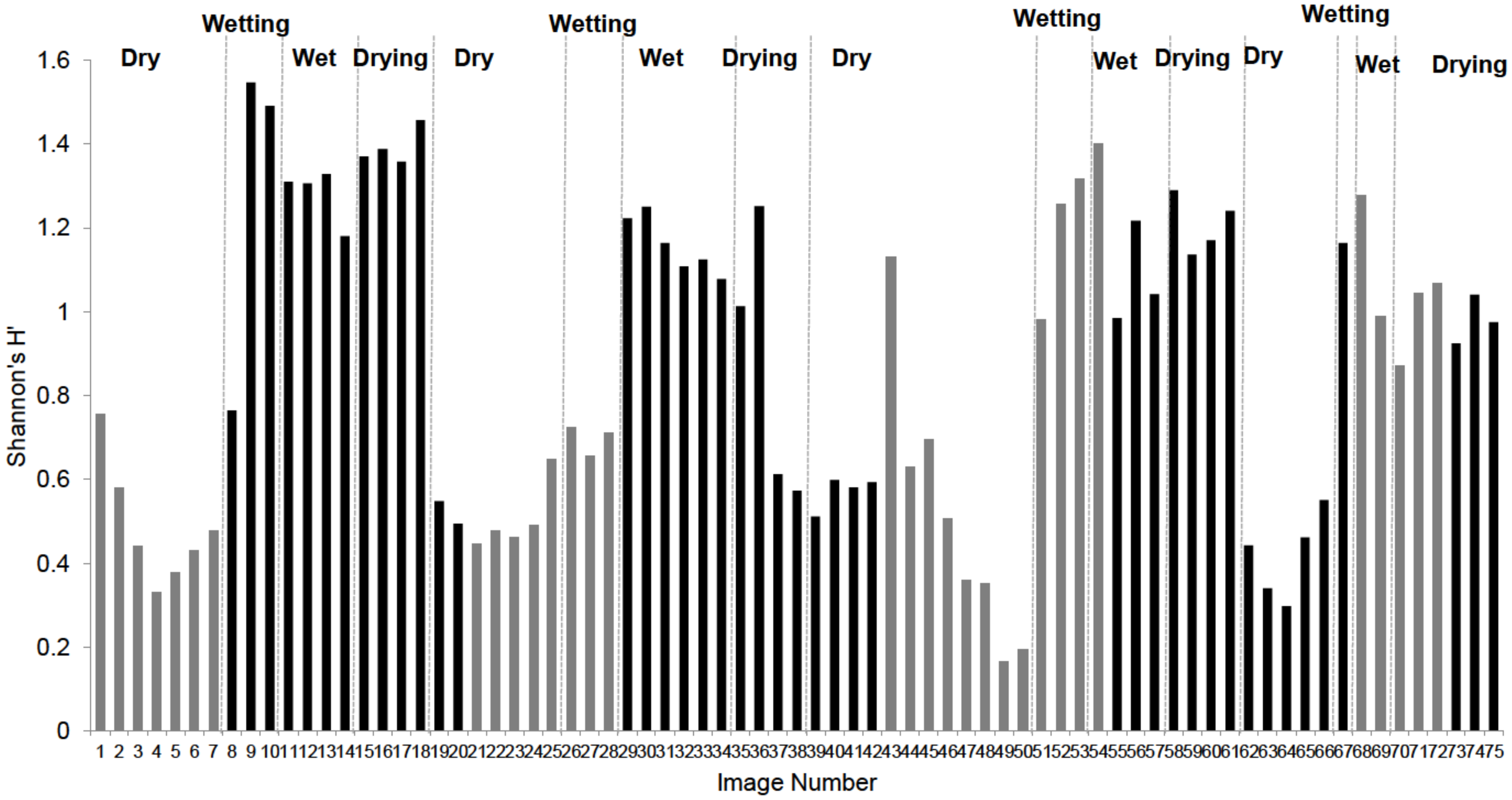

Figure 6.9 Shannon -Wiener Diversity of NDVI class area in the dry, wetting, wet and drying adaptive phases. Image numbers are explained in Table 6.1.

Table 6.5 Differences in NDVI class area and quality, number and directions of NDVI class transitions, probability of NDVI class transitions and NDVI class diversity among events for each adaptive phase. NS = not significant (p>0.05). No test = replication unavailable for a test.

Data type	P values			
	Dry	Wetting	Wet	Drying
Area and quality				
Total area of active NDVI	0.008	NS	0.015	0.017
NDVI Class 2	0.036	NS	0.006	0.011
NDVI Class 3	NS	NS	0.016	NS
NDVI Class 4	NS	NS	NS	0.010
NDVI Class 5	<0.001	NS	0.014	0.008
NDVI Class 6	NS	NS	NS	0.020
Number of transitions				
One way transitions	0.046	No test	NS	NS
Two-way transitions	0.019	No test	NS	0.007
Total transitions	0.001	No test	NS	0.017
Probability of transitions (%)				
Number of transition with probability < 1	0.002	No test	NS	NS
Number of transition with probability 1 to 5	0.028	No test	NS	NS
Number of transition with probability 5 to 10	NS	No test	NS	NS
Number of transition with probability 10 to 20	NS	No test	NS	NS
Number of transition with probability 20 to 50	NS	No test	NS	NS
Number of transition with probability > 50	NS	No test	NS	NS
Diversity of NDVI Class area				
Diversity of NDVI class area	NS	NS	NS	0.011

6.5. Discussion

There is limited empirical evidence demonstrating the application of adaptive cycles (Scheffer 2009), despite the widespread acceptance of resilience theory and the adaptive cycle model of ecosystem change (Holling 1986, Holling and Gunderson 2002). This study showed that an adaptive cycle of vegetation productivity occurred in the semi-arid Narran floodplain in response to flooding and drying. The adaptive cycle repeated in each of four flood events. Vegetation productivity response followed the hypothesised adaptive cycle phases of wetting, wet, drying and dry corresponding to a cycle of conservation, release, reorganization and exploitation. Thus, adaptive cycles are a sound representation of the dynamics of floodplain vegetation response to flooding and drying. Adaptive cycles highlight the complexity of vegetation productivity responses to flooding and drying in contrast to the simpler boom-bust, or related state-transition, models that form the current understanding of semi-arid floodplains (Walker *et al.* 1995). Boom-bust and state-transition models of floodplain productivity emphasise that maximum productivity occurs when water is added to a floodplain in flood events (Bunn *et al.* 2006). Under an adaptive cycle model the presence or absence of water remains a key driver of vegetation productivity. However, vegetation productivity is not confined to periods of floodplain inundation only (cf. Parsons and Thoms 2013) but occurs regardless of the presence or absence of surface water, and differs among phases of floodplain inundation as they cycle through wetting, wet, drying and dry phases.

In all four events, observed floodplain vegetation productivity responses matched those hypothesised in the adaptive cycle model derived from one event (Thapa *et al.* 2015b). The area of vegetation productivity increased in the dry and drying phases and decreased in the wetting and wet phases. The quality of vegetation productivity was also as hypothesized, with higher quality vegetation productivity in the wet and wetting phases, lower quality productivity in the drying phase and lowest quality productivity in the dry phase. The maximum number of transitions between NDVI classes occurred in the wet phase and was dominated by two-way transitions, as hypothesised. The dry phase had the lowest number of transitions, and was dominated by one-way transitions, as hypothesised. The distribution of probability transitions was bimodal in all phases, also as hypothesised, but the degree of bimodality differed between phases. The wetting, wet and drying phases were dominated by smaller probability class changes (i.e. more frequent smaller magnitude changes), whereas in the dry phase higher probability changes (i.e. higher magnitude changes) were more prominent and this was not as hypothesised. Diversity also followed the hypothesised adaptive cycle model with a high diversity of NDVI classes in the wet, decreasing through the drying phase to be lowest in the dry phase. These recurrent patterns of vegetation productivity through the phases of the adaptive cycle demonstrate that the effects of floodplain flooding and drying are consistently reflected in vegetation response. One of the tenets of the theory of adaptive cycles is repetition through phases of conservation, release, reorganization and exploitation where one phase builds the conditions that influence the movement of the system into the next phase (Holling and Gunderson 2002). The movement of Narran floodplain vegetation productivity through the adaptive cycle phases is influenced by the conditions of flooding and drying associated with a hydrological driver of ecosystem change.

Although the adaptive cycle repeated over four events, some differences in vegetation response were observed among flood events. The hydrological character of the four events varied in terms of the area of floodplain inundation and translated into differences in the duration of adaptive cycle phases among events. In particular, the events differed in duration of the wet and wetting phases, but not the dry phase, which was greater than 12 months for each event. In low-gradient floodplains there is a general positive relationship between discharge and the area of floodplain inundation (Murray *et al.* 2006), where larger discharges inundate more floodplain area and therefore connect a greater area under flood (Mertes *et al.* 1995, Hughes 1997). The hydrological character of flood events, that is the timing, magnitude and duration of floodplain inundation, is consistently identified as a prominent influence on landscape patterns of floodplain vegetation (Mertes *et al.* 1995, Capon 2005, Ward *et al.* 2014). The results of this study revealed an inconsistent influence of flood size on vegetation productivity response through the adaptive cycle phases. The larger flood (e.g. Event 1) had a greater area of floodplain inundation (Figure 6.3) but a smaller area of NDVI (Figure 6.4). Thus smaller floods, which are associated with a smaller area of floodplain inundation, had larger areas of NDVI. Differences in NDVI quality, probability and direction of change and diversity among events were inconsistent and differed by adaptive cycle phase. Landscape patterns of floodplain vegetation productivity can be influenced by a range of hydro-geomorphic factors including hydrology (Sims and Thoms 2002), soil character (Reid *at al.* 2011) and floodplain morphology (Scown *et al.* 2015). In a series of experiments designed to test the influence of different flooding and drying regimes on floodplain vegetation Webb *et al.* (2006) demonstrated that prolonged water logging of floodplain soils can inhibit recruitment and vegetation productivity. Thus, longer duration flood events may suppress floodplain vegetation productivity in the wet phase. By comparison, larger scale variations in the nutrient status of floodplain soils have been inferred to influence vegetation productivity across floodplains whereby areas of elevated nutrients are associated with more productive vegetation and faster vegetation productivity response to flooding (Sims and Thoms 2002, Reid *et al.* 2011). However, the systematic variation of soil nutrient concentrations from west to east across the Narran Floodplain, which is a legacy of past geomorphic processes (Rayburg *et al.* 2006), suggests the minimal influence of soil nutrients on the landscape pattern of vegetation productivity response.

The environmental processes influencing vegetation productivity response through the wetting, wet, drying and dry adaptive cycle phases in the Narran floodplain can only be hypothesised at present. Nonetheless, understanding patterns at multiple levels of organisation is an essential first step in deciphering the relationships between ecosystem pattern and process (Turner 1989). The new philosophy of science (Pickett *at al.* 1994) emphasizes the explanation of structures and patterns rather than focusing solely on proving causality using a falsification approach. Experiments can be conducted on plant ecophysiology and inundation interactions to understand the causal mechanisms driving floodplain vegetation productivity responses through the adaptive cycle phases. However, floodplains are complex systems and vegetation responses to inundation may have multi-causal, self-emergent and hierarchically organized properties that can never be fully deciphered with a reductionist approach. Interdisciplinary floodplain research requires information on both the complexity of patterns at multiple scales and detailed experimental studies to increase understanding about the nature of change and the potential influence of multiple drivers on patterns of change.

Resilience is about characterising and understanding change in complex systems (Gunderson and Pritchard 2002, Walker and Salt 2012). Ecologically, resilience can be defined as the capacity of systems to undergo change while maintaining the same fundamental structure, function and feedbacks (Holling 1973, Holling and Gunderson 2002, Walker and Salt 2012). Adaptive cycles are a component of resilience theory and provide a framework for understanding how complex systems undergo change (Holling and Gunderson 2002). The results of this study consistently demonstrated vegetation productivity change through an adaptive cycle in response to flooding and drying. Thus, this study supports the notion of Holling (1973) and Holling and Gunderson (2002) that a resilient systems fluctuates between the four phases of an adaptive cycle. A feature of an adaptive cycle is that it contains an exit point where the system might flip to a different cycle characterised by different structure, function and feedbacks (Holling 1973, Gunderson and Pritchard 2002). Although little is known about the exit from an adaptive cycle, exit points have been characterized as periods of marked change in the stability of key driving factors (Scheffer and Carpenter 2003, Scheffer 2009). When a system approaches a threshold of change, it fluctuates more which is thought to be an indicator of an impending change in state or regime shift (Biggs *et al.* 2009, Scheffer 2009). The transition between the reorganisation and exploitation phases is considered as the point in the adaptive cycle at which a system is more vulnerable to state change (Scheffer *et al.* 2001, Holling and Gunderson 2002,). Example state changes have been observed for lake, coral reef, forest and grassland ecosystems (Scheffer *et al.* 2001, Scheffer and Carpenter 2003, Wolf *et al.* 2007) but it has only been hypothesised thus far that this state change occurs between the reorganisation and exploitation phases of the adaptive cycle. In the Narran floodplain, stability, rather than instability, in vegetation productivity was observed in the reorganisation and exploitation phases of the adaptive cycle. The conservation phase of the floodplain adaptive cycle was found to be the most unstable, with a greater number of transitions between NDVI classes, a greater number of two-way transitions, and transitions characterised by high-frequency or low magnitude changes in NDVI class. The results from the Narran floodplain suggest that in contrast to theory, the exit point occurs in the conservation to release phase when the floodplain is wet, not dry.

6.5.1 Conclusion

This study used the hypothesised floodplain adaptive cycle model of Thapa *et al*. (2015b) to show that the adaptive cycle of floodplain vegetation response to flooding and drying repeated over multiple events. An adaptive cycle model of vegetation productivity improves on current boom-bust, state and transition models for floodplains in semi-arid regions. The adaptive cycle model acknowledges the importance of transitions between phases rather than a focus on a limited number of states – the boom (wet) or bust (dry). Semi-arid floodplains change and do so naturally, but are also increasingly influenced by anthropogenic pressures (Thoms 2003). An enhanced understanding of the complexity of floodplain change using an adaptive cycle perspective will increase our ability to model and manage these valuable but fragile ecosystems into the future.

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Chapter 7 Do adaptive cycles of floodplain vegetation response to inundation differ among vegetation communities?

Abstract

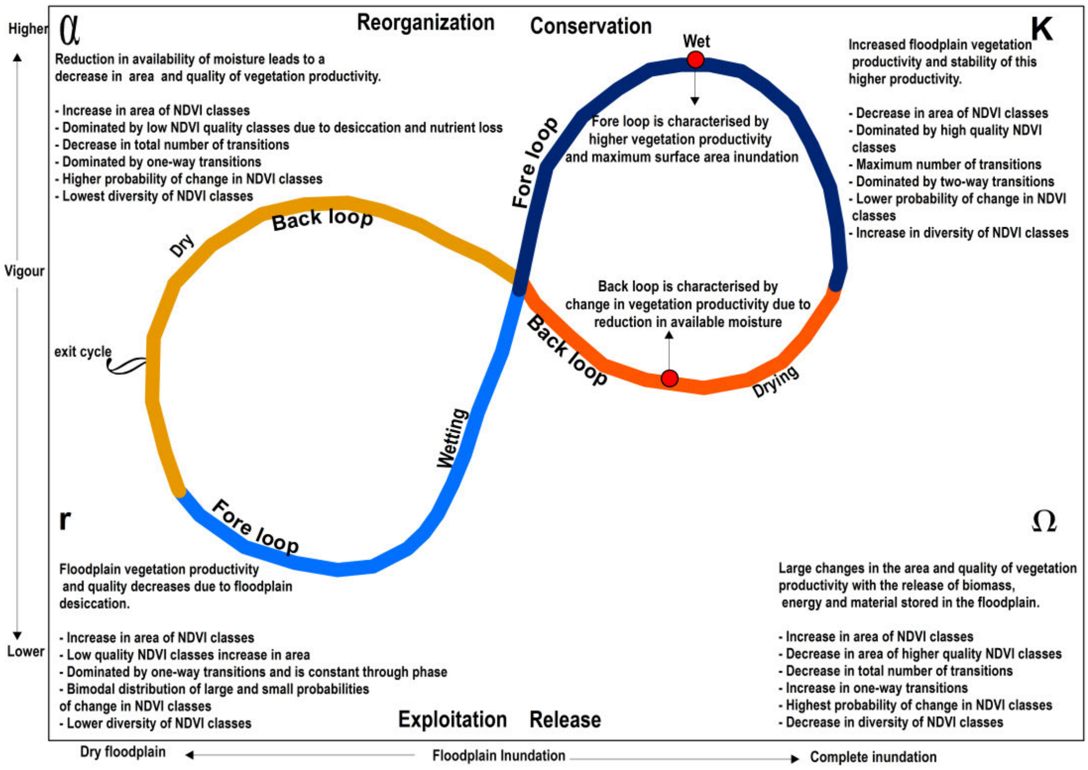
Flooding is a key driver of floodplain vegetation productivity. Adaptive cycles provide a model for examining the productivity of floodplain vegetation communities in response to hydrology. Floodplain inundation drives floodplain vegetation productivity responses through an adaptive cycle of wetting (exploitation phase), wet (conservation phase), drying (release phase) and dry (reorganisation phase) of an adaptive cycle. We examined changes in the productivity of four floodplain vegetation communities (lignum, coolibah, grass and poplar box) through an adaptive cycle and explored how the various strategies employed by these vegetation communities to cope with variation in water availability influence the adaptive cycle over multiple flooding and drying events. All four vegetation communities showed significant differences in vegetation productivity response, as indicated by changes in the Normalized Difference Vegetation Index between the adaptive cycle phases. Differences were evident in the total area of vegetation that showed a productivity response, the quality or the vigour of the response, the trajectory of change (i.e. towards higher or lower productivity) and the probability of change. Although the four vegetation communities exhibited response patterns in relation to flooding and drying that fit the adaptive cycle model, differences were evident in the timing of transitions between adaptive cycle phases and the duration spent in those phases in each vegetation community. Poplar box and coolibah communities showed a higher productivity response during the drying or release phase. By comparison the highest productivity response for the grassland and lignum shrubland was observed during the wetting or exploitation phase. Overall, the results showed the four vegetation communities are sensitive at different points in the adaptive cycle. Knowledge of floodplain vegetation response in each phase of an adaptive cycle will enable better management of floodplains, because management activities can be tailored to adaptive phase patterns associated with each community.

