Response of *Breonadia salicina* in the Sabie River to an extreme flood: Implications for demographic modelling, monitoring and adaptive river management in the Kruger National Park

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Declaration

I hereby declare that the contents of this dissertation comprise my own original work, except where otherwise acknowledged or stated. This dissertation is being submitted for the Degree of Master of Science in the University of the Witwatersrand, Johannesburg, South Africa. It has not been submitted before for any degree or examination in any other university.

Signed on this 17th day of March 2009

Lisa Dowson

Abstract

The Sabie River is a heterogeneous river system and sedimentation has been identified as a threat which may reduce bedrock influence and heterogeneity in this river. This motivated the development of a monitoring programme utilising the demographic profiles of *Breonadia salicina* (*B. salicina*) as an indicator of sediment change along the Sabie River. The negative-J demographic profile of *B. salicina* in the pool-rapid channel type was considered the most sensitive to sedimentation. As part of this monitoring programme, a rule based model was developed as a predictive tool to be used by managers. The *Breonadia* Model was designed to model changes in the demographic profile in response to changes in sedimentation.

In February 2000, an extreme flood occurred in the Sabie River and markedly altered the biophysical template and influenced the structure of the *B. salicina* population. The *Breonadia* model was developed prior to the 2000 flood and there were no empirical data on vegetation response to a flood of this magnitude. Hence, the model may not fully represent the process of vegetation response and recovery as it occurs on the post flood biophysical template. The 2000 flood in the Sabie River provided an opportunity for examining the response of *B. salicina* to a Large Infrequent flood and for directly testing how well the *Breonadia* Model predicts these responses. The *B. salicina* population was always considered to follow a flowering response, producing seeds in order to recover from disturbance. This characteristic was incorporated in the *Breonadia* Model, with the model subsequently being used to predict the likely timeframe of recovery to a Large Infrequent flood disturbance. This study aimed to improve understanding of *B. salicina* population dynamics subsequent to large infrequent floods by examining the different response strategies of the *B. salicina* population after the 2000 large infrequent flood event. This study also re-evaluated the application of the negative-J demographic profile-focused *Breonadia* Model. Assessments were made of the applicability of the *Breonadia* Model and monitoring in the pool-rapid channel type within the context of the SAM framework utilised in the KNP.

The examination of response mechanisms revealed that sprouting is an important mechanism in *B. salicina* that enabled the population to recover from damage caused by the flood. A canonical correspondence analysis showed that sprouting accounted for 56% of the overall variation in recovery response five years after the flood. Flowering accounted for the other 44%. The likelihood of sprouting was higher in more severe damage categories and smaller size-class categories. These response mechanisms were unrelated to the underlying geomorphology at the channel type scale. Thus, while recruitment has been shown to occur in relation to the underlying physical template, the mode of response is related to individual size-class and damage severity. The complex interplay of biotic responses and the multi-scaled physical template suggests that the longer term recovery of the *B. salicina* population in the Sabie River will not be spatially uniform.

The *Breonadia* Model did not withstand direct testing and predicted an overly optimistic level of recruitment following a catastrophic flood event. The data suggest that sprouting continues to limit flowering in adult plants five years after the 2000 flood, therefore limiting recruitment of new individuals. Thus the *Breonadia* Model was updated to take the influence of sprouting on fecundity into account. A penalty to fecundity was determined from field data and extrapolated to include the 10 years after any catastrophic flood.

This study has revealed the importance of disturbance events in influencing response mechanisms, which has an effect the demography of a riparian species. The physical template of the Sabie River forms a complex and patchy template on which riparian vegetation processes occur. However, factors unrelated to the physical template also play a role in influencing riparian vegetation processes. Management of the Sabie River needs to take these complex relationships into account in the context of the variable hydrological regime in order to update and apply valid management strategies to the system.

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Dedication

To Elbert: without your encouragement and support, this would not have been possible.

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CHAPTER 1: ECOSYSTEM DYNAMICS, DISTURBANCE AND PLANT RESPONSE AND THEIR IMPLICATIONS FOR STRATEGIC ADAPTIVE MANAGEMENT

Contrary to previous perceptions that ecosystems regulate towards a climax, stable state, ecosystems are in a continual state of flux (Holling, 1978; Walters, 1986). Limited scientific knowledge of ecosystem fluctuations in time and space poses a problem for conservation management. To deal appropriately with the fluctuating conditions in ecosystems, the discipline of natural resource management has experienced a shift from responding subsequent to fluctuations to a more adaptive pro-active strategy that requires predicting these fluctuations. This enables managers to prepare in advance for possible ecosystem fluctuations by adapting their management strategies (Holling, 1978; Walters, 1986; 1997; Peel *et al*., 1999; Rogers, 2003).

Adaptive management allows for frequent adjustments in management practices through a process of "learning while doing," that enables managers to deal with the uncertainty of ever-changing ecosystems (Walters and Holling, 1990; Walters, 1997). The management approach facilitated by Strategic Adaptive Management (SAM), specific to South Africa, Kruger National Park (KNP) uses management actions as opportunities to learn more about an ecosystem and thus enhance management decision making, even when there is incomplete knowledge of an ecosystem (Rogers and Bestbier, 1997).

Strategic Adaptive Management focuses on strategic planning and links science and management to reach consensus on the acceptable range of fluctuations of the ecosystem being managed, referred to as the desired state (Rogers and Bestbier, 1997). The desired state for the system is then translated into operational goals that provide managers with specific targets or ecological endpoints for the managed ecosystem (Rogers and Biggs, 1999). Selecting an indicator to quantitatively define the desired state enables managers to measure achievement of operational goals for the system. Monitoring for achievement of the operational goals can then focus on the selected indicator. However, monitoring for achievement of these goals remains a reactive strategy. By integrating existing knowledge into models, managers are able to predict adverse system conditions, proactively screen potential management strategies and adapt accordingly (Starfield *at al*., 1990; Walters, 1986; 1997). In addition, models can assist with clarifying problems and improving communication between science and management. Models are also useful in identifying key knowledge gaps and indicating areas that can be examined in future studies (Starfield *et al*., 1990; Walters, 1986; 1997). Thus, models are useful tools that can increase the ability of managers to be strategic and adaptive in allowing the natural fluctuations within a managed system.

However, as models are often initially constrained by available data, it is important to update models as new data become available or as management objectives change (Starfield and Bleloch, 1986). Strong interplay between the modelling process and the collection of monitoring data becomes important, as gaps in the model can highlight which data are needed to improve a model (Starfield and Bleloch, 1986). Thus new events, such as disturbances that occur in an ecosystem, play a role in changing modelled components of that system and are important opportunities to collect new information.

Disturbance events such as hurricanes, fire, flooding or herbivory can change the species composition of the community and can influence the initial response of that system (Sparks and Spink, 1998). The resulting ecological processes that occur after these disturbance events are variable (Turner *et al.*, 1998) and are influenced either by the presence of surviving, disturbance tolerant organisms or residuals, local conditions and chance colonisation events (Wood and Del Moral, 1987). Fluctuating ecosystem conditions limit the value of static management strategies while adaptive management strategies can be applied more appropriately (Holling, 1978; Walters, 1986; 1997; Peel *et al.*, 1999). Adaptive management in the KNP includes adjusting and redefining targets for managed systems to take new, natural fluctuations into account (Mackenzie *et al.*, 1999).

In South Africa, KNP managers apply SAM in order to meet their conservation goals (Rogers and Bestbier, 1997). As part of their management strategy for rivers, park managers have produced a desired state description for the rivers of the KNP. This allows the development of operational conservation goals for the KNP's rivers (Rogers and Bestbier, 1997). These conservation goals fall within the KNP management framework that aims to maintain and improve heterogeneity and diversity within the park.

The Sabie River, within the KNP, is a heterogeneous river system because of the variable underlying geological influence and variable sediment and flow conditions. As a result a variety of habitat types and communities have developed along its length (van Niekerk *et al.*, 1995; van Coller *et al.*, 1997). Sedimentation has been identified as a threat which may reduce bedrock influence and heterogeneity in the Sabie River, with possible detrimental effects on river function and species diversity (van Coller, 1993; Heritage *et al.*, 1997). This threat motivated the development of a monitoring programme utilising the riparian tree *Breonadia salicina* (*B. salicina*) as an indicator of sediment change along the Sabie River

(Mackenzie *et al*., 1999). A rule based model was developed as a predictive tool as part of this programme (Mackenzie *et al*., 1999).

The *Breonadia* Model focuses on changes in the population structure of the tree species *B. salicina* to define the state of the Sabie River's riparian vegetation in relation to the desired state of the river. Changes in the population structure of the *B. salicina* population represent the response of riparian vegetation to changes in bedrock influence in the Sabie River. The *Breonadia* Model included known information about the response of the *B. salicina* population to different flow events. For those flow events where no data existed, assumptions were made about how the population would respond. The model rules and assumptions did not however take all types of hydrological events into account and a list of factors requiring improvement was drawn up by the model developers (Mackenzie *et al*., 1999). Rules and assumptions about large infrequent floods were particularly singled out as being in need of empirical verification.

In February 2000 an extreme flood occurred in the Sabie River resulting in substantial removal of vegetation and changes to the geomorphology and landscape characteristics of the river in a manner that was unprecedented in 60 years of aerial photographic records (Parsons *et al*., 2006). The 2000 flood provided an opportunity to improve understanding of how *B. salicina* was influenced by and recovered from a flood classified as a Large Infrequent Disturbance (LID). This information can then be used to adjust model assumptions and rules about this type of flow event. Improved understanding and updating of management tools such as the *Breonadia* Model will enhance decisions made for management of the Sabie River. This dissertation examines the reproductive response of *B. salicina* to the 2000 flood. Further, the implications of this response for the rules within the model and the application of the *Breonadia* Model in the KNP are discussed.

1.1 The reproductive response of vegetation to disturbance

Spatial and temporal fluctuations in ecosystems are natural phenomena and natural disturbances can be viewed as a source of variation in ecosystems, with some species being dependant on conditions created by disturbance (White, 1979; White and Harrod, 1997). Disturbance events are defined as "any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resource, substrate availability, or the physical environment" (White and Pickett, 1985).

A disturbance to a system will generate a subsequent successional response in the vegetation community (Tilman, 1993). Historically, succession was considered to be directional, and hence, fairly predictable (Odum, 1969). More recently, however, studies have shown that disturbances have specific ecological effects on communities and a number of different viewpoints on succession have started to emerge (Johnson and Miyanishi, 2007). Pickett and White (1985) summarised these emerging successional theories, highlighting conflicting evidence on the role of disturbance in communities. A landscape can be viewed as a mix of patches, with each patch undergoing succession (Pickett and White, 1985) where historical events such as disturbances influence recruitment, growth and mortality. These temporal variations are reflected in a population's demographic profile (Bullock *et al.*, 1996) and play a role in future changes in the community. As a result, studies of population demography can tell us a great deal about the disturbance regime in an ecosystem.

Studies show that dynamic states, where change, disturbance and succession are natural characteristics of the system, produce multiple state trajectories (Westoby *et al.*, 1989; Holling, 1995; Bengtsson *et al.*, 2000; Janssen *et al.*, 2004; Knowlton, 2004; Petraitis and Methratta, 2006). However, disturbance studies still tend to focus on correlating vegetative response to various defined characteristics of disturbance rather than on understanding how disturbances influence the underlying ecological processes (Johnson and Miyanishi, 2007). If studies of disturbance can even partly answer how different disturbances cause an observed ecological effect rather than simply defining what that ecological effect is, then the accuracy of assumptions used to fill in missing data will be greatly enhanced. Increased understanding of how disturbance influences underlying ecological processes such as reproductive response mechanisms will improve the reliability of predictions of response, even for those disturbances for which there are no data (Johnson and Miyanishi, 2007).

Disturbances can occur at a variety of intensities, sizes and frequencies (Turner *et al.*, 1998). Large Infrequent Disturbances (LIDs) are considered to be larger in extent, duration or magnitude than "typical" disturbances affecting a system (Turner and Dale, 1998). Large Infrequent Disturbances include events such as widespread fires, hurricanes, extreme floods and volcanic eruptions. The ecological consequences of small disturbances are generally well studied, however, understanding of larger disturbances, that are infrequent in occurrence, is more limited (Turner and Dale, 1998).

Large Infrequent Disturbances can occur over a spatially large area and cause changes that persist for long periods of time (Turner and Dale, 1998). They can become the driving force behind ecosystem processes (White and Harrod, 1997, Turner and Dale 1998) by generating a template upon which future ecological processes occur and providing an opportunity for recruitment (Grubb, 1977). Despite the perception that large disturbances generate a uniform template by removing vegetation and sediment, a complex, heterogeneous template is instead generated (Glenn-Lewin and van der Maarel, 1992; Turner *et al*., 1998; Turner and Dale, 1998). This patchy template is generated because LIDs are variable in intensity across the landscape. Pre-existing physical and biological patchiness in a landscape also contribute towards variability in disturbance intensity (Turner *et al*., 1998). Thus, disturbances may vary in distribution, frequency, predictability, severity and synergism in the landscape (White and Pickett, 1985). Individual plants will be affected differently by the disturbance resulting in differing mechanisms of response occurring at different scales across species and between individual plants. Disturbance frequency and disturbance severity influence the vegetative response of plants, such as the proportion of a floral community or population that will sprout or produce seed, and the extent to which these responses occur in an individual (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Kennard *et al*., 2002). Thus, because disturbances can vary in the landscape, the subsequent response of vegetation to disturbance is also expected to be patchy.

Tree species that produce large numbers of wind dispersed seeds generally respond well to large disturbances (Baker, 1974). Large disturbances change the availability of resources (Canham and Marks, 1985) and producers of large numbers of seeds are more likely to successfully disperse to suitable areas. Conversely, those species able to regenerate asexually by sprouting, and thus maintain the older life stages, may do better when suitable habitat for recruitment is unavailable after a disturbance (Nakamura and Inahara, 2007).

Sprouting is the ability of a plant to regenerate after disturbance by producing new shoots from the plant's roots or stem (Blake, 1983; Laureysens *et al*., 2003) and is an effective means of regaining above-ground biomass (Sakai *et al*., 1995, Bellingham and Sparrow, 2000; Rydberg, 2000; Laureysens *et al*., 2003; Luoga *et al*., 2004; Tewari *et al*., 2004). Sprouting is also an important alternative to regeneration from the seed under disturbance conditions (Martínková *et al*., 2006). Sprouting gives species the means to persist through both natural and anthropogenic disturbances (Bond and Midgley, 2001); however, this response mode can reduce the ability of residual trees to produce seeds (Keeley and Keeley, 1977). The ability of trees to sprout can be influenced by individual characteristics such as plant age or size (Misra *et al*., 1995., Tewari *et al*., 2004) as well as external factors such as disturbance intensity (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Kennard *et al*., 2002).

Bellingham and Sparrow (2000) proposed a model demonstrating the relationship between disturbance magnitude/frequency and how this would affect the ratio of seeders versus sprouters within a community (Figure 1). Their model suggests a trade-off between sprouting and seed production, with the number of seed producing species in a community generally declining as the proportion of sprouting species increases. The model is also applicable to single species, where the frequency or magnitude of the disturbance would affect the proportions of individuals within a population that sprout versus those that seed. Their model further proposes that sprouting is the dominant response at low disturbance severity, with seeding increasing in dominance as disturbance severity increases. As the disturbance severity continues to increase, sprouting once again becomes the dominant response within a population at very high disturbance severity (Bellingham and Sparrow, 2000). The strength of the sprouting response can decrease in certain species when trees are damaged frequently (Hytönen and Issakainen, 2001) while other species show no decrease in sprouting ability despite several consecutive years of damage. Furthermore, it is suggested that either one or other response will never be the sole response due to the patchy nature of disturbance in time and space (Bellingham and Sparrow, 2000).

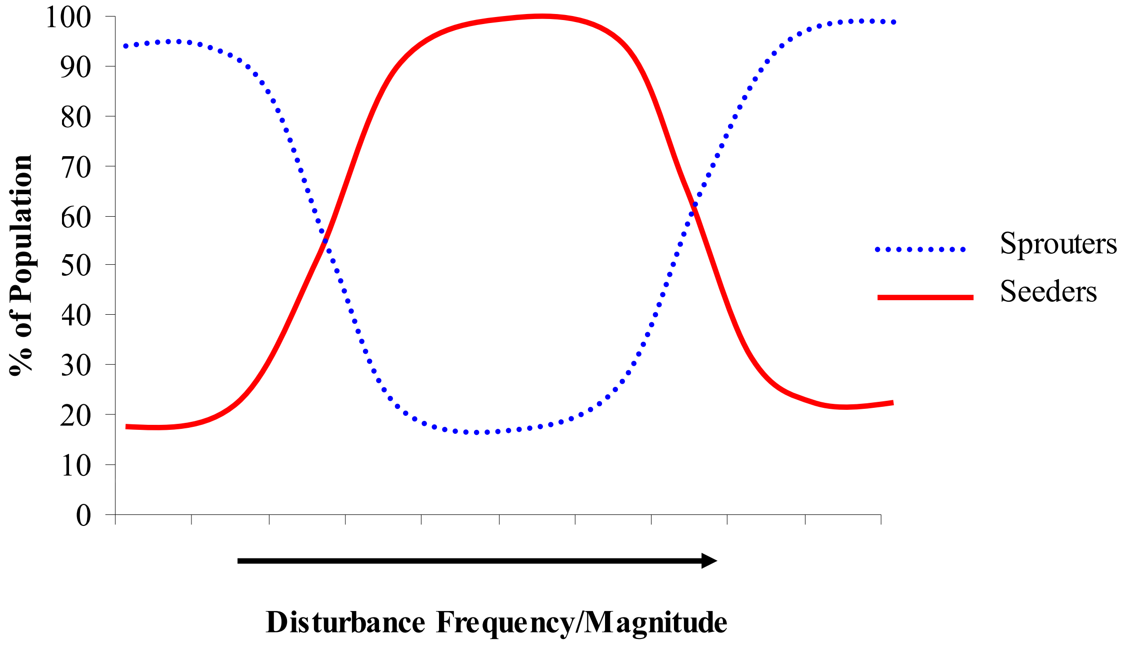

Figure 1: Bellingham and Sparrow model of the trade-off between the proportions of sprouters and seeders within a population in relation to disturbance frequency or disturbance magnitude. From Bellingham and Sparrow, 2000.

Many studies on the response of a species to disturbance have focused on how response mechanisms differ in relation to variations in disturbance intensity or disturbance frequency (Morrison *et al.*, 1995; Vesk and Westoby, 2004; Clarke *et al.*, 2005). A review of the literature on the response of vegetation to disturbance indicates that both damage severity as a direct result of disturbance (Bellingham and Sparrow, 2000) and size-class (Misra *et al.*, 1995; Tewari *et al.*, 2004) also influence vegetation response mechanisms. More recently studies have found that patterns of sprouting response and recruitment subsequent to disturbance show a correlation with competition for resources rather than with disturbance intensity or frequency in woody species (Lamont and Markey, 1995; Bond and Midgley, 2001; Clarke and Knox, 2002; Clarke *et al.,* 2005).

In competitive environments, sprouting trees are favoured because of their ability to persist (Clarke *et al.,* 2005). When competition for resources is low, population recovery is dominated by rapid and successful recruitment; the population generally displays an even-aged structure where most of the population is the same age (Silverton and Lovett Doust, 1993). Sylvie *et al.* (1993) found that even-aged population structures that occur after particularly intense disturbances, such as fires, persist for a limited period (100 years in a Canadian boreal forest), eventually changing to an uneven-aged population structure as the population recovers. Populations affected by less intense disturbances were found to have an uneven-age structure following disturbance (Sylvie *et al.*, 1993).

1.2 Riparian tree reproductive response to disturbance

Riparian areas between terrestrial and aquatic ecosystems form a transitional zone subject to episodic disturbances such as flooding (Swanson *et al.*, 1982). A single disturbance event occurring in a riparian area can manifest at different intensities at different points in space due to pre-existing heterogeneity and differences in elevation within a river channel. Numerous studies have linked the structure of riparian forests to spatial and temporal variations in disturbance and geomorphology (Niiyama, 1987; 1989; Ishikawa, 1988; Hughes, 1990; van Coller *et al.*, 1997; 2000; Robertson and Augspurger, 1999; Shin and Nakamura, 2005). For example, changes in elevation can influence frequency of flooding disturbance temporally or the intensity of disturbance experienced spatially. Higher lying areas will experience flood disturbance only from deeper, less frequent flood events. The flooding depth, duration and flow of these larger floods will be less at higher elevations compared to the same event at a lower lying area. In addition, the nature of flooding disturbance (timing, duration and frequency) will influence erosion and deposition and thus the availability of different habitats for regeneration (Cordes *et al.*, 1997; Dykaar and Wingington, 2000). The nature of disturbance in riparian zones has also been shown to vary along the length of streams, with different types of disturbance being associated with headwaters of streams, middle order reaches and low gradient, meandering streams (Nakamura *et al.*, 2000; Nakamura and Swanson, 2003).

Life history characteristics and regeneration habitat are important factors in regeneration in riparian areas after disturbance (Nakamura and Inahara, 2007). Forest communities occurring in riparian zones are able to survive intense and frequent disturbances through structural and physiological adaptations and utilisation of the underlying geomorphology as habitat for recruitment and growth (Nakamura and Inahara, 2007). As there is variation in the types of disturbance as well as the frequency and intensity of disturbances, there is a range of response strategies and life history characteristics that can be found in affected riparian forest communities. This range of strategies may be important in explaining the relationship between environmental heterogeneity and the organisation of riparian forest communities (Nakamura and Inahara, 2007).

The response strategies of seed production and sprouting in disturbed riparian forests are each supported by a range of life history characteristics (Nakamura and Inahara, 2007). Nakamura and Inahara (2007) list the life history strategies of riparian forest species relying on seed production in order to recover subsequent to disturbance as:

- Production of wind dispersed seeds, thus increasing the likelihood of colonising suitable recruitment habitat over a large area.
- Producing high numbers of seeds to increase the likelihood of colonising all available recruitment habitat.
- Delaying seed dispersal to coincide with seasonal changes in disturbance regimes
- Delaying the germination of seeds to coincide with seasonal changes in germination conditions.

Species that have a sprouting response might employ life history characteristics such as longevity and enhanced stem growth. A sprouting response strategy will thus maintain the existence of a species in areas where seedling recruitment habitat is spatially and temporally unpredictable (Nakamura and Inahara, 2007). Nakamura and Inahara (2007) do not list water dispersed seeds as a life history strategy in disturbed riparian forests. Wind dispersal allows seeds to be dispersed both up and downstream, whereas water dispersed seeds would likely only disperse to downstream areas. The larger area of colonisation resulting from wind dispersal is almost certainly a better strategy than water dispersal of seeds in these communities.

Either seed production or sprouting strategies could increase the likelihood of successful establishment of new individuals in a riparian area subject to flooding disturbance. However, the success of each of these strategies may depend on the patchy spatial variability in conditions subsequent to a disturbance event. Species will therefore exhibit different life history characteristics that enable them to persist in disturbed areas under certain conditions (Nakaura and Inahara, 2007). Further, Bellingham and Sparrow (2000) proposed that individuals within a species can have different response mechanisms, thus individuals within a species can also be expected to exhibit different response mechanisms and life history characteristics in response to different disturbance intensities or frequencies, enabling them to persist subsequent to disturbance. The use of sprouting or seeding strategies by *B. salicina* in response to a large flood disturbance is largely unknown. Individuals of *B. salicina* may exhibit different reproductive responses to disturbance that may depend on the severity of the disturbance in the landscape. In order to better understand ecosystem fluctuations and their implications for SAM, it is necessary to understand the way that *B. salicina* responds to disturbance and the implications for models that use this species as an indicator.

1.3 Objectives and outline of dissertation

As part of the SAM framework, KNP managers are committed to take into account any system changes that result from disturbance events. Disturbance events such as the Sabie River flood in 2000 are used as an opportunity to gain information about changes in river ecosystem processes. This new information can be used to verify and update management tools, such as models and monitoring techniques so they continue to be applicable to the system following disturbances. If new information is not used to update management tools, a stagnation of pro-active strategies and a return to re-active management responses may occur.

The 2000 flood provides a suitable opportunity for directly testing the predictive *Breonadia* Model and for determining how well it predicts the response of *B. salicina* to an extreme flood. The aim of this dissertation is to utilise the 2000 flood in the Sabie River as an opportunity to verify and correct existing assumptions about response to and recovery from disturbance within the existing *Breonadia* Model.

This dissertation will examine vegetation response to disturbance and discuss the implications of variable response mechanisms for management tools utilised as part of a strategic management framework. The *Breonadia* Model will be examined as a case study to show how ongoing research is important to continually improve the value of predictive models as a tool for managers in an adaptive management framework. This will be done in three parts by:

i) Examining the reproductive response of the tree species *Breonadia salicina* to a LID flood in the Sabie River.

ii) Testing the ability of the *Breonadia* Model to predict recovery of the *B. salicina* population in the Sabie River subsequent to a LID flood event.

iii) Using this new information to update the model and compare it to the current version. This will enable managers to utilise an updated version of the *Breonadia* Model in the post-flood era.

CHAPTER 2: THE REPRODUCTIVE RESPONSE OF THE *BREONADIA SALICINA* POPULATION ALONG THE SABIE RIVER

The study of demography examines the causes of changes to populations over time and is a quantitative description of the birth, growth, reproduction and death of individuals within a population (Solbrig, 1980; Silverton, 1982). Different age groups of plants provide useful intervals at which changes in the population size over time can be analysed (Silverton, 1982). Demographic studies search for past environmental influences, including both biotic (such as fecundity and growth rate) and abiotic (such as the underlying physical template) factors that contribute to the current population structure, allowing predictions to be made about future changes in population structure (Harper and White, 1974; Pacala, 1987; Pavlik and Barbour, 1988). The structure of a population is represented as a demographic profile that gives an indication of the number of individuals in each age or size category in the population.

Variation in the intensity or frequency of disturbance events changes the reproductive response of woody species, resulting in a change in the mode of recruitment (Bellingham and Sparrow, 2000), thus influencing the demography of species. In the Sabie River, previous studies have focused on the close relationship between riparian vegetation and the underlying physical template, suggesting that the demography of *B. salicina* is predominantly shaped by changes to this template. There is very little current understanding of the reproductive response of *B. salicina* to disturbance and the role it may play in shaping populations in the Sabie River independently of changes to the underlying physical template (Section 1.2). This chapter will summarise the existing knowledge on the influence of the underlying physical template in shaping the *B. salicina* population in the Sabie River and why these characteristics make the species suitable as an indicator species in the KNP. The chapter will then go on to examine whether reproductive response may also play a role in shaping the demographic profiles of this species by influencing recruitment of new individuals.

