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Influences of river flows on recruitment success of Fynbos Riparian Vegetation along selected high gradient streams in the Western Cape, South Africa

A thesis submitted in fulfillment of the requirements for the degree of Magister Scientiae

by

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Key words

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Abstract

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Riparian vegetation occurs in two distinct zones, the wet bank and the dry bank. Knowledge on how the flow regime influences the zonal structure of riparian vegetation is required to mitigate the adverse effects of water resource utilization on riparian vegetation.

The first objective of this study was to determine whether flow exerts a physical influence on zonal structure pre- or post-recruitment. An examination of the survival of seedlings and saplings was conducted along Western Cape rivers to investigate seedling persistence and survival on lateral zones. A comparison of the ratios of seedlings, saplings and adults in different riparian zones for the years, 2004, 2011 and 2013, was carried out. The results suggest that in general seeds are deposited randomly on the banks, where they germinate and become seedlings. Seedlings that become established at locations unsuitable for their persistence into adulthood are removed either by high flows or perish during dry conditions. Thus, lateral zonation eventually develops due to species differences in tolerance to conditions at different positions on the banks.

The second objective was to explore the effects of the reduction in dry season low flows on the recruitment success of riparian species at sites upstream and downstream of abstraction points. At most sites plants were arranged into different lateral zones and the numbers of species between upstream and downstream sites were not significantly different. There were significant differences in the abundances between up- and downstream sites, with the loss of herbaceous plants and sedges at downstream sites, both of which favour moist conditions. Also, in the absence of dry season flows, the seedlings of dry bank tree species recruited closer to the channel than those at the sites with summer flows. The shifting of the dry bank into the channel narrows the channel, which may affect the hydraulic pressures exerted during floods.

The spatial arrangement in the riparian zone has as much to do with flow conditions post recruitment as it does with conditions during recruitment. This shows that the structure of riparian plants is determined not only by whether or not the minimum flows are met, this points to the need to reinstate the naturally variable flow and adopting a holistic approach for the understanding and management of aquatic systems.

May 2014

Declaration

I declare that *Influences of river flows on recruitment success of Fynbos Riparian Vegetation along selected high gradient streams in the Western Cape, South Africa* is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Full name.................................... Date..................................

Signed...

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1 Introduction

Vegetation in the riparian zone grows in distinct lateral bands, broadly divided into the wet bank and the dry bank (Reinecke and Brown 2013). The arrangement of plant communities is a response to water availability, channel morphology, sediment supply and surface-groundwater interactions (Swanson *et al.* 1982; Naiman *et al.* 2005; Camporeale and Ridolfi 2006; Gurnell *et al.* 2011), and the life cycles of many riparian species have been found to be closely linked to the natural variation of flow of a river (Poff *et al.* 1997; Friedman and Auble 2000; Pettit *et al.* 2001).

Diversion and abstraction of water from rivers for off-stream use by humans affects the volume of water left in the stream and therefore the extent and frequency of inundation and drying along the banks. Since the flow regime of a river controls the distribution and abundance of riverine species and balances the ecological integrity of flowing water systems (Poff *et al.* 1997), changes to the flow regime affect the structure of riparian vegetation through effects on the life cycles of the individual species making up the communities with knock-on effects to most other parts of the ecosystem (Naiman *et al.* 2005). The need to allocate water for the maintenance of ecosystem functions in rivers has been widely recognised (Poff *et al.* 1997; Richter *et al.* 2003; Postel and Richter 2003; Brown and King 2003) and is being put into practice in many parts of the world (Tharme and King 1998; Richter *et al.* 2006). In South Africa, the National Water Act requires that an Ecological Reserve is defined for all or part of a “significant” water resource in the country (Section 16 of NWA, 1998). However, the allocation of water for ecosystem maintenance, requires a knowledge of how changes in river flows, including flooding, affect the functioning of the riparian vegetation, so that the need for this water can be motivated. Understanding, and if possible quantifying, these links aids prediction of how riparian communities would change in response to altered flow regimes, and thus what flows (quantity and quality) are required to maintain them.

This study seeks to investigate the physical influences of flow on the functionality of the structure of riparian vegetation (lateral zonation) through investigation of its effect (flow) on the recruitment phases of key riparian species. The central assumption of this study is that recruitment of vegetation in the riparian zone of rivers is controlled to a greater extent by the flow regime. There are two parts to the study. The first part focuses on temporal changes in

Fynbos riparian systems of the Western Cape to assess the possible influences of flow on the recruitment pattern of plant communities on the riparian lateral zones. The second part concentrates on the effects of diminished summer low flows on recruitment (seedlings and saplings) of riparian vegetation.