Keywords: NDVI, floodplains, resilience, adaptive cycles, riparian vegetation communities

7.1. Introduction

Change is an intrinsic feature of ecosystems (Pickett and White 1985, Likens 1992, Holling and Gunderson 2002) and understanding how and why ecosystems change is central to ecosystem science (Sutherland *et al.* 2013). However, changes in ecosystems are rarely simple because responses to drivers of change are mediated through a range of interactions and feedbacks between biotic and abiotic components and processes that make up most ecosystems. These interactions and feedbacks ensure that ecosystems, like other complex systems, are characterized by self-organization, nonlinear dynamics and the potential for multiple stable states (Holling and Gunderson 2002, Dearing 2008, Folke *et al.* 2010, Walker and Salt 2012). Complex systems are also characterised by resilience; the capacity to recover from disturbance and maintain the same structure, function and feedbacks (Walker and Salt 2012). Resilience theory proposes that complex systems have dynamic trajectories that often do not tend towards stable or equilibrium conditions; rather they move through an adaptive cycle. The adaptive cycle is a key component of resilience theory (Holling and Gunderson 2002) that provides a metaphor for understanding change in complex systems (Holling 1986, Gunderson and Holling 2002, Jax 2010, Walker and Salt 2012). Adaptive cycles characterize change as a cyclic process comprised of four phases: exploitation (r), conservation (K) release (Ω) and renewal (α) (Holling 1973, Gunderson and Holling 2002).

Thapa *et al.* (2015b) argued that dryland floodplain vegetation dynamics are best understood using an adaptive cycle model, whereby floodplain inundation drives vegetation response through a cycle of exploitation, conservation, release and reorganization (Figure 7.1). The dryland floodplain adaptive cycle starts as floodwater inundates the floodplain (the wetting phase) and initiates the exploitation phase of the adaptive cycle (Figure 7.1). During this phase, vegetation productivity increases as water is exploited through photosynthesis in the previously moisture-limited system. Initial productivity following wetting should be relatively low because prior to wetting the amount of photosynthetically active biomass is expected to be low, thus limiting the capacity of the system for primary production. However, as the exploitation phase proceeds, the amount of photosynthetically active biomass increases and overall rates of productivity per unit area increase accordingly. Assuming continued water availability, the capacity of vegetation to exploit available water will be curtailed by the physiological and biochemical limits to photosynthesis of individual plant species and/or by access to other potentially limiting resources such as light or nutrients. At this point, the system will enter the conservation phase. The conservation phase is a period of greatest vegetation productivity. Variation in productivity during this time is expected to be relatively low, with minor fluctuations occurring as a result of factors other than water availability, such as interspecific competition, grazing, and phenological cycles of growth and senescence in individual species. The contraction of surface water (the drying phase) reinitiates moisture limitation and triggers the release phase of the adaptive cycle, during which tightly bound resources in vegetation and soil are released and become a source for reorganization and renewal. Vegetation productivity is expected to decrease during this period. There will also be a higher probability of change in vegetation productivity due to release of biomass, energy and material stored in the floodplain during the conservation phase. Further desiccation of the floodplain occurs until it reaches a dry phase of no surface water availability. The dry phase corresponds to the reorganization phase of the adaptive cycle. During the dry phase vegetation may reorganize in to the same state that existed prior to the onset of wetting, or may exit to a new state (Holling 1973, Scheffer and Carpenter 2003).



Reduction in availability of moisture leads to a decrease in area and quality of vegetation productivity.

- Increase in area of NDVI classes
- Dominated by low NDVI quality classes due to desiccation and nutrient loss
- Decrease in total number of transitions
- Dominated by one-way transitions
- Higher probability of change in NDVI classes
- Lowest diversity of NDVI classes

Fore loop is characterised by higher vegetation productivity and maximum surface area inundation

Back loop is characterised by change in vegetation productivity due to reduction in available moisture

Increased floodplain vegetation productivity and stability of this higher productivity.

- Decrease in area of NDVI classes
- Dominated by high quality NDVI classes
- Maximum number of transitions
- Dominated by two-way transitions
- Lower probability of change in NDVI classes
- Increase in diversity of NDVI classes

Floodplain vegetation productivity and quality decreases due to floodplain desiccation.

- Increase in area of NDVI classes
- Low quality NDVI classes increase in area
- Dominated by one-way transitions and is constant through phase
- Bimodal distribution of large and small probabilities of change in NDVI classes
- Lower diversity of NDVI classes

Large changes in the area and quality of vegetation productivity with the release of biomass, energy and material stored in the floodplain.

- Increase in area of NDVI classes
- Decrease in area of higher quality NDVI classes
- Decrease in total number of transitions
- Increase in one-way transitions
- Highest probability of change in NDVI classes
- Decrease in diversity of NDVI classes

Figure 7.1 The hypothesised adaptive cycle model of semi-arid floodplain productivity. The adaptive cycle starts as floodwater inundates the floodplain in the wetting (exploitation) phase. The wet (conservation) phase is the phase of maximum inundation. The drying (release) phase starts with the contraction of water from the floodplain and the dry (reorganisation) phase occurs with desiccation of the floodplain. The cycle reflects changes in two properties: the X -axis corresponds to connectedness along a continuum from a dry floodplain to complete inundation and the Y- axis corresponds to low to high vegetation vigour. The exit from the cycle, indicated at the left of the figure, is the stage where there is potentiality a change in state (after Thapa *et al.* 2015)

Implicit in the adaptive cycle model Thapa *et al*. (2015b) is that the passage of floodplain vegetation through the four phases is controlled not only by water availability, but also physiological factors that control the capacity and rate of vegetation response to wetting and drying. This is likely to vary among plant species, depending on the adaptive strategies plants employ to cope with high levels of variability in water availability (Noy-Meir 1973, Stafford-Smith and McAllister 2008). Noy-Meir (1973) identified three functional categories to describe the strategies desert vegetation employs to cope with variability in water availability. Poikilohydric species such as algae and lichens maintain all plant parts under extreme change in hydration. Ephemeral species maintain no photosynthetically active parts during extreme dry phases. Ephemerals persist in reserve form during dry periods and are replenished with the initiation of a new pulse of moisture. Drought persistent species include all perennials that maintain some photosynthesis throughout dry phases. Stafford Smith and McAllister (2008) adapted the Noy-Meir (1973) categorisation to produce five functional response strategies of desert organisms, of which three apply to plants: in-situ persistent, refuging persistents and ephemerals.

These functional categories can be applied to plants found on floodplains in dryland regions. Floodplain trees in dryland regions, for example, are drought persistent (Noy-Meir 1973) or in-situ persistents (Stafford Smith and McAllister 2008) that maintain photosynthesis during dry times by utilising extensive and deep root systems to access limited water in the vadose zone (Noy-Meir 1973, Engel *et al*. 2005, Stafford Smith and McAllister 2008, Roberts and Marston 2011). In addition, many floodplain tree species (e.g. *Eucalyptus coolabah*) have low transpiration rates, which allow them to persist under conditions of low soil moisture during extreme dry periods (Roberts and Marston 2011). At the other extreme of flooding, a common adaptation among floodplain *Eucalyptus* is to produce adventitious roots during long periods of inundation (Gomes and Kozlowski 1980). In contrast, many grasses and shrubs found on arid and semi-arid floodplains can be categorised as ephemerals in that they persist in reserve form during dry periods. Reserve forms vary among ephemerals. Herbaceous ephemerals, for example, frequently rely on a large persistent seed bank to survive dry periods. These seeds remain dormant in the soil during long dry periods and only germinate once water becomes available (Capon 2007, Reid *et al*. 2011). Perennial grass and shrub ephemerals, by contrast, maintain biomass above and/or below ground in a dormant form. Upon wetting, these plants respond rapidly to increased water availability and grow fast during large resource pulses to increase biomass, set seed and replenish storage organs (Noy-

Meir 1973, Stafford Smith and McAllister 2008). The capacity to respond rapidly among these ephemerals is aided by adaptations such as a concentration of root biomass in surface soils, allowing them to quickly and efficiently access newly available moisture and nutrients that are concentrated in the upper 30 cm of soil (Reid *et al*. 2011, Roberts and Marston 2011, Collins *et al*. 2014).

Different response strategies among different vegetation types can result in clear productivity patterns at landscape scales. Parsons and Thoms (2013) studied vegetation productivity responses on a dryland floodplain during dry, wet and rain resource states. They found clear patterns in productivity associated with the major vegetation communities. Floodplain woodland communities, for example, maintained their greenness through all three resource states, whereas, grassland and shrubland communities were largely inactive during the dry resource state (Parsons and Thoms 2013). During the wet resource state all vegetation communities responded by increasing their greenness, but the highest response was observed in grassland and shrubland communities.

In this study we further test the Thapa *et al*. (2015b) model by exploring how the various strategies employed by dryland floodplain plants to cope with variation in water availability influences the adaptive cycles these plants exhibit at the community level of organisation. The study utilises four floodplain vegetation community types to explore response to wetting: coolibah (*Eucalyptus coolabah*) woodland, poplar box (*Eucalyptus populnea*) woodland (both in situ persistents), grassland and lignum (*Duma florulenta*) shrubland (both ephemerals). Based on the adaptive cycle model (Figure 7.1) we examine four hypotheses about adaptive cycles exhibited by vegetation communities in response to flooding. First, the major vegetation communities will exhibit an adaptive cycle in response to flooding. However, following from the plant strategy frameworks of Noy-Meir (1973) and Stafford-Smith and McAllister (2008) and vegetation response patterns observed by Parsons and Thoms (2013) we expect that the adaptive cycles exhibited by vegetation communities will differ. Thus, our second hypothesis is that the capacity of ephemerals to respond quickly should ensure that grassland and lignum shrubland enters the exploitation phase earlier after the initiation of wetting and proceeds to the conservation phase quicker than the woodland coolibah and poplar box communities. The third hypothesis is that the capacity of in-situ persistent woodland communities to access scarce water should ensure that these communities enter the release and reorganisation phases later than grassland and lignum shrubland. Our fourth hypothesis is that the amplitude of response to wetting over the course of adaptive cycles should be greater in grassland and lignum shrubland communities, reflecting their adaptive strategy of dormancy during periods of water scarcity.

7.2. Study area and methods

7.2.1 Study area

The Narran floodplain extends between 29° 40' – 29° 57' S and 147° 16' – 147° 30' E and covers an area of 296 km^2. Located within the lower Condamine Balonne Catchment, in the northern-most part of the Murray Darling Basin, NSW, south east Australia (Figure 7.2) the landscape of the Narran floodplain is geomorphologically complex with numerous lakes, channel networks and dissected floodplain surfaces. The geology of the Narran floodplain is dominated by Quaternary alluvial sediments composed of moderately to highly weathered sedimentary rocks (Galloway *et al.* 1974). The soil types in this landscape consist of hard setting red-brown earth (*red and brown Chromosols*), pellitised clays (*Lunettes*), deep grey (*Grey Vertosols*), brown (*Brown Vertosols*) and black self-munching, cracking and non-cracking clays. The higher elevated areas of the Narran floodplain landscape consist of hard and soft red earth, gilgai clays and sandy rises (NFRPC 2004).

The climate of the Narran floodplain is semi-arid with average maximum summer and winter temperatures of 36° C and 19° C respectively. Average annual rainfall (1940 – 2009) is 448 mm at Collarenebri (Station 048038) and average annual evaporation at Cobar is 2,250 mm . Rainfall is highly variable within and between years: the lowest annual rainfall was 144 mm in 2002 and the highest was 957 mm in 1950. Most rainfall in the Condamine Balonne River catchment occurs in the well-watered uplands in the summer months (November – February) associated with tropical monsoonal activity. As a consequence, flows into the Narran floodplain are highly variable. The long term mean annual discharge (1965 – 2009) of the Narran River is 128,717 ML (Wilby Wilby, Gauge 422016), with the largest recorded annual discharge exceeding 690,000 ML in 1983 and the lowest annual discharge of 1003 ML recorded in 2002. The Narran floodplain remains dry approximately 60% of the time (Rayburg and Thoms 2009). Thus, there are periodic dry and wet resource states in the Narran floodplain arising from variability in Narran River hydrology (Murray *et al.* 2006).

The Narran floodplain contains several vegetation communities (NFRPC 2004) but is dominated by four major vegetation community types (Figure 7.2), which were selected as the focus for this study. Extensive areas of the floodplain are dominated by the perennial shrub lignum (*Duma florulenta*). Lignum shrubland occupies 11,242 ha (38%) of the floodplain area, mostly in the north western and the central part of the Narran floodplain and along the main channel of the Narran River (Figure 7.2). Lignum shrubland may also feature a very sparse overstorey of woodland species such as coolibah (*Eucalyptus coolabah*), river red gum (*Eucalyptus camaldulensis*), black box (*Eucalyptus largiflorens*), poplar box (*Eucalyptus populnea*), leopardwood (*Flindersia maculosa*), gidgee (*Acacia cambagei*), white cypress pine (*Callitris glaucophyll),* and smaller shrub/tree species such as river cooba (*Acacia stenophylla*) and eurah (*Eremophila bignoniiflora*).

The second major vegetation community of the Narran floodplain is grassland, covering 4,163 ha (14%) of the floodplain area. Grassland consists of Mitchell grass (*Astrebla spp*), neverfail (*Eragrostis setifolia*), box grass (*Paspalidium constrictum*), kangaroo grass (*Themeda triandra*) and Warrego summer grass (*Paspalidium jubiflorum*) interspersed among clumps of trees and shrubs. Grassland is mostly found in the south eastern and central western part of the floodplain (Figure 7.2). The third major vegetation community type is a complex of riparian and mixed woodlands that cover 2,616 ha (9%) of the floodplain area. This community complex (hereafter referred to as coolibah woodland) is dominated by coolibah, but other tree species such as belah (*Casuarina cristata*), gidgee, leopardwood, mulga (*Acacia aneura*), black box, river red gum, poplar box, and whitewood (*Atalaya hemiglauca*) are also interspersed through the coolibah woodland. Common shrubs within coolibah woodland include lignum, eurah, river cooba, budda (*Eremophila duttonii*), spiny saltbush (*Rhagodia spinescens*) and wild orange (*Capparis mitchellii*). The fourth major vegetation community type is poplar box woodland, which covers 1,218 ha (4%) of the floodplain area. This community is dominated by poplar box but other tree species such as coolibah, leopardwood, mulga, belah, whitewood, wilga (*Geijera parviflora),* mulga and white cypress pine also occur within the community. The remaining community types were excluded from the study. A small area of mixed woodland, mostly dominated by leopardwood and gidgee and shrubs such as spiny saltbush covers 65 ha (0.2%) of the floodplain area, mostly in the north eastern and north western part of the floodlain (Figure 7.2). Crops and annual pastures also occupy a significant area of the Narran floodplain, covering 4,784 ha (16%). The remaining 5,495 ha (19 %) of the Narran floodplain is covered by lakes and barren ground. The Narran floodplain was gazetted as National Park in 1988 and listed as a Ramsar wetland of international importance in 1999.