2.1 The study area

The Sabie River is a perennial river with a catchment area of 7,096km^2 (Chunnet, 1990). The river originates in the Mpumalanga region of South Africa (Figure 2) and flows a distance of 210km before its confluence with the Inkomati River in Mozambique. The river flows for 106km through the KNP (Mackenzie *et al.*, 1999), which forms the study area.

Despite being perennial in nature, the Sabie River experiences high flow variability (Rountree *et al.*, 2000). Flooding events are associated with summer thunderstorms. The

Sabie River catchment falls within a semi-arid to sub-tropical climate, experiencing a decreasing annual rainfall gradient along its length, with most precipitation occurring in the west outside of KNP (1800-2000mm) and decreasing towards the east (450-650mm). Evaporation is lowest in the west (1400mm) and highest in the east (1700mm) (Heritage *et al.*, 1997).

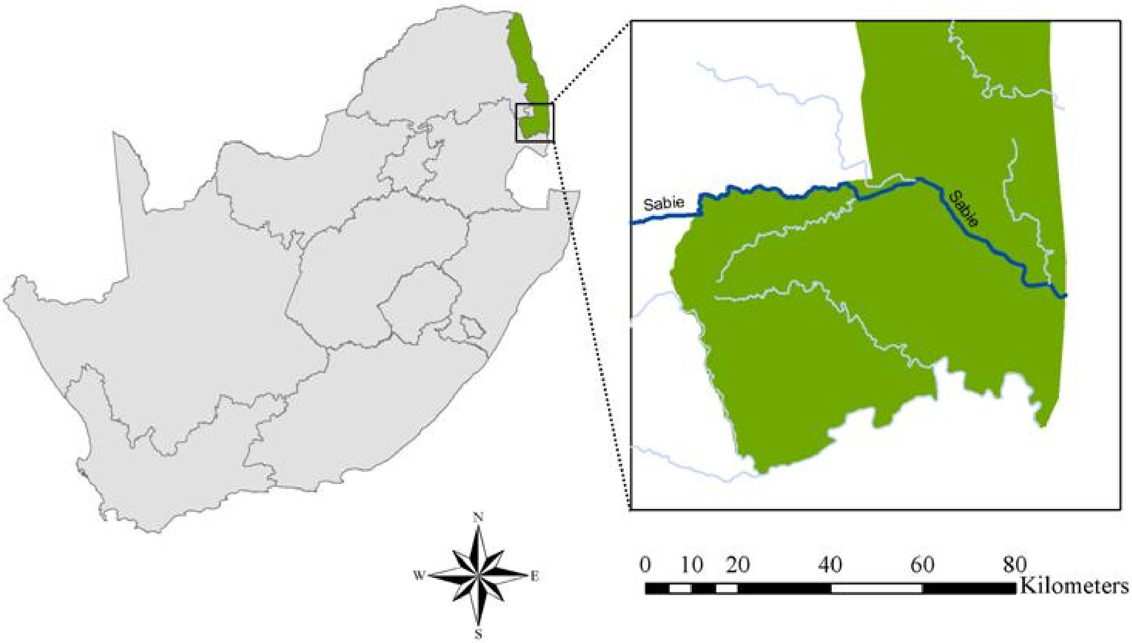

Figure 2: Location of the Sabie River within the Kruger National Park, South Africa. The Sabie River flows from west to east in the Southern area of the Park as indicated.

A complex geology consisting of sedimentary, extrusive and intrusive igneous and metamorphic rock underlies the Sabie River and influences river geomorphology resulting in a variable physical template (van Niekerk and Heritage, 1993; Cheshire, 1994). The resulting spatially variable template causes continuously changing conditions of sediment movement and water flow (Rogers and O'Keeffe, 2003), forming different physical features along the river's length as a consequence.

A hierarchical geomorphic-based classification system (catchment, unit grouping, plan form, channel types and morphological units) has been used to describe the Sabie River (van Niekerk *et al.*, 1995). This study was conducted at the channel type and geomorphic unit scale, rather than at the catchment, unit or plan form scales, as these are the scales relevant to this project. At the channel type scale, the river is both bedrock and alluvium influenced, creating a mixed bedrock-alluvial system. Five major channel types have been described: single thread (continuous pool), pool-rapid (rapids separating pools), braided (braiding restricted by the macro-channel), bedrock anastomosing (multiple bedrock controlled channels) and mixed anastomosing (multiple alluvium controlled channels over a bedrock base) (van Niekerk *et al*., 1995). Each channel type comprises a specific combination of in-channel geomorphic features, each being associated with specific channel types (Mackenzie *et al.*, 1999). Rock geomorphic features include cataracts, rapids, pools and riffles. Core, braid, point and lateral bars make up sedimentary features while lateral deposits and weathered bedrock make up the macro-channel bank (van Niekerk *et al*., 1995).

The upstream sections of the Sabie River, outside of the KNP, are subjected to anthropogenic activities, including large-scale forestry and fruit farming (O' Keefe and Rogers, 2003). Approximately 30% of the Sabie River’s Mean Annual Runoff (MAR) is lost, mostly to commercial activities of this type (O' Keefe and Rogers, 2003). Water abstraction has altered the flow regime of the river, resulting in reduced stream flow. This reduced flow leads to a decrease in sediment transport capacity and an increase in sediment storage in the river, with a projected loss of bedrock influence.

The KNP management objectives are to conserve structural, functional and compositional diversity in all their facets and fluxes (Rogers and Bestbier, 1997). Increases in sediment would reduce geomorphic heterogeneity, which would in turn reduce species diversity and thus alter hydrological and ecological processes (van Coller, 1993; Heritage *et al*., 1997). A monitoring programme utilising the population structure of *B. salicina* as an indicator of the effect of sediment change on riparian vegetation in the Sabie River (Jewitt *et al*., 1998; Mackenzie *et al*., 1999) was developed, as part of the KNP management system to conserve diversity.

2.2 Size, age and stage-based approaches for investigating tree demographics

A number of factors including competition (Gates, 1978), changes in mortality rates (Ford and Diggles, 1981) and uneven growth rates (Ford, 1975) may account for the occurrence of different profiles in plant populations. Determining the age structure of populations to describe ecological and evolutionary dynamics is a fundamental issue in population biology and many studies on woody species have focussed on age distribution (e.g. see Knowles and Grant, 1983; Kalisz and McPeek, 1992). Age structured demographic studies of woody species most commonly utilise the technique of dendrochronology, or tree ring dating (Fritts, 1976; Fritts and Swetnam, 1989) to determine tree age. One of the challenges to studying the demography of plant populations is the aging of plants, and deciding what comprises a single demographic unit, because individuals are not necessarily physiologically independent (Solbrig, 1980). Variability in growth rates and problems with aging of plants makes it difficult to utilise age structure descriptions of many plant populations (Solbrig, 1980; Kirkpatrick, 1984; Stewart, 1986).

As an alternative to a dendrochronological approach, measurements such as height or trunk diameter of individual trees can be used as surrogates for age in demographic studies. Various parameters of plant size include diameter at breast height (Platt *et al.*, 1988), tree height, mean crown diameter (Shaltout and Ayyad, 1988) and mean basal area (Butler, 1988), which have been used to infer the age of individuals. However, without a strong relationship between size and age, it is not possible to directly infer age from size measurements, and thus a third approach utilising the stage of development of individuals can be used in demographic investigations.

Stages of development, sometimes referred to as biological age, are related to specific stages of growth associated with both the age and the size of individuals (Robbins, 1957). Changes in morphology, anatomy, physiology or biochemistry occur at different stages in a plant's lifecycle, making it possible to characterise an individual plant's biological age by its stage of development (Gatsuk *et al.*, 1980). It has further been suggested that the age-state of a plant determines its role within a population rather than the number of years which the plant has lived (Gatsuk *et al.*, 1980). Age states are useful predictors of population development and in conjunction with more formal plant age analyses, are also useful in tracing historical influences to the present population structure (Harper, 1977).

A dendrochronological investigation on the suitability of tree ring dating for aging *B. salicina* found that the species did not provide ring structures suitable for age determination (de Fontaine and Rogers, 1995). However, a stage-based demographic investigation of the *B. salicina* population on the Sabie River found that the population structure is strongly related to the underlying physical template, with specific demographic profiles occurring in different channel types and geomorphic units (de Fontaine and Rogers, 1995). The occurrence of negative-J, unimodal and bimodal demographic profiles indicates that there are periods of strong recruitment followed by periods of decreased recruitment. These fluctuations in recruitment levels were considered to be the result of fluctuations in the availability of suitable recruitment habitat as a result of the influence of flow events (de Fontaine and Rogers, 1995).

However, although increases in the availability of suitable recruitment habitat will result in increased recruitment levels thus influencing the demographic structure of a population, there are additional factors that play a role in shaping populations. Disturbance events themselves, such as floods, can have a direct influence on the structure of a population by uprooting or damaging established trees (Turner and Dale, 1998). Demographic and disturbance studies often make correlations between population structure and disturbance intensity. However, these studies seldom examine the underlying mechanisms behind the influence of disturbance on demography (Nakamura and Inahara, 2007). Trees may have different response mechanisms in response to different disturbance intensities. Response mechanisms, such as sprouting, can have an influence on recruitment of new individuals. Disturbances of a new level of intensity may prompt a different response in a population to those responses previously recorded. Floods of differing magnitudes provide opportunities to examine the influence of different disturbance intensities on population structure and how populations respond to these events. Thus in the case of *B. salicina*, modes of response subsequent to disturbance may also play a role in the formation of specific demographic profiles.

2.3 The demography of the Sabie River *Breonadia salicina* population

There is very little literature available on the biology of *B. salicina* with most of the current knowledge coming from the work of Palgrave (1983), de Fontaine and Rogers (1995), van Coller *et al.* (1997) and Mackenzie *et al.* (1999). These studies al suggest that the influence of disturbance on the underlying physical template indirectly plays a role in shaping sub-population structures of *B. salicina.* This is due to site heterogeneity influencing habitat availability (de Fontaine and Rogers, 1995). *Breonadia salicina* is an abundant tree species that is easy to locate along the length of the Sabie River and is easy to identify at all times of the year (de Fontaine and Rogers, 1995). *Breonadia salicina* is limited to the riparian zones of permanent rivers in eastern Mozambique and the Limpopo and Mpumalanga provinces of South Africa, extending further southwards into northern Kwazulu Natal (Van Wyk and van Wyk, 2000). Adult individuals range from 10 to 40 meters in height. Pale mauve flowers forming compact, round auxiliary heads are produced from December to March (Palgrave, 1983). *Breonadia salicina* produces clusters of small, brown, two-lobed fruit capsules 2-3mm in length. The two-winged seeds are produced from June to July (Palgrave, 1983).

Mackenzie (unpublished data, CWE, University of the Witwatersrand (UWITS)) observed that seeds are produced every year and have been found on all geomorphic features of the Sabie River. Due to the winged nature of the seeds, it was assumed that they are wind dispersed (De Fontaine and Rogers, 1995) and no studies have been conducted on the viability of the seeds after prolonged exposure to water. However, the close proximity of this species to the active river channel combined with the discovery of seeds and germinants on all geomorphic units, away from adult trees, implies that the seeds may also be water dispersed. The ready availability of seed in the system implies that establishment of new individuals of *B. salicina* would be primarily limited by habitat availability (de Fontaine and Rogers, 1995).

The population is sensitive to changes in bedrock availability along the Sabie River and was thus selected as an indicator of biotic response to changing sedimentation conditions (van Coller, 1993; Mackenzie *et al*., 1999; Mackenzie, unpublished data, CWE, UWITS). Establishment of new individuals is reliant on the availability of exposed bedrock as individual seedlings must anchor themselves in crevices in the exposed bedrock to ensure successful establishment. Individuals that do not germinate in bedrock crevices are washed away by high flow events. Increases in sedimentation will therefore result in reduced establishment of new individuals because sediment blankets anchoring sites.

Three types of demographic profiles were found to occur in the *B. salicina* population along the Sabie River: negative-J, unimodal and bimodal (Figure 3) (de Fontaine and Rogers, 1995). Each of these demographic profiles was found to be associated with specific geomorphic features of the hierarchical geomorphic-based classification for the Sabie River. Flow events in the river influence the geomorphic template, washing out sediment resulting in bedrock becoming exposed or conversely depositing sediments over underlying bedrock. This results in fluctuations in the extent of exposed bedrock and sediment over time, with the different channel types being affected differently due to a variety of factors such as channel width and steepness (Rountree, unpublished data, CWE, UWITS). As a result of the differential effects of the different channel types, each channel type is dominated by specific geomorphic features. As the *B. salicina* demography at any one point in space is influenced by the patterns of fluctuation between bedrock and sediment, each channel type shows a specific demographic profile based on the dominant geomorphic unit and the frequency of fluctuations within that channel type. More detailed explanations of these demographic profiles are provided below.

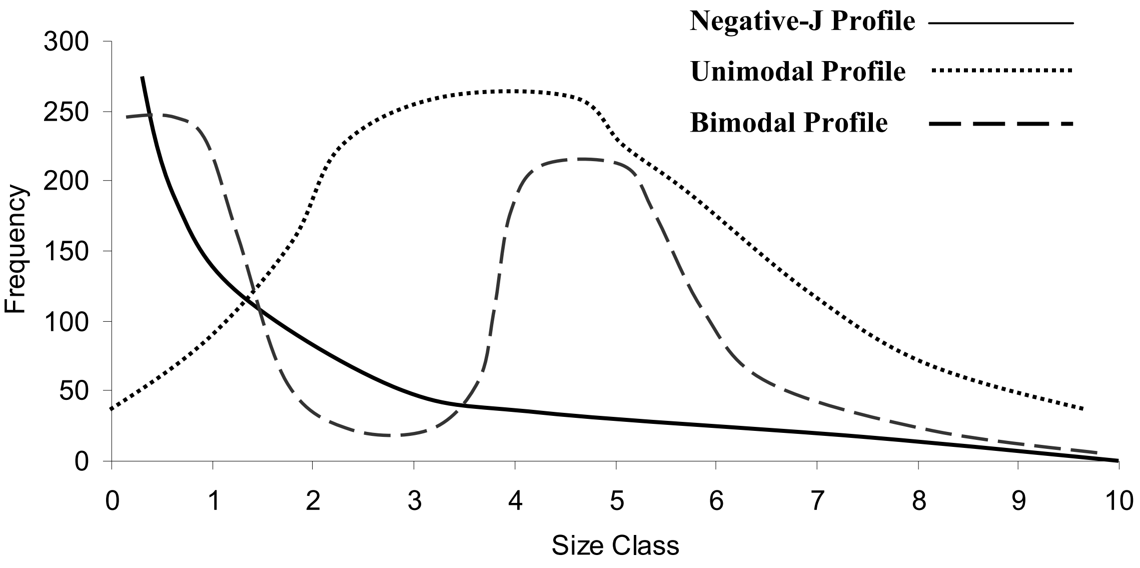

Figure 3: Hypothetical negative-J, bimodal and unimodal, demographic profiles. Similar profiles to these hypothetical examples have been found associated with the *Breonadia salicina* population in the Sabie River.

a) Negative-J Profile

Negative-J profiles indicate uneven age or size distributions within a population of long-lived species (Platt *et al*., 1988). De Fontaine and Rogers (1995) found that *B. salicina* sub-populations in the Sabie River that are described by a negative-J curve were associated with exposed bedrock in the anastomosing channels at the geomorphic unit scale. Given that a high frequency of smaller size-classes indicates a high establishment rate, de Fontaine and Rogers suggested that exposed bedrock represents the most important site of *B. salicina* establishment. Readily available seed implies that habitat availability is the regulating factor on establishment rates (de Fontaine and Rogers, 1995). A rapid decrease in frequency in the large size classes indicates either a high mortality rate or a change in site availability. This demographic profile is likely to respond most quickly to increases in sedimentation as the high establishment rate is limited by a loss of suitable exposed bedrock habitat.

b) Unimodal Profile

In the anastomosing channel type, the unimodal profile indicates that a period of high recruitment occurred historically, and that recruitment levels have since declined. This indicates that hydrological events have caused changes within the channel that have in turn resulted in a decline in recruitment. De Fontaine and Rogers (1995) suggested that the active channel may have switched from one side of the macro channel to the other, undercutting sediment deposits and exposing bedrock for recruitment, resulting in sufficient temporal variation to create the unimodal profile. This profile appears to develop through time from negative-J profiles. A decline in seedling recruitment in populations displaying a negative-J profile creates a sudden decrease in smaller size-classes, resulting in the peak of one of the larger size-classes. This profile indicates that suitable site availability for recruitment has declined in the recent past.

Unimodal profiles in sub-populations of *B. salicina* in the Sabie River were associated with highly vegetated and braided channels. This profile suggests that a single disturbance event had influenced the species demographics in these subpopulations (de Fontaine and Rogers, 1995). Low levels of seedling recruitment were found to occur in these channel types due to the limited availability of exposed bedrock.

c) Bimodal Profile

A number of factors including competition (Gates, 1978; Rabinowitz, 1979), changes in mortality (Ford and Diggle, 1981) and varying growth rates (Ford, 1975) influence the development of bimodal profiles. Bimodal profiles show two peaks in the frequency of size-classes. Bimodal profiles appear to develop in the same way as unimodal profiles, where a decline in available habitat reduces recruitment of new individuals. However, in bimodal profiles, seedling recruitment increases and declines twice within the lifespan of the oldest trees in the population due to changes in recruitment levels, creating two peaks on the size-class frequency graph (Argen and Zackrisson, 1990). Thus, differing population profiles can develop over time as channel type, and thus the availability of suitable habitat for recruitment, changes.

In the Sabie River, past and current disturbance events are considered to play a role, specifically in wide bedrock anastomosing channels, resulting in the formation of a bimodal demographic profile. Thus, differences in channel type as a result of disturbance events influence the population structure of *B. salicina*.

2.4 A hypothesis of the *Breonadia salicina* population response to increased sediment in the Sabie River

From Section 2.3 it is clear that previous studies found that different demographic profiles occur in the Sabie River population of *B. salicina* as a direct result of different characteristics in the underlying physical template. An increase in sediment accumulation is considered to have a detrimental effect on biodiversity in the Sabie River (van Coller, 1993; Heritage *et al.*, 1997). Increases in sediment accumulation are also hypothesised to have a particular effect on the negative-J *B. salicina* population structure, enabling KNP managers to utilise the species as an indicator of increases in sedimentation (Mackenzie *et al.*, 1999) (Figure 4).

Initially the negative-J structure is found on exposed bedrock (Figure 4a). As sedimentation increases there is a decrease in suitable recruitment habitat and thus an associated decrease in the number of newly established germinants. During this initial phase of sediment accumulation, there is no noticeable change in density of the larger size-classes due to the initial loss of suitable recruitment habitat (Figure 4b). Over a longer period of time, the reduction in recruitment is more noticeable and this starts to have a "push-through" effect on the larger size-classes as there are fewer smaller individuals growing into the larger sizes classes (Figure 4c). Ultimately, it is expected that there will be a significant reduction in density of the larger size-classes. This will reduce seed production within the population, resulting in reduced recruitment of new individuals and eventually leading to local extinction (Figure 4d).

The initial, rapid response of negative-J *B. salicina* population structure to a loss of bedrock substrate is due to the influence sedimentation has on recruitment of new individuals (Mackenzie *et al.*, 1999). Early indicators of change within a system are valuable as they allow for a quick response to potential problems, however, natural fluctuations within a population can make it difficult to observe detrimental changes in the system (Noss, 1990). Long-term studies of ecological processes in a system can give an indication of which fluctuations are responses to normal disturbances and which are as a result of outside influences or impact (Noss, 1990).

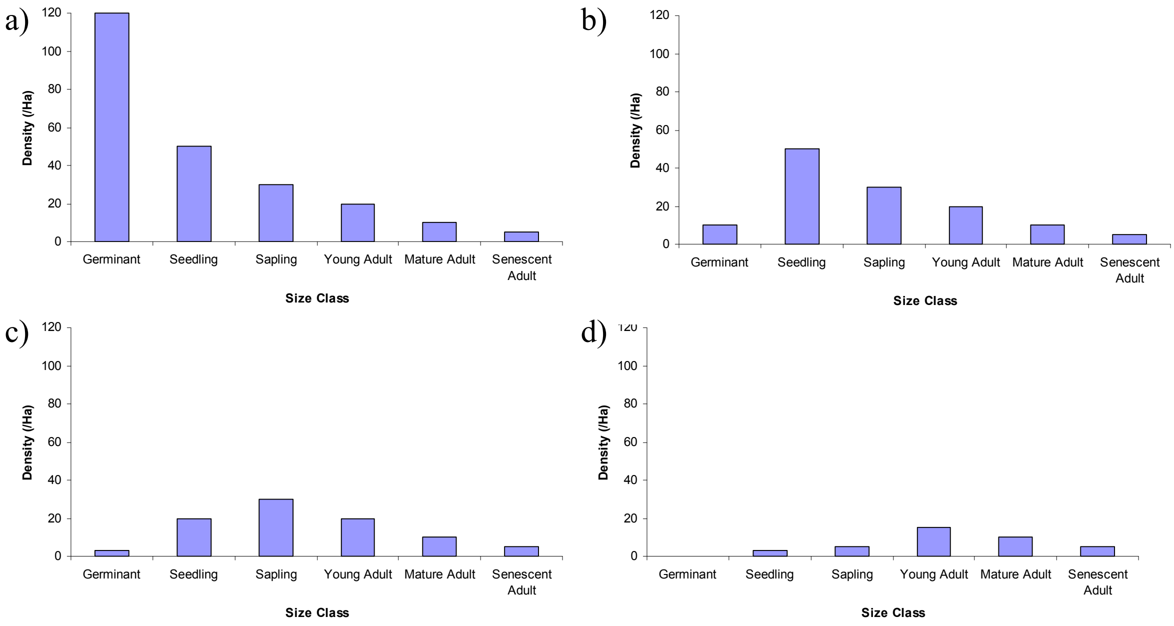

Figure 4: The hypothesised effect of long-term sediment accumulation on the population structure of *Breonadia salicina* within bedrock geomorphic units (Mackenzie *et al.*, 1999) where a negative-J profile occurs initially (a) and increases in sedimentation result in reduced recruitment in the germinant size-class (b). Over a longer period of time, the reduced recruitment of germinants results in the density in the larger size-classes becoming reduced as there are fewer new individuals to grow into the larger size-classes (c). Eventually, the decrease in recruitment results in a reduced density across all size-classes in the population (d).

De Fontaine and Rogers (1995) attributed changes in the population structures to variations in recruitment and mortality. For example, the negative-J profile associated with exposed bedrock in the Sabie River was assumed to be a result of strong, unlimited recruitment of new individuals with mortality rates increasing with increasing size class. Seed availability did not limit recruitment and thus, a change in habitat availability was expected to be the primary limiting factor on recruitment. The other demographic profiles found in the *B. salicina* sub-populations, and associated with different geomorphic units, were attributed to periods of limited recruitment due to changes in recruitment habitat availability. Fluctuations in habitat availability lead to phases of recruitment alternating with periods where recruitment is limited to non-existent, thus resulting in the formation of uni- and bimodal demographic profiles in the anastomosing channel types. The responsiveness of the *B. salicina* population to changes in sedimentation makes this species a good indicator of the biological response to changes in sedimentation in the Sabie River (Mackenzie *et al.*, 1999).

2.5 *Breonadia salicina* as an indicator of changes in sedimentation

Indicators are widely used as a convenient tool for assessment of environmental conditions (Thomas, 1972; Zonneveld, 1983), including trends in populations, habitat extents and measuring the impacts of specific pressures on a population (EASAC, 2005). An indicator species is defined by Landres *et al.* (1988) as, "an organism whose characteristics (e.g. presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient, or expensive to measure for other species or environmental conditions of interest." Thus, changes in species sensitive to particular environmental conditions within a system can be monitored to provide managers with a surrogate measure of changes to that environmental condition (Madejón *et al.*, 2005). When monitoring at a species-population level, the indicator species can signal the effects of environmental fluctuations on a number of other species with similar requirements (Noss, 1990). For example, when monitoring an indicator species to provide a measure of change in habitat availability; if the availability of habitat is maintained for the indicator species, then the assumption is that habitat will also be available for other species requiring similar conditions (Landres *et al.*, 1988).

Certain ecological criteria should be met when selecting an indicator (Landres *et al.*, 1988). Changes in the environmental condition of interest must have a cause and effect on the indicator; in other words, the indicator must be directly sensitive to changes in the environmental condition of interest. If the indicator is simply sensitive by showing a correlative change in response to changes in specific environmental conditions, it becomes difficult to separate other factors that may also influence the indicator in a similar way. A good indicator should also have low variability in its response to changes in the environmental condition of interest.

The demographic profiles of the *B. salicina* subpopulations associated with the different channel types were found to be either unimodal or bimodal (De Fontaine and Rogers, 1995). The negative-J profile only emerged at the finer, geomorphologic unit scale when exposed bedrock patches within different channel types were examined. The negative-J profile is not noticeable at the channel type scale as most channel types include high densities of the larger size classes, established on previously exposed but now sediment covered bedrock. However, when only exposed bedrock in the anastomosing channels is examined at the geomorphic unit scale, the negative-J profile emerges (de Fontaine and Rogers, 1995). This profile is therefore strongly associated with exposed bedrock and considered to be sensitive to increases in sediment.

The previous study by Mackenzie *et al.* (1999) was only conducted in the four most common channel types within the KNP reach of the Sabie River. The continuous pool channel type was omitted. Of the four main channel types found in the Sabie River, the pool-rapid channel type was considered to be the most sensitive to increases in sedimentation due it its physical characteristics (Heritage *et al.*, 1997). Thus, pool-rapid channels were expected to show the earliest change in population structure as a result of increases in sedimentation and were therefore made the focus of the *Breonadia* Model and the associated monitoring programme.

The *Breonadia* Model groups the size-classes of *B. salicina* into six functional groupings which are associated with reproductive characteristics of the tree (germinant, seedling, sapling, young adult, mature adult and senescent adult) (Mackenzie *et al.*, 1999). These functional categories will be referred to as size classes for the remainder of this dissertation as the basis of their definition is basal diameter.