Accordingly, the main hypotheses for the study were: (1) lateral zonation of plants in the riparian zone is determined by factors that are exerted after recruitment; (2) sites that lack summer low flow will have less clear lateral zonation than sites that have a completely natural flow regime; and, (3) more seedlings will establish in the channel at sites with no summer low flows when compared with sites with natural summer flows and the marginal zone will be narrower in response to abstraction.

The focal points of each chapter are as follows:

- Chapter 1: introduction to and motivation for the study.
- Chapter 2: a literature review, which addresses the links between lateral zonation and flow, recruitment dynamics, effects of flow modification on riparian community structure, environmental flows and adaptive management.
- Chapter 3: investigates the positions of recruitment and whether these were dictated by seed distribution patterns or physical events following deposition.
- Chapter 4: investigates whether the absence of dry season low flows in particular plays any kind of functional role in the positioning of plants on the river bank, especially in their recruitment phase.
- Chapter 5: concludes the study.

Chapters 2 - 4 of this thesis were written as papers but have been streamlined to reduce repetition in the dissertation. To this end, the abstracts were removed, and the introductions and methods of data collection and analysis were cross-referenced between chapters where applicable.

1.1 Study area description

Most parts of South Africa receive summer rainfall (Reason and Mulenga 1999). The Western Cape, however, is characterized by a Mediterranean type climate with hot and dry summers followed by cold and wet winters (Sieben *et al.* 2009; Gasith and Resh 1999). Precipitation is mostly in the form of rain with more than 60% falling between April and September. Rainfall is between 400 and 750 mm, but most mountainous areas receive about 1000-2000 mm per year and can exceed 3000 mm (Sieben 2002).

This region is recognised for the Cape Floristic Region (CFR), with two major biomes: the Fynbos Biome (most plants are sclerophyllous) and the Succulent Karoo (semi-arid and mostly supports succulent flora) (Moor and Day 2013). This vegetation is highly diverse and is fire adapted. According to Mucina and Rutherford (2006), the headwaters of south-western Cape rivers are characterized by a Fynbos Riparian Vegetation community typified by the small trees *Brabejum stellatifolium, Metrosideros angustifolia* and *Brachylaena neriifolia* (Holmes *et al.* 2005).

The study was conducted in two catchments in the Western Cape, the Berg Catchment and Breede Catchment. Six upper-foothill rivers were selected, of which five were in the Breede catchment: Elands, Molenaars, Sandrifskloof, Morraineskloof and the Keurhoek. The Breede catchment is home to the wide Breede River valley, which is surrounded by mountain ranges with the Franschhoek and Du Toit Mountains to the west, and the Hex River Mountains to the north. Rainfall varies greatly with a mean annual precipitation of 250 mm per annum in north-eastern areas and the southwest mountainous regions receiving about 3000 mm of rain per annum (DWAF 2004b). The Elands River drains from the Hawequas Mountain and joins the Molenaars River at the Hugenot Tunnel before joining the greater Breede River. The Sanddrifskloof, Morraineskloof and the Keurhoek Rivers are situated in the Hex River Valley, which is bordered by the Kwadousberg Mountains in the south and the Matroosberg mountains to the north (Breede Valley Municipality 2003). These three rivers drain into the Hex River. The Sanddrifskloof River joins the Hex River at the Sandhills village, while the Morraineskloof and the Keurhoek Rivers are both tributaries of the Amandel River, which flows into the Hex River shortly after they join. The region is heavily cultivated with vineyards and is well known for its table grape production being responsible for 90% of the total national supply (Breede Valley Municipality 2003).

The sixth river was the Jonkershoek River, which is in the Berg catchment. The Jonkershoek River has its source to the south-east of Stellenbosch in the Hottentots Holland Mountains. The mountain range has high plant diversity and reputedly has the best quality of drinking water in the region (Sieben 2002). The dominant land-use is commercial agriculture, particularly orchards for the production of citrus fruit, and vineyards for wine production (DWAF 2004a).

1.2 Definitions

The following definitions apply in the study:

Riparian vegetation: refers to the riverine plant community that is adjacent to the active channel and is sustained by generally moist conditions along river margins. This vegetation is distinctly different in species composition from the neighbouring terrestrial communities (Reinecke 2013).

Riparian zone and or riparian area: The area adjacent to the active channel of a river that is influenced by the flow regime of the river (Reinecke *et al.* 2007). The two words are used interchangeably.

Tree:	A woody plant of any life stage developing from a single stem.
Seedling:	A tree of height less than 0.3 m.
Sapling:	A tree of height between 0.3 m and 1.9 m.
Adult:	A tree of height ≥ 2 m.