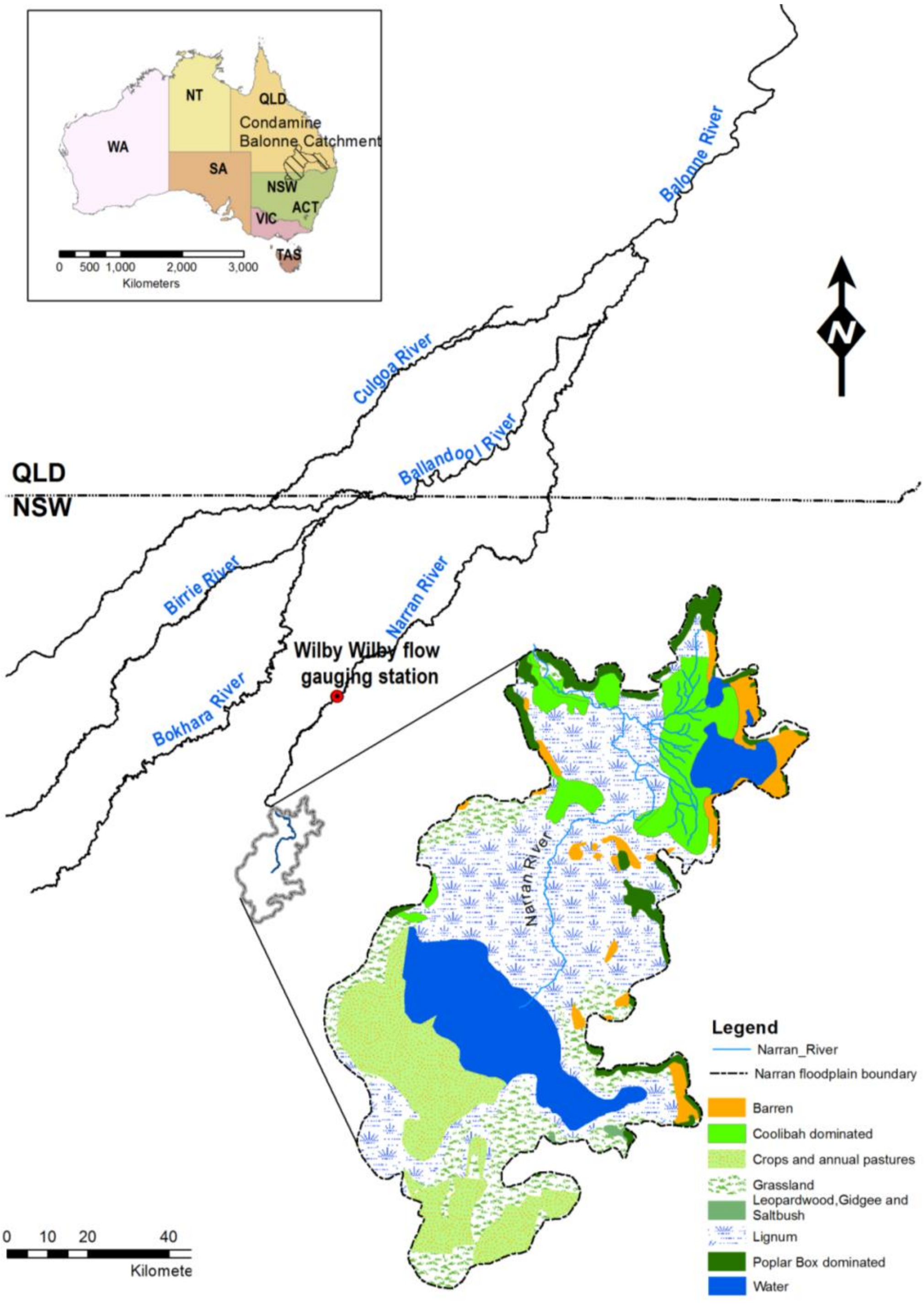


Figure 7.2 Location of the Narran floodplain within the Condamine Balonne Catchment and the distribution of vegetation communities within the Narran floodplain. Vegetation communities are derived from (NFRPC 2004).

7.2.2 Methods

7.2.2.1 Satellite Image selection and delineation of adaptive cycle phases

Remotely sensed Landsat TM/ETM+ satellite images were used to track vegetation productivity through dry and flood periods in the Narran floodplain. A detailed description of image selection and allocation of images to adaptive cycle phases is given in (Thapa *et al.* 2015b). In summary, dry and wet periods were identified from the hydrological (Narran River at Wilby Wilby) and rainfall (Collarenebri) records. A dry period is no flow or flow below the long-term 95th percentile flow, combined with below average rainfall. A flood period is defined as flow above 13,000 MLD, which is that flow required to initiate floodplain inundation (Thapa *et al.* 2015b). The availability of high-quality, cloud-free Landsat satellite images (Path 92, Row 81) corresponding to dry and flood periods was examined. From the pool of high-quality satellite images four dry years (1987, 1993, 2002, and 2007) and four flood years (1988, 1994, 2004, and 2008) were selected, corresponding to paired flood-dry events. A sequence of images was selected at approximately monthly intervals in each year. The dry period image sequence stopped when rain occurred, and the flood period image sequence stopped when floodwater completely contracted and dry images started. Images were cropped to a standard floodplain area and resampled to 25 metre resolution. Overall, 75 images were extracted across the four events (for detail see Table 3.1). Phases of the adaptive cycle for each event were delineated from the area of floodplain inundation (Thapa *et al.* 2015b). The wetting phase is an initial expansion of floodwater across the floodplain. The wet phase is a phase of maximum flood inundation. The drying phase is associated with the contraction of floodwaters. The dry phase is associated with no surface water availability. Based on the area of flooding and the trajectory of flood inundation (expanding, contracting, no surface water) each of the 75 images was allocated to the corresponding wetting, wet, drying or dry phase of the adaptive cycle.

7.2.2.2 Calculation of NDVI and Delineation of Vegetation Community Types

The Normalised Difference Vegetation Index (NDVI) is a greenness measure calculated from red and near infrared (NIR) reflectance properties of vegetation. The NDVI is strongly correlated with photosynthetic activity and hence is a surrogate of vegetation productivity (Lillesand and Kiefer 2000, Wang *et al.* 2004, Farina 2006, Wen *et al.* 2012). The NDVI was calculated in each image as the normalized differences of the spectral reflectance of NIR and visible (red) using equation 1.

$$NDVI \ = \rho nir - \rho red \ / \ \rho nir + \rho red \qquad (1)$$

where ρ represents the spectral reflectance values of spectral bands of Landsat TM/ETM+ image nir (Band 4) and red (Band 3). Entropy analysis and moving window analysis was used to form the 473,142 NDVI pixel values into a minimum number of NDVI groups accounting for the greatest variance in the data set (Parsons and Thoms 2013). Six NDVI classes emerged. Class 1 (NDVI <0) is no greenness. Class 2 (NDVI 0-0.072), Class 3 (NDVI 0.073-0.207), Class 4 (0.208-0.459), Class 5 (NDVI 0.460-0.666) and Class 6 (NDVI >0.666) represent a continuum of increasing vegetation productivity.

Spatial distribution of the four major vegetation communities in the Narran floodplain (lignum shrubland, grassland, poplar box woodland, coolibah woodland) were extracted from a published 1:50000 map of vegetation communities and land cover types (Parsons and Thoms 2013). The accuracy of this mapping has been verified and ground-truthed (NFRPC 2004, Murray *et al*. 2006, Rayburg and Thoms 2009). The vegetation community map was overlain with the NDVI Class data to determine the area of NDVI Classes 1-6 associated with each vegetation community in each of the 75 images (belonging to a specific adaptive cycle phase). This data set formed the basis for extracting variables representing vegetation productivity dynamics.

7.2.2.3 Analysis of vegetation productivity through the adaptive cycle phases

Four elements of NDVI were used to examine vegetation community productivity through the wetting, wet, drying and dry phases of the adaptive cycle: total area of NDVI; quality of NDVI; number and direction of NDVI class transitions and probability of NDVI class transitions. The total area of active vegetation vigour (NDVI classes 2-6), hereafter termed total response area, was calculated for each image. The quality of vegetation vigour (individual NDVI classes 2-6), hereafter termed response quality, was also calculated for each image.

Pair-wise transitions between NDVI classes were calculated on a pixel-by-pixel basis between sequential images (hereafter termed periods). In each vegetation community, each pixel was classified into a change class C_{ij} which represents a change from NDVI class *i* to NDVI class *j*. A total of 36 C_{ij} were possible among the six NDVI classes, comprising six constant classes and 30 change classes. First-order Markovian transition models (Weng

2002, Rogers and O'Keeffe 2003, Bolliger *et al.* 2009) were used to model the number and direction of NDVI class change and the probability of NDVI class changes between sequential images. The Markovian transition model consists of each NDVI class C_{ij} present in each period and the probability P_{ij} of each C_{ij} occurring. Periods were allocated to the corresponding wetting, wet, drying or dry phase of the adaptive cycle. The total number of changes and the direction of changes (one-way or two-way) between NDVI classes was tallied from a pictorial representation of the Markovian transition model (e.g. Appendix 3). A change direction ratio of one-way to two-way changes was also computed. The probability of change P_{ij} was calculated based on the proportion of the total area of NDVI class *i* that transitioned to NDVI class *j*. These probabilities were then categorized as very small (<1%), small (1-5%), small to moderate (5-10%), moderate to large (10-20%), large (20-50%) and very large (>50%).

7.2.2.4 Multivariate data analysis

Differences in area and quality of NDVI response, the number and direction of changes and the probability of changes between adaptive cycle phases and vegetation communities were determined using permutational multivariate analysis of variance (PERMANOVA). For these analyses a sample was considered as the image (area and quality; n= 75 x four vegetation communities), or the period between sequential images (the number and direction of changes and probability of changes; n= 67 x four vegetation communities). The response variables were the range of variables that characterised each image and community combination with respect to total area and quality of NDVI classes, number and direction of changes (one-way and two-way) and probability of change classes.

Resemblance matrices were calculated using the Bray Curtis similarity coefficient to compare image/period x vegetation community combinations with respect to the area and quality of NDVI, the number, direction and probability of changes. These matrices were used as inputs in PERMANOVA (Anderson *et al.* 2008) to determine whether significant differences could be detected between the four vegetation communities and adaptive cycle phases and to determine whether there were differences between communities within the adaptive cycle phases.

7.3. Results

There was a significant difference in NDVI responses between the four Narran floodplain vegetation communities and their adaptive cycle phases (Figs 3–14). These differences in NDVI response were evident for all variables: response area and quality, number of changes, direction of changes and the probability of change. The greatest differences between adaptive cycle phases and vegetation communities were observed in area and quality followed by direction of change data.

7.3.1 Differences between the coolibah woodland community adaptive phases

The total response area (i.e. NDVI Classes 2-6) for coolibah woodland was greater during the dry phase than the wetting, wet and drying phases (Figure 7.3). Response quality also differed between the phases (Figure 7.3). During the wetting phase NDVI Class 4 contributed most to the total response area, followed by NDVI Class 3, NDVI Class 2 and NDVI Class 5 while NDVI Class 6 contributed the least. During the wet phase, greenness was generally higher, with the area occupied by NDVI Class 4 and 5 both increasing and the area occupied by NDVI Class 3 and 2 decreasing. The response area occupied by NDVI Class 6 remained very low. There was a further moderate increase in NDVI during the drying phase, with increases in the response area occupied by NDVI Class 4 and 5, an increase in the response area occupied by NDVI Class 3 and a further decline in the response area occupied by NDVI Class 2. During the dry phase, NDVI values declined with the response area occupied by NDVI Class 2 and 3 increasing and the area occupied by NDVI Class 4 and 5 decreasing. NDVI Class 6, representing the highest vegetation greenness, did not occur during the dry phase (Figure 7.3). In summary, the total area of coolibah woodland showing greenness was higher in the dry phase than the wetting, wet and drying phases. However, the degree of greenness in coolibah woodland was greater in the drying phase followed by wet, wetting and dry phases.

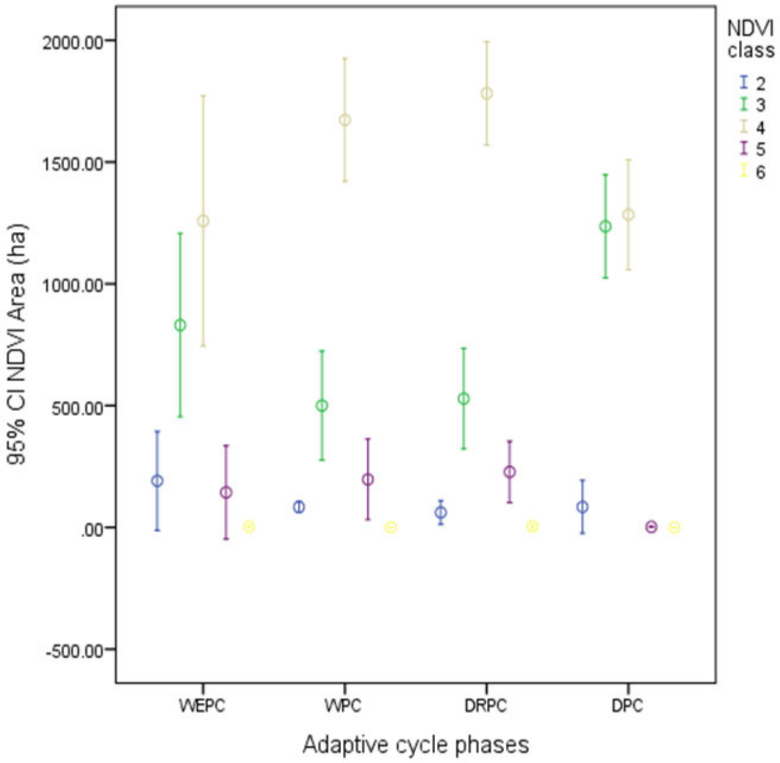


Figure 7.3 The area of NDVI Classes 2-6 for coolibah woodland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPC = wetting phase coolibah, WPC = wet phase coolibah, DRPC = drying phase coolibah and DPC = dry phase coolibah.

The total number of changes among the NDVI classes differed markedly between phases. Overall, the greatest number of changes occurred during the wet phase (293) followed by the drying (287), dry (125) and wetting (65) phase. The total number of changes was influenced by the number of periods sampled. The wetting phase had 5 periods, while the wet, drying and dry phase had 15, 20 and 27 periods respectively. Thus, the average number of changes per period was highest in the wet and drying phase, followed by the wetting phase with the lowest number of changes overall in the dry phase (Figure 7.4).

One-way and two-way directional changes occurred in all phases (Figure 7.4) but the change direction ratio of one-way to two-way changes differed among the four phases. During the wetting phase a total of 23 one-way changes and 42 two-way changes occurred. In comparison, the wet phase had 44 one-way and 249 two-way changes and the drying phase had 59 one-way and 228 two-way changes. Finally, the dry phase had 43 one-way and 82 two-way changes. Overall, the change direction ratio was lower in the wet phase (mean = 0.21) compared to the dry phase (mean = 0.65). For all phases a regular pattern in the change direction ratio was observed between the NDVI classes of the coolibah woodland community, whereby the ratio was lowest during the wet phase, followed by the drying phase and with the highest ratios observed during the dry and wetting phase of the adaptive cycle**.**

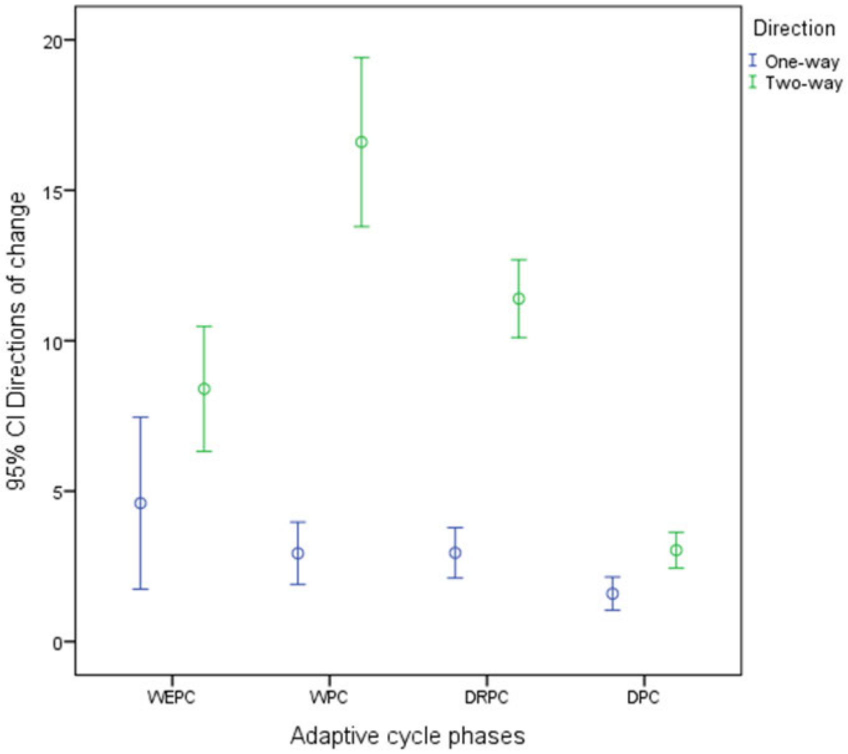


Figure 7.4 Direction of change (one-way or two-way) between coolibah woodland NDVI classes in the dry, wetting, wet and drying phases of the adaptive cycle. WEPC = wetting phase coolibah, WPC = wet phase coolibah, DRPC = drying phase coolibah and DPC = dry phase coolibah

The probability of change between NDVI classes was dominated by changes with a very small probability of change (that is, most changes affected a small proportion of area) and these very small probability changes were the most common probability type in all phases. However, differences were evident in the distribution of probability of change classes between the phases. During the wetting phase the very small probability of change class was largest, followed by the small and large probability of change classes, with the lowest number of changes in the very large probability of change class (Figure 7.5).

The wet phase followed a similar pattern, with very small and small probability changes most abundant and with relatively few intermediate and very large probability changes. The wet phase differed from the wetting phase in that the number of large probability changes was greater (Figure 7.5). The drying phase was also dominated by very small and small probability changes, with very few changes in the intermediate probability class. The drying phase contrasted with the wetting and wet phases in that the number of very large probability changes was relatively high. Finally, the dry phase differed to other phases due to the substantially lower number of changes in all probability classes, but also in the relatively large number of relatively high number of large and very large probability changes compared to small and intermediate probability changes (Figure 7.5).