2.6 Thresholds of Potential Concern for the loss of bedrock influence in the Sabie River

The state of flux of ecosystems, and the limited understanding thereof, requires that managers deal with uncertainty in order to manage ecosystems effectively. Strategic Adaptive Management includes the development of a desired state for the system being managed and operational goals that provide managers with specific endpoints or targets for ecosystem management (Rogers and Bestbier, 1997; Rogers and Biggs, 1999; Rogers *et al.*, 2000). The condition targets or defined limits of acceptable change used in KNP, named Thresholds of Potential Concern (TPCs), are thresholds warning of the potential development of undesirable ecosystem states (Rogers and Biggs, 1999). Thresholds allow for natural variability in the system and the associated changes in the indicator, and define upper and lower limits of acceptable change for the system within its defined desired state (Figure 5). In other words, TPCs represent hypothetical thresholds of flux. These thresholds are defined by translating the desired state of the system into operational goals and include both a spatial and a temporal range of acceptable flux, thus accounting for the variability and heterogeneity of ecosystems (Rogers *et al*., 2000).

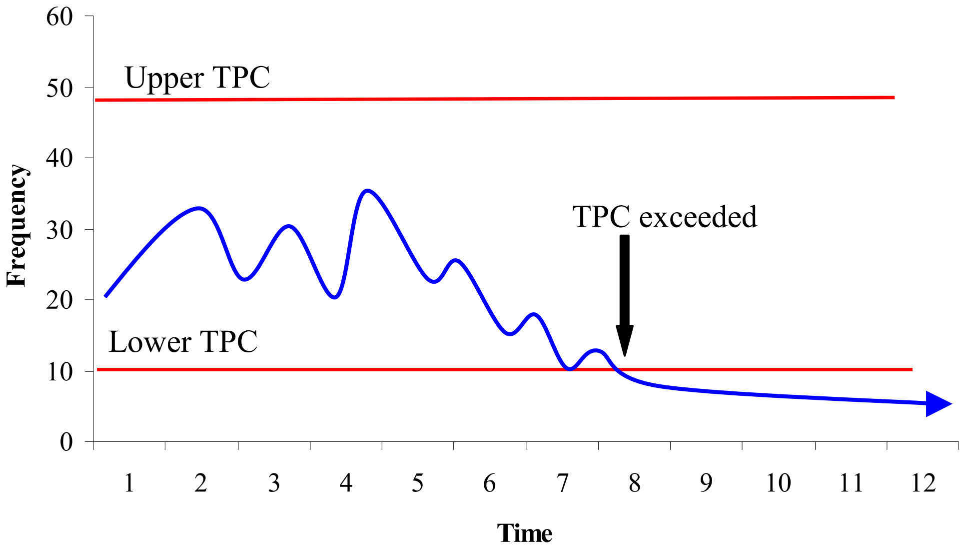

Figure 5: Conceptualisation of a Threshold of Potential Concern. In this example, the hypothetical frequency of occurrence of the indicator species mostly fluctuates over time due to natural variability between a defined upper and lower Threshold of Potential Concern. Management action is prompted when the frequency of the indicator approaches or reaches one of the thresholds that define the bounds of the desired system state.

A loss of bedrock influence in the macro channel of the Sabie River in the KNP is assessed through three TPCs (Mackenzie *et al*., 1999). These TPCs concentrate on the population structure in terms of the size-class density of *B. salicina* in the bedrock sections of the pool-rapid channel type. Fluctuations in the population's structure are acceptable as long as a negative-J shaped population structure persists across all size classes other than the germinant size class of *B. salicina* (Mackenzie *et al*., 1999). The negative-J population structure represents a high abundance of the smaller size-classes and a decrease in abundance as size-class increases and is associated with high levels of recruitment and mortality. Unacceptable changes to the population structure based on the expected ecological response of the *B. salicina* population to increases in sedimentation in the Sabie River will result in one or more of the TPCs being exceeded. These thresholds are defined in relation to a change from the characteristic negative-J profile (see Table 1 and Figure 6) along with the characteristic negative-J structure associated with exposed bedrock in the Sabie River.

In Table 1, the equation defining the characteristic negative-J profile is described. A more detailed description of each of the three defined TPCs is also provided. Each of these descriptions explains how the shape of the curve representing the change in densities across the size classes of *B. salicina* changes from the characteristic negative-J profile. The TPCs should be audited at least once every four years. If any of the TPCs is exceeded, auditing should be done more frequently, following the protocol set out by Mackenzie *et al.* (1999).

Table 1: Definition of the negative-J structure and the Thresholds of Potential Concern for loss of bedrock influence in the Sabie River from Mackenzie *et al.* (1999).

Definition	**Description**
Defined negative-J	Densities (y) per size class (x) that fit the ideal negative-J structure in pool-rapid channels are defined by the following equation: $y = 0.004x^2 - 0.602x + 22.536$ Significant variation from this equation results in the TPCs defined below being exceeded.
TPC for reduced recruitment	Any change in the population structure resulting in a flatter J-curve as a result of lower frequencies in the small size-classes so that the log of the population J-curve equation x-coefficient reaches -0.68. This is associated with reduced establishment of the smaller size-classes as a result of a loss of suitable bedrock establishment sites.
TPC for reduced density	Any change in population structure resulting in a reduced frequency in all size-classes so that the log of the population J-curve equation constant reaches 4.04. This change is associated with a loss of density across all size-classes, resulting in a shift of the curve downwards, and a lowering of the y-axis intercept.
TPC for a reduced correlation to the defined negative-J	Any change in the *B. salicina* population structure from the defined negative-J structure to unimodal, bimodal or positive-J so that logged, its correlation (r^2) to the logged defined negative-J profile is reduced such that $r^2 \leq 0.926$.

The modelled germinant size-class is excluded from the population structure utilised in the TPC. Large numbers of germinants are found all along the Sabie River on all habitat types. Including the germinant size class would result in an apparent negative-J profile occurring everywhere in the Sabie River. Most germinants will not successfully establish and thus they should be excluded to prevent a false impression of a negative-J profile. The TPCs have been defined by assuming growth rates for each size-class of *B. salicina* as there are no data on *B. salicina* growth rates. The rapid recruitment of new germinants and quick recovery of *B. salicina* back to a negative-J profile had been observed after high flow events occurring in the Sabie River (Mackenzie, pers. comm., CWE, UWITS). Table 1 contains the defined negative-J profile for the Sabie River that is utilised in the *Breonadia* Model. The defined negative-J profile is thought to change in one of three ways as a result of increases in sedimentation, hence the definition of three TPCs (Mackenzie *et al.,* 1999).

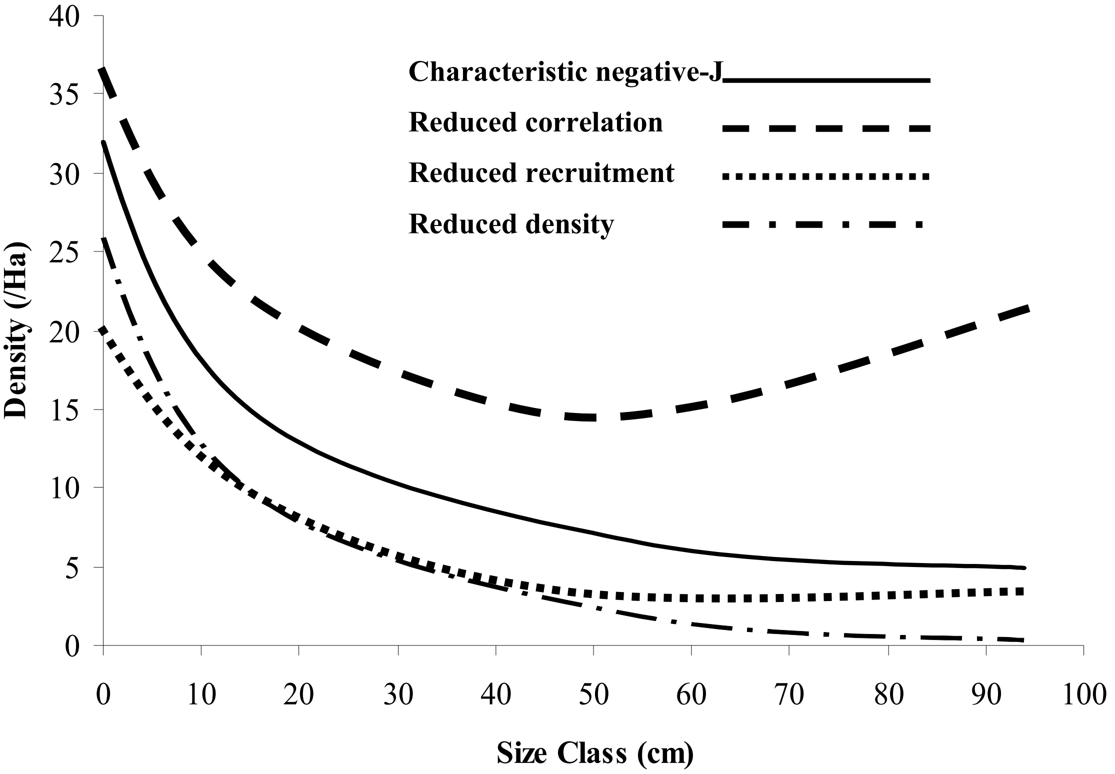

Figure 6: Conceptualisation of how the population can change from the Negative-J structure to exceed threshold according to the defined Thresholds of Potential Concern for *B. salicina* population structure in the Sabie River, Kruger National Park.

A reduction in recruitment as a result of increasing sedimentation, as previously discussed, is likely to be the earliest noticeable change to the structure. The smaller size classes will show a reduction in frequency, although the larger size classes are unlikely to be affected in the short term (Figure 6).

The TPC for a reduction across all size classes would most likely occur as a longer term result of increasing sedimentation (Section 2.4). As this TPC has been defined specifically to give a warning of increasing sedimentation, it is important to interpret any changes to the population profile in the context of what is occurring in the river. This type of change to the negative-J profile can be seen as a reduced density across all size classes (Table 1). The general shape of the negative-J profile will not necessarily be lost.

Any change to the population profile, such that its correlation to the defined negative-J profile is reduced, forms the basis for the final TPC. A reduced correlation could occur simply as a reduction in recruitment or as an overall loss of density across all size classes. A reduced correlation to the defined negative-J profile could also occur as a result of very long-term increases in sedimentation (Section 2.4).

Natural and acceptable fluctuations within the system influence the profile. Natural disturbances can cause changes in population structure, resulting in the defined TPCs being exceeded. Thus, any changes to the population structure of *B. salicina* such that any one or more of the defined TPCs is reached must be interpreted within the context of the particular disturbance events (Mackenzie *et al*., 1999). For example, high flow events can remove individuals from the smaller size-classes of the population resulting in a change from a negative-J population structure to a unimodal profile. However, in the year following a high flow event, if suitable habitat is available, the seedling class is expected to recover, resulting in a return to the negative-J structure. A temporary loss of the negative-J structure as a direct result of flow events rather than as a result of a loss of bedrock influence should not be treated as a cause for concern by managers. These fluctuations in the population structure are as a result of natural variation within the system. Fluctuations within the defined TPCs that can be explained by natural fluctuations in the system are acceptable, indicating that the desired state of flux in the system has been maintained. If natural fluctuations in the system result in the TPCs being exceeded, it becomes necessary to redefine the TPCs. This allows new and acceptable fluctuations to be taken into account where researchers may not have had previous knowledge about particular types of events and how they affect the population structure of *B. salicina* (Mackenzie *et al*., 1999).

2.7 Flood disturbance and exceeding TPCs

During 2000, severe flooding occurred in areas of Southern Africa, including in the Sabie River. At the peak of the flood, discharge reached an estimated 3000m^{3}sec^{-1} where the Sabie River enters the Kruger Park and 7000m^{3}sec^{-1} where the river exits the park at the

Mozambique border 120km downstream (Heritage *et al*., 2001). Typical wet season base flows in the Sabie River are in the order of 15-20m^{3}sec^{-1}. The flood return interval was estimated to be 90-200 years (Smithers *et al*., 2001) and Parsons *et al*. (2005) classes the flood as a Large Infrequent Disturbance (LID).

Large infrequent flood disturbances have been defined as having either a water depth or flow volume greater than two standard deviations of the mean from a record of several decades or longer (Resh *et al*., 1988). In a flooded area, the flood intensity may be highest in low elevation areas that are inundated for a longer duration (Sparks and Spink, 1998) or in areas where velocity is greatest. Floods also have patchy effects as they can both erode and deposit sediment. Nutrient availability can change (Canham and Marks, 1985) and the availability of certain habitat types can be affected.

Large floods can also have an impact on riparian vegetation as individuals from all size-classes can be damaged or removed, significantly changing the population structure in the short term. Large disturbances frequently leave a heterogeneous pattern of patches consisting of a mix of biotic and abiotic legacies (Turner and Dale, 1998). Different successional processes and responses can occur in the different patch types. Examination of the different vegetation interactions occurring in the different patch types can give insight into mechanisms behind different vegetation responses to flood disturbance.

The 2000 flood disturbance in the Sabie River played a direct role in shaping sub-populations of *B. salicina* by uprooting and damaging individual trees, substantially reducing the overall density of the species (Parsons *et al*., 2006). Other studies have suggested that both the frequency and intensity of disturbance can directly influence the response strategy of individual trees, thus shaping the subsequent population structure in terms of the recruitment of new individuals (Keeley and Keeley, 1977; Bellingham and Sparrow, 2000). Consequently, it is possible that a combination of both the underlying template and disturbance effects play a role in shaping the different population profiles observed in the Sabie River. Thus the demography and response of *B. salicina* is expected to be strongly related to the geomorphic template as well as to the size of individuals and the direct impact of the flood on individuals.

Disturbance events, such as the 2000 Sabie River flood, can reduce dominance exerted by particular species and enable new individuals to colonise and establish (Canham and Marks, 1985). However, competition can be strong and plants with good response strategies are more likely to establish successfully. Woody plants, such as *B. salicina*, can follow a number of response modes after a disturbance event which may influence the future dominance and success of the species (Kennard *et al*., 2002). Severe disturbance events or changes in disturbance frequency can also change the predominant response of woody species, resulting in a change in the mode of recruitment (Bellingham and Sparrow, 2000). The *Breonadia* Model utilised by KNP managers was designed on the assumption that recruitment is the only response that occurs in the *B. salicina* population. Thus, it is important to examine the response mechanisms that occur in the population subsequent to the 2000 flood to determine whether different response mechanisms occur subsequent to a flood of this magnitude, and whether any new response mechanisms are sufficient to influence the demographics of the *B. salicina* population in the Sabie River.

2.8 Aim: To examine the different response mechanisms in *Breonadia salicina* subsequent to a large infrequent flood

Previous studies on *B. salicina* have hypothesised that changes in demography in the Sabie River population are as a result of changes to the underlying physical template. As this species is utilised as an indicator species, it is important to have a full understanding of all the influences on demography to prevent misunderstanding of changes occurring in the population structure that could lead to incorrect management procedures being implemented in the Sabie River.

Other studies of riparian species (e.g. Morrison *et al*., 1995; Vesk and Westoby, 2004; Clarke *et al*., 2005) have demonstrated that variations in disturbance can result in different reproductive responses being expressed by residual trees, influencing demography independently of changes to the underlying physical template. No previous studies have focused on reproductive response mechanisms of *B. salicina* and it has always been assumed that this riparian tree species relies solely on seed production as its reproductive strategy.

This chapter will examine the response mechanisms expressed by *B. salicina* subsequent to the 2000 flood disturbance. In addition the trade-off between these response mechanisms (sprouting and flowering) will be examined. Finally, this chapter will determine whether response mechanisms are in any way related to the underlying physical template or whether it is independent factors such as disturbance intensity (inferred by flood damage) or size-class of the individual trees that influence recruitment.

2.9 Methods

2.9.1 Data collection

Fieldwork was conducted four years after the 2000 flood as this was the expected time frame for recovery of the *B. salicina* population back to a negative-J profile subsequent to a LID flood event (Mackenzie *et al.*, 1999). Reproductive response data were collected in May 2005 as the brown, lobed fruits that develop after flowering are visible on trees in May.

As the previous studies on *B. salicina* suggest that response is related to the underlying geomorphological template, it was important to evaluate the response of *B. salicina* in all four channel types in the Sabie River. This gave an indication of where recruitment was occurring in the river and also of how the *Breonadia* Model outputs in terms of recruitment compare with what is occurring in the river.

Sampling was conducted utilising the methods of Mackenzie *et al.* (1999) so that the data would be comparable. Belt transects of 20 meters in width were placed across half the river channel from the top of one macro-channel bank to the main channel. Sixteen sites (see Figure 7) comprising four sites located in each of the four common channel types (pool-rapid, mixed anastomosing, bedrock anastomosing and braided) were selected.

Each site position and area was measured using a Global Positioning System (GPS) and tape measures. The following features were recorded for all *B. salicina* individuals found at each site:

- Basal diameter (in millimetres, measured above the basal swelling and below the lowest branches).
- Each individual was placed into a basal diameter size-class category as defined by Mackenzie *et al.* (1999). These size-classes are utilised in the *Breonadia* model and are related to life history class rather than evenly allocated size-classes (Table 2).
- Flood damage category (uprooted, pushed over, dead, damaged or broken branches, broken or damaged main stem). The severity of flood damage was assumed to infer disturbance intensity as experienced by each individual.
- Additional disturbance factors such as fire were recorded.
- The presence of coppice shoots on individuals was noted.
- The presence and abundance of flowers/fruits on individuals. Flowers/fruits were placed into one of the following four abundance categories based on a visual estimate: no fruit/flowers, few fruits/flowers, average fruits/flowers and abundant fruits/flowers.

Table 2: The functional size-class definitions used in the *Breonadia* Model. Individuals are classified into life-stage size-classes based on their basal diameters.

Size-class category	Basal diameter (cm)
Germinant	0-0.025
Seedling	0.025-3
Sapling	3-10
Young Adult	10-20
Mature Adult	20-70
Senescent Adult	>70

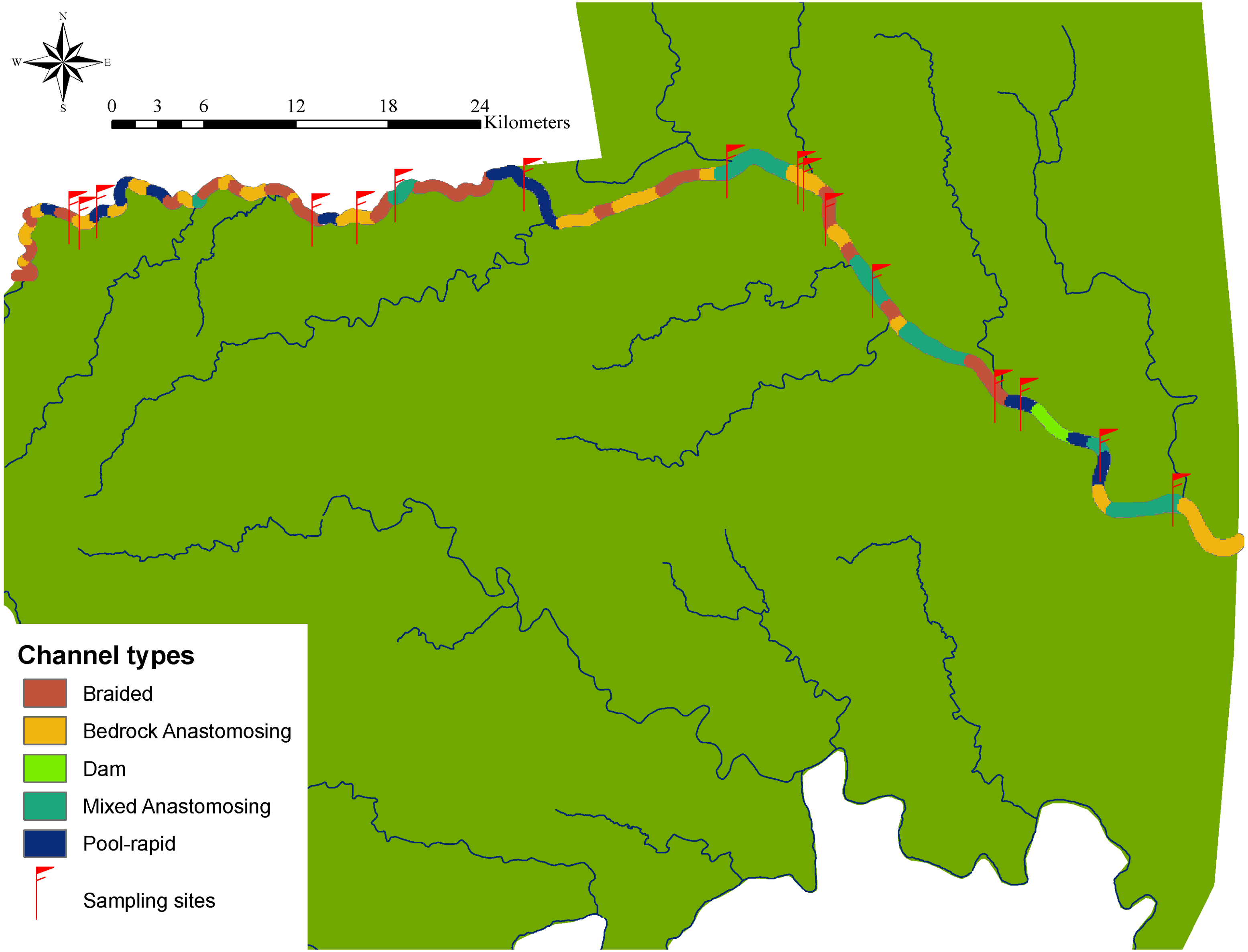

Figure 7: Locations of the sixteen sampling sites along the Sabie River, Kruger National Park.

2.9.2 Examining the reproductive response of *B. salicina* to the 2000 flood

Evidence from other studies suggests that response may be influenced by size-class (Misra *et al.*, 1995; Tewari *et al.*, 2004), damage intensity (Bellingham and Sparrow, 2000) or the underlying physical template (Grubb, 1977; White, 1979; Picket and White, 1985; White and Harrod, 1997). As such, the following three relationships were considered.

a) Flowering response in relation to sprouting response

Several studies have found that sprouting inhibits flowering in woody species. A graphical comparison of flowering/fruiting strength was made between the sprouting and non-sprouting categories in *B. salicina* to determine whether sprouting is likely to inhibit the expected flowering response. A comparison independent of channel type was sufficient for this purpose as the influence of geomorphology on response mechanisms will be examined later in this chapter. It is important to note that this simple comparison can give an indication of whether a sprouting response limits flowering and thus whether it should be considered a factor influencing population demography in the *Breonadia* Model. A Wilcoxon signed rank test (non parametric) was conducted to determine whether there is a statistical difference in the proportions of trees flowering between sprouting and non sprouting group subsequent to the 2000 flood. The test was conducted using sites as replicates to remove site-site variability from the analysis.

b) Sprouting and flowering response across channel types

Previous studies have shown that *B. salicina* population structure is related to channel types in the Sabie River. Conversely, other studies have shown that the population structure in other woody species can be influenced by response mode in response to disturbance. Hence, causality between response mode and channel type in *B. salicina* was deemed worthy of investigation since this too could affect the output of the *Breonadia* Model.

Each tree was placed into either a sprouting or a non-sprouting category. The percentage of trees in each category was calculated separately at each site, and the mean across sites was obtained for each channel type. Seedlings and germinants that were recruited after the flood were excluded as they did not show any sprouting response to the flood and hence skewed the data in favour of non-sprouting response.

In addition, one-way ANOVA was used to test for significant differences in the sprouting response across the channel types. The sampling sites were used as replicates within each channel type. The test was conducted at an alpha value (significance level) of 0.05. If the calculated F value (measurement of the difference between samples) is less than the critical F value at a 95% confidence limit, the Null Hypothesis is rejected and the alternative hypothesis that the proportional contribution of sprouting differs across channel type is accepted.

The same series of tests was performed to detect differences between the occurrence of a flowering response and channel type. However, in this case four categories for flowering were used: abundant, average, few and no flowers. In each test, the Y variable being analysed was the summary of sprouting response or flowering response respectively.

c) The combined influence of channel type, size-class and damage class on flowering and sprouting response to the 2000 flood

Many factors, including size-class and damage intensity, can influence reproductive response of trees to disturbance. The relationship between response mode and channel type in *B. salicina*, as well as the joint effect of size-class and damage intensity, should therefore be examined. These joint relationships are important since they are only considered as marginal factors in the existing *Breonadia* Model and a joint consideration could improve the accuracy of the model output. Hence, a forward correspondence analysis was performed to establish the effects of these three factors, jointly.

A direct gradient analysis using canonical correspondence analysis (CCA) from the programme CANOCO (Ter Braak and Šmilauer, 1988) was used to determine the environmental variables associated with the pattern of response shown in the adult size-classes of *B. salicina*. The environmental variables were channel type, size-class and damage class. The non-adult size-classes (germinants, seedlings and saplings) were excluded as they are too young to display a flowering response.

As data were collected four years subsequent to disturbance, it is expected that some trees will be sufficiently recovered to produce flowers. Thus adult trees were placed into one of four possible categories to represent response subsequent to the 2000 flood:

- No response. Adult trees in this category showed no response at the time of the field survey. There was no evidence of a sprouting response or of flowers or fruits on the tree.
- Flowering response. These trees displayed evidence of flowers and fruits at the time of data collection. They had no evidence of any sprouting response.
- Sprouting response. Adult trees displaying evidence of sprouting and no flowers or fruits at the time of the field survey were placed into this response category.
- Flowering and sprouting response. Both a sprouting response and evidence of flowering were observed on these trees.

The environmental factors (channel type, size-class and damage class) were categorised, and each category ranked in order from smallest to largest size-class and least to most severe damage categories. The channel types were ranked braided, pool-rapid, bedrock anastomosing and mixed anastomosing, as channel type was utilised as an environmental variable in this analysis. Four damage categories were used: no damage, loss of branches, trees being pushed over and trees experiencing breakage of the main stem. The same size-class categories as defined by Mackenzie *et al*; (1999) were utilised (Table 2).

CANOCO includes an automated forward selection that summarises both the marginal and the conditional effects of each explanatory variable (ter Braak and Smilauer, 1988). Forward selection of environmental variables was carried out in CANOCO to determine which variables contributed most to the variation in the response of *B. salicina*.

2.10 Results

A total of 410 living trees were sampled across the sixteen sites. A table of sample size for each size-class in each of the sites is presented below (Table 3).