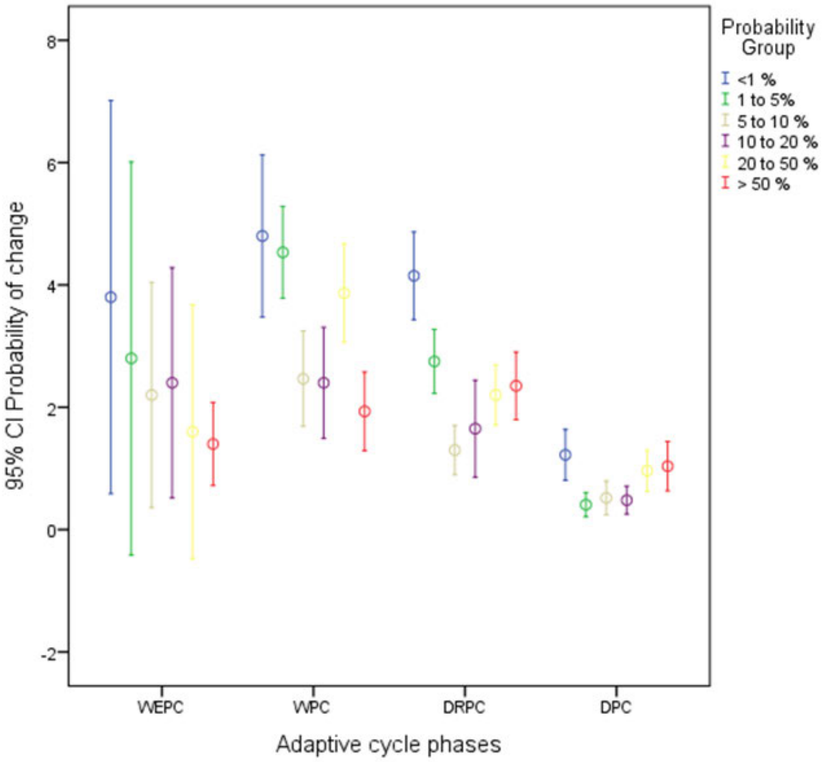


Figure 7.5 Distribution of the probability of NDVI class changes for coolibah in the wetting, wet, drying and dry phases of the adaptive cycle. WEPC = wetting phase coolibah, WPC = wet phase coolibah, DRPC = drying phase coolibah and DPC = dry phase coolibah.

7.3.2 Differences between the grassland community adaptive cycle phases

The total response area for grassland (NDVI Class 2-6) was also greater during the dry phase than the wetting, wet and drying phases (Figure 7.6). Response quality also differed between the phases (Figure 7.6). During the wetting phase NDVI Class 3 had the greatest contribution to the total response area, followed by NDVI Class 5, NDVI Class 4 and NDVI Class 6, whereas NDVI Class 2 contributed the least to the total response area. During the wet phase, greenness was generally higher, with the area occupied by NDVI Class 3 and 4 both increasing and the area occupied by NDVI Class 5 and 2 decreasing. The area occupied by NDVI Class 6 remained low. There was a further moderate decrease in greenness during the drying phase, with increases in the area occupied by NDVI Class 3 followed by NDVI Class 4, an increase in the area occupied by NDVI Class 2 and a further decline in the area occupied by NDVI Class 5 followed by NDVI Class 6. Finally, during the dry phase there was a greater increase in NDVI Class 3 area. However, in the other NDVI classes, greenness declined further in area and, to a lesser extent, NDVI Class 4, Class 2, and NDVI Class 5. NDVI Class 6 (representing the highest vegetation greenness), did not occur during the dry phase (Figure 7.6). In summary, the total area of grassland community showing greenness was higher in the dry phase than the wetting, wet and drying phases. However, the degree of greenness in grassland community was greater in the wetting phase followed by the drying, wet and dry phases.

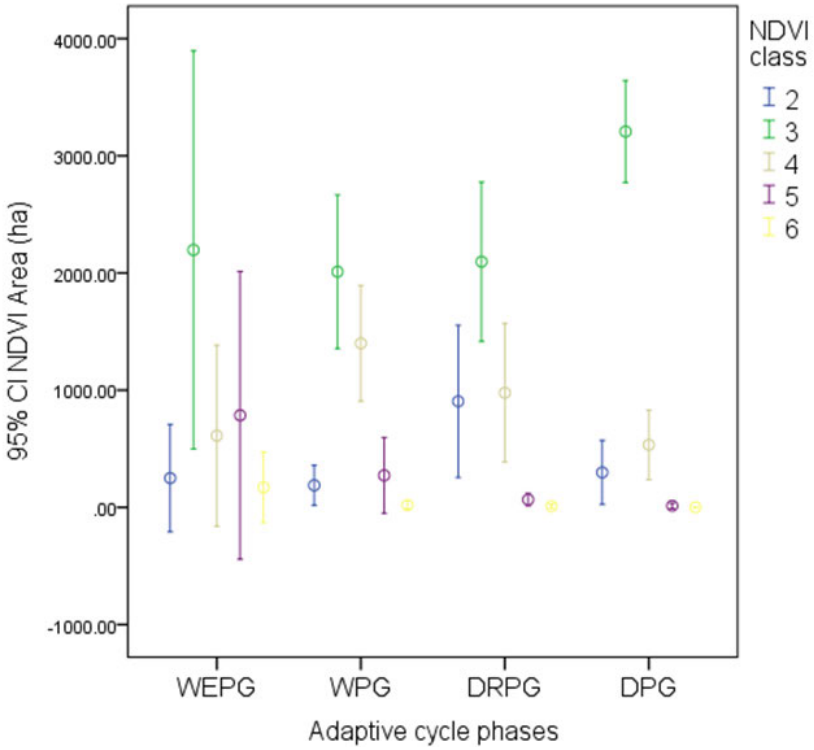


Figure 7.6 The area of NDVI Classes 2-6 for grassland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPG = wetting phase grassland, WPG = wet phase grassland, DRPG = drying phase grassland and DPG = dry phase grassland.

The total number of changes among NDVI classes also differed markedly between the phases. Overall, the greatest number of changes occurred during the wet phase (244) followed by the drying (215), dry (210) and wetting (52) phases (Figure 7.7). The total number of changes was again influenced by the number of periods sampled. Thus, the average number of changes per period was highest in the wet (mean = 16, range = 11-26) and drying (mean = 11, range = 5-22) phases, followed by the wetting phase (mean = 10, range = 6 -16) with the lowest number of changes overall in the dry phase (mean = 8, range = 4-15; Figure 7.7).

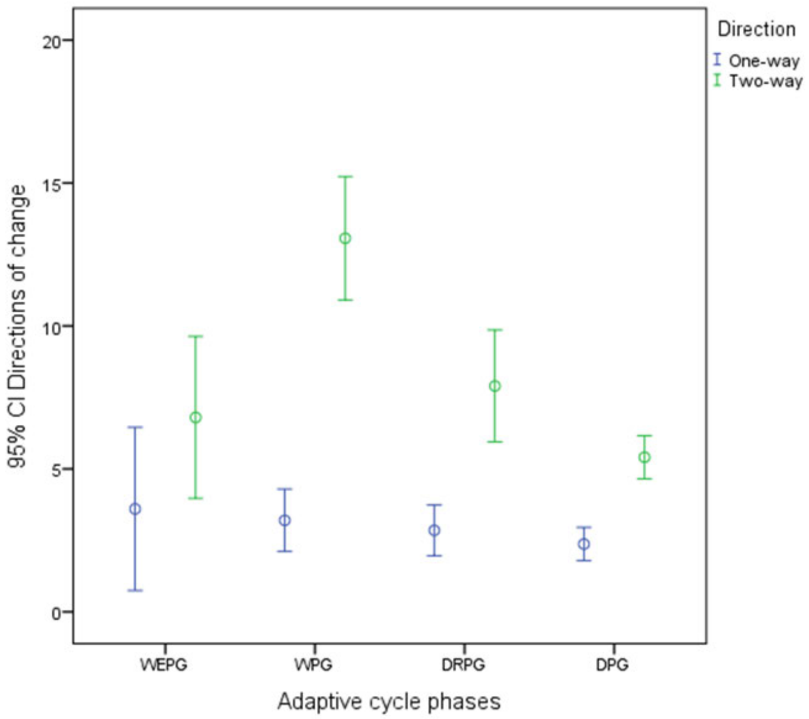


Figure 7.7 Direction of change (one-way or two-way) between grassland NDVI classes in the dry, wetting, wet and drying phases of the adaptive cycle. WPG = wet phase grassland, DRPG = drying phase grassland and DPG = dry phase grassland.

Both one-way and two-way changes occurred in all the phases (Figure 7.7). During the wetting phase a total of 18 one-way changes and 34 two-way changes occurred. In comparison, the wet phase had 48 one-way and 196 two-changes and the drying phase had 57 one-way and 158 two-way changes. Finally, the dry phase had 64 one-way and 146 two-way changes (Figure 7.7). For all phases a regular pattern in the change direction ratio was observed, whereby the ratio was lowest during the wet phase, followed by the drying phase and the highest ratios observed during the wetting and dry phases of the adaptive cycle. The change direction ratios were lower in the wet phase (mean = 0.25) compared to the wetting (mean = 0.54) and dry (mean = 0.51) phases.

Like the coolibah woodland, very small probability changes were the most common changes in all phases, with differences evident in the distribution of probability of change classes between the phases. During the wetting phase most changes were very small probability changes. The next most common changes were very large and small probability changes with the lowest number of changes being intermediate and large probability changes (Figure 7.8).

The wet phase followed a similar pattern, albeit with more changes overall, being dominated by very small and small probability changes and with relatively few intermediate and very large probability changes. The wet phase differed from the wetting phase in that the number of large probability changes was greater (Figure 7.8). The drying phase was also dominated by very small, large and very large probability changes with very few intermediate probability changes. The drying phase contrasts with the wetting and wet phases due to the relatively small number of very low and low probability changes. Finally, the dry phase was dominated by very small and very large probability changes, with lowest numbers of intermediate probability changes (Figure 7.8).

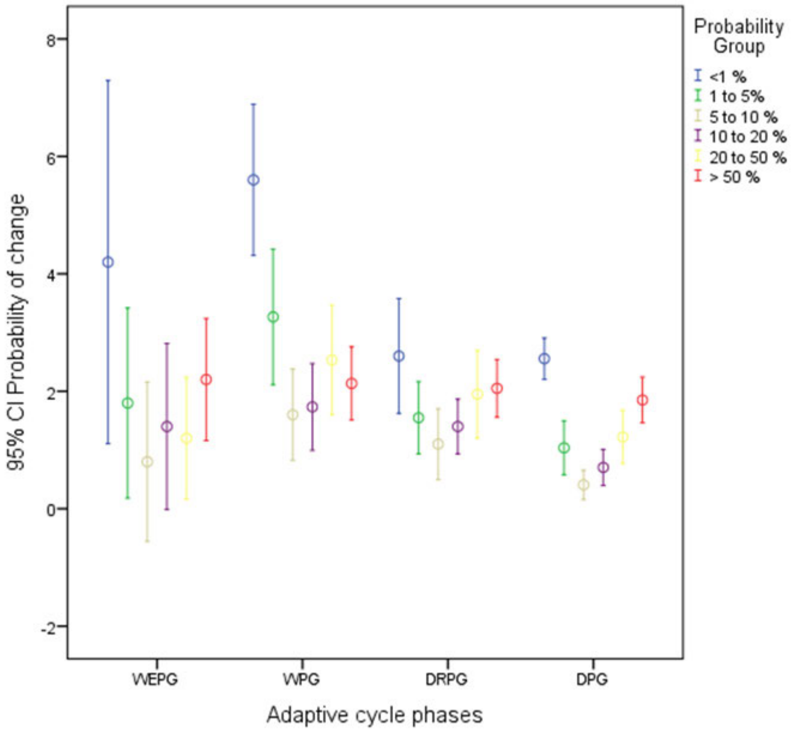


Figure 7.8 Distribution of the probability of NDVI class changes for grassland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPG = wetting phase grassland, WPG = wet phase grassland, DRPG = drying phase grassland and DPG = dry phase grassland.

7.3.3 Differences between the lignum community adaptive cycle phases

The total response area for lignum (NDVI Class 2-6) was greater during the dry phase than the wetting, drying and wet phases (Figure 7.9). Response quality within lignum differed between the phases (Figure 7.9). During the wetting phase NDVI Class 3 covered the greatest response area, followed by NDVI Class 4, NDVI Class 5 and NDVI Class 2. NDVI Class 6 contributed the least to the total response area. During the wet phase, there was a sharp increase in the contribution of NDVI Class 4, and a smaller increase in NDVI Class 5. In contrast, the response area of NDVI Class 3 decreased from that of the wetting phase. The area occupied by NDVI Class 2 and 6 decreased slightly from the already low levels of the wetting phase. There was a decrease in greenness during the drying phase, with areas occupied by NDVI Class 4, 5 and 6 all falling and areas occupied by NDVI Class 2 and 3 rising. Finally, during the dry phase the area occupied by NDVI Class 3 area rose further to the highest level across all phases. The areas occupied by NDVI Classes 2, 4, 5 and 6 all fell (NDVI Class 6 did not occur during the dry phase) (Figure 7.9). Thus, the total area of lignum shrubland community showing greenness was higher in the dry phase than the wetting, wet and drying phases. However, the degree of greenness in the lignum community was greater in the wetting phase followed by the wet, drying and dry phases.

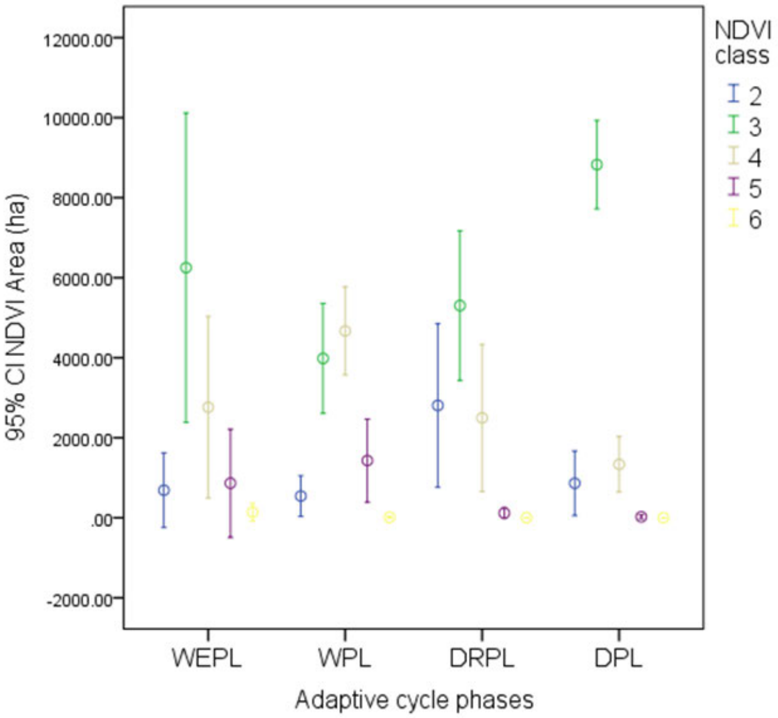


Figure 7.9 The area of NDVI Classes 2-6 for lignum shrubland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPL = wetting phase lignum, WPL = wet phase lignum, DRPL = drying phase lignum and DPL = dry phase lignum.

The total number of changes among the NDVI classes differed markedly between the phases. Overall, the greatest number of changes occurred during the wet phase (275) followed by the drying (250), dry (200) and wetting (63) phases (Figure 7.10). When the number of periods sampled in each phase is considered, the average number of changes per period was highest in the wet (mean = 18, range = 8-29) and drying (mean = 13, range = 5-20) phases, followed by the wetting phase (mean = 13, range = 9-17) with the lowest number of changes in the dry phase (mean = 7, range = 3-11; Figure 7.10).

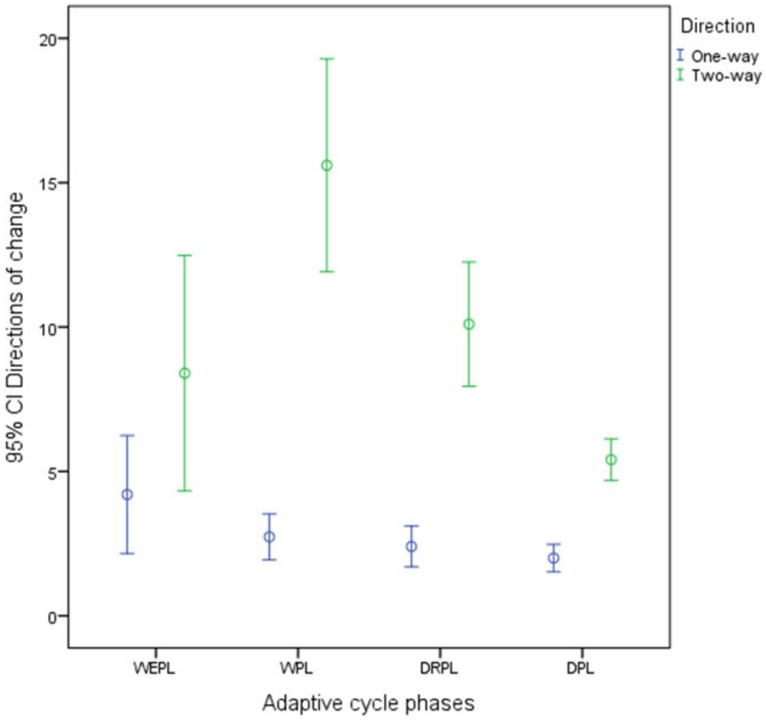


Figure 7.10 Direction of change (one-way or two-way) between lignum shrubland NDVI classes in the dry, wetting, wet and drying phases periods of the adaptive cycle. WEPL = wetting phase lignum, WPL = wet phase lignum, DRPL = drying phase lignum and DPL = dry phase lignum.