Table 3: Sample size of each size class in each of the sixteen sites

Channel Type	Germinant	Seedling	Sapling	Young Adult	Mature Adult	Senescent Adult
Braided Sites			1	1	2	
					3	2
Pool-rapid Sites		4	1	4	4	1
		1	1	16	19	1
				7	4	
		20	1		6	
Mixed Anastomosing Sites	1	36		3	9	
	10	18	2	1	5	
	8	12	1		2	
		6	7	1	11	2
Bedrock Anastomosing Sites	14	52		1	4	1
			1	1	3	
	18	36		1	19	2
		10	6		7	

Two modes of reproductive response to the 2000 flood were observed in the *B. salicina* population in the field. A number of adult trees were flowering at the time of data collection and many trees across all size-classes displayed a sprouting response as a result of disturbance from the 2000 flood.

a) Flowering response in relation to sprouting response

Sprouting trees showed a decreased likelihood of producing flowers (only 40% produced flowers) compared to non-sprouting trees (90% produced flowers) (Figure 8). In addition, trees that were flowering but not sprouting produced more flowers than those that were also sprouting. The Wilcoxon signed rank test comparing flowering between sprouting and non sprouting trees demonstrated that there was a significant difference in the percentage of flowering trees between the sprouting groups ($z=3.162$, $P<0.005$). This indicates that sprouting significantly reduces the likelihood of flowering in residual trees, despite data only being collected four years subsequent to the 2000 flood. This trend is attributed to trees expending energy on sprouting and thus regaining biomass rather than producing seeds. It is expected that individual sprouting trees will recover and regain biomass until eventually they will be sufficiently recovered to produce flowers. The influence of sprouting on the ability of trees to produce flowers has repercussions for recruitment of new germinants in the post-flood era.

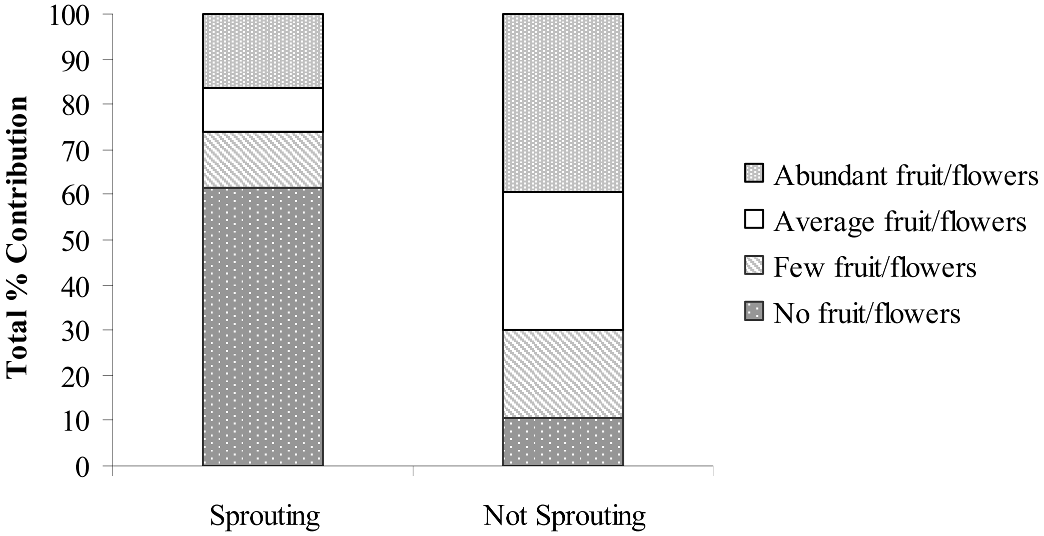

Figure 8: Total percentage contribution of each fruiting/flowering class across each sprouting class for residual trees.

b) Sprouting and flowering response across channel type

The proportional contribution of the sprouting response was similar across the bedrock anastomosing (72%), mixed anastomosing (76%) and pool-rapid (72%) channels but much lower in the braided channel type (35%) (Figure 9). However, in the braided channel type, most residual trees surveyed were large adults located a greater distance and elevation from the main channel than adults in the other channel types. In this position, trees would experience a lower intensity of flood and this may account for the low proportion of sprouting individuals.

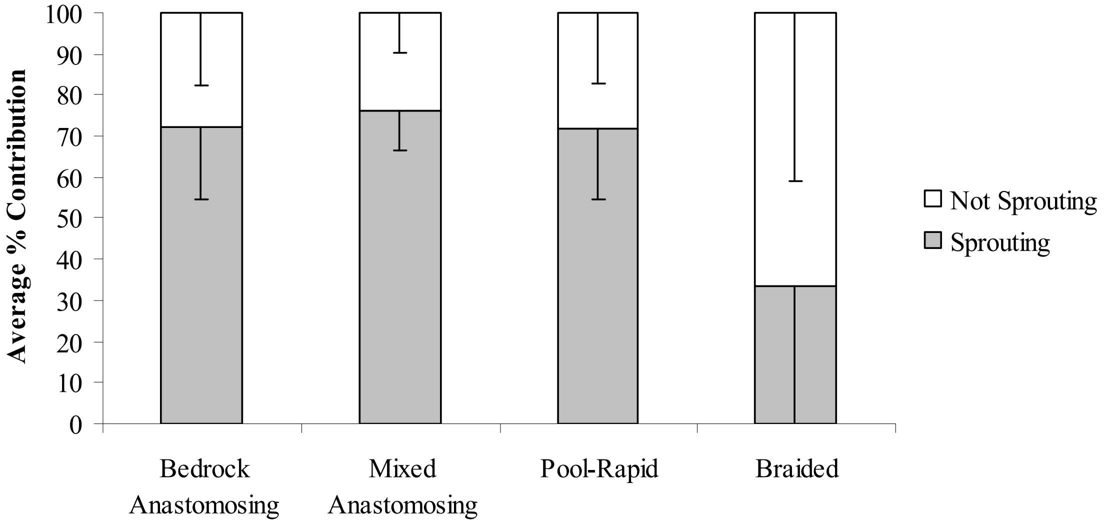

Figure 9: Percentage contribution ±Standard Error (S.E.) of sprouting and non-sprouting trees within each channel type. The S.E. bars indicate one standard deviation.

These data show that sprouting is a dominant response mechanism in the *B. salicina* population subsequent to LID flood disturbances with more than 70% of all trees recorded displaying this mechanism of recovery. There was no significant difference in the proportion of the sprouting response in trees among channel types (Table 4) suggesting that the degree of sprouting in *B. salicina* is not related to the underlying physical template at the channel type scale.

Table 4: One-way ANOVA results for difference in sprouting response type across channel types.

ANOVA						
Source of Variation	**Sum of Squares**	**Degrees of Freedom**	**Mean Squares**	**F**	**P-value**	**F Critical**
Between Groups	0.389	3	0.129	0.963	0.444	3.587
Within Groups	1.481	11	0.134			
Total	1.871	14				

More than 45% of all trees in all channel types did not show any evidence of fruit or flower production (Figure 10). The proportion of flowering trees was highest (52%) in the mixed anastomosing channel type. This is the channel type that also has the highest density of post-flood recruits and the highest density of adult trees. The likelihood of flowering was lowest in the pool-rapid (35%) and braided (32%) channels.

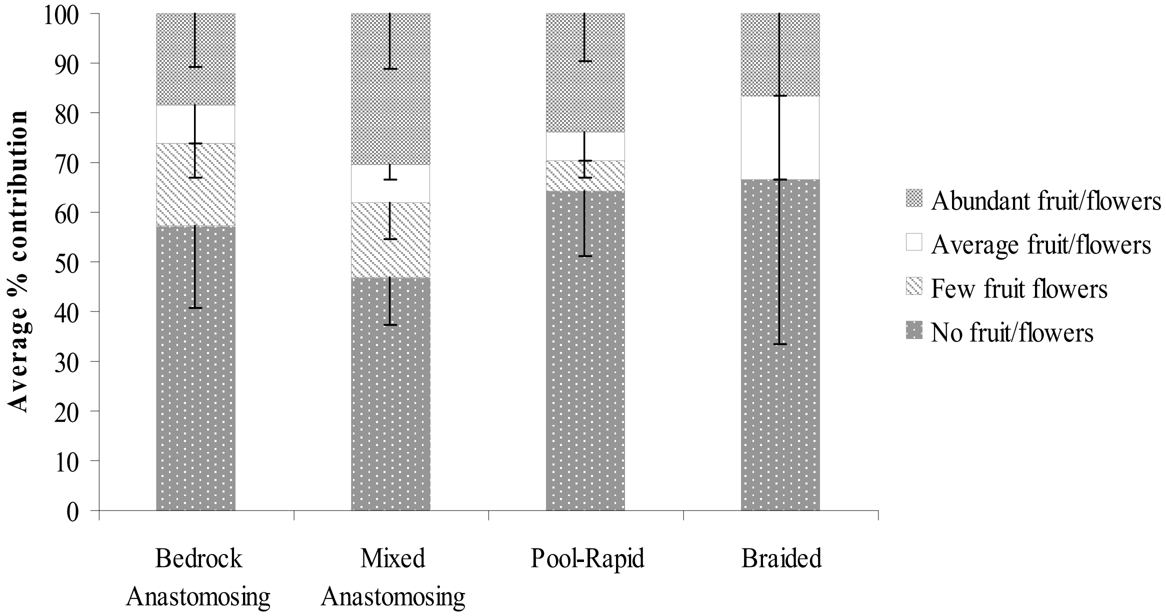

Figure 10: Mean percentage contribution (±S.E.) of each fruiting/flowering class in each channel type. The S.E. bars indicate one standard deviation.

There was no significant difference in the proportion of the flowering response among channel types (Table 5). Hence, the null hypothesis that there is no difference in the amount of flowering observed in the different channel types is accepted. In other words, the incidence of flowering in *B. salicina* is not related to the underlying physical template at the channel type scale. Thus it appears that neither the proportional occurrence of the flowering response nor the sprouting response is associated with a particular channel type. This suggests that response subsequent to disturbance is influenced by factors other than the underlying physical template such as size-class and disturbance intensity.

Table 5: One-way ANOVA results for difference in flowering response type across channel types.

ANOVA						
Source of Variation	**Sum of Squares**	**Degrees of Freedom**	**Mean Squares**	**F**	**P-value**	**F Critical**
Between Channel Types	0.088	3	0.029	0.247	0.861	3.587
Within Channel Types	1.316	11	0.119			
Total	1.405	14				

c) The influence of channel type, size-class and damage class on response mechanisms

Flood damage is negatively correlated with the "flowering" and "no response" categories (Figure 11), indicating that these response types are more likely to occur in trees that experience little to no flood damage and less likely in trees experiencing more severe forms of flood damage. Size-class is negatively correlated with both the "sprouting" and the "sprouting and flowering" response types, indicating that sprouting is more likely to occur in the smaller than the larger size-classes.

The automated forward selection procedure in CANOCO selected flood damage and size-class as the variables describing differences in response categories. Channel type was not identified as a variable explaining the variation in response categories in *B. salicina* by the automated forward selection. Response mechanisms in the *B. salicina* population were strongly influenced by flood damage, explaining 56% and 22% of the variation respectively but not by channel type (Table 6 and Figure 11).

Table 6: Canonical Correspondence Analysis: The results of the forward selection.

	Lambda	**P**	**F**
Flood Damage	0.56	0.002	62.90
Size-class	0.22	0.002	11.83
Channel Type	0.03	0.114	2.04

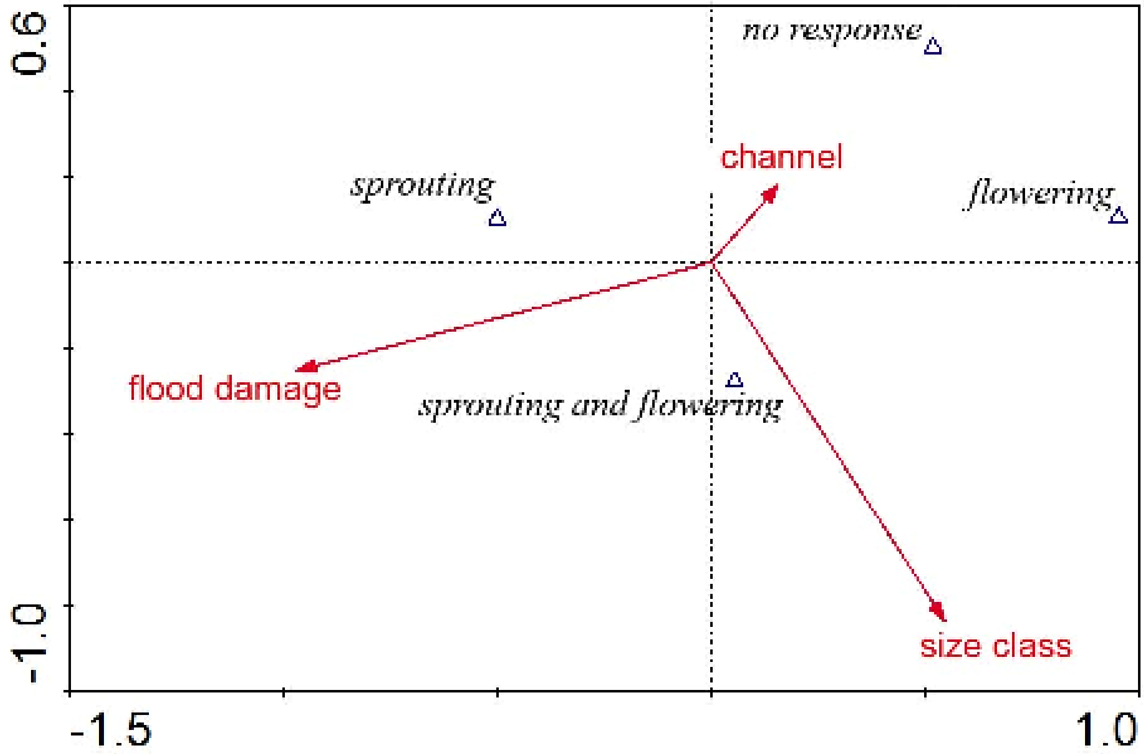

Figure 11: An ordination diagram output from CANOCO based on the canonical correspondence analysis. Adult trees were placed in one of four possible response type groups (triangles) to determine how much of the variation in response can be explained by channel type, flood damage and size-class (lines).

2.11 Discussion

Despite sprouting having been observed in *B. salicina* prior to the 2000 flood, its importance as a response mechanism has not previously been considered. The high levels of available *B. salicina* seed in the Sabie River led to assumptions that recruitment was the dominant response in the population and that seed availability would not be a factor limiting recruitment in this species (Mackenzie *et al.*, 1999). Factors such as high seedling mortality and competition for resources influence population structure and can preclude the development of even-aged stands of *B. salicina* and support suggestions that this species is a seeding species. However, the results of this study show that the *B. salicina* population displays a sprouting response to a large infrequent flood, suggesting that recruitment may not be the only response mechanism as previously thought. The population has limited long-term seed viability, no evidence of seed storage (Mackenzie *et al.*, 1999), and a range of uneven sized population profiles (de Fontaine and Rogers, 1995). These characteristics are associated with sprouting species rather than with flowering species indicating that *B. salicina* will not necessarily display rapid recovery through recruitment after disturbance.

Based on data collected subsequent to other flood events, *B. salicina* displayed a strong recruitment response to disturbances, including in response to a large flood in the Sabie River in 1996 (Mackenzie, unpublished data, CWE, UWITS). The high frequency of sprouting and the related low frequency of flowering in sprouting individuals subsequent to the 2000 flood recorded in this study suggest that fewer seeds will be produced when sprouting is a dominant response. Other studies found that sprouting can have a significant influence on seed production and hence on demography (e.g. Bellingham and Sparrow, 2000; Kennard *et al*., 2002; Kozlowski, 2002; Shea *et al*., 2004; Martínková *et al*., 2006) as species that place energy reserves into sprouting, are less likely to produce seeds immediately subsequent to disturbance (Keeley and Keeley, 1977). This may be sufficient to reduce recruitment and thus drive changes to the demographic profile.

In addition, the response of *B. salicina* to the Sabie River flood in 2000 was found to be strongly related to the intensity of disturbance experienced by individual trees and to the size of individual trees rather than to the underlying physical template at the channel type scale. Thus, changes in the availability of habitat for recruitment may influence successful recruitment and therefore demography to some extent. Further, a dominant sprouting response to LIDs may influence demography by limiting seed production and reducing recruitment of new individuals across the underlying physical template. This demonstrates that recruitment of *B. salicina* in the Sabie River is patchy in two ways. Firstly, seed production itself is related to the patchiness of disturbance, with different individuals experiencing different disturbance intensities due to their location in the channel. Secondly, once seeds have been produced and dispersed, recruitment will be patchy but related to the underlying physical template and the location of suitable recruitment habitat. However, the seeds of *B. salicina* are winged and have been found widely dispersed throughout the Sabie River (Mackenzie *et al*., 1999). The patchiness in terms of seed production will therefore only influence the availability of seed and thus the total number of newly recruited individuals at the whole river scale. The spatially patchy production of seed by adult trees will not influence the patchy location of new individuals. Therefore the combination of the patchy underlying physical template and the patchy nature of disturbance influences the location and the number of new recruited trees. This drives changes to the demographic profiles in the Sabie River.

It is important to remember that the *B. salicina* demographic profile in the Sabie River is modelled as part of the management strategy for the Sabie River. Any oversights in the modelling of how this species responds to and recovers from disturbance could have significant repercussions for future management of the Sabie River. Management of the Sabie River relies partly on predictions made with the *Breonadia* Model, which does not take a sprouting response into account. It is therefore important to examine whether the sprouting response observed in the field subsequent to the 2000 flood does actually play a role in shaping the demography of *B. salicina* in the Sabie River.

The *Breonadia* Model does not take a sprouting response into account and relies on the assumption that seeds are not limited in the Sabie River. The model is therefore likely to over-estimate recruitment after LID flood events. In the model, recovery of the population subsequent to disturbance occurs rapidly after a modelled LID flood event due to the assumption that the flowering and seed production will be the same as observed subsequent to other disturbance events; in other words, that recruitment is the only response mechanism to all disturbance events (Mackenzie *et al.*, 1999). Examining and understanding the underlying mechanisms, such as response mechanisms, can improve predictions about changes to disturbances for which there are no data (Johnson and Miyanishi, 2007). This would be beneficial as the *Breonadia* Model does not define a relationship between change in disturbance intensity and changes to the demographic profiles of *B. salicina*. It is therefore important to examine the actual demography of *B. salicina* subsequent to the 2000 flood and compare this to what could be expected if the species did not show a sprouting response as represented by the *Breonadia* Model. If the sprouting response shown in the *B. salicina* population has a significant or a long-term effect on the population demography, this has important implications for continued use of the *Breonadia* Model in its current format and for management of the Sabie River in the KNP.

CHAPTER 3: TESTING THE *BREONADIA* MODEL OUTPUT: A COMPARISON WITH THE *BREONADIA SALICINA* POPULATION DEMOGRAPHY FOLLOWING THE 2000 FLOOD

The *Breonadia* Model was developed on existing knowledge and data and is envisaged being used as an ongoing learning tool, to be updated as more long-term data on *B. salicina* response to changes in geomorphology and hydrology becomes available (Mackenzie *et al.*, 1999). Some of the information for refining and improving the model will come from monitoring data that are collected by KNP staff as part of the evaluation of sedimentation in the Sabie River, while the remainder will be collected as part of specific research projects. Hydrological disturbance events provide an opportunity to test the model and identify un-modelled variability due to specific hydrological events. Disturbance events of different magnitudes have different influences on subsequent system processes, resulting in different vegetation responses. Thus it is important to examine the response of *B. salicina* to all hydrological disturbances for which there were no data at the time of model development. The 2000 flood provided the opportunity for examining the response of *B. salicina* to a LID flood disturbance; an event for which there were no data.

This lack of data resulted in the development of assumptions about population response. Thus, it was assumed that the response of the *B. salicina* population would be similar to that shown in response to other, smaller flood events for which there were data (Mackenzie *et al.*, 1999). The *B. salicina* population monitored in the pool-rapid channel type was therefore expected to recover from the 2000 flood by means of seedling recruitment to a negative-J population structure. However, from Chapter 2, sprouting is a significant response mechanism occurring in the Sabie River *B. salicina* population subsequent to a LID flood event. As a sprouting response can have a significant influence on the ability of trees to produce seeds, thus influencing recruitment and the demographic profile (Bellingham and Sparrow, 2000; Kennard *et al.*, 2002; Kozlowski, 2002; Shea *et al.*, 2004; Martínková *et al.*, 2006), it is important to test the *Breonadia* Model against independent post-flood data. The model's population structure output at the time showing recovery to a negative-J structure can be directly compared to independent field data collected subsequent to the 2000 flood for the same period. This will indicate whether the recovery of the *B. salicina* population is significantly different from how this recovery is represented in the *Breonadia* Model.

Before testing any model, it is important to understand the underlying mechanisms and rules of that model. Understanding how the rules within the *Breonadia* Model are applied will ensure that the correct data are collected in order to test the model and if necessary update it. This chapter will provide a description of how the *Breonadia* Model generates a demographic profile for *B. salicina* in the pool-rapid channel type in the Sabie River before testing that output against data collected subsequent to the 2000 Sabie River flood.

3.1 Development of the *Breonadia* Model

Sedimentation in the Sabie River reduces bedrock influence, terrestrialises the riparian zone and aids reed encroachment and invasion by alien vegetation (Mackenzie *et al*., 1999). As objectives of previous research in KNP, conducted by the Kruger National Park Rivers Research Programme was to predict the biological consequences of these changes in the Sabie River (Breen, 1994). These specific problems were better managed by developing a number of small, specific conceptual models for each problem (Mackenzie *et al*., 1999). This suite of models (the BLINKS Models) was developed as a prototype predictive tool and included a geomorphological model, a riparian vegetation model and a fish assemblage model.

An extreme drought during the 1992/1993 wet season and a 1:50 year return period flood during February 1996 provided opportunities to study riparian vegetation response to these types of hydrological events. This knowledge was used to improve the BLINKS models. Despite this, an evaluation by Mackenzie *et al.* (1999) found that these models produced coarse results that did not contribute towards a specific achievable management objective. A new rule-based model, relying on the responses of a single indicator species, *B. salicina*, was developed by Mackenzie *et al.* (1999) following a pragmatic approach whereby managers identified specific management goals prior to model development. Changes in the *B. salicina* population structure were used as an indicator of riparian vegetation response to increases in sedimentation in the Sabie River. The defined TPCs for sedimentation in the Sabie River were utilised during model development to filter out unnecessary system components so that the pragmatic model only included essential components (Mackenzie *et al*., 1999).

The *Breonadia* Model is used to predict how hydrology, rainfall, size-class longevity, fecundity, survival and density dependence influence the negative-J demographic profile of the *B. salicina* population in the pool-rapid channel type. A Decision Support System (DSS) within the model the allows users to evaluate these predicted changes to the population structure in terms of the TPCs, informing managers which factors are likely to result in one or more of the defined TPCs being exceeded. When trends from long-term data indicate the population structure is approaching threshold conditions, the *Breonadia* Model may be used to simulate multiple scenarios to find a corrective strategy with the highest chance of success. Mackenzie *et al*., (1999) envisaged park decision makers using the model to, "run TPC audits of scenarios of potential management actions." Mackenzie *et al.*'s (1999) suggested scenarios included planting trees along the river, scenarios of catchment development and altered hydrological regimes due to dams, so that managers could access goal achievement under specified conditions.

3.1.1 How changes in population structure are calculated in the Breonadia Model

The *Breonadia* Model is a rule based model that utilises population projection matrices and a time step process as described by Caswell (1989), where specific changes occur for each individual tree, depending on the size-class in which it is placed. The *B. salicina* population was broken down into different functional size-classes (Table 2) where individuals have a staying time before they can grow into the next size-class (Mackenzie *et al*., 1995). This time step process in the *Breonadia* Model follows a size-class life cycle similar to the conceptual life cycle presented by Caswell (1982) (Figure 12) where each individual within a particular size-class has a survival percentage (related to mortality) as well a chance of growing into the next size-class (related to staying time) each year.

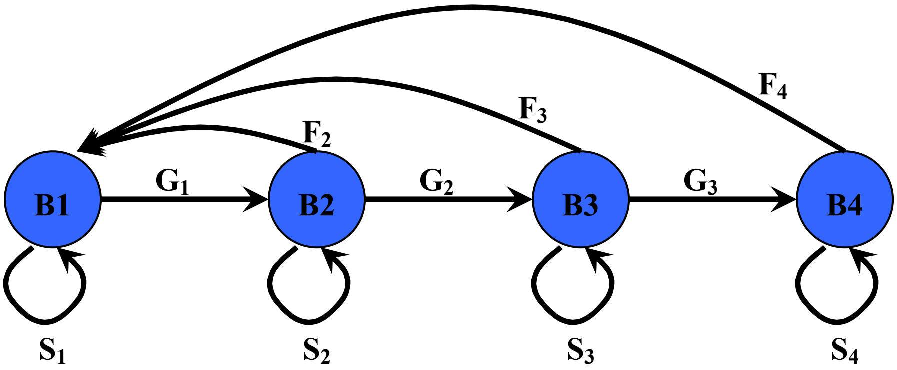

Figure 12: Conceptual size-class life cycle where individuals grow no more than a single size-class per yearly time interval. B represents the organisms within a specific size-class (size-class 1 through to 4), G represents the growth probability of the organisms within each size-class, F the fecundity of each size-class and S the survival probability for organisms within each size-class. (Caswell, 1982).

The benefits of demographic modelling are that existing data can be used in a number of ways (Manning and Martin, 2000, unpublished data):

- Estimating the probability of populations reaching a certain size in the future and how this probability can change depending on changes to driving factors such as climate and resources.
- Simulating the response of a population to both known and hypothesised management conditions.
- Enabling sensitivity analysis to determine which points in the lifecycle of individuals within a population have the greatest impact on population growth. This is useful for pinpointing the nature and timing of management intervention so that the best results are achieved.
- Improving monitoring protocols. Demographic models can help researchers to determine which data are the most valuable.
- Transferring understanding to other species.

In the *Breonadia* Model, the survival and growth likelihoods are influenced by a number of environmental factors (such as population density, rainfall and hydrology) and individual characteristics (such as current size-class). The number of germinants produced by each adult individual (fecundity) is also influenced by environmental inputs and individual factors in a similar way. Mortality in the smaller size-classes is influenced by rainfall, flood characteristics, substrate type and geomorphic position. Larger size-classes are not directly dependant on substrate or rainfall as they have better anchorage and water table access and modelled mortality occurs as a result of high flow events and the survival probability for the size-class.

A conceptualisation of how changes to population structure are calculated in the *Breonadia* Model (Figure 13) demonstrates how the population structure is influenced by input data as well as important internal feedback mechanisms in order to produce a population structure for year of data (Mackenzie *et al*., 1999). Environmental inputs to the model include rainfall, hydrology or flow characteristics, substrate change and geomorphic position. Hydrology input is in the form of daily discharge and can be generated from either real data, scenario flows or generated from the Agricultural Catchments Research Unit model (Schulze, 1995). Daily flows are placed into specific hydrological states and the frequency of each of these hydrological states influences the likelihood of individuals staying or moving from their size-class as well as their survival. Geomorphology input into the model is selected by the user as one of seven scenarios of changing substrate. These scenarios comprise the changing proportions of each of the different substrate types. Output from the geomorphology model (Jewitt *et al.*, 1998) can be used as a user input into the *Breonadia* Model. Daily rainfall makes up another model input and influences the survival probability of germinants and seedlings, except in severe droughts when adult survival and fecundity are also reduced.

Daily inputs are used to determine the occurrence of rainfall and flow events throughout the year, resulting in each year's time step being classified in terms of its rainfall and hydrology. Daily rainfall is used to calculate the occurrence of dry and wet periods throughout the year. The periodicity of these rainfall periods influences the survival of the germinant and seedling size-classes, with wet periods increasing their survival probability and dry periods decreasing this probability. Similarly, the *Breonadia* Model utilises the daily hydrological input data to determine the occurrence of nine possible hydrological events. The frequency of these different hydrological events invokes a set of rules for the hydrological state of the river for that year.

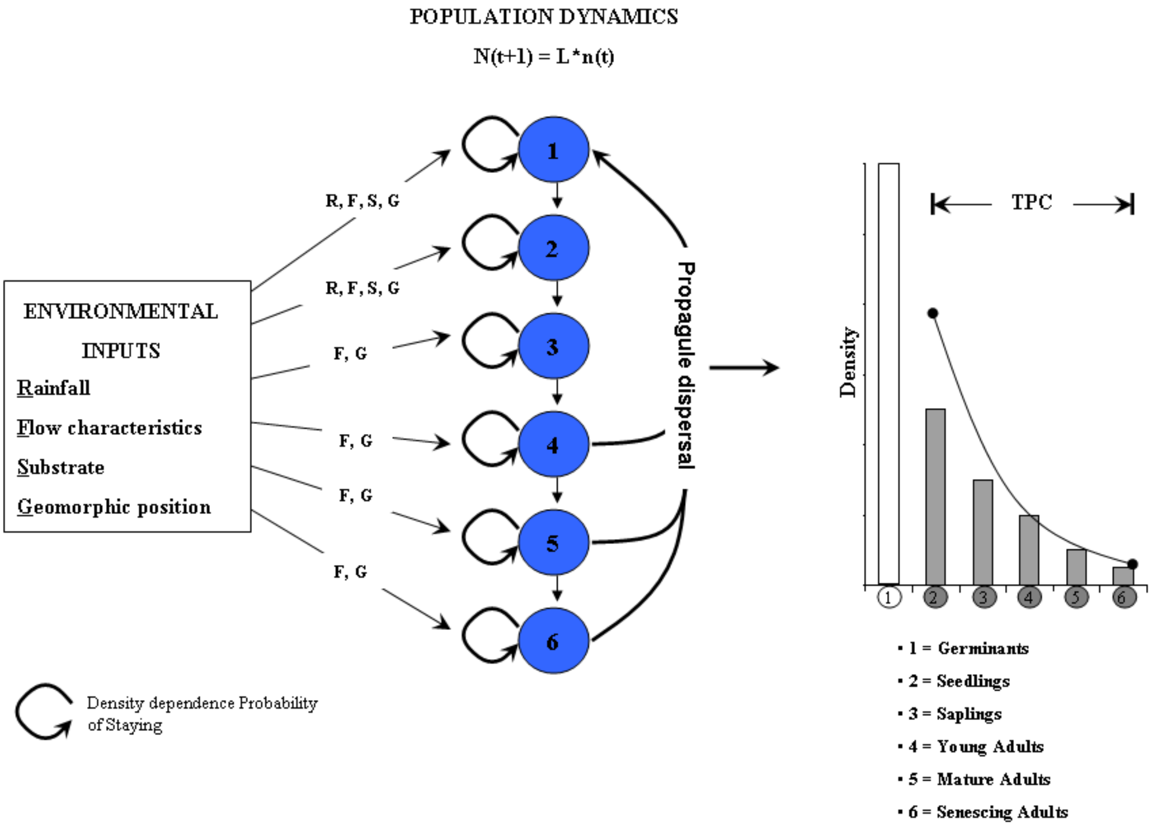

Figure 13: Conceptualisation of the *Breonadia* pragmatic model. The basis of the model is a population matrix model where the population (n) at time t + 1 is equal to the transition matrix multiplied by the population at time t. Density dependence and

propagule dispersal are important feedback mechanisms. The output of the model is a population structure of non germinant individuals, from which the TPC may be assessed. (R = rainfall, F = flow characteristics, S = substrate, G = geomorphic position). From Mackenzie *et al* (1999).

Changes to the physical substrate influence the survival probability of the different size-classes in the model. Specific substrate change scenarios in the model may be selected by the user or alternatively, the model can calculate substrate change according to hydrological events by selecting the hydrological link scenario. This is useful for KNP managers, as they can measure the effect of a managed flow regime in the Sabie River by using the *Breonadia* Model to test how a specific flow regime will change the physical substrate and thus the *B. salicina* population structure.

A general overview of the structure of the *Breonadia* Model shows how the input variables (hydrology, geomorphology and rainfall) influence fecundity, survival and the probabilities of staying or going from a particular size-class (Figure 14, Mackenzie *et al*., 1999). Size-class longevity was also considered to be an important input by the model developers, however, growth and size-age data were limited at the time of model development and thus this input was estimated from data for other tree species. Model developers made it possible for users to alter the longevity input when more data became available.

Three feedback mechanisms within the model operate at each yearly time interval to influence the output of each subsequent yearly time interval. These mechanisms are:

a) Fecundity, which is affected by the density of each size-class during that same year. Mackenzie *et al*. (1999) defined fecundity in the *Breonadia* Model as the number of germinants produced per adult tree. It is important to note here that this does not refer to the number of seeds produced by each adult (seeds are assumed to be produced in unlimited quantities) but rather the number of seeds produced by each adult that successfully germinate. Thus fecundity is influenced by hydrology, geomorphology and rainfall in any particular year as these are factors that can influence seed germination and establishment. The population density of each size-class at time t directly influences the number of germinants produced by that size-class at time t+1. Size-classes with a lower density produce fewer germinants as there are fewer adults to produce germinants. The timing of hydrological and rainfall events then has a further influence on the number of germinants. High flow events that occur close to germination time reduces the number of germinants as high flows are known to wash away unanchored germinants. Lack of rainfall also reduces germinant numbers as their root systems are not deep enough to reach baseflows.

b) Density dependence acts on each size-class as there is a limit to the number of individuals that can occupy the available space. Abundance for each size-class is combined with a density coefficient to calculate a density dependence function.

c) The population structure at any one time is added to the matrix in the subsequent time interval and divided on the basis of substrate type proportion (Mackenzie *et al*., 1999).

These data are used to influence 21 separate matrices of variables within the model over a user specified number of time intervals. The output is generated in the form of a 14 size-class population structure which is then further summed into the six functional size-classes defined by Mackenzie *et al*. (1999) including the new germinants recruited that year. The resulting population structure each year then is checked for compliance against the TPCs.

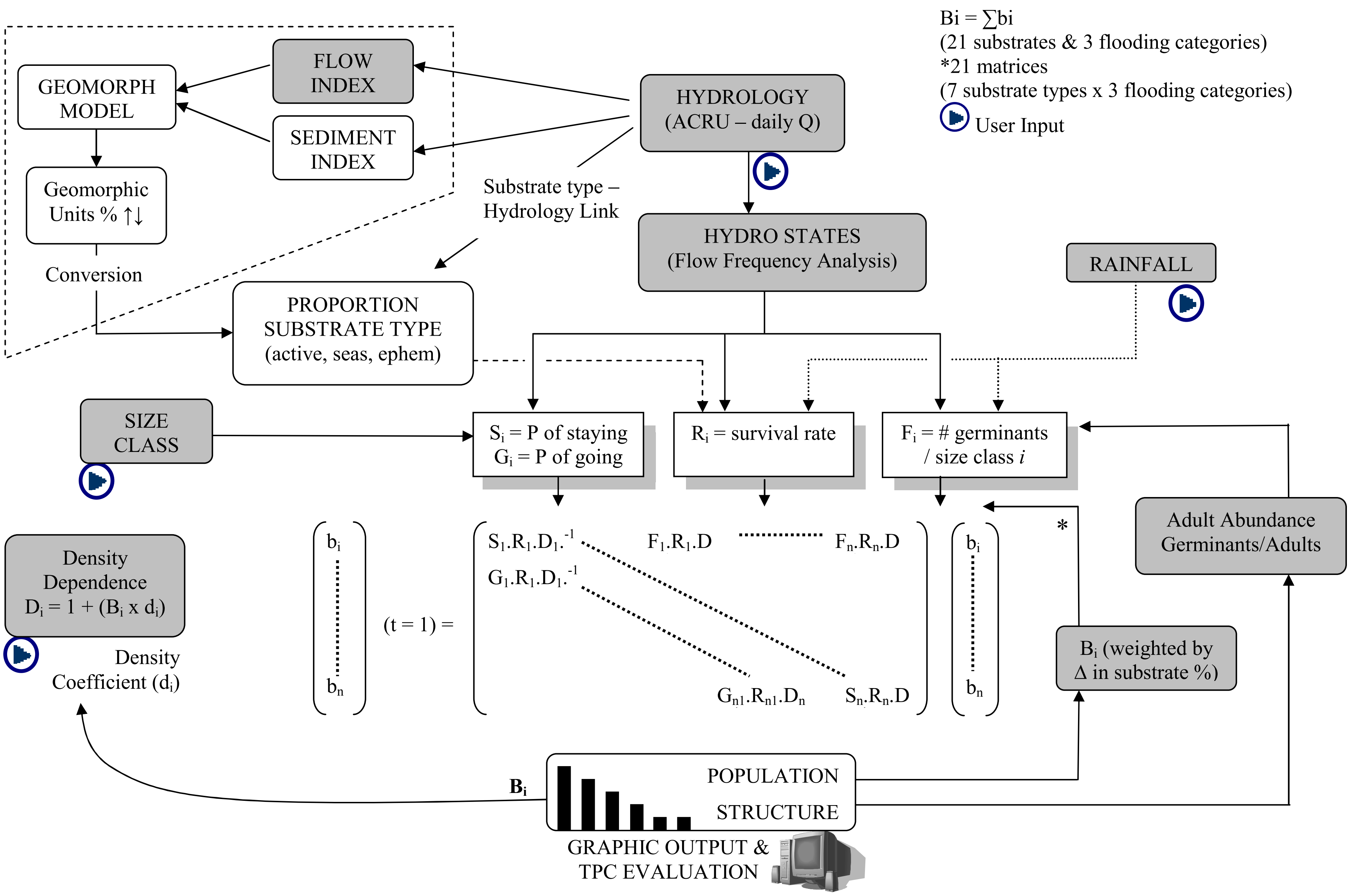

Figure 14: Conceptual diagram of the Breonadia Model structure. From Mackenzie et al. (1999).

3.1.2 The modelled influence of flood events on population structure

The *Breonadia* Model utilises daily hydrology data to define the occurrence of one of nine hydrological states in the Sabie River. These hydrological states were selected in order to represent functionally meaningful flows for vegetation (Mackenzie *et al.*, 1999). The daily hydrological data undergo frequency analysis each year and the resulting frequency of each of the nine hydrological states is defined. The frequencies of these states are then used to invoke rules about the occurrence of hydrological events such as no flow events and floods of differing magnitudes. These hydrological events have been ranked in order of influence such that the model only takes the most important event in a year into account. The *Breonadia* Model at present is unable to calculate the compounded influence of multiple hydrological events in a year. The *Breonadia* Model refers to LID flood events as "catastrophic floods." A "no flow" event overrides all other hydrological events. A "catastrophic flood" overrides all other high flow events.

Hydrological events can be used to influence the substrate input in the *Breonadia* Model on a yearly time-step basis, rather than selecting a specific substrate change scenario. The hydrological influence on substrate consists of estimates based on a general understanding of the geomorphology of the Sabie River (Mackenzie *et al.*, 1999). Thus, a specific hydrological regime can be used to estimate change in sedimentation levels in the Sabie River, which is then used to influence the modelled *B. salicina* population structure.

The occurrence of a catastrophic flood in any particular year in the model results in a specific influence on each of the flooding zones in the Sabie River, actively removing sediments and thus exposing bedrock. For example, in the active zone, exposed bedrock substrate increases by 15% of its current proportion, replacing loose alluvium (Mackenzie *et al.*, 1999). Seasonally flooded zones experience a 10% increase in bedrock and loose alluvium substrate decreases by 10% of the original bedrock proportion. In ephemeral zones, mudsilt increases by 5% of its original proportion, replacing parent soil.

Flood events also influence the survival of individual trees. Floods remove trees; smaller trees are more likely to be removed from the population as a result of a flood. There were no data on the removal of trees due to a catastrophic flood at the time of model development. Data about the influence of the 1996 1:50 year flood on the survival of trees in different size-classes were collected and used to generate a probability of removal for each size-class. The 1996 flood was not classified as a LID flood by Mackenzie *et al.*, (1999). Instead, the size-class removal probability values from the 1996 1:50 year flood were increased by a factor of four to represent the influence of a LID flood on the *B. salicina* population (Mackenzie *et al*., 1999). The flood removal probabilities are generated for each size-class in the active, seasonal and ephemeral flood zones of the river.

3.1.3 The modelled influence of Large Infrequent Disturbance floods and auditing Thresholds of Potential Concern

The modelled response of the *B. salicina* population after a LID flood relies solely on the recruitment of new individuals as germinants (Mackenzie *et al.*, 1999). The timing of hydrological events in the model reduces recruitment subsequent to that particular event. For LID floods (catastrophic flood category in the model), it was assumed that resulting tree damage would inhibit flowering and thus seed production from occurring the following spring. The *Breonadia* Model therefore does not model any recruitment of new germinants in the year following a catastrophic flood (Mackenzie *et al.*, 1999). Subsequent to this, modelled adult trees are assumed to recover from the disturbance and normal recruitment calculations continue, with fecundity once again being influenced by population density, rainfall and substrate availability.

The *Breonadia* Model also assumes that catastrophic floods result in a decrease in population density as a direct result of uprooting and tree death. A study by Parsons *et al.,* (2006) confirms that this is the case for the Sabie River *B. salicina* population subsequent to the 2000 flood. This decrease in population density has a dual feedback influence on recruitment. Firstly, a low population density results in fewer adult trees available to produce new seedlings (negatively weights recruitment). Secondly and conversely, a low population density results in decreased competition for physical space in the environment (positively weights recruitment). The modelled amount of suitable substrate availability subsequent to a catastrophic flood is increased, reducing modelled competition for suitable recruitment habitat and increasing the modelled fecundity values, i.e. increasing the modelled number of germinants produced per adult tree for that year. This is due to the effect of catastrophic flood disturbances opening up new areas for recruitment. Overall, these factors positively weight the fecundity values in the model, promoting recruitment subsequent to catastrophic floods.

It is important to clarify here that while modelled fecundity in the *Breonadia* Model is defined as the number of germinants per adult, it only relates to those germinants produced per adult tree that have sufficient resources (such as suitable habitat) to enable them to germinate and establish, and excludes those germinants that in reality would germinate and then die in the same growing season due to competition for resources. Fecundity in the *Breonadia* Model is modelled in this way because the assumption about unlimited seed in the system would otherwise result in unrealistically high numbers of modelled germinants. Essentially, the model first calculates population density (from the other size classes), rainfall and substrate availability and then calculates the number of germinants that can utilise those resources. This reduces processing within the model and simplifies the calculations made when running the model.

The response of the *B. salicina* population to natural disturbance events, such as LID floods, and the resulting changes to the demographic profile are fluctuations that must be taken into account when monitoring changes in the population. It is important to differentiate between demographic changes that are as a result of natural disturbance events and changes that are as a result of increased sedimentation in the Sabie River. Changes to the *B. salicina* population structure as a result of natural fluctuations such as floods are acceptable and should not be of concern to managers. However, limited knowledge of the population response to different disturbances highlights the importance of incorporating mechanisms that allow for these natural fluctuations. The TPCs are defined to take these natural fluctuations into account. When a new disturbance occurs, the TPCs can be exceeded. When a natural disturbance that is not human induced or altered causes one or more of the TPCs to be exceeded, the TPCs can be redefined to take these natural fluctuations into account. However, the process of redefining the TPCs is unlikely to take all possible events into account. For this reason, when any TPC is exceeded, this should be evaluated in the context of flow events (Mackenzie *et al.*, 1999) since it is expected that the TPCs can be exceeded by natural disturbance events. In the case of the TPCs that define fluctuations in the negative-J profile, waiting periods on monitoring after natural disturbances were proposed so that the population structure has time to recover from the disturbance (Mackenzie *et al.*, 1999). These waiting periods allow the population structure to recover from the flood event back to a defined negative-J population structure before monitoring continues. Mackenzie *et al.* (1999) developed a TPC auditing protocol that relies on the expected time of recovery from specific disturbances. TPCs can remain exceeded for a longer than expected period of time due to additional disturbance events that occur during the recovery period. This is acceptable if this can be attributed to natural events. However, if recovery takes longer than expected and there are no additional disturbance events, this would be a cause for concern. The auditing protocol includes an action path for both of these scenarios (Mackenzie *et al.*, 1999).

For example, changes to the population structure as a direct result of flood events may be sufficient to indicate that one or more of the TPCs has been exceeded if monitoring continues immediately after disturbance events. The 2000 Sabie River flood resulted in a loss of vegetation and change in the river's biophysical template that was unprecedented in 60 years of aerial photographic records (Parsons *et al.*, 2006). The stripping of the larger size-classes of *B. salicina* by the flood caused all three defined TPCs for *B. salicina* to be exceeded (Figure 15). The modeled LID flood event occurred in Year Six of the entire time-step scenario (Figure 15). Recovery back to a negative-J shaped profile occurred four years later, in Year Ten (Mackenzie *et al.*, 1999). Although the negative-J profile re-appeared after a four year period, it can be seen that the three defined TPCs remain exceeded for a number of further years. This is partially due to continued recovery from the LID flood event and partially due to subsequent disturbance events.

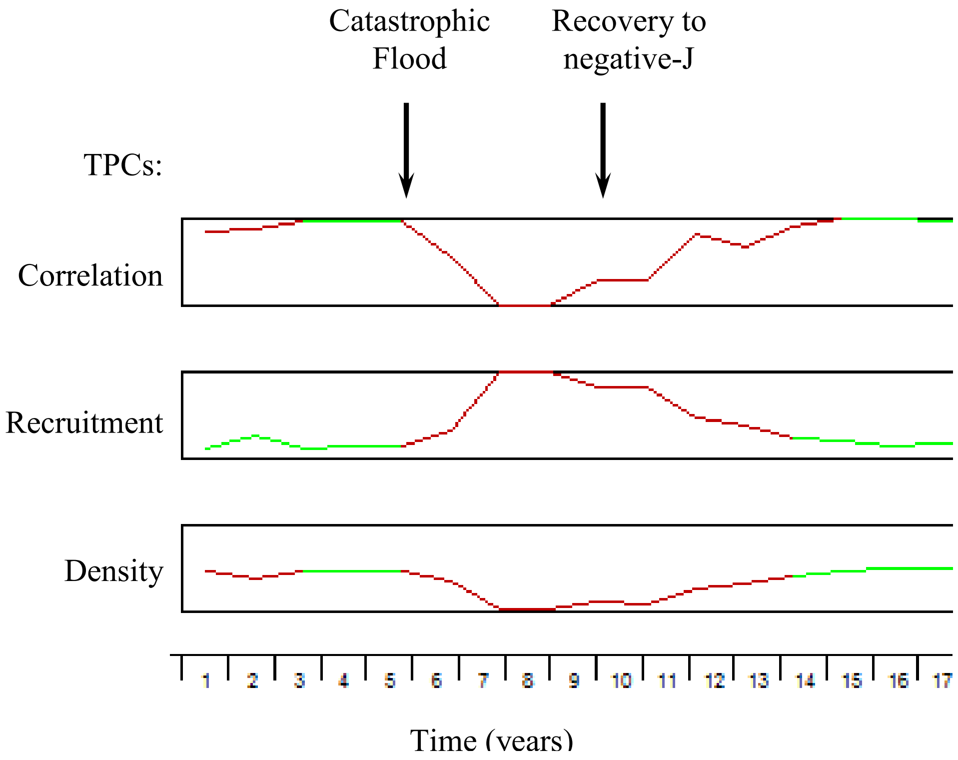

Figure 15 : A screenshot of the TPC audit output generated from the Breonadia Model (Mackenzie *et al.*, 1999). The green sections show where TPCs are within the thresholds, red sections show where each TPC has been exceeded. This output includes a catastrophic flood and the subsequent years, demonstrating how all three TPCs were exceeded as a result of a catastrophic flood. Recovery to a negative-J profile occurs after four years; however, the TPCs remain exceeded due to following events. The changes in density, recruitment and correlation are changes within the defined TPCs for monitoring *B. salicina* as outlined in Section 2.4.

The *Breonadia* Model was used to generate predictions of when the population was likely to return to its pre-flood negative-J structure after hydrological events in order to stipulate the length of waiting period after events of different magnitudes (Mackenzie *et al.,* 1999). The modelled recovery back to a negative-J profile after a catastrophic flood, such as occurred in 2000, was found to occur after a four year time interval . The waiting period until TPC auditing can continue was set at the expected four year recovery period plus an additional year by the model developers; thus a five year waiting period has been put in place after catastrophic floods. The model prediction about response subsequent to the flood indicates that seedlings should occur at high abundances (greater than 800 seedlings per hectare) four years subsequent to the flood.

3.2 Refinement of the *Breonadia* Model as a management tool

It is important to remember that an incomplete dataset was used to build the *Breonadia* Model. Gaps in the information were filled by assumptions and information from other, similar systems. Incomplete models still provide a useful function for managers; however, when the opportunity arises new data can be used to refine models, thus increasing the strength of models as management tools (Starfield *et al.*, 1990; Walters, 1986; 1997).

The *Breonadia* Model can be refined in a number of different ways. Firstly, new field data that are independent from data used to develop the model can be used to directly test the model. A model output is generated that is comparable to this independent data by running the model and producing an output for the same conditions under which the field data were collected. The model output is then compared directly to the field data. This gives an indication of how sound the model is when applied to new situations. Long-term monitoring data, as well as ongoing research, provide additional information on the relationships between the *B. salicina* population and fluctuations in the physical characteristics of the Sabie River. This can facilitate ongoing improvement of the model by application of new information to areas of the model that had to be estimated at the time of model development.

Secondly, the *Breonadia* Model may also be refined by directly addressing the inherent assumptions on which it is based. An example of an inherent assumption in the model is the assumption that *B. salicina* seed production does not limit establishment in the Sabie River. This is based on observations of seeds and new germinants in large numbers all along the Sabie River throughout the year (Mackenzie *et al.*, 1999). This assumption was incorporated into the model by not placing a seed availability limit on the recruitment of new individuals.

The model developers instead placed the following limits on the recruitment of new germinants:

- Availability of suitable exposed bedrock habitat (substrate type). Exposed bedrock is required for successful establishment of new individuals.
- Population density of *B. salicina*. Individuals compete for resources and as such, low *B. salicina* population density promotes recruitment. However, a low population density also negatively weights recruitment of new germinants, as there are fewer adults to produce seeds.

The following factors influence the survival of germinants but do not influence the number of new germinants produced in any single year:

- Hydrological events (magnitude and timing). The magnitude of hydrological events, or their timing, influence the survival of new individuals in their first year. Seeds are dispersed from April to July and lose their viability by December of any one year (Mackenzie *et al.*, 1999). The timing of hydrological events can influence recruitment by resulting in germinant mortality.
- Rainfall (occurrence of wet and dry periods through the year). Similarly to hydrological events, the occurrence of dry and wet periods and their frequency and duration influences the survival of new individuals in their first year.

3.3 Testing the *Breonadia* Model

Testing of any model requires a data set independent of the initial data used in model development; the initial data set is used to adjust the model parameters during model development and is therefore bound to the model while the second data set is used for independent validation (Starfield *et al.*, 1990). Use of the first data set for model development as well as testing will lead to over-fitting of the data and falsely reported error rates that are lower than those that will occur when the model is applied (Duda *et al.*, 2000). Large discrepancies in the model output from the test data indicate that the model is not effective on new independent data (Starfield *et al.*, 1990).

At the time the *Breonadia* Model was developed, there was no independent data set to test the model and the model was instead tested by evaluating the model outputs against different flow scenarios. Previous understanding of the indicator species, *B. salicina*, was used to develop expectations of how the population would respond to various flow scenarios (de Fontaine and Rogers, 1995; van Coller *et al.*, 1997). These scenarios were then compared to model outputs for the same flow scenarios in order to highlight any inadequacies in the model, being used in a feedback mechanism to improve the reliability of the model output (Mackenzie *et al*., 1999).

Monitoring data collected and recorded over long periods of time (more than several years) can be used to further refine the *Breonadia* Model. Population monitoring data used to audit the TPC should be collected at five year intervals at specified monitoring sites and can also be used to update the population structure as a model input update. Monitoring data can be used to refine the model in specific four ways (Mackenzie *et al*., 1999):

- To test the model output.
- To address inherent assumptions made in the model.
- To improve variable and parameter estimation in the model.
- To upgrade the substrate-hydrology link.