Both one-way and two-way changes occurred in all the phases (Figure 7.10). During the wetting phase a total of 21 one-way changes and 42 two-way changes occurred. In comparison, the wet phase had 41 one-way and 234 two-way changes and the drying phase had 48 one-way and 202 two-way changes. Finally, the dry phase had 54 one-way and 146 two-way changes (Figure 7.10). For all phases a regular pattern in the change direction ratio was observed between the NDVI classes of the lignum shrubland community, whereby the ratio was lowest during the wet phase, followed by the drying phase and with the highest ratios observed during the wetting and dry phases. The change direction ratio was significantly lower in the wet phase (mean = 0.25) compared to the wetting phase (mean = 0.63).

Like coolibah and grassland, very small probability changes were the most common probability type in all phases but differences were evident in the distribution of probability of change classes between the phases. During the wetting phase very small probability changes were most abundant followed by small and large probability changes. The lowest change was noticed in the very large probability of change classes (Figure 7.11). The wet phase followed a similar pattern to the wetting phase, with the important difference that all probability changes were more abundant (Figure 7.11). The drying phase was also dominated by very small and small probability changes with very few intermediate probability changes. The drying phase contrasts with the wetting and wet phases largely because probability changes are relatively low and very large probability changes relatively high. Finally, the dry phase differed to other phases due to the substantially lower number of changes, but also in the relatively large proportion of very small and very large probability changes (Figure 7.11).

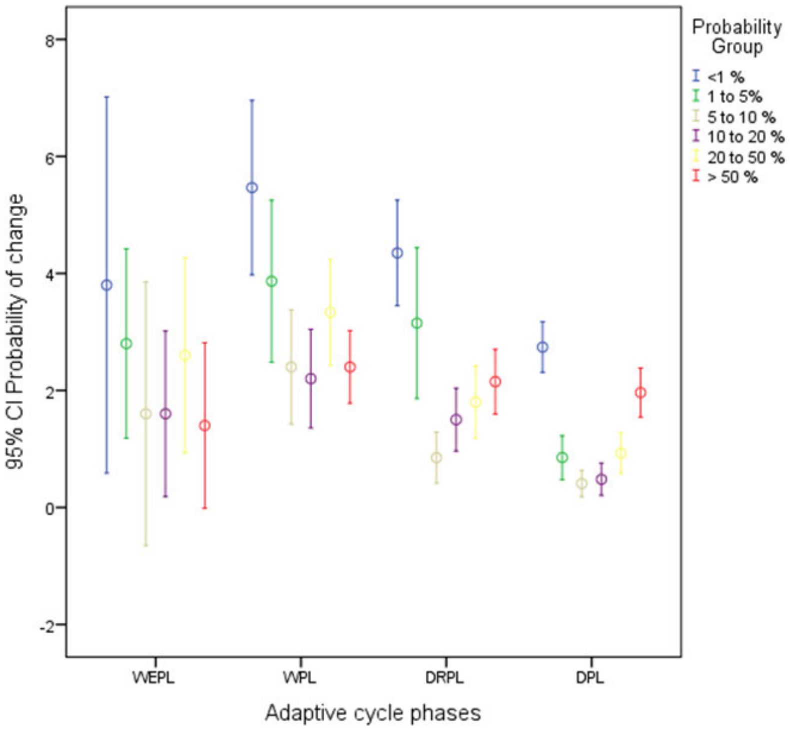


Figure 7.11 Distribution of the probability of NDVI class changes for lignum shrubland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPL = wetting phase lignum, WPL = wet phase lignum, DRPL = drying phase lignum and DPL = dry phase lignum.

7.3.4 Differences between the poplar box woodland community adaptive cycle phases

The total response area for poplar box woodland was greater during the dry phase than the drying, wet and wetting phases (Figure 7.12). Response quality within poplar box woodland also differed between the phases (Figure 7.12). During the wetting phase NDVI Class 3 contributed the most to the total response area, followed by NDVI Class 4, NDVI Class 5, NDVI Class 2 and NDVI Class 6. During the wet phase, response quality was similar with the area of NDVI Class 3 and 4 clearly highest and the area of the other classes very low. In contrast to the wetting phase, however, NDVI Class 4 covered a greater area than NDVI Class 3 during the wet phase. There was a decrease in greenness during the drying phase, with an increase in the area occupied by NDVI Class 3 and NDVI Class 2 and a decrease in the area of NDVI Class 4. There was also a decrease in the area of NDVI Class 5. NDVI

Class 6 representing the highest greenness did not occur during the drying phase. Finally, during the dry phase, greenness increased slightly with small increases in the areas occupied by NDVI Class 3, and NDVI Class 4 and a decline in the area in NDVI Class 5. In the drying phase NDVI Class 6 did not occur during the dry phase (Figure 7.12). In summary, the total area of poplar box woodland showing greenness was higher in the dry and drying phases than the wet and wetting phases.

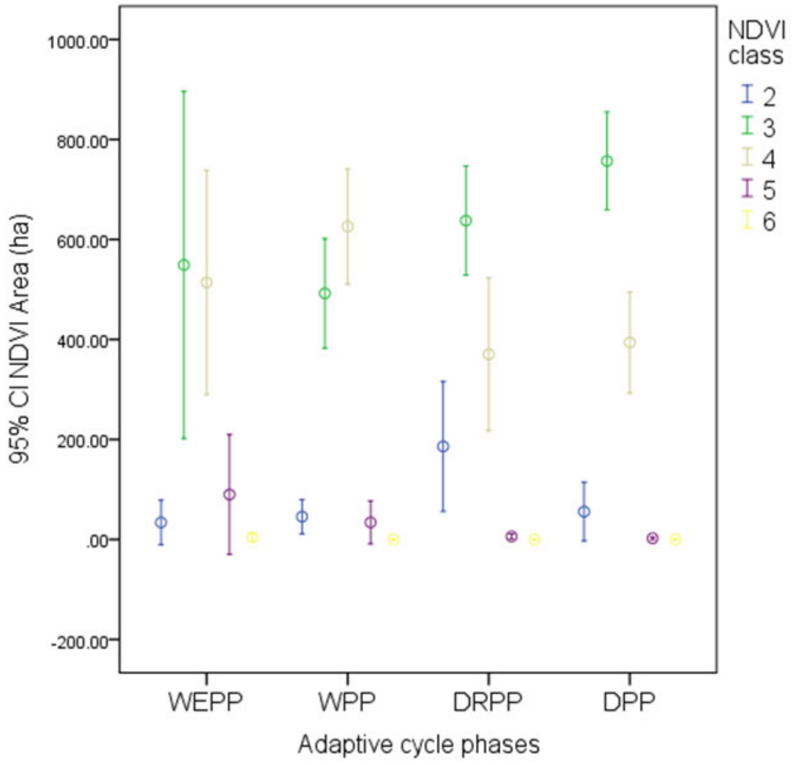


Figure 7.12 The area of NDVI Classes 2-6 for poplar box woodland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPP = wetting phase poplar box, WPP = wet phase poplar box, DRPP = drying phase poplar box and DPP = dry phase poplar box.

The total number of changes among the NDVI classes differed markedly between the phases. Overall, the greatest number of changes occurred during the wet phase (224) followed by drying (192), dry (179) and wetting (57) phases (Figure 7.13). The total number of transitions was influenced by the number of periods sampled. Thus, the average number of changes per period was highest in the wet (mean = 15, range = 9-24) and wetting (mean = 11, range = 9-14) phases, followed by the drying phase (mean = 10, range = 5-16) with the lowest number of changes overall in the dry phase (mean = 7, range = 3-11; Figure 7.13).

Both one-way and two-way directional changes occurred in all the phases (Figure 7.13). During the wetting phase a total of 18 one-way changes and 39 two-way changes occurred. In comparison, the wet phase had 28 one-way and 196 two-way changes and the drying phase had 47 one-way and 145 two-way changes. Finally, the dry phase had 53 one-way and 126 two-way changes (Figure 7.13). For all phases a regular pattern in the change direction ratio was observed between the NDVI classes, whereby the ratio was lowest during the wet phase, followed by the wetting phase with the highest ratios observed during the drying and dry phases of the adaptive cycle. The change direction ratio was lower in the wet phase (mean = 0.18) compared to the dry phase (mean = 0.51).

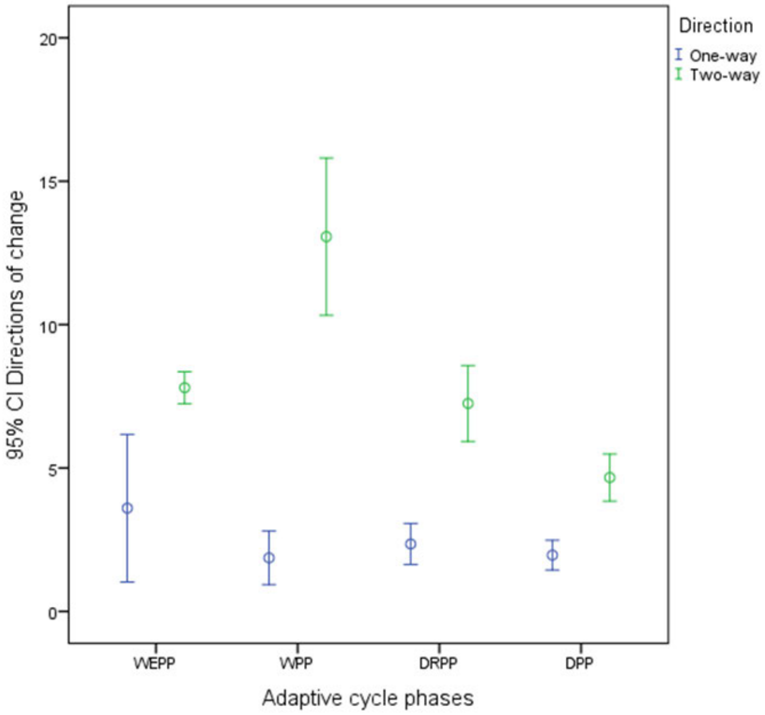


Figure 7.13 Direction of change (one-way or two-way) between poplar box woodland NDVI classes in the dry, wetting, wet and drying phases of the adaptive cycle. WEPP = wetting phase poplar box, WPP = wet phase poplar box, DRPP = drying phase poplar box and DPP = dry phase poplar box.

Like the other vegetation communities, very small probability changes were the most common change in all phases (Figure 7.14). During the wetting phase small probability changes were the next most common change type, followed by large and very large probability changes, with the fewest changes being intermediate probability changes (Figure 7.14). All probability changes except very large, were more common during the wet phase, with the greatest increases in intermediate and large probability changes (Figure 7.14). There were fewer changes of all probability types during the drying phase, with the greatest decline in small to moderate probability changes. Finally, there were fewer still changes during the dry phase, although there was a slight increase in the number of very large probability changes (Figure 14).

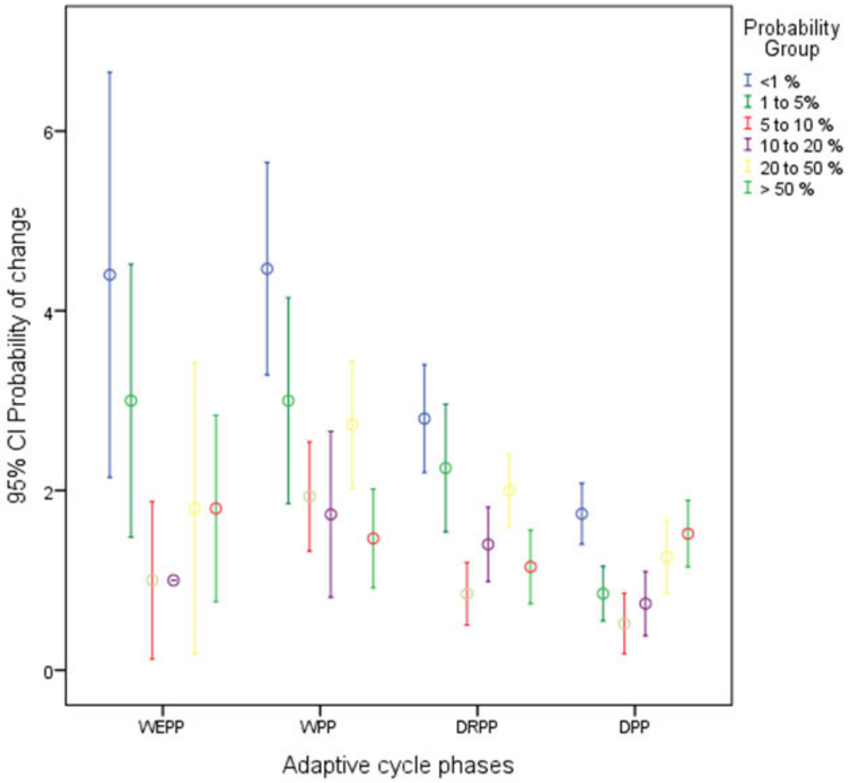


Figure 7.14 Distribution of probability NDVI class changes for poplar box woodland in the wetting, wet, drying and dry phases of the adaptive cycle. WEPP = wetting phase poplar box, WPP = wet phase poplar box, DRPP = drying phase poplar box and DPP = dry phase poplar box

7.3.5 Multivariate analyses

Permutational MANOVAs showed significant differences in the area and quality of response between the four vegetation communities (pseudo F = 65.031, $p < 0.001$) and between the adaptive cycle phases (pseudo F = 12.835, $p < 0.001$). There were also significant differences between vegetation communities within the different adaptive cycle phases (pseudo F = 3.0917, $p < 0.001$). The pairwise comparison of response quality between the four vegetation communities showed that all were significantly different (Table 7.1). Similarly, pairwise comparisons across phases showed significant differences between the dry, wet, and drying phases for all four vegetation communities. However, the pairwise comparisons between grassland and lignum shrubland responded similarly during the wetting phase (Table 7.1).

Table 7.1 Pairwise permutation MANOVAs for individual vegetation communities, adaptive cycle phases and vegetation communities within adaptive cycle phases using NDVI area and quality data. p values are provided and p > 0.05 is non-significant (NS).

Comparison	*p* value			
Vegetation community	Coolibah	Grass	Lignum	Poplar box
Coolibah				
Grass	< 0.001			
Lignum	< 0.001	< 0.001		
Poplar Box	< 0.001	< 0.001	< 0.001	
Adaptive cycle phases	Dry	Wetting	Wet	Drying
Dry				
Wetting	< 0.001			
Wet	< 0.001	= 0.023		
Drying	< 0.001	= 0.105 NS	= 0.002	
Vegetation communities	Adaptive cycle phases			
	Dry	Wetting	Wet	Drying
Coolibah - Grass	< 0.001	= 0.03	< 0.001	< 0.001
Coolibah - Lignum	< 0.001	< 0.001	< 0.001	< 0.001
Coolibah – Poplar box	< 0.001	= 0.032	< 0.001	< 0.001
Grass – Lignum	< 0.001	= 0.196 NS	< 0.001	= 0.002
Grass – Poplar box	< 0.001	= 0.01	< 0.001	< 0.001
Lignum – Poplar box	< 0.001	= 0.003	< 0.001	< 0.001

Permutational MANOVAs also indicated significant differences in direction of change between vegetation communities (pseudo F = 28.823, $p < 0.001$) and phases (pseudo F = 10.123, $p < 0.001$). There were also significant differences between vegetation communities within adaptive cycle phases (pseudo F = 3.0414, $p < 0.001$). The pairwise comparisons of direction of change showed significant differences between communities during dry and wet phases for all four communities, but less consistent patterns during the wetting and drying phases (Table 7.2). During the wetting phase there were significant differences between coolibah and lignum, grassland and poplar box and lignum and poplar box. By comparison, during the drying phase all vegetation communities differed significantly ($p < 0.005$) (Table 7.2).

Table 7.2 Pairwise permutation MANOVAs for individual vegetation communities, adaptive cycle phases and vegetation communities within adaptive cycle phases using direction of change data. p values are provided and p > 0.05 is non-significant (NS).

Comparison	*p* value			
Vegetation community	Coolibah	Grass	Lignum	Poplar Box
Coolibah				
Grass	< 0.001			
Lignum	< 0.001	< 0.001		
Poplar Box	< 0.001	< 0.001	< 0.001	
Adaptive cycle phases	Dry	Wetting	Wet	Drying
Dry				
Wetting	< 0.001			
Wet	< 0.001	= 0.034		
Drying	< 0.001	= 0.007	= 0.006	
Vegetation communities	Adaptive cycle phases			
	Dry	Wetting	Wet	Drying
Coolibah - Grass	< 0.001	= 0.204 NS	= 0.003	< 0.001
Coolibah - Lignum	< 0.001	= 0.013	< 0.001	< 0.001
Coolibah – Poplar box	< 0.001	= 0.091 NS	< 0.001	< 0.001
Grass – Lignum	< 0.001	= 0.081 NS	= 0.012	= 0.005
Grass – Poplar box	< 0.001	= 0.01	< 0.001	< 0.001
Lignum – Poplar box	< 0.001	= 0.006	< 0.001	< 0.001

Permutational MANOVAs indicated significant differences in probability of change between vegetation communities (pseudo F = 2.3056, $p < 0.001$) and phases (pseudo F = 42.484, $p < 0.001$). There were also significant differences between vegetation communities within adaptive cycle phases (pseudo F = 2.4519, $p < 0.001$). Pairwise comparisons showed a significant difference between grassland and coolibah communities but no significant differences for the remaining comparisons (Table 7.3). Pairwise comparison of communities across all phases showed coolibah to be the only community to differ from the other communities and these differences were not consistent across phases. Coolibah differed from grass, lignum and poplar box during the dry phase and from grass and poplar box during the wet and drying phases (Table 7.3).