However, no long-term database containing monitoring data has been maintained and thus it is difficult to update and refine the *Breonadia* Model as envisioned by the model developers. Despite this, even data collected over a short period of time can provide valuable input for addressing some aspects of model refinement as well as for providing an independent data set with which to test the model. Snapshot data can also be focused to target specific aspects of the *Breonadia* Model that require updating. A list of aspects of the model identified as requiring improvement was made by the model developers (Mackenzie *et al*., 1999). These aspects are discussed below in more detail.

i) The substrate-hydrology link relationship in the model is based on the limited understanding of geomorphological response to changing flow conditions at the time of model development (Mackenzie *et al.*, 1999). Model developers recommend developing a detailed geomorphological model to provide better predictions of change in substrate type. An interim alternative would be to collect empirical substrate type proportion data as part of the monitoring programme in conjunction with hydrological event data. Both of these options require detailed long-term data, and are beyond the scope of this dissertation.
ii) Improving variable and parameter estimation should focus on improving model estimates that were based on poor data or intuitive understanding of *B. salicina* at the time of model development (Mackenzie *et al.*, 1999). Model developers conducted sensitivity analyses to determine which parameters should be prioritised for updates. Of the 50 listed parameters, half are substrate related. The remaining parameters are

related to growth rates, a variety of hydrological events or to specific factors influencing particular size classes. The data from this study can however be used to improve the estimates on the influence of catastrophic floods on fecundity across all size classes.

iii) Model developers also provided a list of twelve assumptions made in order to set up the rules in the *Breonadia* Model. If any assumptions need to change as a result of research or new information, the hard coding of the model would need to be changed by rewriting the code for the appropriate rule. The twelve assumptions made to complete the rules setup in the *Breonadia* Model are:

- Fecundity and survival after small hydrological events (high flows, very small floods, extreme low flows and intermediate flows) are unknown; these hydrological events are excluded from having any influence in the *Breonadia* Model.
- Growth rates of the different size classes are considered independent of substrate and flooding frequency.
- Drought and rainfall don't influence growth rates.
- Damage caused by flooding doesn't influence growth rates.
- Size classes in the model can't skip size classes within one year.
- Density dependence is independent of substrate type and inundation frequency; the self regulatory effect of density dependence is the same on different substrate types.
- All adult size classes are affected in the same way in terms of survival by density dependence.
- Fecundity is independent of substrate type.
- All adult size classes are affected the same way in terms of fecundity by density dependence.
- Hydrological events override all other previous hydrological events (no combined effects); multiple hydrological events have no effect.
- Herbivory has no effect on the population.
- Equal densities of *B. salicina* occur on different substrates.

Targeted research is required to address these assumptions; however, most of the assumptions require data recorded over long periods of time (several years and longer). Data used to test the model should be collected regularly and should include the population densities of each size-class in the monitoring sites (Mackenzie *et al.*, 1999). This ensures data are more likely to be available both before and after all hydrological events. Additional data to that collected, as part of the monitoring programme, would be required. This should include monitoring the growth of labelled individuals, examining changes in substrate and growth in addition to population structure and density in response to difference hydrological events. Recording of regular long-term monitoring data as well as any additional data appropriate to addressing the listed assumptions on which the *Breonadia* Model is based should be a priority if this model is to improve in value as a management tool. Additionally, the limited data on which the model is based resulted in the development of rules that, although not assumptions, do not take the influence of less frequent events or condition into account. For example, as discussed in Section 2.3, the *Breonadia* Model relies on population density and substrate availability to limit recruitment in the population. This relies on the assumption that seed production is not a limiting factor within the Sabie River, a characteristic of negative-J populations.

Proper testing of the model output requires collection of data before and after a hydrological event. This model test was not possible over the 2000 LID flood event as no data were recorded immediately prior to the flood event and hydrological data during and after the flood were limited. Direct model testing as suggested by the model developers was thus not possible within the scope of this project. However, as the *Breonadia* Model is a tool for predicting changes to the population structure, a direct evaluation of the model output against comparable field data will still provide a useful test of the predictive capabilities of the model. This assessment will help determine whether the assumptions about recovery of *B. salicina* to a LID flood event are significantly different from what occurs in the field.

3.4 Aim: Examining the post-flood demography of *B. salicina* and testing the *Breonadia* Model

The aim of this chapter is to examine the ability of the *Breonadia* Model to capture changes in population structure subsequent to a catastrophic flood. This will be done by comparing what is expected (in terms of population response and structure following the flood) from the model predictions and to what is observed from the field data.

This chapter will make two comparisons. Firstly, the output from the *Breonadia* Model will be directly compared to demographic data collected at the monitoring sites in the Sabie River. These monitoring sites were selected specifically for the monitoring programme associated with the *Breonadia* Model and as such data from these sites will be directly comparable to the output from the *Breonadia* Model. However, the monitoring sites are located in both pool-rapid and bedrock anastomosing channels. Previous studies of *B. salicina* indicate that recruitment and thus the different demographic profiles are strongly associated with specific channel types in the Sabie River (de Fontaine and Rogers, 1995; van Coller *et al.*, 1997; Mackenzie *et al.*, 1999). The negative-J profile was found to be associated with bedrock sections of the anastomosing channels rather than pool-rapid channels. Thus this chapter will also make a direct comparison between the *Breonadia* Model output and each of the four channel types in the Sabie River. This will determine where in the river template response, recovery and demographic profile most closely matches the model output so that the application of the model and the monitoring programme can be re-evaluated. A re-evaluation of the model will assist with identifying knowledge gaps within the model assumptions about *B. salicina* population structure in the Sabie River and response to LID flood events.

3.5 Methods

The demography data were collected in the spring (September) of 2004, so that seeds would have had time to germinate following seed production and dispersal in autumn. Transects were sampled using the methods of Mackenzie *et al.* (1999) (described in Chapter 2) so that all data would be comparable with outputs generated from the *Breonadia* Model. For the analysis in this chapter, two data collections were made. Firstly, data were collected at the nine monitoring sites (Figure 16) associated with the *Breonadia* Model in order to provide data for direct testing of the model. Secondly, data were collected at the same sixteen sites examined in Chapter two of this dissertation (Figure 7) to compare the model output with each of the four channel types in the Sabie River.

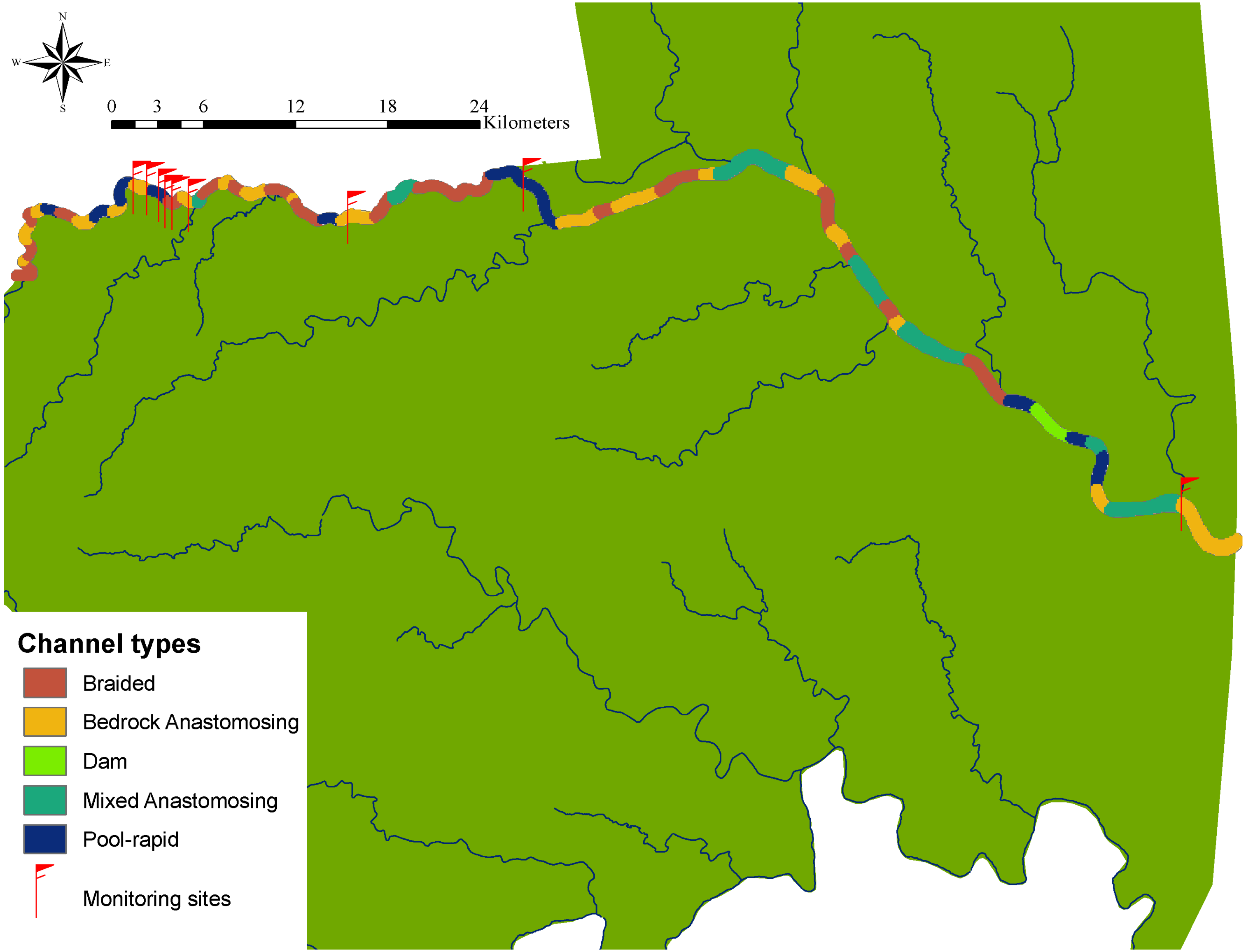

Figure 16: Locations of the nine monitoring sites along the Sabie River, Kruger National Park

For the analysis in this chapter, only basal diameter (in mm, measured above the basal swelling and below the lowest branches) was recorded for each *B. salicina* individual found at each site. The basal diameter was used to place each tree into a basal diameter size-class category as before (Table 2). The area of each site was recorded in hectares. The data from the monitoring sites and each of the four channel types were represented as the density of trees (number of trees per hectare) within each of the functional size-classes as the *Breonadia* Model only produces a size-class density output. The mean density of trees in each size-class at each site was calculated for the monitoring sites and for each of the four channel types.

The *Breonadia* Model was run to generate the size-class density output for the "hydrology link" scenario in order to include the influence of hydrology on substrate. Actual flow for a catastrophic flood event in the Sabie River could not be used due to the absence of a complete flow record for the flood period. Instead, a catastrophic event is modelled by adding the appropriate increases in flow to historical flow data. The model output for the hydrological scenario with an added catastrophic flood was generated, resulting in population structure and flow summaries for each year time step. The flow summary was examined to determine in which year the catastrophic flood occurred. The modelled population structure for the period four years subsequent to the catastrophic flood event was recorded and used to plot a size-class density curve to represent the expected population profile.

This modelled population profile was then visually compared to the size-class density curve generated from the monitoring sites. Similarly the *Breonadia* Model density size-class output was compared to the size-class densities observed in each of the four channel types to examine the applicability of the *Breonadia* Model to specific channel types.

3.6 Results

3.6.1 Direct test of the *Breonadia* Model output against monitoring site data

The *Breonadia* Model output for four years post flood displayed very high recruitment levels (>2500/ha) and a return to a negative-J profile (Figure 17). The logarithmic scale of the y-axis here emphasises the strong recruitment demonstrated in the *Breonadia* Model prediction and contrasts strongly with the population structure observed at the nine monitoring sites in the Sabie River where no recovery to a negative-J profile and few new recruits were found (Figure 18). The monitoring sites displayed a unimodal profile, with the peak density occurring in the seedling and sapling size classes.

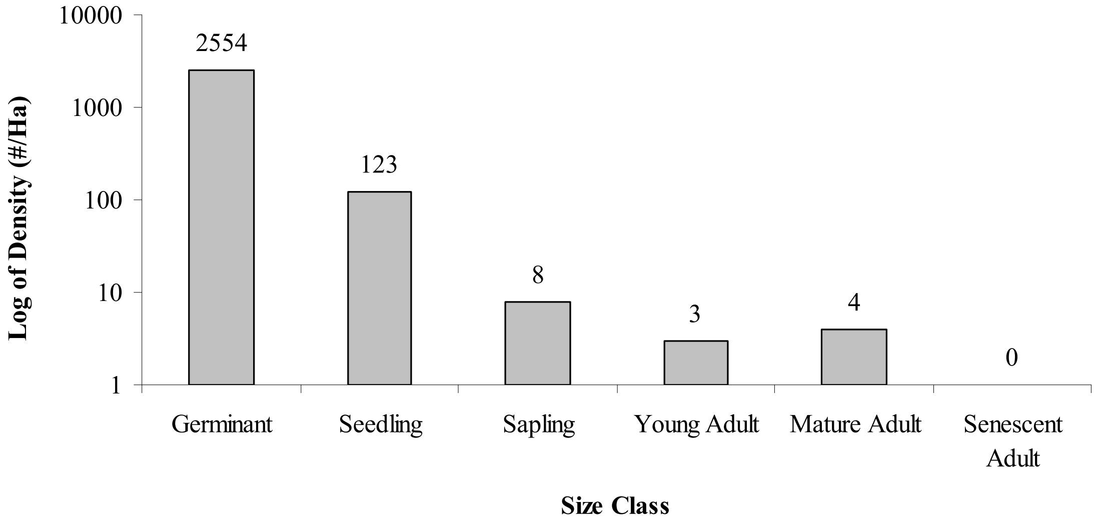

Figure 17: Model density size-class category output for the hydrology link scenario for a four-year post catastrophic flood period. The data values indicate the actual density values for each size-class. The logarithmic scale (base 10) on the y-axis emphasises the unrealistic nature of the *Breonadia* Model prediction.

The high level of recruitment predicted using the *Breonadia* Model is attributed to two factors in the setup of the rules in the model:

- The *Breonadia* Model rules are set up to interpret an increase in suitable bedrock habitat as a decrease in competition for physical space.
- Similarly, the decrease in total tree density due to flood stripping is interpreted as a decrease in competition for physical space.

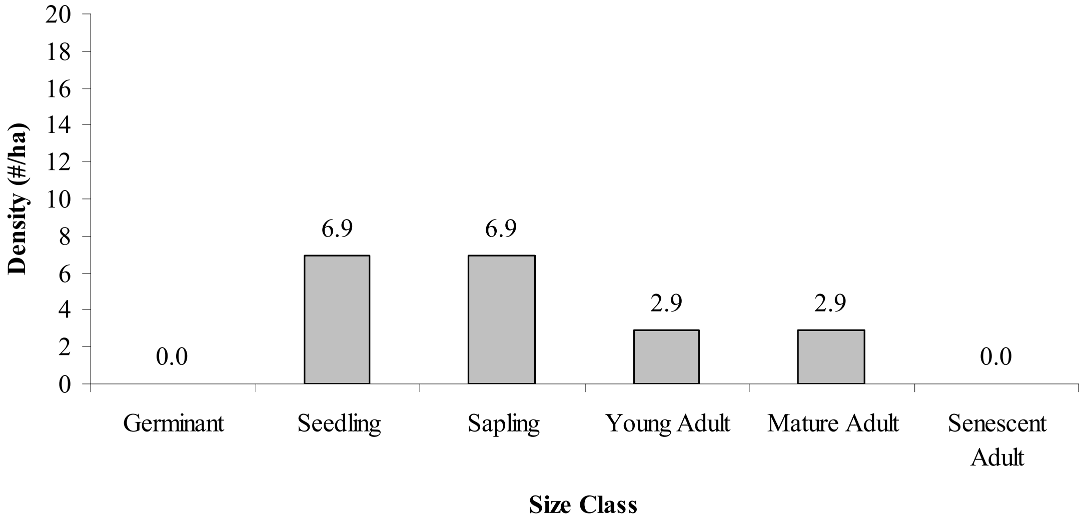

Figure 18: The observed total size-class densities in 2004 of the *Breonadia salicina* population at the nine monitoring sites. The data values indicate the actual density values for each size-class.

These graphs suggest that the size-class density profile of the *Breonadia* Model output is very different from the profile that occurs in the monitoring sites. Thus the *Breonadia* Model incorrectly predicted the population structure of the *B. salicina* subpopulation in the monitoring sites after a hydrological event of the magnitude of the 2000 Sabie River flood.

3.6.2 Comparison of the *Breonadia* Model output with the demographic profile in the four channel types

The sub-population in the braided channel (Figure 22) did not fit any of the recognised pre-flood demographic profiles for the *B. salicina* subpopulations within the Sabie River (Section 2.3), instead showing low densities overall but a trend towards increased density with increasing size-class. *Breonadia salicina* sub-populations in the bedrock anastomosing, mixed anastomosing and pool-rapid channels (Figure 19 to Figure 21) all showed a bimodal demographic profile, with the first peak occurring in the seedling size-class and the second in the larger mature adult size-class. While all showing bimodal profiles, the density of trees in each of these three channel types varies, with the lowest density occurring in the pool-rapid channel type. Also, although the higher densities in the seedling size class imply that recruitment is occurring strongly after the flood event, most of these individuals showed evidence of flood damage and are residuals from before the 2000 flood. It is important to remember that the germinant size-class is excluded from evaluation of the demographic profile in the *Breonadia* Model.

Thus, even where recruitment has occurred after the flood, it has not resulted in a recovery to a negative-J profile anywhere in the Sabie River. The density of recruitment after the 2000 flood was greatest at the sites which had the highest density of reproductive trees, namely in the mixed anastomosing (Figure 20) channel type, followed by the bedrock anastomosing channel type (Figure 21).

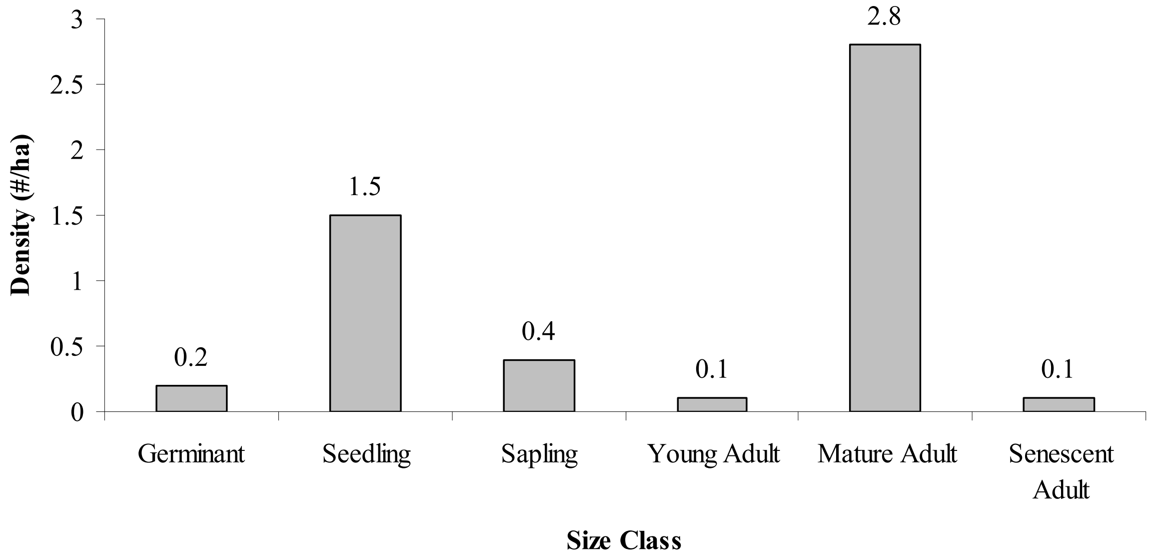

Figure 19: The *B. salicina* subpopulation size-class density in the pool-rapid channel type. Numerical values indicate the actual density in each size-class.

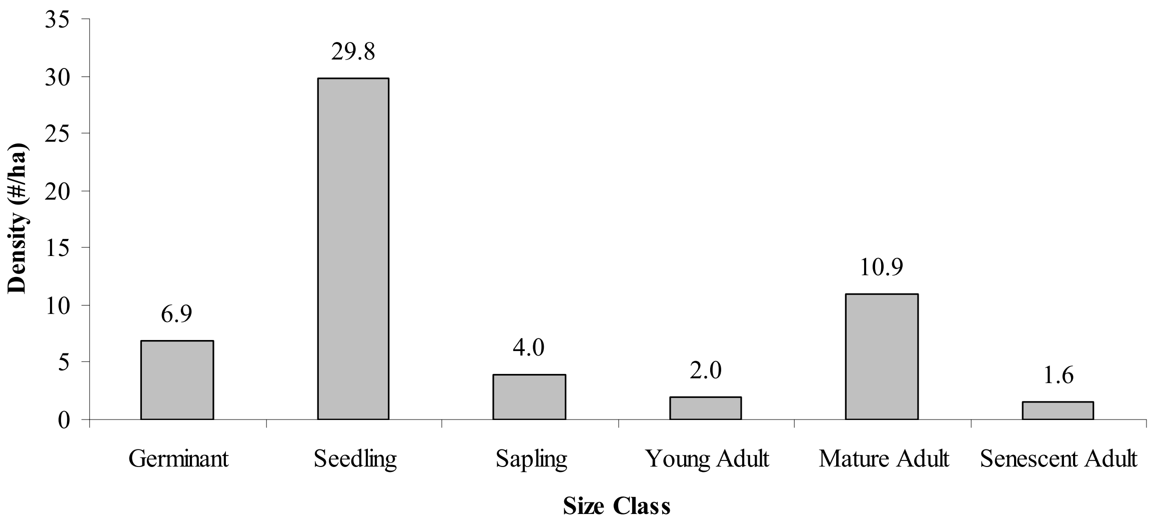

Figure 20: The *B. salicina* subpopulation size-class density in the mixed anastomosing channel type. Data values indicate the actual density in each size-class.

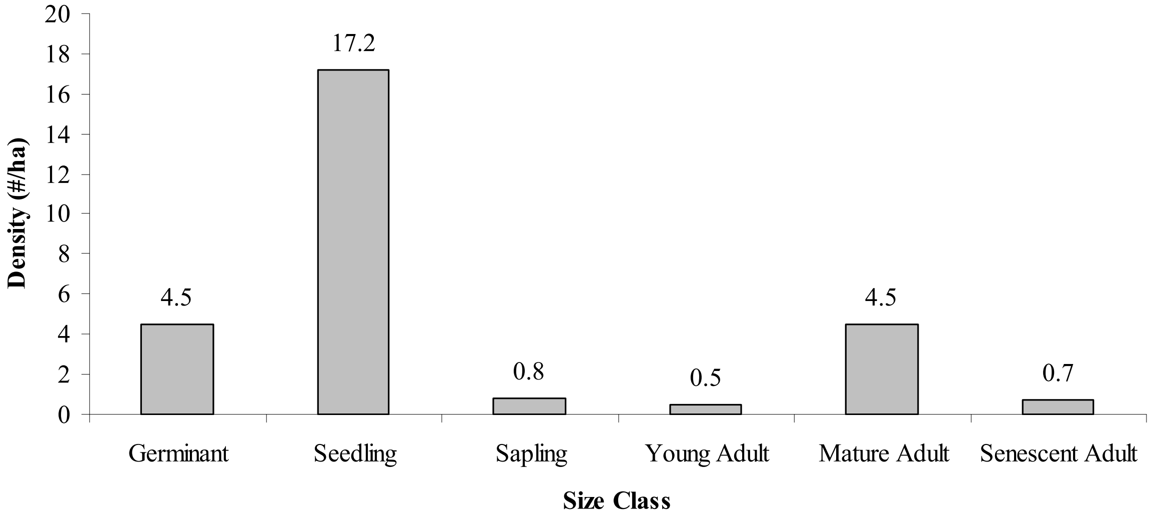

Figure 21: The *B. salicina* subpopulation size-class density in the bedrock anastomosing channel type. Data values indicate the actual density in each size-class.

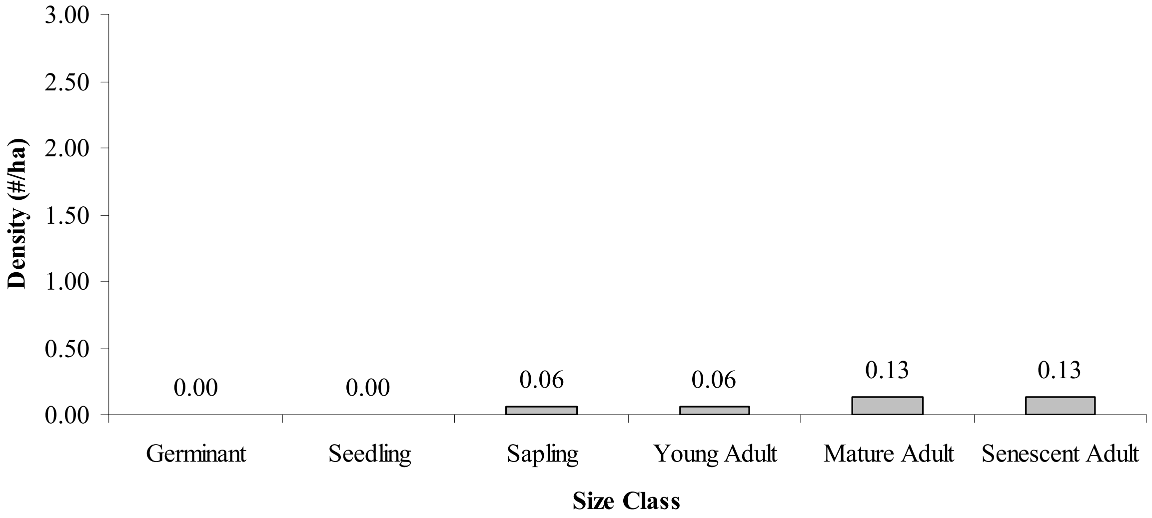

Figure 22: The *B. salicina* subpopulation size-class density in the braided channel type. Data values indicate the actual density in each size-class.

These graphs suggest that subsequent to the 2000 flood, the demographic profiles of *B. salicina* did indeed vary between channel types. However, recruitment of new germinants did not appear to be particularly high in any particular channel type. Thus, recruitment would be expected to occur most strongly in those channel types that display the greatest likelihood of flowering (Section 2.10) implying that recruitment occurs close to parent trees and that widespread dispersal of *B. salicina* seeds is more limited than suggested by the literature.

Despite that the monitoring sites are located in a mix of pool-rapid and bedrock anastomosing channels, the unimodal profile recorded in the monitoring sites does not match the bimodal profile recorded in the bedrock anastomosing channels and in the pool-rapid channels. The monitoring sites had very low densities of trees compared to what was found in specific channel types. This could be due to localised variation of flood waters, possibly resulting in the removal of more trees in the monitoring sites. As can be seen from Figure 16, the monitoring sites were predominantly located in the upstream reaches of the Sabie River whereas the locations of sites for each of the channel types were spread along the entire reach of the Sabie River within the KNP. This suggests a pattern of disturbance and recruitment that is related to the longitudinal profile of the Sabie River.

The small difference in size-class profiles between all four of the channel types in the Sabie River implies that demography is associated with the underlying physical template, despite that reproductive response also plays a role in levels of recruitment of *B. salicina* in the Sabie River. That the size-class profile found in the monitoring sites does not match the profile found in any of the four channel types suggests that the monitoring sites are not a good representation of the demography in any one of the four channel types.