Table 7.3 Pairwise permutation MANOVAs for individual vegetation communities, adaptive cycle phases and vegetation communities within adaptive cycle phases using probability of change data. p values are provided and p > 0.05 is non-significant (NS); * no p value

Comparison	*p* value			
Vegetation community	Coolibah	Grass	Lignum	Poplar Box
Coolibah				
Grass	< 0.003			
Lignum	> 0.181 NS	> 0.091 NS		
Poplar Box	> 0.098 NS	> 0.107 NS	> 0.061 NS	
Adaptive cycle phases	Dry	Wetting	Wet	Drying
Dry				
Wetting	< 0.001			
Wet	< 0.001	< 0.001		
Drying	< 0.001	= 0.185 NS	< 0.001	
Vegetation communities	Adaptive cycle phases			
	Dry	Wetting	Wet	Drying
Coolibah - Grass	< 0.001	= 0.401 NS	= 0.01	= 0.002
Coolibah - Lignum	< 0.001	= 0.948 NS	= 0.867 NS	= 0.336 NS
Coolibah – Poplar box	= 0.004	= 0.319 NS	= 0.021	< 0.001
Grass – Lignum	*	= 0.671 NS	= 0.157 NS	= 0.059 NS
Grass – Poplar box	= 0.215 NS	= 0.586 NS	= 0.534 NS	= 0.144 NS
Lignum – Poplar box	= 0.117 NS	= 0.618 NS	= 0.116 NS	= 0.06 NS

7.4. Discussion

The productivity response of vegetation within the Narran floodplain has previously been shown to have a distinct pattern that is consistent with an adaptive cycle (Thapa *et al.* 2015b). The current study demonstrates that productivity responses for major vegetation community types in the Narran floodplain are also consistent with an adaptive cycle. All four vegetation communities showed significant differences in vegetation productivity responses between the adaptive cycle phases. These differences in vegetation community productivity response were evident in relation to the total area of vegetation that showed a productivity response, the quality of the response, the number and direction of changes and the probability of change. Moreover, the adaptive cycle response is repeated within each of the major communities over a sequence of flooding and drying events.

7.4.1 Different vegetation communities have a different adaptive cycle

Although adaptive cycle responses were evident for all communities, there were also important differences between communities in their pattern of vegetation productivity response over the course of the adaptive cycle phases. These differences are evident in the timing of transitions between adaptive cycle phases, the duration each community spent in those phases and the amplitude of the responses. These differences were largely as hypothesised based on the categorisation of grasses and lignum as ephemerals and coolibah and poplar box woodland as in-situ persistents (Noy-Meir 1973, Stafford Smith and McAllister 2008). For example, productivity responses to inundation began earlier and productivity increased faster in grassland and lignum shrubland than in the coolibah woodland community. Grassland and lignum shrubland thus commenced the exploitation phase earlier than coolibah. Moreover, because grassland and lignum shrubland responded more rapidly, the peak in productivity or vigour also occurred earlier in these communities than in coolibah woodland. Thus, grassland and lignum shrubland began the conservation phase earlier and after a relatively short period in the exploitation phase.

Associated with this early response and rapid increase in vigour, grassland and lignum shrubland also exhibited a large contrast in vigour between the dry phase and the wetting and wet phase, with small areas of the high NDVI classes (Class 4, 5 and 6) during the dry phase but larger areas during the wet phase. In contrast, coolibah woodland responded later and more slowly to the increase in water availability. Productivity in coolibah woodland was relatively low during the wetting phase and highest during the drying phase, a time when the productivity of grassland and lignum shrubland had already begun to decline. Thus, coolibah woodland spent a longer period in the exploitation phase, entered the conservation phase later in the cycle and maintained high productivity through the drying phase. Coolibah woodland also exhibited a weaker contrast in vigour across phases, with areas belonging to the higher NDVI classes substantial throughout the cycle.

Poplar box woodland, however, did not respond as predicted over the wetting and drying cycles. As long-lived woody plants, poplar box were expected to be in-situ persistent (Noy-Meir 1973, Stafford Smith and McAllister 2008) and thus respond more slowly to increased water availability and maintain relatively high vigour through dry periods. Despite this, the response pattern observed in poplar box woodland was closer to that of lignum shrubland or grassland than coolibah woodland. For example, the vigour of poplar box was higher during the wetting and wet phases with the greatest areas of NDVI Class 4 and 5 occurring during these phases and relatively smaller areas of NDVI Class 4 and 5 occurring during the drying phase (Figure 7.12). The apparently rapid and short response of poplar box to inundation may reflect the position of these communities on the Narran floodplain in relation to elevation. Poplar box are situated at relatively high elevations and would only be inundated during very large floods. Thus, the observed responses may reflect local rainfall rather than the inundation events. Because rainfall is likely to precede flooding and result in a shorter period of high soil moisture, this may account for the relatively rapid and short-lived productivity response in poplar box. A further factor that may have contributed to the productivity response pattern in poplar box is the relatively sparse canopies of these woodland communities. Sparse canopy cover means that observed NDVI changes within a community are likely to be more strongly influenced by responses in the understorey, which may include a high proportion of ephemeral plant species. Further studies incorporating on-ground measurements are needed to establish the likely importance of either or both of these proposed mechanisms. Uncertainty around the nature of the response in poplar box woodland notwithstanding, the transitions between phases of the adaptive cycle appear, in general, to be driven by hydrology, but interactions between the driver and the ecology of the dominant species in each vegetation community results in different adaptive cycles.

This complex response in semi-arid floodplain vegetation communities to changing water availability is not unexpected and is consistent with the strategies that the dominant species within each community use to cope with extreme variation in water availability. Grasses and lignum, for example, may be characterised as using fluctuating persistent or ephemeral strategies, relying on adaptations that facilitate their rapid growth when water becomes available (Noy-Meir 1973, Stafford Smith and McAllister 2008), and thus a rapid transition into an exploitation phase and subsequently to a conservation phase. Likewise, once surface soil water becomes limiting, the adaptive strategies of grasses and lignum are to shed most green leaves and persist in reserve form for the duration of dry conditions or to set seed that is stored in a persistent seed bank that can germinate once water becomes available again (Noy-Meir 1973, Burrows 1990, Brock and Casanova 1997, Chong and Walker 2005, Roberts and Marston 2011).

The response pattern exhibited by coolibah, on the other hand, is consistent with a drought persistent or in-situ persistent strategy, whereby adaptations are directed at maintaining vigour through harsh periods rather than responding rapidly to sporadic and short-lived increases in water availability. Coolibah utilise extensive and deep root systems to access limited water in the vadose zone (Engel *et al*. 2005, Roberts and Marston 2011) and have low transpiration rates which allow them to persist even when soil moisture is very low (Horner *et al*. 2009, Roberts and Marston 2011). Coolibah woodland species may also rely on a stem succulent strategy during the dry phase which would enable them to store water in their trunks. This capacity has been demonstrated in other eucalyptus species in semi-arid regions of Australia (Roberts and Marston 2011, Yan and Dickinson 2014). Ground water has been shown to be an important source of water for arid and semi-arid floodplain woodland species (Scott *et al*. 2008, Horner *et al*. 2009, Roberts and Maston 2011). Thus, it is possible that coolibah has the capacity to access deep soil water or the ground water due to their deep taproot systems (Scott *et al*. 2008, Horner *et al*. 2009, Roberts and Maston 2011). However, the regional groundwater in the Narran floodplain is, on average, 100 m below the floodplain surface (Roberts and Marston 2011). While it is possible that there may be small areas of relatively shallow groundwater, which taproot systems of coolibah may be able to access, it is unlikely that such areas could account for the responses observed in the coolibah woodland community.

7.4.2 Implications for floodplain vegetation community resilience

Although our hypotheses about adaptive cycles exhibited by the major vegetation communities were largely supported by the results, some aspects of this study were contrary to our initial predictions. Theoretically, systems are more vulnerable to change state (i.e. exit from the adaptive cycle to a different cycle) during the transition between the reorganisation and exploitation phase of the adaptive cycle (Holling and Gunderson 2002, Scheffer *et al.* 2003). This is associated with increased instability and the predominance of more frequent and larger magnitude changes (Holling and Gunderson 2002). However, over multiple adaptive cycles each of the four vegetation communities showed that the conservation, or wet phase, was more dynamic in all five response variables (i.e. area and quality of response, number and direction of change and the probability of change). This contradicts adaptive cycle theory that the conservation phase is the phase of relative stability, and that the reorganisation and exploitation phases are phases of instability. Thus in dryland floodplain ecosystems our results suggest that because instability occurs in the wet phase (conservation) this is probably where the exit to a new state occurs. When systems approach a threshold of change in state, they begin to fluctuate more than usual (Walker and Salt 2012). It is at this point that the chance of crossing a major threshold or tipping point and moving to a new state is greatest. Based on the adaptive phase showing greatest variability this study suggests that the potential for change in state in the Narran floodplain is highest at the transition between the wet (conservation) and drying (release) phases. Knowledge of floodplain vegetation response in each phase of an adaptive cycle will enable better management, because monitoring and management for resilience requires information about changes in the magnitude and frequency of change so that movement towards a tipping point can be detected (Biggs *et al.* 2009).

Resilience refers to a system’s ability to respond to change and still retain the same structure, function and feedbacks without moving into an alternate regime (Holling 1973, Holling and Gunderson 2002). Vegetation communities of the Narran floodplain have been shown to maintain state over the course of extreme variability in water availability. Our data shows that all four vegetation communities transitioned between wetting, wet, drying and dry phases of an adaptive cycle presenting similar patterns from cycle to cycle irrespective of the duration between the phases and of different flood magnitudes. Our results thus support the notion of

Holling (1973) and Holling and Gunderson (2002) that resilient systems fluctuate within the same basin of attraction.

Although this study demonstrated repeated adaptive cycles among the individual vegetation communities, further study is needed to confirm the findings and address some inconsistencies and uncertainty. For example, detailed field studies would establish relationships between eco-physiological factors and observations of vegetation productivity in the adaptive cycle phases. In particular, the unexpected patterns observed for poplar box woodland communities may be better understood with such field-based monitoring. It should also be noted that changes in productivity are not the only biological responses likely to occur as a result of wetting and drying. Phenological responses such as flowering, seed set, germination and recruitment are all important to the maintenance of individual communities over time and are likely to exhibit distinct patterns over the course of cycles of wetting and drying. Whether patterns in these responses can be considered as following distinct and repeated adaptive cycles and whether they can provide insight as to the sensitivity of floodplain plant communities to potential changes in state over the course of the adaptive cycle remains to be seen and is an obvious direction for future study.

7.4.3 Conclusion

This study used the adaptive cycle framework to explore functional change in a complex system (Thapa *et al*. 2015b) and as a foundation to assess change and stability in a system. Restoration of degraded floodplain vegetation and maintaining floodplain integrity is a core element of semi-arid floodplain river management initiatives. Understanding of adaptive cycles makes us more aware of the importance of transitions, dominance of the different phases and frequency of the individual transitions in driving change in vegetation communities. The different responses that we observed between adaptive phases in each vegetation community over multiple events will enable better management by identifying likely times when a community might exit an adaptive cycle and change state. The natural variability of wetting and drying has already changed in the Condamine-Balonne Catchment with the advancement of land and water resource development activities (Sheldon *et al*. 2000, White *et al*. 2010) and may further alter with climate change (CSIRO 2008, Finlayson *et al*. 2013). The knowledge of different adaptive cycle phases of floodplain vegetation and the possibility of state change will help to restore degraded floodplain vegetation and have significant implications for understanding the overall functioning of semi-arid floodplain ecosystems.

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	Author's Name (please print clearly)	% of contribution
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Chapter 8 Thesis synthesis

8.1. Introduction to synthesis

Australian dryland floodplain river ecosystems are characterised by extreme hydrological variability (McMahon 1979, Finlayson and McMahon 1988). Thus, variability in the duration, frequency, magnitude and timing of flooding and drying of floodplains is a major feature of these ecosystems (Thoms 2003, Sheldon *et al.* 2010). The high biodiversity of floodplain ecosystems compared to other global ecosystems (MEA 2005) is maintained, in part, by these hydrological variations as well as highly productive soils, which combine to influence the resilience of floodplain vegetation communities over time (Whited *et al.* 2007). In Australia, floodplain ecosystems are a valuable resource in terms of the ecosystem goods and services they provide and the agricultural production they support. The ecosystem services provided by the rivers, wetlands and floodplains of the Murray-Darling Basin have been valued at $187–302 million per year (Thoms and Sheldon 2000), while irrigated agricultural production from Australia's floodplains has been valued at more than $10 billion per year (Thoms and Sheldon 2000). However, floodplain ecosystems are also a threatened resource, largely because of agriculture and the water resource development that supports it (MEA 2005, Tockner *et al.* 2008).

Ecosystem changes are rarely simple (Pickett and White 1985, Likens 1992, Jax 2010). This is because their responses to drivers of change are mediated through a range of interactions and feedbacks between biotic and abiotic components and the process complexity in space and time. Thus, understanding change requires both an explicit understanding of how ecosystems change and the key drivers of change (Sutherland *et al.* 2013). Relatively little is known about the longer-term response of vegetation productivity to flooding and drying across floodplain landscapes (Capon 2007, Parsons and Thoms 2013). Moreover, the majority of floodplain vegetation research has tended to focus on patterns and processes at the relatively smaller plot or transect scales. Understanding the dynamics of an ecosystem requires not only a focus on functional connections and boundaries but also the hierarchical nature of ecosystems and the scale of resolution at which change is studied (Pickett *et al.* 2003). Applying this to floodplain ecosystems, understanding how vegetation productivity changes over time in response to flooding and drying events is a key knowledge component for modelling floodplain resilience in the face of increasing disturbance (Capon 2003, Scown *et al*. 2015). The productivity of floodplain vegetation is an indicator of floodplain ecosystem resilience,but one that has received limited attention in the scientific literature. Thus, this thesis addresses the knowledge gap of floodplain vegetation productivity responses to flooding and drying events at two levels of organisation: the whole floodplain landscape and individual vegetation community types.

The main aim of this thesis was to examine the functional response to flooding and drying within the Narran floodplain-wetland complex. This dryland floodplain ecosystem is characterised by a highly variable flooding and drying regime through time and represents an ideal system in which to study ecosystem change within the context of a highly variable hydrological driver. In order to achieve this aim, four research objectives were addressed through four research manuscripts presented in Chapters 4–7 of this thesis (Table 8.1). The results of this thesis have contributed an improved understanding of change in floodplain vegetation productivity by developing a resilience-based floodplain adaptive cycle model. In this adaptive cycle model, vegetation productivity is the ecosystem responder and hydrology, or floodplain flooding and drying, the main driver of change. The approach taken focuses on the changes in floodplain NDVI, a surrogate of vegetation productivity, over multiple flooding and drying events in the whole floodplain landscape and four different vegetation communities. The method of investigation can be applied to other dryland floodplain ecosystems to understand change in vegetation productivity in response to flooding and drying. Thus, it represents a significant contribution in understanding the response of floodplain vegetation to flooding and drying, with the application of the adaptive cycle model for understanding change in ecosystems.

This synthesis of the research undertaken to produce this thesis is organised into four sections. The first section summarises the key results of each research manuscript and how each adds to the body of knowledge on vegetation productivity in dryland floodplain ecosystems (Table 8.1). The second section argues the philosophical content of this thesis, with a focus on floodplain ecosystem change. The third section outlines the application of this study of floodplain vegetation productivity to floodplain management and finally, the fourth section discusses the future research prospects that emerge from this thesis.

Table 8.1 A summary of research undertaken in this thesis and the contributions emerging from this thesis

Manuscript number	Manuscript aims	Thesis chapter	Key results	New contribution
Manuscript 1	Manuscript 1 examined the differences over time in NDVI values between and within the dry and wet resource states to see if these differences were consistent at the entire landscape and vegetation community scale. Further, this study examined what drives differences in NDVI in terms of climate and flow.	Chapter 4	• NDVI differed significantly between wet and dry resource states. • A significant difference in NDVI was observed between and within the sequences of wet and dry resource states. Thus, not all wet and dry states were the same. • The pattern of response was similar with the availability of water but differed between vegetation communities. • The effect of discharge on NDVI was significantly greater than rainfall, but the combination of discharge and rainfall was associated with the highest response in NDVI. Moreover, the NDVI response differed between vegetation communities.	• This manuscript is the integrated study of floodplain vegetation productivity to flooding and drying in the whole floodplain landscape and in four vegetation communities. Further, this study used climate and flow data to better understand the variability in flooding and drying by incorporating high resolution Landsat satellite imagery at approximately monthly intervals over twenty years. • Thus, the results of Manuscript 1 led to thinking of alternative ways to examine the functional vegetation responses to flooding and drying using a model that can better reflect functional processes than the simple two state boom-bust model. An adaptive cycle model that has been used in understanding change in general may help us to understand the complexity of floodplain vegetation productivity.
Manuscript 2	Manuscript 2 examined how semi-arid floodplain vegetation productivity changed in response to floodplain flooding and drying and to evaluate whether the observed responses correspond to an adaptive cycle or a two state boom-bust model of change.	Chapter 5	• Productivity of floodplain vegetation in response to flooding was hypothesised to be more complex than the boom-bust model and shows an adaptive cycle of exploitation (wetting), conservation (wet) release (drying) and reorganization (dry) phases. • In addition to the complexity of vegetation productivity response through the dry, wetting, wet and drying phases, there was a distinct hysteretic loop in the relationship between productivity and floodplain inundation. • There are two interacting elements to the hypothesised floodplain adaptive cycle model. The first describes the progression of flooding	• A hypothesised adaptive cycle model was developed to better understand change in vegetation productivity response to flooding and drying. • A distinct hysteresis was observed in the relationship between floodplain inundation and vegetation productivity • Thus, the results of Manuscript 2 led to thinking about the efficacy of the adaptive cycle in multiple flooding and drying events. Not all floods are the same and they differ in magnitude, timing and duration. Different sized floods may make the application of the adaptive cycle untenable if the adaptive cycle does not hold over multiple events.

Manuscript number	Manuscript aims	Thesis chapter	Key results	New contribution
			as the key driver of vegetation productivity through the adaptive cycle and the second describes the progression of vegetation productivity response to that key driver through the phases of the adaptive cycle.	
Manuscript 3	Manuscript 3 examined adaptive cycles of floodplain vegetation in multiple events to determine if an adaptive cycle repeats and how it is influenced by different sized flood events.	Chapter 6	• The adaptive cycle repeated over multiple events through a cycle of wetting, wet, drying and dry phases. • The character of wetting and drying was similar over multiple events, but the phases varied in relation to different flood events. Multiple flooding and drying sequences showed that the point in the cycle where greatest stability occurs is the reorganization (dry) phase. However the conservation (wet) phase was the most dynamic phase and was not stable over time.	• A change in state or regime shift in floodplain vegetation may be most likely during the transition between the conservation and release phase because this phase showed the highest instability. In contrast, a change in state may be least likely during the transition from the reorganization to exploitation phase because this phase was the most stable. These inferences are counter to those hypothesised based on adaptive cycle theory. • Thus, the results of Manuscript 3 led to a refinement of the adaptive cycle framework through comparison of the responses of individual vegetation communities over multiple flooding and drying events.
Manuscript 4	Manuscript 4 examined four individual vegetation community responses to multiple flooding and drying events to test if adaptive cycles differ among vegetation communities.	Chapter 7	• The adaptive cycle repeated in four vegetation communities over multiple events but the pattern of vegetation productivity response differed between communities. • Timing and amplitude of peaks and troughs in productivity also differed between communities. • Overall, higher productivity response was observed in grassland and lignum shrubland compared to coolibah and poplar box woodland. Differences reflect the eco-physiological amplitude of dominant species within each community.	• This study highlights how different strategies adopted by different vegetation communities influences change in vegetation productivity response to inundation. Thus, different responses that we observed between adaptive phases in each vegetation community over multiple events will enable better management by identifying likely times when a community might exit an adaptive cycle and change state. • Therefore, the floodplain adaptive cycle model is a better model to track change in vegetation productivity in response to flooding and drying than the simple two state boom - bust model of change

8.2. Summary of the key research results emerging from this thesis

The core of this thesis is the four research manuscripts submitted to various scientific journals. The thesis had a sequential series of hypotheses, with the results of initial studies leading into and aiding the development of subsequent hypotheses. Manuscript 1 (Chapter 4) entitled “The semi-arid floodplain vegetation productivity response to flooding and drying” submitted to the *Journal of Arid Environments*, examined monthly differences in NDVI values between and within a series of dry and wet resource events at two different levels of organisation; the floodplain landscape and the vegetation community level. In previous studies, the response of floodplain vegetation productivity has been modelled to change between two states: a dry ‘bust’ state associated with very limited water availability and thus very low vegetation productivity; and a wet ‘boom’ state of relatively abundant water availability and an overall increase in vegetation productivity (Walker *et al.* 1995, Bunn *et al.* 2006, Sims and Coloff 2012, Sternberg *et al.* 2012). The results of my study found NDVI values to be highly variable between and within the multiple flooding and drying events. Furthermore, variability in NDVI occurred at both levels of organisation. This dynamic response to multiple flooding and drying events suggests that a simple boom and bust model may not be appropriate for conceptualisation of dryland floodplain vegetation dynamics, and that an alternative model of functional responses in vegetation productivity needs to be explored (Table 8.1). The accepted, simple, two-state boom and bust model does not account for the processes that may occur in transition to and from dry and wet resource states. It is suggested that an adaptive cycle model, a key component of resilience theory used in understanding change in ecosystems (Holling 1973, Holling and Gunderson 2002) is an alternative model that better reflects the complexity of floodplain vegetation productivity responses to flooding and drying (Table 8.1).

Manuscript 1 explores change in vegetation productivity response to flooding and drying in an integrated way using high spatio-temporal resolution satellite imagery at the two levels of organisation by considering multiple flooding and drying sequences. Examination of multiple sequences of flooding and drying events in an integrated way is useful in understanding and predicting floodplain vegetation dynamics and the trajectory of change. The over time, multi-event understanding is critical to the ability to manage the complex semi-arid systems and make predictions about future dynamics. Thus, Manuscript 1 provides a study design that contributes to understanding change in floodplain vegetation productivity response to flooding and drying.

Overall, the results of Manuscript 1 revealed a highly complex relationship between hydrological and ecological processes on the Narran floodplain. The complex response depended on scale of observation, where the entire landscape responded similarly over multiple events to the availability of moisture, but varied among the vegetation communities. This led me to hypothesise about alternative ways to examine functional hydro-ecological change in vegetation response using a model that better explains complexity of floodplain flooding and drying processes than the relatively simple two-state boom and bust model.

Manuscript 2 (Chapter 5) entitled “An adaptive cycle hypothesis of semi-arid floodplain vegetation productivity in dry and wet resource states” has been published in the journal *Ecohydrology*. The aim of this manuscript was to examine whether the observed responses in floodplain vegetation productivity (NDVI) to floodplain flooding and drying corresponded to an adaptive cycle (Table 8.1). Manuscript 2 is the first empirical study to apply an adaptive cycle model to a semi-arid floodplain and provides an alternative approach to understanding the complexity of change in vegetation productivity in response to floodplain flooding and drying. The study utilised a pixel-by-pixel change analysis and a series of Markovian transitional models to track change in vegetation productivity through a floodplain flooding and drying sequence. Markovian transition models have been used to understand the dynamics of landscape change since the 1980s (Usher 1979, Weng 2002, Bolliger *et al.* 2009), and this manuscript applies Markovian transition models to examine the functional response of floodplain vegetation to flooding and drying.

The study described in Manuscript 2 revealed a hysteresis in the relationship between floodplain inundation and productivity. The hysteresis observed in Manuscript 2 indicates congruence between vegetation response to flooding and drying and the hypothesised adaptive cycle model. The adaptive cycle was shown to be made up of four hydrologically based phases: wetting, wet, drying and dry. The wet phase was more dynamic, by comparison the dry phase was uniform in vegetation productivity. Thus, adaptive cycles seem to occur in semi-arid floodplain ecosystems in response to floodplain inundation. Further, the

Markovian transition model demonstrated complexity in the area and quality, number and direction, probability and diversity of change in NDVI in the phases of the adaptive cycle. In addition to the complexity of NDVI change through the dry, wetting, wet and drying phases, a distinct hysteretic loop was observed in the relationship between vegetation productivity and floodplain inundation. This hysteretic pattern resembles an adaptive cycle through the dry, wetting, wet and drying phases. Based on the observed pattern of vegetation productivity response, I hypothesised an adaptive cycle model for the Narran floodplain where floodplain inundation drives vegetation productivity through a cycle of exploitation (wetting phase), conservation (wet phase), release (drying phase) and reorganisation (dry phase). Overall, Manuscript 2 demonstrated that change in vegetation productivity follows the four phases of an adaptive cycle.

The strong relationship between vegetation productivity and flooding and drying raised questions regarding the efficacy of the adaptive cycle in multiple flooding and drying sequences. Floods differ in magnitude, timing and duration. Patterns of changes in vegetation productivity associated with flooding and drying may, therefore, vary in accordance with variation in flood magnitude, timing and duration. Therefore, Manuscript 3 (Chapter 6) posed questions about the efficacy and repeatability of the adaptive cycle in multiple flooding and drying events associated with floods of different characters. Manuscript 3 entitled “Adaptive cycles of floodplain vegetation response to multiple flooding and drying events” was submitted to the journal *Hydrology and Earth System Sciences*. Manuscript 3 followed the approach outlined in Manuscript 2 (Chapter 5) but investigated multiple events. The aim of Manuscript 3 was to determine if adaptive cycles repeat over multiple events and how the adaptive cycle is influenced by flood events of different character (Table 8.1).

The findings of Manuscript 3 were that the adaptive cycle repeated over different flood events. However, the character of the adaptive cycle for each event differed in character of each phase. Thus, vegetation productivity changes through the adaptive cycle in response to flooding and drying but, was complex and varied between multiple events. Two of the phases, the release (drying) and reorganization (dry) were as expected as they maintained higher stability in all events. In contrast, the exploitation (wetting) and conservation (wet) phases were not as expected. In the exploitation (wetting) phase it was hypothesised that limited vegetation productivity would occur and that productivity would be stable but the data showed substantial instability in vegetation productivity in this phase with no decrease in vegetation productivity. Similarly, it was also hypothesised that the conservation (wet) phase would be stable because of ample resource availability. However, data from multiple events showed that the conservation phase is dynamic and not stable, with a greater number of changes, two-way directional changes and a higher probability of large magnitude changes. This contradicts adaptive cycle theory, which suggests that the conservation phase is the phase of relative stability and that the reorganization and exploitation phases are phases of instability. Another result that was not expected was the location of the exit point from the adaptive cycle where there is the potentiality of state change. The exit point from an adaptive cycle is characterized by high instability. In the Narran floodplain, the pattern of changes that indicate when, according to adaptive cycle theory, an exit from the cycle or change in state was not observed between the reorganization and exploitation phases of the adaptive cycle as hypothesised by adaptive cycle theory. Rather, the pattern indicative of a higher potential for a change in state was observed between the conservation and release phases. This is a significant finding suggesting that potential for a change in state in dryland floodplains is highest at the transition between the wet (conservation) and drying (release) phases (see details in Chapter 6 and 7 of this thesis).

Although the adaptive cycle repeated, the observed complexity of response over multiple events raised questions about why adaptive cycle phases may differ slightly between multiple events. Component floodplain vegetation communities may respond differently between phases, as they utilise different adaptation strategies to cope with variation in water availability. That variation may influence the adaptive cycle within a vegetation community. Application of the adaptive cycle framework in the Narran floodplain was further refined through comparison of the adaptive cycles of individual vegetation communities over multiple flooding and drying events. Manuscript 4 (Chapter 7), entitled “Do adaptive cycles of floodplain vegetation response to inundation differ among vegetation communities?”, was submitted to the journal *PLOS ONE*. The main aim of Manuscript 4 was to refine the adaptive cycle framework (Chapter 5 and 6) through comparison of the response of different vegetation communities within the Narran floodplain over multiple flooding and drying events (Table 8.1).

The four vegetation communities (grassland, lignum shrubland, coolibah woodland and poplar box woodland) followed an adaptive cycle in response to flooding and drying, although differences in adaptive cycle phases were observed between vegetation communities. The differences were evident in the timing of transitions between each of the adaptive cycle phases. Grassland, lignum shrubland and poplar box woodland productivity response occurred earlier in the adaptive cycle than in coolibah woodland communities. Higher quality vegetation productivity was observed in grassland and lignum shrubland vegetation communities than in the coolibah and poplar box woodland communities. Grassland and lignum shrubland had low NDVI during the dry phase; by comparison woodland maintained relatively high NDVI during the dry phase. This observed response was consistent with the adaptive strategies that plant species use to cope with extremes in resource availability. Grassland and lignum shrubland can be characterised as using the fluctuating persistent or ephemeral strategies suggested by Noy-Meir (1973) and Stafford Smith and McAllister (2008) for semi-arid vegetation communities. In contrast, the NDVI pattern exhibited by the woodland communities - especially coolibah - was consistent with the drought persistent or in-situ persistent strategy of Noy-Meir (1973) and Stafford Smith and McAllister (2008), which means they can maintain their vigour even during the harsh periods. Poplar box woodland, however, did not respond as predicted; the response pattern observed in poplar box woodland was closer to that of grass and lignum shrubland than coolibah. This contradicts the Noy-Meir (1973) and Stafford Smith and McAllister (2008) semi-arid floodplain woodland adaptation strategies. These unexpected results in poplar box woodland may reflect the position of these communities on the Narran floodplain in relation to elevation. Thus, the observed responses may reflect local rainfall rather than inundation events. Because rainfall is likely to precede flooding and result in a shorter period of high soil moisture, this may account for the relatively rapid and short-lived productivity response in poplar box. A further factor that may have contributed to the productivity response pattern in poplar box woodland is the relatively sparse canopies of these woodland communities.

Despite the differences between vegetation communities described above, over multiple adaptive cycles the conservation or the wet phase was the most dynamic in all variables (area and quality of response, number and direction of change and the probability of change) in each of the four vegetation community types. The results of Manuscript 4 also contradict adaptive cycle theory that the conservation (wet) phase is the phase of relative stability and that the reorganization (dry) and exploitation (wetting) phases are phases of instability.

8.3. Contribution to the broader scientific knowledge

8.3.1 Semi-arid floodplain ecosystems

Semi-arid floodplain ecosystems are characterised by change, driven largely by high spatial and temporal variability in inundation by floodwater. Subsequently, semi-arid floodplains have been described as boom and bust ecosystems (Walker *et al*. 1995, Bunn *et al*. 2006). The two state boom and bust model of hydro-ecological processes is a widely accepted model for large semi-arid floodplains subject to high inundation variability, and suggests that variability plays a major role in the integrity of floodplain ecosystems (Leigh *et al*. 2010). During extended periods of limited water availability, a bust period that may last for years, floodplain primary and secondary productivity is low (Arthington *et al*. 2010, Parsons and Thoms 2013). On the other hand, a boom period stimulates a rapid increase in floodplain productivity that may last for months across large semi-arid floodplains (Thoms 2003, Bunn *et al*. 2006, Leigh *et al*. 2010). The findings of this thesis demonstrate that flooding and drying is more complex than as predicted by a simple boom and bust model of change and varied in different events over time and between different vegetation communities. The wet or the boom period was more dynamic than the dry period and NDVI varied significantly between floods of different sizes (see Chapter 4, 5, 6 and 7 of this thesis). Moreover, this thesis suggests that placing emphasis on semi-arid floodplain ecosystems as consisting of two states does not account for the processes that may occur in the transitions between the dry and wet states.

Resilience theory proposes that complex systems hold dynamic trajectories that do not tend towards stable or equilibrium conditions, rather such systems move through an adaptive cycle (Holling and Gunderson 2002). The findings of this thesis support this proposition in relation to semi-arid floodplain ecosystems. The results of this thesis add a deeper understanding of functional change in vegetation response to flooding and drying events by introducing an adaptive cycle model. The thesis presents the first empirical studies of adaptive cycles in floodplains (see Figure 5.9). The adaptive cycle model views change in vegetation productivity as a continuing process through a cycle of exploitation, conservation, release and reorganization (see Chapters 5, 6 and 7 of this thesis). The exploitation phase of the adaptive cycle corresponds to wetting of the floodplain, where vegetation exploits the availability of water and begins to increase in productivity. The conservation phase of the adaptive cycle corresponds to maximum inundation and is a period of increased vegetation productivity and stability of this productivity, due to ample water availability. Contraction of flood water triggers the drying of the floodplain and corresponds to the release phase of the adaptive cycle, where vegetation productivity is expected to decrease in area and quality due to release of biomass, energy and material stored in the floodplain in the prior conservation phase. As the floodplain dries further, vegetation productivity moves into the reorganization phase of the adaptive cycle, where floodplain vegetation may reorganise in the same state or exit the cycle to a different state. Thus, this thesis suggests that a floodplain adaptive cycle is a better model to track change in vegetation productivity response to flooding and drying. The semi-arid floodplain adaptive cycle model developed in this thesis demonstrates the wet phase to be more dynamic than the dry phase (see Chapter 5, 6 and 7), suggesting that change in state may occur while transitioning from the conservation to release phase, a new finding which needs further research in relation to the applicability of the adaptive cycle model.

8.3.2 Value of a landscape approach using remote sensing techniques

Much of the current knowledge of floodplain vegetation comes from small-scale studies, based on information collected at sites, transects or in plots (Brock and Casanova 1997, Stienhard and Volk 2003, Warwick and Brock 2003, Capon 2005, Capon *et al*. 2009, Reid *et al*. 2011). Typically the results of these studies are up-scaled to the entire floodplain. Small-scale approaches may adequately characterise floodplain vegetation patterns but these characterisations will only hold for that scale of observation (van Coller *et al.* 2000, Gillson 2004). Ignoring cross scale effects is one of the most common reasons for failure in environmental science (Pickett et al., 2003) and natural resource management (Walker and Salt 2012). Thus, a multi-scaled approach can provide a clearer understanding of influencing processes.