The negative-J shaped output from the *Breonadia* Model also did not appear to resemble the size-class profile found in any of the four channel types. From the application of the *Breonadia* Model we would expect recruitment to be highest in the pool-rapid channel type as the negative-J profile was associated with this channel type in the monitoring programme (Mackenzie *et al.*, 1999). The results from this study show a very similar profile in the pool-rapid channel type to both the mixed anastomosing and the bedrock anastomosing channel type, but lower overall densities of trees and lower levels of post disturbance recruitment. The review of the literature (Section 2.3) indicated that a negative-J profile was associated with exposed bedrock habitat in the anastomosing channel types and not with the pool-rapid channel type. The negative-J profile and the pool-rapid channel type were chosen for monitoring because these are considered to be the most sensitive profile and channel type to increases in sedimentation. The *Breonadia* Model therefore simulates how changes in the pool-rapid channel type will influence a negative-J profile, a situation that does not occur naturally. This has implications for the application of the *Breonadia* Model in terms of the channel type to which it is applied.

3.7 Discussion

Harper (1997) suggests that demographic data can be used to generate hypotheses about underlying geomorphic processes. In the case of *B. salicina* in the Sabie River, the different size-class profiles are known to be associated with specific features of the underlying template (de Fontaine and Rogers, 1995) and establishment is associated with specific geomorphic features. The strong relationship between the different profiles and the underlying physical template of the Sabie River is considered to be a result of long-term changes to the underlying template due to changing flow conditions, and of disturbance events influencing the underlying physical template in the short term. Both of these explanations result in changes in bedrock availability. Changes to the underlying template do not necessarily influence established individuals but will influence current levels of recruitment. The relationship between recruitment and the physical template suggests that the underlying physical template would influence the recovery of *B. salicina* sub-populations from flood disturbance (de Fontaine and Rogers, 1995), where fluctuations in the levels of availability of suitable habitat will result in alternating periods of high and low recruitment levels. However, although there was some re-distribution of sediment within the river, limited habitat availability seems an unlikely explanation for the limited recruitment observed in the field after the 2000 flood due to the following factors:

- Vegetation was stripped from the channel as a result of the flood leaving areas open for establishment (Parsons *et al*., 2006).
- Some sediment was also flushed from the system, leaving an abundance of exposed bedrock suitable as recruitment habitat in the river (Rountree, pers. comm., CWE, UWITS).
- The overall density of *B. salicina* was significantly reduced as a result of the 2000 flood (Parsons *et al*., 2006), it is therefore unlikely that recruitment in the post-flood era is limited by density dependence.

An alternative explanation for limited recruitment observed in the field after the 2000 flood is that seed is limited in availability due to decreases in the density of mature adult trees as well as changes to fecundity in residual adult trees. This is contrary to model predictions, which are based upon the availability of habitat and limited competition after such an event. Thus there is an inherent problem with the model's assumption that seeds are not a limiting factor to the recruitment of *B. salicina* following disturbance. Although, the model does incorporate penalties to fecundity after disturbance events, these are applied only in the first year after an event and do not take compounding events or longer term effects, such as changes to fecundity due to the effect of sprouting, into account.

The difference in the size-class profile in the monitoring sites and the output of the *Breonadia* Model can be attributed to the exclusion of sprouting as a response mode in the model. Previous demographic analyses of the sub-populations of *B. salicina* in the Sabie River revealed that environmental heterogeneity and thus the availability of suitable habitat for recruitment of new individuals is the central factor that drives the demographic profile of these sub-populations (da Fontaine and Rogers, 1995). However, this study suggests that after a catastrophic flood the shape of sub-population profiles is strongly influenced not only by the availability of suitable habitat, but also by the availability of seed in the system as a result of the influence of a sprouting response. High proportions of adult *B. salicina* showed a reduced ability to produce flowers as a result of the sprouting they showed in response to the 2000 flood (Chapter 2). Thus, contrary to previous studies on *B. salicina*, disturbance events also play a direct role in the shaping the demographic profiles observed in this species, rather than only influencing population structure through changing the underlying physical template.

The 2000 flood had a direct influence on the demographic profiles of the sub-populations of *B. salicina* occurring in each of the channel types in the Sabie River by stripping vegetation across all size-classes (Parsons *et al.*, 2006). In addition the subsequent response modes, namely the influence of sprouting on flowering ability and thus recruitment of new individuals, also influenced the population structure among channel types. However, the lack of any patterns in population structure or even response mode across channel types indicate that the influence of the physical template on population structure is not occurring at the channel type scale in the Sabie River after the 2000 flood. Rather it is the direct influence of the flood resulting in differing levels of damage severity and the subsequent response modes of individual trees that will influence seed production in *B. salicina*. Once seeds are produced, recruitment will continue to be influenced by the underlying physical template as successful establishment will only occur in suitable habitat. However, widespread and abundant dispersal of seeds produced after the disturbance is necessary before recruitment can be influenced predominantly by the underlying template throughout the Sabie River. Thus, subsequent to disturbance, there is a complex interplay between both the response modes which influence seed production and the underlying physical template which influences recruitment and establishment of new individuals. These conclusions about sprouting as an important recovery mechanism in *B. salicina* populations challenge some of the underlying assumptions in the *Breonadia* Model.

Based on the observations of this study, it appears that the underlying model assumption about unlimited seed availability in the Sabie River is false. The very high population density prior to the 2000 flood may have contributed enough seeds such that seed availability did not limit recruitment at that time. However, after the 2000 flood, the overall population density, including the density of seed producing size-classes is reduced. There are therefore fewer adults to produce seeds over a larger suitable area. In addition to this, sprouting further reduces the ability of many these adult trees to produce seeds until they recover sufficient biomass. The limited viability and little evidence of storage in a seed bank of seed in the *B. salicina* population (Section 2.11) will further limit seed availability after a large flood. Thus it appears that the discrepancy between model prediction and field data is a consequence of limited seed production and storage in the Sabie River after a LID. The underlying model assumption of unlimited seed availability is therefore flawed and the rules governing recruitment response in the *Breonadia* Model need to be modified.

The *Breonadia* Model also predicts an increase in suitable substrate availability in response to flood disturbance (see Section 3.1.2). The rules set up in the *Breonadia* Model interpret an increase in suitable bedrock habitat (a consequence of the catastrophic flood) as a decrease in competition for physical space. The model rules include the assumption that a catastrophic flood event will scour and remove sediment from the river, resulting in increased bedrock habitat availability. This results in a modelled increase in the number of new germinants. However, the 2000 flood didn't remove sediment from the river, but redistributed it differently in the river (Rountree, pers. comm., CWE, UWITS). Therefore, although the availability of suitable recruitment habitat could potentially be increased in the modelled sites on the river, this does not necessarily mean that habitat availability is increased everywhere in the Sabie River. Thus, assuming that the limited seed produced is distributed all along the Sabie River, the recruitment that does occur after a catastrophic flood is likely to be highest where the most bedrock habitat occurs. From this study, it appears that the highest densities of new germinants occurred in the anastomosing channels (Section 3.6). From these results it seems likely that these channel types had the highest levels of available recruitment habitat. However, the anastomosing channels were also found to have the highest densities of adult residuals, many of which did produce flowers, fruits and therefore seeds. This suggests that recruitment may also correlate to proximity to flowering adults.

The *Breonadia* Model accounts for the direct influence of a catastrophic flood on the overall population density, where density is decreased as a direct result of a catastrophic flood due to trees being uprooted or killed during the flood. This overall decrease in modelled population density triggers model rules to positively weight the number of new germinants produced, due to the reduction in competition for resources and physical space. It is more likely that despite an availability of suitable bedrock habitat in the field, the decrease in adult trees results in lower seed production, further limited by adult trees that sprout rather than producing flowers in response to the flood.

The *Breonadia* Model cannot adequately predict the recovery of a pre-flood negative-J profile after disturbance events that result in a dominant sprouting response. If KNP managers use the model subsequent to these types of disturbance, the model outputs will not compare with response in the field. When managers compare outputs from the *Breonadia* Model to demographic profiles in the Sabie River, it will appear that the population in the river did not recover from the disturbance in the expected time frame. The demographic profiles recorded in the river will also be sufficiently different to indicate TPC exceedence. It is therefore important to either update the TPCs themselves to take these changes to the population profile into account, or to increase the waiting period after disturbances before monitoring and auditing of the TPCs continues (Section 3.1.3).

The results from this study, combined with previous studies on *B. salicina* (da Fontaine and Rogers, 1995; Mackenzie *et al.*, 1999), indicate that it is a combination of the underlying physical template and individual life history characteristics that play a role in shaping the demography of *B. salicina* populations. This chapter also highlights two updates that must be made to the *Breonadia* Model, firstly it must take sprouting into account; secondly, TPC auditing must consider a slower recovery of the population than previously expected.

CHAPTER 4: REDESIGN OF THE BREONADIA MODEL AND THE ASSOCIATED MONITORING PROGRAMME USED IN THE KRUGER NATIONAL PARK

4.1 Introduction

As shown in Chapter 3 of this dissertation, the *Breonadia* Model does not accurately describe the response of the *B. salicina* population in the pool-rapid channel types, where monitoring for sedimentation occurs because the model is based on underlying assumptions about response mechanisms and limitations on recruitment that may not always apply to the Sabie River (Section 3.1.1). New knowledge about the response ecology of the indicator species raises concerns about the continued relevance of the *Breonadia* Model and the implications of using incorrect data in the post flood era. The rules in the *Breonadia* Model should be updated to take the influence of sprouting on recruitment into consideration.

The aim of this chapter is to update the *Breonadia* Model and the associated monitoring programme to be more applicable in the post-flood era by taking the influence of sprouting into account. This aim can be achieved by meeting the following objectives:

- By updating the *Breonadia* Model so that it can take the influence of sprouting into account. This update must be made so that end users can easily change the penalty weighting values.
- By updating the actual rainfall and hydrology with more recent data in the *Breonadia* Model so that actual rainfall and hydrology values rather than modelled or scenario data can be used.
- By updating the monitoring programme in terms of the location of monitoring sites, such that unnatural increases in sedimentation can be monitored, and in terms of data collected, such that long-term data on the influence of sprouting on recruitment may be obtained.
- By using the updated version of the *Breonadia* Model to recalculate the required waiting period after the occurrence of LID flood events before TPC auditing can continue.

4.2 Redesign of the *Breonadia* Model

4.2.1 Accounting for sprouting in relation to fecundity

A strong sprouting response in the *B. salicina* population influences recruitment of new individuals by limiting flowering and thus the production of seeds within the Sabie River. This influence on the ability of trees to produce flowers is expected to decrease over time as sprouting individuals recover lost biomass. This study provided only a snapshot of the influence of sprouting on flowering at a time frame five years after the flood. However, sprouting is expected to influence the ability of trees to flower over several years and thus any updates made to the *Breonadia* Model must allow for penalties to fecundity to be applied over several years.

The *Breonadia* Model calculates a fecundity value each year based on the number of adult trees in the population. Mature adults have the highest fecundity, followed by senescent adults and then young adult trees. The fecundity of adult trees is further influenced by the flooding zone (active, seasonal and ephemeral) in which they are located in the event of a flow event. Subsequent to this, population density and habitat availability place further limits on fecundity, with fewer germinants being produced if the adult population density is low and if habitat availability is limited.

Fecundity is calculated by applying weighting factors to adult trees due to their current size-class, the adult density and hydrological events that occur in that year. The fecundity output is presented as a number of germinants produced from the adults in each flooding zone (active, seasonal and ephemeral). The number of germinants is then influenced by rainfall for that year, with the calculated fecundity values being increased for wet years and decreased for dry years (Mackenzie *et al*., 2003). Hydrological events also play a role in the survival of new germinants.

Subsequent to the 2000 flood, population density was low, and habitat availability high, thus the limit on recruitment in the model after a flood of this magnitude is due to a low population density resulting in low recruitment. However, the *Breonadia* Model does not take into account that the production of germinants in the field, which is further limited by the occurrence of a sprouting response in many adult tees.

The *Breonadia* Model can be updated to take the influence of sprouting into account by applying a penalty to the model calculated fecundity value, with the penalty decreasing over time as trees recover biomass, and thus flowering ability over time. However, as the field data were collected five years after the flood, it is necessary to extrapolate the change in the influence of sprouting on flowering over time. If the input of the sprouting influence on fecundity is made easily changeable by end users, these values can be easily adjusted if long-term data collection is imposed in order to improve information on this change over time.

4.2.2 Calculating the influence of sprouting on fecundity

In species where regeneration via seedling production is poor due to sporadic fruit production (Chidumayo, 1997), seed predation (Chidumayo, 1997), limited seed dispersal (Chidumayo, 1992) or low seedling survival (Grundy, 1995; Chidumayo and Frost, 1996), regeneration can be best promoted by sprouting. Sprouting species following this pattern of regeneration tend to store energy underground and produce few seeds (Keeley and Keeley, 1997). In species that rely strongly on seed production as a means of regeneration, disturbance may promote sprouting in the species as a means of regaining lost biomass (Bellingham and Sparrow, 2000; Rydberg, 2000; Laureysens *et al*., 2003; Luoga *et al*., 2004; Tewari *et al*., 2004). Sprouting in adult trees in response to disturbance has been found to reduce the ability of trees to produce seeds (Bellingham and Sparrow, 2000). These typically seed producing species are expected to recover sufficient biomass over time so that seed production can resume. Thus, immediately after a disturbance of sufficient magnitude, adult trees that sprout in response to flood damage are expected to have a reduced likelihood of flowering. The likelihood of flowering (and hence seed production) in the population is expected to increase over time as trees recover lost biomass. The influence of sprouting on fecundity in the *Breonadia* Model can be taken into account by applying a penalty to the fecundity calculated. In order to simulate the recovery of biomass and the associated increase in seed production, the penalty to fecundity can be decreased over time.

All data on adult size-classes were used in order to calculate the influence of sprouting on flowering (Section 2.10). The percentage of trees falling into each response category (flowering, no response, sprouting, both flowering and sprouting) was calculated for each of the adult size-classes. The sum of the percentages of trees falling into the sprouting/not flowering (41% for young adults) and the not sprouting/not flowering (2% for young adults) category was used as the penalty to fecundity for that size-class for the fifth year after a catastrophic flood (Table 7).

Table 7: Percentage contribution of each response type for young adult trees five years subsequent to the 2000 flood.

	Flowering	**Not flowering**
Sprouting	32.65	40.82
Not sprouting	24.08	2.45

When the *Breonadia* Model was run in a step by step process, where the result of each step in the model is determined before running the next step, it was found that although the model calculates a fecundity value for each adult size-class, the size-class fecundity values are combined and output as a fecundity value per flooding zone (active, seasonal and ephemeral). This is so that the influence of rainfall and hydrology, which are related to flooding zones, can be applied to further modify the fecundity values. The data collected for this project was not stratified by flooding zones, therefore the relationship between sprouting and flowering in the field data had to be extrapolated to what was expected in each of the flooding zones along the Sabie River.

A 3-dimensional matrix was drawn up in order to guide the extrapolation process. The matrix included the fecundity percentage penalty for each size-class for the year that data collection occurred (Red circle, Figure 23). These data were used to estimate the flowering percentage penalty expected in each flooding zone for the same time period. Flowering was expected to be more limited in the active zone, with flowering likelihood increasing through the seasonal and ephemeral zones. Trees in the seasonal zone were assumed to have the same flowering penalty as the total penalty calculated for each size-class as trees in this zone were assumed to receive average levels of flood damage. An increased penalty value was applied to the active zone (green circle, Figure 23) and a decreased value to the ephemeral zone (blue circle, Figure 23) such that the average of the penalties from all three flooding zones was equal to the actual penalty applied to that size-class. This process was applied to each size-class.

These values were then used to extrapolate the change in flowering penalty against time over a total of a 10 year period. Values were extrapolated back in time, with penalties increasing to 100% for the year immediately after the 2000 flood. Penalty values extrapolated forward in time were decreased gradually until a penalty of 0% was achieved across all size-classes and flooding classes at a time frame of 10 years after the flood.

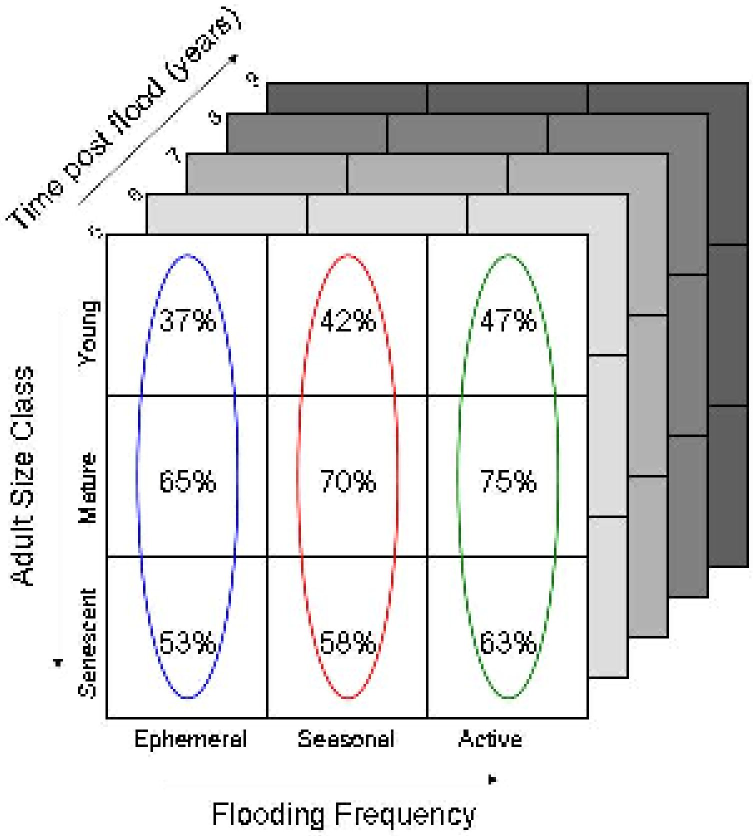

Figure 23: Conceptual representation of the 3D matrix used to calculate the changes in flowering penalty with time across flooding zone

The *Breonadia* Model generates a fecundity value for each flooding zone which increases or decreases based on the rainfall and hydrology that year. Thus, the size-class penalty values generated for each flooding zone for each time period were averaged to obtain an mean penalty value across all adult size-classes for each flooding zone for each year following the flood. These means were then used to generate a flowering penalty text document that could be utilised to adjust fecundity in the *Breonadia* Model following catastrophic floods. The accessibility of these values in a text file enables users to change the penalty values to more suitable figures as knowledge about sprouting influence on fecundity in the *B. salicina* improves.

4.2.3 Code adjustments to the *Breonadia* Model

Mackenzie *et al.* (1999) recommended that a detailed fecundity study be conducted on *B. salicina* as there are numerous factors that either limit or promote fecundity in the population and that may need to be incorporated as model updates in the future. A detailed fecundity study was beyond the scope of this dissertation. However, it has been established from this study that sprouting does limit flowering. This therefore provides an explanation for the far lower levels of recruitment than expected to be observed in the field. The change in this influence over time has only been estimated for the purposes of this model update. It was therefore important to create a user-modifiable input that can be used to both improve the estimates of the change in influence of sprouting on fecundity over time as well as take other influences into account. The format of the fecundity penalty input text file is such that it could even be generated by the model in the future, taking a multitude of factors into account, rather than being purely modifiable by end users.

The Breonadia Model was written in Visual Basic 6. Four changes were made to the Visual Basic code in order to apply penalties to fecundity values calculated by the *Breonadia* Model.

- The first step was to create an input file that holds the penalty values to fecundity so that it could be read and used by the model. This file is a simple text file so that the end user can easily make adjustments to the fecundity values when necessary.
- The second change was made to model initialisation. Each time the model is executed, an initialisation sequence runs in order to reset the model. This creates the variable for catastrophic flood penalties and resets the model to prevent values generated in previous model runs from influencing new runs. The new initialisation is shown in green in Figure 24.
- Thirdly, a new function was created, allowing the model to read the catastrophic flood penalties input data. This is the process of identifying whether a catastrophic flood event has occurred in the last 10 years or not so that the correct penalties can be applied to fecundity. This procedure is carried out for each year time-step after the flow frequency analysis is conducted and is indicated in red (Figure 24).
- The fourth change was to apply the penalties to the model calculated fecundity values. The penalties are applied to fecundity after the initial model-calculated fecundity (related to population density and habitat availability) and before the final factors weighting fecundity are applied (rainfall and hydrology) in order to model how fecundity is really influenced as closely as possible. Fecundity is firstly reliant on the availability of adult trees (population density), then on the ability of these adults to produce seeds (flood damage penalty to fecundity). Finally, the survivorship of new germinants is influenced by rainfall and hydrology events following germination. This final adjustment to the fecundity calculation is shown in blue (Figure 24).

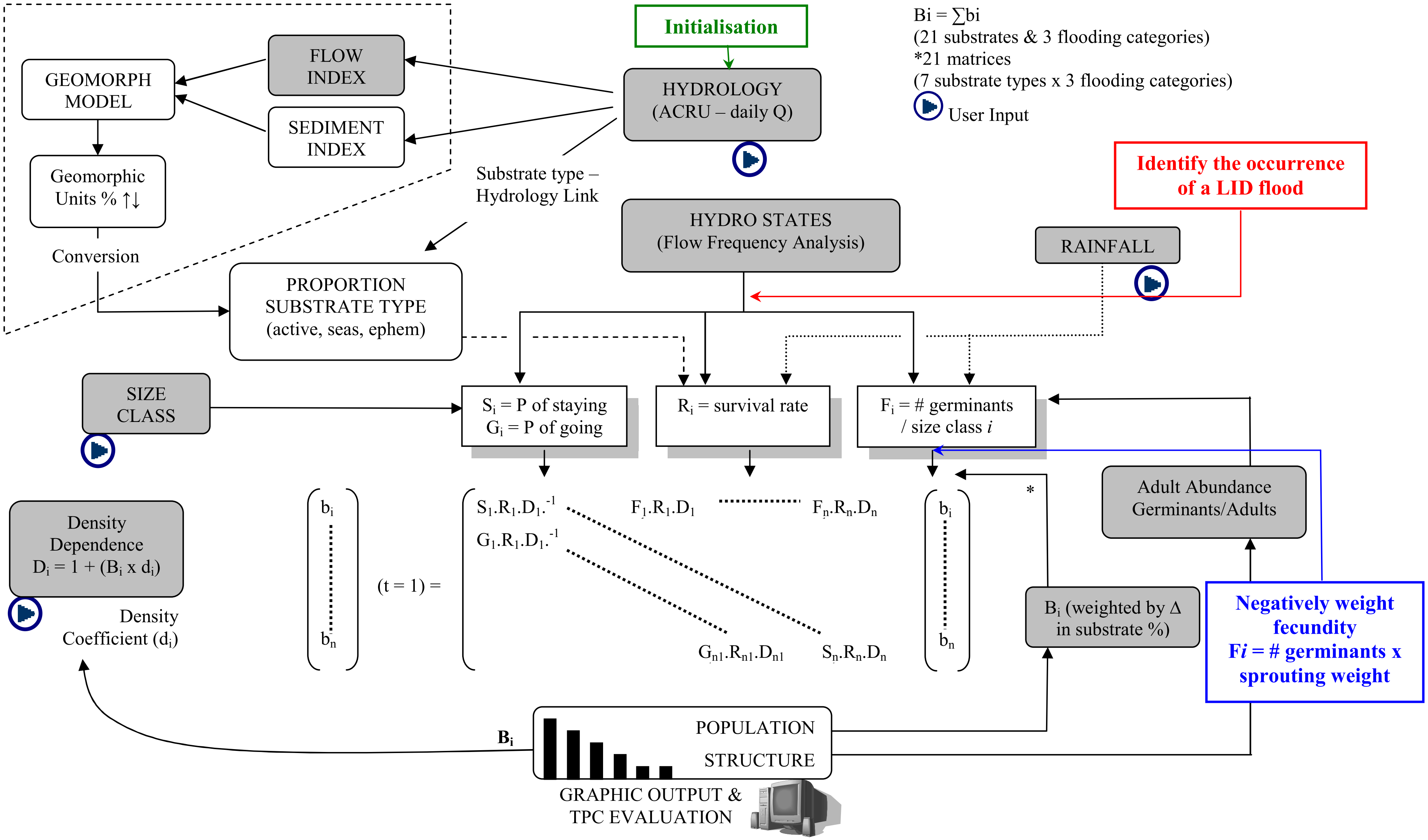

Figure 24: Conceptual diagram of the Breonadia Model structure (from Mackenzie *et al.*, 1999), showing where the adjustments to take sprouting into account were applied (shown in red).

4.2.4 Rainfall and hydrology updates to the *Breonadia* Model

The rainfall and hydrology data associated with the previous version of the *Breonadia* Model is limited to 1930 to 1993 and does not include the actual rainfall and hydrology associated with a catastrophic flood in the Sabie River. The model instead relied on modelled data or the addition of this event to historical or modelled rainfall and hydrology values. Actual hydrology and rainfall data for the Sabie River for the weather stations and gauging stations located near to the Skukuza and Lower Sabie rest camps in the KNP were obtained from KNP.

Although the *Breonadia* Model was designed for data input updates to be made easily by users, documentation for the *Breonadia* Model does not stipulate the exact format for these data, nor does it provide any indication as to which data were used to create the input files. The more recent data obtained from the park included an overlap period with the current rainfall and hydrology data used in the model in order to ensure that the same data format was used as far as possible.

The overlap of data (40 years) indicates that the daily rainfall input data for the model is the daily maximum rainfall recorded at the Skukuza rest camp weather station. The hydrology data recorded at the two gauging stations appears to be an average of the flow recorded at each of the two weirs. The downstream weir, located near the Lower Sabie rest camp, was destroyed in the 2000 flood and there is a gap in the data for a few years after the flood before the weir was rebuilt. Hydrological modelling of the relationship between flow at the two weirs and the average flow in the KNP section of the Sabie River could be used to complete the missing hydrology data in the future, however, this was beyond the scope of this dissertation. Thus, only a new rainfall input file has been added to the model; this file would only be used once a new flow input file has been generated. The original historical rainfall input file has been retained as it is associated with the historical flow data.