Hierarchy theory is a theory of scaled systems (O'Neill *et al*. 1988). Hierarchy theory provides a framework for integrating pattern and process of floodplain ecosystems and the influence of pattern and process across different levels of organisation. By linking, geomorphological, hydrological and ecological hierarchies, we can place hierarchy into an applied context to view the complex riverine ecosystem from a truly multidisciplinary perspective (Dollar *et al*. 2007). Dollar *et al*. (2007) described how agents, or drivers, of change operate over different spatial and temporal scales. Organisms perceive the landscape at different resolutions and extents of patchiness depending on their size and they will respond differently to hydrological and geomorphological processes operating at different scales.

This thesis represents an advance on previous studies as an approach for characterising and understanding landscape scale patterns in vegetation communities in large floodplains for several reasons. First, direct measurements of the change in vegetation productivity over large areas is impractical with field based studies, particularly in spatially heterogeneous landscapes because they require high intensity sampling to characterise spatial patterns and are thus time consuming and expensive. Remote sensing satellite data have proven extremely useful for detecting change in vegetation pattern and process over various scales (Mertes 2002, Farina 2006, Sims and Colloff 2012, Wen *et al*. 2012) and offer a more cost-effective approach for regular monitoring of vegetation cover change over large areas (Lillesand and Kiefer 1994).

Second, the thesis monitored change over a 20 year period and over multiple flooding and drying cycles which meant that both long-term trajectories of change and cyclic patterns in vegetation productivity response to flooding and drying could be detected and explored. Many previous studies of floodplain vegetation productivity using remotely sensed data have been limited to one or two snapshots (e.g. Sims and Thoms 2002, Parsons and Thoms 2013) and thus were not able to investigate vegetation productivity dynamics in either the short or long term.

Third, the thesis used high resolution, multi-spectral imagery. Studies that have used remote sensing derived NDVI images to assess change in vegetation productivity over time have tended to use very coarse resolution satellite data such as MODIS or AVHRR (e.g. Sims and

Colloff 2012, Wen *et al*. 2012). However, recent studies suggest that examining change in vegetation vigour in semi-arid regions with low resolution data highlight results may be limited. This is because semi-arid regions have scattered trees or tree patches which may be lost in coarsely resolved data. Further, NDVI values at low resolution may be influenced by the effects of aggregation from the surrounding cover types (Munyati and Mboweni 2012). Thus, medium to high resolution satellite data such as Landsat and SPOT may better capture the dynamics of vegetation productivity (Munyati and Mboweni 2012).

Fourth, the thesis incorporated climate and flow data over these multiple periods to unpack the influence of both rainfall and flooding as sources of water on vegetation productivity response. Previous studies, both field-based and remote sensing based, have reported a positive correlation between productivity and flooding or rainfall in an individual basis in an semi-arid regions (e.g. Nightingale and Phinn 2003, Al-Bakri and Suleiman 2004, Westbrooke *et al*. 2005, Hassler *et al*. 2010, Sims and Colloff 2012, Wardle *et al*. 2013, Travers and Eldridge 2013). However, these studies did not use flooding and rainfall in an integrated way over multiple events as this thesis has done. This study confirmed that flooding was the key driver, but flooding and rainfall in combination generated the highest productivity.

Finally, the study design of this thesis combined the use of high resolution multispectral remote sensing imagery, a 20-year time series, and hydrological and rainfall records with an adaptive cycle model and Markovian transition analysis. The use of the adaptive cycle model and the Markovian transition analysis allowed for the complex, landscape and vegetation community level patterns of change associated with transitions between wet and dry states to be better understood than the boom bust models applied in previous studies. Thus, integrated approaches taken in this thesis have enhanced our knowledge of understanding change in of semi-arid floodplain vegetation productivity response to flooding and drying.

8.3.3 Floodplain resilience

Floodplains are resilient systems (Capon *et al*. 2009, Colloff and Baldwin 2010). Resilience is defined ecologically as the capacity of a system to undergo change or disturbance and still retain the same structure, function and set of feedbacks without moving into an alternative regime (Holling 1973, Holling and Gunderson 2002, Folke *et al*. 2004, Walker *et al*. 2004).

Systems that are not resilient cannot absorb disturbance and may collapse into a different state that has different structure, function and feedbacks (Scheffer *et al.* 2001, Walker *et al.* 2004). These types of changes are called regime shifts and have been reported in many ecological systems. For example, eutrophication may cause a switch from clear to turbid water conditions in shallow freshwater lakes (Scheffer and Carpenter 2003); fire and grazing may cause a switch from grassland to shrubland (Wolf *et al.* 2007); elevated turbidity with high phytoplankton biomass has resulted in a switch from submerged vegetation to floating plants in tropical lakes (Scheffer *et al.* 2003); and coral dominated reef ecosystems can switch to algae dominated reefs through a combination of human and natural disturbances (Hughes 1994). Regime shifts have also been reported in semi-arid floodplains. Walker and Salt (2012), for example, reported that the river red gum woodlands of the Murray River floodplain, Australia, have passed a threshold of water availability and are dying because of over extraction of water. Likewise, Whalley *et al.* (2011) reported a regime shift associated with the invasion of exotics plants in the Gwydir wetlands and Macquarie Marshes in northern NSW, Australia. The most compelling evidence of regime shift has been observed in shallow lake systems (Capon *et al.* 2015). However, other studies question the possibility of regime shifts. Capon *et al.* (2015) report that there was no strong evidence for regime shifts and changes between multiple or alternative stable states in a review of the effects of disturbances in freshwater ecosystems. This thesis has examined change in floodplain vegetation productivity response to flooding and drying using a key component of resilience theory - the adaptive cycle framework. Overall the vegetation response of the Narran floodplain was complex but indicative of a resilient ecosystem. The productivity of floodplain vegetation in the Narran cycled through the four phases of an adaptive cycle and the pattern was repeated despite variation in flood character. The Markovian transition models showed a dynamic response in vegetation productivity cycling through the four phases of an adaptive cycle. One of the major characteristics of resilience theory is that resilient systems always fluctuate between the four phases of an adaptive cycle (Holling and Gunderson 2002, Walker and Meyers 2004, Walker *et al.* 2004, Folke *et al.* 2010). Thus, in terms of the adaptive cycle component of resilience theory, semi-arid floodplains are resilient systems as they show consistency in pattern in relation to the various phases, which may be considered evidence of the system retaining the same function, structure and feedbacks.

The other new finding of this thesis is the potential for change in state or exit from the adaptive cycle. Under an adaptive cycle framework a change in state (regime shift) or exit from the cycle is most likely to occur while transitioning from the reorganisation to the exploitation phase. However, the semi-arid floodplain adaptive cycle model developed in this thesis did not show a change in state while transitioning from the reorganization to exploitation phase. Rather, vegetation productivity in the reorganization and exploitation phases was found to be stable over multiple flooding and drying events. In contrast, the conservation phase was more dynamic and not stable over multiple flooding and drying events, with a higher and larger number of high frequency low magnitude changes. The reorganization phase showed a smaller number of low frequency high magnitude changes. Resilience theory suggests that when a system approaches a threshold it fluctuates more than usual (Biggs *et al*. 2009, Walker and Salt 2012). This suggests that the change in state or exit from the cycle in the Narran floodplain may happen while transitioning from the conservation to release phase where high instability was observed. Theoretically the conservation phase is the most stable phase due to ample resource availability coupled with a balance in competition for those resources that supposedly ensures stability (Holling 1973, Holling and Gunderson 2002). The potential point of change in state of the Narran semi-arid floodplain system contradicts adaptive cycle theory, and further research is needed to test if this point of exit repeats in other floodplain ecosystems.

8.3.4 Ecosystem change

Change is an intrinsic feature of ecosystems (Likens 1992) and understanding how and why ecosystems change is central to ecosystem science (Sutherland *et al*. 2013). Studies have shown that change over time in ecosystems is driven by both internal and external influences (Holling 1986, Holling and Gunderson 2002, Sutherland *et al*. 2013). Thus, ecosystem change is rarely simple because responses to drivers of change are mediated through a range of interactions and feedbacks between biotic and abiotic components and processes (Pickett and White 1985, Sutherland *et al*. 2013). These many interactions and feedbacks ensure that ecosystems are characterised by self-organisation, hysteresis, non-linear dynamics and the potential for multiple stable states (Holling and Gunderson 2002, Dearing 2008, Folke *et al*. 2010 Walker and Salt 2012). Semi-arid floodplains are dynamic, constantly changing complex ecosystems. This reflects their structure and function being highly variable in time and space (Rogers and O'Keeffe 2003, Thoms 2003, Bunn *et al.* 2006, Stromberg *et al.* 2009, Stromberg *et al.* 2013). Semi-arid floodplains are characterised by long periods of no surface water availability interspersed by periods of floodplain inundation (Colloff and Baldwin 2010). Changes in vegetation productivity occur in response to this variable flooding and drying, but this change is not well understood. The findings of this thesis enhance our knowledge of change in semi-arid floodplain vegetation in response to flooding and drying. There have been no other published studies of this type, and this is the first quantitative study of an adaptive cycle in floodplain ecosystems. The research represents a significant contribution to knowledge of the response to floodplain vegetation to flooding and drying, and highlights the value of using an adaptive cycle model and Markovian transition models to examine the complexity of change. This study suggests a complex response of floodplain vegetation productivity to flooding and drying in the Narran floodplain and shows that vegetation productivity transitions over time through the four phases of an adaptive cycle.

Overall, this thesis employed a resilience-based adaptive cycle model to improve understanding of vegetation productivity change using high resolution monthly Landsat satellite images of multiple flooding and drying sequences at the landscape and vegetation community levels. Further, the study results also demonstrated an adaptive cycle at two distinct levels of organisation, hence top-down constraints and smaller scale bottom-up influences were observed on the spatial pattern of change in vegetation productivity responses. The nature of change observed was more dynamic and varied over time than that previously reported in the literature for floodplains (see Chapter 4, 5, 6 and 7). The frequency, direction and probability of change between NDVI classes differed between dry and wet resource states. These characteristics of change were consistent over multiple events and also between different vegetation community types. Change in vegetation productivity in semi-arid floodplains in response to flooding and drying cannot therefore be perceived as a two state boom and bust model where vegetation is either productive or not. Changes in vegetation productivity were observed during the dry or the bust period, albeit with a one way direction of change and stability over multiple events. By comparison during the wet phase the overall response was more complex than that perceived by a simple two state model. Vegetation productivity response during the wet resource state was more complex with multi-directional two-way changes. Further vegetation productivity also varied among multiple flooding events of different flood sizes. Thus, the emphasis on floodplain productivity as consisting of two states may not account for the potential complexity in response to water availability (Thapa *et al*. 2015b).

Despite variation across different flood sizes the adaptive cycle repeated over multiple events over twenty years (see Chapter 6 and 7). The demonstrated complexity of vegetation productivity changes in response to flooding suggests that understanding the dynamics of change in these floodplains in relation to hydrological processes is amenable to an adaptive cycle approach. Under an adaptive cycle framework, change in floodplain vegetation productivity is viewed as a constant and dynamic cycle of exploitation, conservation, release and reorganization, rather than existing between two boom or bust states.

8.4. Application of this study to management

The findings of this thesis have implications for management and monitoring of change in floodplain vegetation productivity in response to flooding and drying. Many studies of floodplain vegetation are focused at the scale of field plots, transects or single geomorphic units like the riparian zone and have limited temporal range (e.g. Brock and Casanova 1997, Warwick and Brock 2003, Capon 2005, Capon *et al*. 2009, Reid *et al*. 2011). The results of this thesis suggest that different management strategies may need to be employed in different phases of the adaptive cycle and at the whole floodplain versus vegetation community level. Vegetation productivity varied over time in multiple events and also differed between vegetation communities and the four phases of an adaptive cycle. Semi-arid floodplain vegetation communities cycled among the four phases of an adaptive cycle and thus are resilient and always return to their initial phase after undergoing transitions through different phases. Although response in different phases of inundation differed between the vegetation communities and different adaptive cycle phases over the course of multiple flooding and drying events, individual vegetation communities further showed that the conservation or the wet phase was more dynamic. Because instability occurs in the wet or conservation phase this is probably where the exit to a new state may occur. The location of the exit point in the wet phase may suggest that more water in floodplains is not always the optimal management solution and it is the cycling around the adaptive phases that is important. Further, floodplain management needs to be cautious in delivering environmental water, since we equally need to manage the wetting, wet, drying and dry phase for the overall integrity of floodplain ecosystems. Vegetation monitoring also needs to be focussed at the individual community level and monitoring can be better if we consider each of the four phases and vegetation community adaptive cycles separately (see Chapter 7 of this thesis). Knowledge of floodplain vegetation response in each phase of an adaptive cycle and the possibility of state change will enable better management and may support restoring overall integrity in floodplain ecosystems.

Overall, the results of this thesis showed that different communities were sensitive at different points in the adaptive cycle. The knowledge of floodplain vegetation response in each phase of an adaptive cycle will enable better management by identifying likely times when a community might enter and exit the adaptive cycle. Further, the knowledge of different phases and potential for changing state will have significant implications for restoring the overall functioning of semi-arid floodplain ecosystems, because monitoring and management for resilience requires information about the magnitude and frequency of change so that movement towards a tipping point can be detected (Biggs *et al*. 2009). Thus, knowledge of floodplain vegetation response in each phase of an adaptive cycle will enable better floodplain management.

8.5. Future research prospects emerging from this thesis

The findings of this thesis showed that floodplain vegetation productivity response to flooding and drying was more complex and dynamic than was previously thought. The findings also raised new questions about the processes of change and the reasons behind the differences in the observed phases of an adaptive cycle between and within multiple events and between and within the vegetation communities. However, there are several limitations of this study that require further research to address limitations and further examine causal driving processes. Calculations of the expansion and contraction of surface water, from which the adaptive cycle phases were determined, was limited in this study. The use of Landsat satellite data may not be the best way of extracting floodplain surface water availability due to its low temporal resolution. Landsat images capture the surface of the earth every sixteen days. This interval hinders capture of finer resolution expansion and contraction of floodwaters in the floodplain landscape if expansion and contraction occurs on a shorter duration than sixteen days. The alternative would be to use SPOT high resolution satellite sensors (Munyati and Mboweni 2013), which can capture an image every four to five days. However, the SPOT sensor doesn't provide a long historical archive, having only been launched in 1986 and SPOT images are much more expensive to acquire than Landsat images. However, use of SPOT images in future research may provide a finer level of detail that can be used to improve the derivation of adaptive cycle phases based on hydrology.

This study relied upon remotely gathered data to demonstrate adaptive cycles amongst the individual vegetation communities. Detailed field studies to verify the remote sensing observations would be of benefit. Detailed field studies would have allowed us to make physio-ecological observations of the factors associated with vegetation productivity through the adaptive cycle phases. For example, the unexpected results in poplar box woodland may be better understood with detailed field based study (see Chapter 7 of this thesis). Thus, a future avenue of research should consider field based examination of vegetation productivity response to supplement and validate the satellite image NDVI measurements.

Another factor that could be improved with field based study is to be able to examine the role of factors other than productivity that may be important in adaptive cycle responses. Possible reasons for differences in the adaptive cycle among vegetation communities may be other environmental variables besides hydrology that influence vegetation productivity responses such as soil nutrient availability, temperature, seasonality, grazing pressure and sub-surface water storage. These environmental variables may be supporting differences in response in the adaptive cycle of the vegetation communities. Studies have shown maximum temperature and soil nutrient distributions to influence productivity patterns (Fu and Burgher 2015) and vegetation community structure and function (Yan and Dickinson 2014). In field based studies, Roberts and Marston (2011) found that maximum and minimum temperature influences germination, and vegetation growth rate. Similarly, Fu and Burgher (2015) also showed maximum temperature is the key driver of change in greenness of semi-arid floodplain vegetation. Besides temperature, soil nutrient availability and distribution also influences vegetation productivity (Baldwin *et al*. 2013, Fu and Burgher 2015). However, Reid *et al*. (2011) suggested that soil nutrients may not vary significantly across large semi-arid floodplains and may have little influence on vegetation productivity response. Thus, there may be other reasons for the observed differences in response through the adaptive cycle that were not examined in this study. Future research is needed to examine whether these other environmental variables influence adaptive cycles of vegetation response to flooding and drying.

This thesis used NDVI as a surrogate of vegetation productivity. NDVI is broad indicator of relative vegetation productivity response and several studies have shown that NDVI saturates at an optimum level (Sims and Colloff 2012, Xu *et al*. 2012) where NDVI is no longer sensitive to variation in vegetation vigour. If NDVI is found to be saturated at the higher productivity level, above this it is no longer sensitive to vegetation growth (Asner *et al*. 2005, Sims and Colloff 2012). To overcome this limitation of NDVI saturation, total biomass productivity per unit of area would be another way of measuring vegetation productivity. The results derived from NDVI and other quantitative measures of the actual productivity response will be the better way to monitor change in vegetation productivity in multiple flooding and drying events. Thus, an avenue of future research should combine both the actual biomass production and the relative measures of productivity such as NDVI. Combining these two approaches in future studies may provide an improved understanding of change in vegetation productivity of semi-arid floodplains.

The other future research question arising from this thesis is the efficacy of the adaptive cycle model in other dryland floodplains. Dryland floodplains in different parts of the world may have different functional processes due to differences in local geomorphology, vegetation composition and hydrological regimes. A future follow up study on the efficacy of the adaptive cycle in different dryland systems would be academically very useful to see if the adaptive cycle model holds in different places and the factors influencing the character of adaptive cycle phases in different dryland floodplains.

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APPENDICES