The updated version of the *Breonadia* Model was used to generate a predicted size-class density output for the period four years after the 2000 flood (Figure 25). Compared to the output for the same period from the previous version of the model (Figure 17), the predicted density of germinants is reduced by approximately 62% from a density of 2554 germinants per hectare in the old model version to 924 per hectare in the updated model version. This level of recruitment is still significantly higher than the density of new germinants actually observed in the monitoring sites for the same period. The updated version of the model predicts a return to a negative-J population structure eight years subsequent to a catastrophic flood in comparison to a four year recovery period predicted with the previous model version.

If the missing flow data is modelled, it is recommended that this more recent hydrological data including the catastrophic flood and the matching rainfall data be used to indirectly test this updated version of the *Breonadia* Model based on the actual flow and rainfall conditions. The outputs generated from the *Breonadia* Model in Figure 25 and Figure 26 have been generated from modelled flow and rainfall data. The updated model output for the same period as data collection (Figure 25), predicts low densities of individuals in the larger size-classes, which is similar to what was found in the field data. However, the model output still shows high levels of recruitment compared to the levels of recruitment currently observed in the river. There are a number of possible explanations for this phenomenon.

Firstly, the updated model output was based on modelled rainfall and flow data rather than actual rainfall and hydrology data. Thus the high rainfall that occurs in the modelled data after the disturbance event may be higher than the actual rainfall that occurred in the river catchment, increasing modelled fecundity and thus recruitment.

Secondly, the calculated change in the ability of adult trees to produce viable seed that was used to generate penalties to fecundity over time in the model may be incorrect. Long-term examination of the influence of sprouting on fecundity in *B. salicina* would improve these estimates.

Thirdly, the *Breonadia* Model was developed to represent changes in a negative-J structured subpopulation and was applied to the pool-rapid channel type in the Sabie River. Evidence from other studies (de Fontaine and Rogers, 1995; van Coller *et al*., 1997) indicates that a negative-J profile is not associated with this channel type. Thus the model has been developed around a vegetation-geomorphology relationship that does not exist, which raises further questions about the overall applicability of the model. The negative-J profile is located on exposed bedrock in both mixed anastomosing and bedrock anastomosing channels. Simply changing the location of the monitoring sites may resolve this issue. However, the processes whereby the *Breonadia* Model determines the change in substrate in relation to hydrology, and the subsequent response of the vegetation to changes in the substrate needs to be examined to determine whether the model appropriately represents this relationship as it occurs in anastomosing channels.

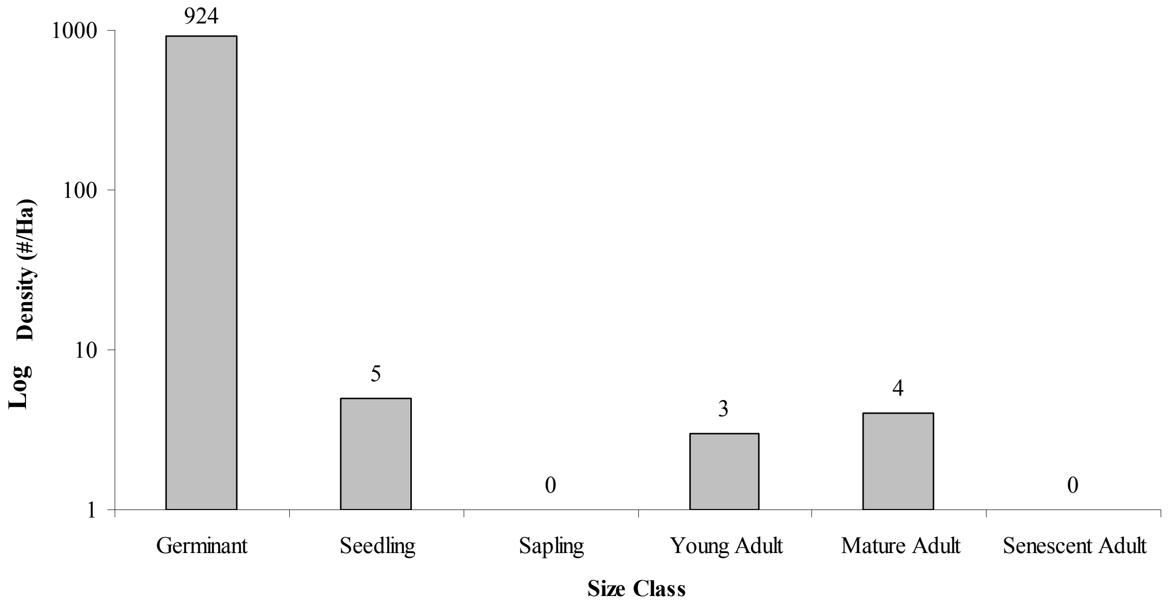

Figure 25: Updated *Breonadia* Model output for the period four years subsequent to a catastrophic flood. The TPC audit function in the model indicates that there is not yet a return to a negative-J population structure.

Figure 26: Updated *Breonadia* Model output for the period eight years subsequent to a catastrophic flood. The TPC audit function in the model indicates the population structure at this time period falls within the acceptable limits of all three of the defined TPCs and that there is a return to a negative-J population structure.

4.3 Recommendations for redesign of the *Breonadia* Monitoring programme

4.3.1 Location of the monitoring sites

Monitoring of the *B. salicina* population currently occurs in pool-rapid channel types as these channels were considered the most sensitive to changes in sedimentation. The loss of a negative-J profile in the monitoring sites alerts managers to increases in sediment in the Sabie River. There are two problems associated with the location of monitoring sites in pool-rapid channels.

Firstly there are implications associated with monitoring for a demographic profile that is not associated with this particular channel type. As this population profile does not occur here, data could indicate increases in sedimentation, although this might not be the case. Alternatively, the population structure may not change and may not indicate vegetation response to sedimentation despite increases in sedimentation occurring elsewhere in the river. Further, recent work by Mark Rountree (unpublished data, CWE, UWITS) suggests that pool-rapid channels may be too sensitive to sedimentation as they show a natural tendency to switch between braided and pool-rapid states. Monitoring in these locations is likely to indicate when transition periods occur rather than indicating any real sedimentation threat.

Second, the density of *B. salicina* in pool-rapid channels is very low relative to the other channel types, with less than 1% of the Sabie River's *B. salicina* subpopulation being located in bedrock sections of the pool-rapid channel type (Heritage *et al.*, 1995). At these densities, loss of a single tree could substantially influence the population profile, thus inferring a potential sedimentation problem. The low density of trees in the pool-rapid channel type also potentially increases the sensitivity of this channel to sedimentation.

Based on the population size-class density data for each of the four channel types, it is recommended that monitoring be located in bedrock areas of mixed anastomosing channels. The mixed anastomosing channel shows the most rapid response in terms of recruitment following the 2000 flood. A negative-J *B. salicina* profile is associated with exposed bedrock in both mixed anastomosing and bedrock anastomosing channels; however, bedrock anastomosing channels are very stable and are likely to be the last location in the Sabie River to experience increases in sedimentation (Mark Rountree, pers. comm., CWE, UWITS). Managers in the KNP should therefore monitor changes to the *B. salicina* population in the bedrock sections of the mixed anastomosing channels in the Sabie River.

4.3.2 Further improving fecundity data in the *Breonadia* Model

As well as providing managers with a direct measure of changes in the response of indicators to changing environmental conditions, monitoring data facilitate comparisons between outputs generated from the *Breonadia* Model and what is occurring in the field. This makes it possible to directly test the model following any fluctuations in environmental conditions, assisting with identifying knowledge gaps in the model rules.

This study identified the influence of sprouting on seed production in *B. salicina*. Future collections of monitoring data should include data on sprouting and flowering in residual trees in order to determine how much of an influence sprouting has on flowering and how this influence changes over time. A detailed fecundity study, possibly including other factors that influence seed production in the species, would help improve the recruitment predictions of the model, further enhancing its predictive capabilities. Despite a waiting period on monitoring being in place subsequent to flood events, ongoing regular monitoring is important to collect more data on the changing relationship between sprouting and flowering and its influence on fecundity.

4.3.3 Waiting period after catastrophic floods

The waiting periods after flood disturbances allow the *B. salicina* population to recover from the disturbance, thus preventing the resulting change in population structure from being attributed to increases in sedimentation. Different disturbance severities influence the population differently, and thus waiting periods of different lengths are applied depending on the severity of the disturbance and the expected time required for the population to recover.

In the updated version of the *Breonadia* Model, modelled recovery to a negative-J profile occurs eight years after a catastrophic flood event. Thus monitoring for vegetation response to sedimentation should recommence nine years after a LID flood disturbance.

Disturbance events and the resulting changes to ecosystem structure and function make it essential to continuously update and modify management tools such as models and monitoring programmes in order to maintain strategic and adaptive management of fluctuating ecosystem conditions. The changes to the *Breonadia* Model and the associated monitoring programme recommended in this chapter will improve the applicability of the model and monitoring of vegetation responses to sedimentation in the Sabie River.

4.4 Conclusion

As a result of the patchiness in disturbance intensity and the subsequent modes of response, recovery of the *B. salicina* population in the Sabie River did not follow the expected recruitment strategy. It is important to note that the expected recovery was based on the recovery observed after other, smaller disturbance events. This new information on recovery in response to LID floods makes it necessary to update the *Breonadia* Model.

This study also revealed a number of flaws in the application of the *Breonadia* Model. The *Breonadia* Model was designed to predict changes in a negative-J profile of *B. salicina* as this profile was found to be associated with exposed bedrock, which is vulnerable to sedimentation. The pool-rapid channels were selected for monitoring as this channel type was considered to be the first channel type to show the effects of increasing sedimentation. However, the negative-J profile was never found to be associated with a pool-rapid channel and thus monitoring for and predicting changes in a negative-J profile in this channel type does not provide any indication of changes in sedimentation in the Sabie River. It is therefore recommended that monitoring programme be amended so that data are collected at the appropriate locations in the Sabie River.

CHAPTER 5: THE EFFECTS OF LARGE INFREQUENT FLOOD DISTURBANCES ON PLANT POPULATION RESPONSE AND THE IMPLICATIONS FOR USING RIPARIAN INDICATOR SPECIES

5.1 The reproductive response of riparian tree species to Large Infrequent Disturbances

Demographic studies of plant populations are useful for describing the changes in the structure of populations in relation to changes in the physical environment (Harper and White, 1974; Harper, 1977; Pacala, 1987). Disturbance events of differing intensities influence the subsequent vegetation response patterns in a number of studies (Bellingham and Sparrow, 2000; Kennard *et al.*, 2002; Kozlowski, 2002; Shea *et al.*, 2004; Martínková *et al.*, 2006). Demographic studies following disturbance events provide insight into response mechanisms that may not have been observed in the population previously, or that have not been considered to be significant previously. These response mechanisms can influence the dominance and success of species after a disturbance event (Kennard *et al.*, 2002). In the Sabie River, the *B. salicina* population displayed a strong sprouting response following the 2000 flood. Sprouting was not previously considered to be a significant response strategy. More than 65% of residual *B. salicina* in the river landscape showed clear evidence of flood damage, many of which displayed a sprouting response.

Other studies on the 2000 Sabie River flood revealed that, as with other types of large infrequent disturbance, a heterogeneous template was left behind in the river landscape, consisting of a mix of biotic and abiotic patches (Parsons *et al.*, 2005; Parsons *et al.*, 2006). The structure and composition of the riparian vegetation in the Sabie River was found to differ amongst these patches and multiple trajectories of riparian vegetation response are expected at different spatial and temporal scales (Parsons *et al.*, 2005; Parsons *et al.*, 2006). At the channel type scale, this study found that recruitment in *B. salicina* is also patchy, with the density of post flood recruited individuals varying among channel types (Section 3.6). This is expected as successful establishment of *B. salicina* is dependant on the amount of available bedrock, which is in turn related to the heterogeneous template left behind by the flood. However, although the response mode of *B. salicina* in terms of post flood recruitment may be directly related to the underlying template, and thus patchy, response in terms of sprouting and flowering were found to be strongly associated with size-class and damage intensity. These modes of response are thus likely related to individual tree life history. The mechanisms of seed dispersal of *B. salicina* suggest that the seeds are spread widely over all geomorphic unit types in the Sabie River. This is supported by observations by Mackenzie *et al.* (1999). Thus, several layers of patchiness exist, but the patchiness of recruitment is likely to be different to the patchiness of individual response modes such as sprouting and flowering. This patchiness in response and recovery is not unexpected as it is a similar result to that found in a number of other studies (Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Kennard *et al.*, 2002).

Compared to other studies on reproductive response to catastrophic disturbances, these results are not unexpected. An experimental hurricane study (Cooper-Ellis *et al.*, 1999) found that the population structure stabilised subsequent to disturbance through a combination of sprouting, recruitment of new individuals and increased growth rates in smaller size classes. While this study did not examine growth rates, both recruitment and sprouting contributed to recovery of the population following catastrophic disturbance in the Sabie River. This supports Bellingham and Sparrow's (2000) hypothesis about response, which proposed that neither sprouting nor flowering will ever be the sole response subsequent to disturbance. A study on population recovery in Yellowstone National Park after catastrophic wildfires found that vegetation cover in the most severely burned patches was not driven by dispersal from other areas (Turner *et al.*, 1997). Instead, vegetation cover increased initially as a result of sprouting residuals and eventually from a recruitment pulse three years after the original catastrophic disturbance, suggesting local dispersal from these sprouting residuals. These results are similar to what was found in this study, where recruitment is highest in channel types with the highest density of adult residuals. However, in this study, due to the lack of long-term data from immediately after the 2000 flood, it is impossible to determine when recruitment began to occur after the flood disturbance. The data from this study are limited as it is not possible to determine whether there was a mix of sprouting and flowering responses immediately after the 2000 flood or whether flowering only occurred after adult trees had first recovered by sprouting. The fact that even four years after the flood disturbance, sprouting still inhibits flowering in residual trees suggests that the process occurring in the Sabie River is similar to what is occurring in Yellowstone National Park. However, trees in the Sabie River that experienced lower levels of damage, and thus lower disturbance intensity were more likely to be flowering. These individuals may occur in patches in the river that equate to less severely burned patches in Yellowstone National Park. These similarities suggest that catastrophic disturbances induce similar responses in plant communities in different ecosystems. This study also found that recruitment may also be related to proximity to adult residuals which is a similar result to that found after the Yellowstone fires (Turner *et al.*, 1997). If this is the case, recruitment is very likely to correlate to response mechanisms, as individual adults that produce seeds rather than sprouting are likely to have high densities of new germinants nearby.

Recruitment of new *B. salicina* individuals is related to the underlying physical template and associated with areas of exposed bedrock (de Fontaine and Rogers 1995). As recruitment of *B. salicina* only occurs in the active channel (de Fontaine and Rogers, 1995; Mackenzie *et al.*, 1999), and many large adult trees are located at a distance from the active channel (Mackenzie, pers. comm., CWE, UWITS), response mechanisms could also be influenced by trends in the physical location of the different size-classes. Although individual tree response modes are influenced directly by factors including size-class and damage severity (Misra *et al.*, 1995., Tewari *et al.*, 2004, Bellingham and Sparrow, 2000; Bond and Midgley, 2001; Kennard *et al.*, 2002), the location of the different size-classes of *B. salicina* in the river channel could influence the severity of disturbance to which they are exposed because LIDs may have different severities in different locations (Turner *et al.*, 1998). Thus the underlying physical template may indirectly play a role in the response mechanisms of individuals following disturbance in terms of damage intensity. Therefore, as well as the post flood template influencing recruitment after disturbance, the pre disturbance template may be influencing the response mode of residual trees after disturbance in the Sabie River and thus longer term changes in the population structure of the plant populations.

5.2 Does the influence of reproductive response reduce the value of *Breonadia salicina* as an indicator species?

The different demographic profiles observed in the Sabie River *B. salicina* population (unimodal, bimodal and negative-J) result from changing levels of recruitment over time in the different channel types of the river. The negative-J profile is associated with a channel type where the level of recruitment has remained high, whereas unimodal and bimodal profiles indicate that the level of recruitment has changed historically due to changes in the availability of suitable habitat.

A disturbance event like the 2000 flood can directly influence the demographic profile of a subpopulation by removing trees across all size-classes. Disturbance events may also indirectly influence the demographics of a subpopulation by affecting recruitment. Sprouting has an important influence on the population structure by limiting recruitment after catastrophic floods. Thus, the demographic profile indicates changes in recruitment levels as a result of changes in seed availability due to sprouting rather than only as a result of changes in suitable habitat availability. However, the output from the updated version of the *Breonadia* Model suggests that a return to a negative-J profile can occur eight years after periods where seed availability appears to limit recruitment (Figure 26) and that this period of limited recruitment is unlikely to cause a lasting change to a negative-J profile. This suggests that the periods of limited recruitment that result in the formation of unimodal and bimodal profiles must occur over longer periods of time. If the levels of recruitment return to the high levels associated with the negative-J profile within an eight year period of a disturbance, recruitment is sufficient and the time frame short enough to prevent the dip in recruitment that would otherwise result in the formation of a unimodal profile.

Once the population has stabilised and returned to a negative-J profile, it will be possible to continue monitoring for increases in sedimentation in the Sabie River as before. However, the long-term influence of catastrophic disturbances on the underlying physical template and the subsequent ecological processes implies that vegetative processes and therefore the demographics of plant species will be similarly influenced over long periods of time. It is important that the monitored characteristic of an indicator change specifically in response to changes in the environmental condition being monitored and not to other factors that may influence the indicator in a similar way (Landres *et al*., 1988). The 2000 flood influenced the response mechanisms occurring in the *B. salicina* population, thereby influencing the population structure subsequent to the disturbance. The negative-J profile of *B. salicina* may be too sensitive to the effect of sprouting on recruitment. If this demographic profile is changing in response to changing response mechanisms as well as in response to the underlying physical template, the species is less valuable as an indicator of changing sediment levels in the Sabie River.

The 2000 flood also resulted in a subsequent reduction in recruitment in the *B. salicina* population due to the effect of the sprouting response on seed production. However, from the *Breonadia* Model output, it seems unlikely that this reduced recruitment will have a lasting influence on the demographic profile of those subpopulations displaying a persistent negative-J profile. The reduction in recruitment as a result of a sprouting response to the disturbance does not appear to limit seed production enough over a long enough period of time to result in a change to a unimodal profile. The subpopulations of *B. salicina* displaying a negative-J profile are therefore sufficiently persistent to recover from this disturbance, and remain sensitive to long-term increases in sedimentation in the Sabie River. This strengthens the suitability of *B. salicina* as an indicator of increasing sediment as it does not seem likely that the negative-J profile will change permanently to a unimodal profile as a result of the 2000 flood, rather, the population will recover to a stable negative-J profile and monitoring of this profile can continue.

Monitoring plays an important role where indicators are used as the focus of model development. Field monitoring of indicators is central for not only for detecting the response of indicators to changes in environmental conditions, but for identifying knowledge gaps in associated models. Models may be developed on incomplete knowledge, including gaps that are filled by assumptions or are not taken into account. In many cases this is not a problem as sufficient knowledge may exist to develop a complete working model and gaps in the existing model are likely to be detected during model development as part of the process of model refinement.

Disturbances, such as the 2000 flood in the Sabie River can, however, act as a mechanism for new and unexpected changes in ecosystems (Turner and Dale, 1998), strongly influencing system processes. These events should therefore be utilised as opportunities to gain new information about changes in ecosystem processes.

A continuation of monitoring following disturbance may show that model outputs do not match what is happening in the field. This indicates a gap in the model's representation of the processes it attempts to emulate. Examination of the *B. salicina* monitoring sites after the 2000 flood indicated that no recruitment was occurring despite model predictions of a strong recruitment response. This gives an indication that the recruitment response in the species is limited following this disturbance, implying that an ecological process not previously considered may be influencing the dominance of different response mechanisms.

Although the negative-J subpopulations do take longer than was initially expected to recover back to the pre-flood profile due to the sprouting response, the 2000 flood does not have serious implications for continued use of *B. salicina* as an indicator species. This longer recovery period does however influence monitoring for sedimentation immediately following catastrophic disturbances. The updated version of the *Breonadia* Model shows a return to a negative-J profile eight years after the disturbance event. Thus the waiting period for monitoring subsequent to a disturbance of this magnitude must increase from five to nine years.

The long waiting period before monitoring recommences has implications for management as the lack of monitoring will result in changes in sedimentation levels remaining undetected during this period. Managers should use the *Breonadia* Model to determine those environmental conditions that limit the response of the subpopulation by recruitment during the waiting period in order to remain aware of increases in sedimentation levels.

5.3 The implications of disturbance for the *Breonadia* Model

The development of models as part of the adaptive management process enables managers to integrate learning gained from management decisions implemented as experiments with learning gained from tests utilising model scenarios (Walters, 1997). This enables managers to deal with the uncertainty of ever-changing ecosystems (Walters and Holling, 1990; Walters, 1997). Continuous examination of changing ecosystem conditions results in an accumulation of knowledge, allowing models to be updated and improved to take new processes and fluctuations into account, thereby increasing their strength as a management tool (Walters, 1997). However, in many management plans, adaptive management planning does not proceed beyond the initial stage of model development to field experimentation, thus leading to stagnation in pro-active strategies (Walters, 1997).

When disturbance has an influence on the components used in a model, a comparison between how the model predicts response to that disturbance and how response actually occurs can be used to identify knowledge gaps in the model structure. This slow progression of model development is crucial if modelling tools are to be updated and remain applicable to fluctuating systems, allowing managers following pro-active strategies to change their management strategies accordingly.

A greater understanding of the mechanics behind responses to disturbance could be very valuable for a model such as the *Breonadia* Model. This model currently focuses on finding direct relationships between changes in the underlying substrate and the population demography. Although this is the primary relationship that shapes the *B. salicina* population, simply extrapolating the observed effects of disturbance events to similar events of differing magnitudes does not result in correct predictions. An understanding of why individuals respond in certain ways may be more useful. For example, in the *B. salicina* population, sprouting and flowering correlate with size-class and flood damage. The magnitude or severity of disturbance events is likely to result in different probabilities of individuals in each size class receiving specific levels of damage from that disturbance. Johnson and Miyanishi (2007) suggested that even partial understanding of how disturbances cause an observed ecological effect rather than simply defining the ecological effect could greatly improve the accuracy of assumptions made about events for which no data is available. This approach to interpreting data could greatly benefit models such as the *Breonadia* Model that rely on incomplete data sets to make predictions about the effects of disturbance and anthropogenic influences on a managed system.

Simple models can work very well even when designed around incomplete datasets, because the models themselves can be used to determine which data are most useful. A study by the British Forestry Commission (Rennolls and Blackwell, 1986) found that forest ecosystems could be maintained in a consistent condition, as long as events that occurred (including management regimes) were the same as those for which there were previous data on which to base a model. The study found that their yield-table based model was unable to predict how forests will respond to new influences, such as hypothetical management regimes. Similarly, an examination of a rule-based model used to predict the vegetation structure in rangelands in Australia found that the model had varying levels of success at predicting the effects of climate change and disturbance (Campbell *et al.*, 1999). A better understanding of the relationship between plant functional attributes and plant functional types as well as how plant functional attributes relate to differing climates and disturbance regimes was required to improve the predictive capabilities of this model (Campbell *et al.*, 1999). Johnson and Miyanishi (2007) suggested that even partial understanding of how disturbances cause an observed ecological effect could greatly improve the accuracy of assumptions made about disturbance events for which no data are available. This study has shown that the sprouting response in *B. salicina* is related to both size-class and the level of damage for each tree. A more detailed understanding of the mechanics behind each response would allow for predictions to be made about the probability of the response shown by a particular individual. If it is possible to find a correlation between the likelihood of specific types of damage and perceived disturbance intensity, this could be extrapolated across a range of disturbance events, even for those for which there are no data. Although the updates made to the *Breonadia* Model as part of this study now allow the model to take sprouting into account, reworking the model to take the causative factors behind response types into account would require far more detailed reworking of the hard coding within the model. The changes made through this study may be sufficient as the *Breonadia* Model is designed to predict changes to the monitored demographic profile in the Sabie River. However, if sprouting is found be significant for a wider range of disturbances, it may be more valuable to model the likelihood of each individual following a specific response mechanism based on the underlying mechanisms rather than generating a correlation from what data is available. This may require the generation of new assumptions about how individual trees perceive flood damage; in other words, what damage categories affect differently sized trees for different disturbance intensities. This would improve confidence in the predictive capabilities of the model for disturbance events for which KNP managers have no data.

5.4 The implications of disturbance for adaptive river management in the Kruger National Park

Fluctuating ecosystem conditions are difficult to manage, however, adaptive management allows for adjustments in management practices that enable managers to deal with continually changing ecosystem conditions and limited knowledge (Holling, 1978; Walters, 1986; Peel *et al.*, 1999). As the *Breonadia* Model did not take the variable response mechanisms of *B. salicina* into account, continued auditing of the TPCs may falsely indicate that the population structure has changed and indicate an increase in sedimentation in the Sabie River. As part of the SAM framework, KNP managers utilise system changes as a result of disturbance as an opportunity to verify and update management tools such as the *Breonadia* Model. If management tools do not take new ecosystem conditions into account, these tools will no longer be applicable to the system to which they are applied. This study updated the *Breonadia* Model and reconsidered the application of the associated monitoring programme as part of the ongoing learning process as a part of SAM in the KNP. Ongoing updates such as these will continue to facilitate pro-active management and learning in the KNP.

Although fluctuations in climate are natural and expected as part of natural ecosystem processes, a number of studies have expressed concern that industrial development may cause changes to climate that result in amplified levels of fluctuation, including in South Africa (Benhin, 2006). It seems unlikely that the effects of amplified changes in factors such as rainfall on managed systems can be predicted from historical data (van Wageningen and du Plessis, 2007). However, predictive models that operate by calculating the mechanics behind ecological effects rather than simply extrapolating from known correlations to events for which we have data may prove to most useful in the longer term to generate more likely predictions of these effects. Models like the *Breonadia* Model were developed so that they could be used to test the likely effects of management decisions, such as controlling flow regimes (Mackenzie *et al.*, 1999). If the likely long-term trends in rainfall and flow, including amplified fluctuations, can be estimated, these data can very easily be input into the *Breonadia* Model in its current format. The model can then be used to predict the likely effect that these will have on the riparian zone, and also to test what contingency plans can counter these effects.

This study has revealed the importance of disturbance events in shaping the longer term demography of species utilised as indicators and these management tools. The physical template of the Sabie River forms a complex and patchy template on which riparian vegetation processes occur. Management of the Sabie River needs to continue to take this complex relationship and the variable hydrological regime into account to update and apply valid management strategies to the system. This study has also demonstrated the importance of updating management tools so that they can take account of new variability. Continual updating and application of predictive tools promotes the assessment of goal achievement and strategic adaptive management of ecosystems.

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