Lateral zones: Sub-sections of the riparian area where groups of plants preferentially grow in association with one another based on their shared habitat preferences and adaptations to withstand prevailing hydro-geomorphological conditions (Reinecke 2013).

Recruitment or recruitment phase: The phases of a plant’s life cycle including flowering, fruit and or seed production, plus the seedlings and saplings life stages.

Pre-recruitment influences: Factors that have an influence on the position of seedlings and saplings before the seeds are deposited at site.

Post recruitment influences: Factors that have an influence on seedlings and saplings after seeds are deposited at sites.

Environmental Flows: Water that is left in a river system, or released into it, for the specific purpose of maintaining the ecological condition of that river (King *et al*. 2003a).

Adaptive management: The adjustment of management plans informed by monitoring results (King *et al.* 2003a; Brown and King 2006).

2 Literature review

2.1 Flow and the structure of the riparian vegetation in lateral zones

Riparian zones are among the most structurally-complex and biologically-diverse terrestrial landscapes on earth (Merritt and Wohl 2002). The term ‘riparian zone’ refers to areas directly adjacent to the wetted channel of a water course or waterbody that support vegetation communities, that are distinctly different from neighbouring terrestrial communities (Reinecke *et al.* 2007). In the case of rivers, the vegetation in these areas typically shows a distributional relationship to the flow regime of the river (Reinecke and Brown 2013). The vegetation zones occupy a three-dimensional transitional area (longitudinal, lateral and vertical) between aquatic and terrestrial ecosystems and serve as a passageway for the exchange of materials and energy from the one ecosystem to the other (Naiman and Decamps 1997; Naiman *et al.* 2005; Kondolf *et al.* 2006; Reinecke *et al.* 2007; Richardson *et al.* 2007).

Healthy riparian zones help to maintain the form of rivers by binding soils and strengthening river banks (Thorne 1990). Trees and shrubs increase channel roughness, thus resistance to flow, which reduces the velocity of the flow in the channel and may lead to deposition of fine sediments and seeds in these areas (Chaimson 1989; King *et al.* 2003b). Riparian vegetation also acts as a buffer against sediments, fertilizers, pesticides and other matter draining from the surrounding landscape through direct chemical uptake (Dosskey *et al.* 2010). Riparian zones also provide migratory corridors for animals and breeding; feeding or nursery grounds for a variety of floral/faunal communities (Naiman *et al.* 1993; Brode and Bury 1984), and provide food and shelter for people and wildlife.

Holmes *et al.* (2005) recorded that South Africa has three biogeographical vegetation types related to rainfall: (i) areas that receive rainfall in the winter or year around comprise mainly fynbos; (ii) summer rainfall areas encompass the grassland and savanna biomes; and the low rainfall or arid area consists of the succulent and (iii) Nama Karoo biomes. Riparian vegetation in the fynbos region varies from forest to tall herbland (Sieben and Reinecke 2007). The riparian vegetation community in the upper reaches of fynbos rivers is characterized by small trees (3 - 10 m high) of *Brabejum stellatifolium*, *Metrosideros angustifolia* and *Brachylaena neriifolia* (Holmes *et al.* 2005; Galatowitsch and Richardson 2005). It has been described as closed-scrub fynbos, hygrophilous mountain fynbos, or broad sclerophyllous closed-scrub (Reinecke *et al.* 2007; Sieben and Reinecke 2007).

The structure of riparian vegetation varies along rivers in response to changes in various factors including or such as channel morphology, flow regime, sediment supply and surface-groundwater interactions (Swanson *et al.* 1982; Camporeale and Ridolfi 2006; Gurnell *et al.* 2011). Riparian zones interact with the landscape in three dimensions: longitudinally as a vegetated strip along the channel from river source to its mouth; laterally as a channel with its associated banks and floodplain, which defines the area over which floods have an influence; and vertically between the bank, river bed and groundwater (Ward 1998; del Tánago and de Jalón 2006).

Germination success of riparian seeds is influenced by factors such as the flow regime and flooding pattern, soil characteristics, temperature fluctuations, light conditions and competition (Kellog *et al.* 2003; Kunstler *et al.* 2009). Survivorship of riparian plants, however, is mainly controlled by substratum texture and soil moisture, while the pattern of river discharge plays a crucial role in the establishment of saplings (Naiman *et al.* 2005). Thuiller *et al.* (2007) suggest that variability about these environmental factors reduces the importance of competition between species and individuals.

According to Naiman and Decamps (1997), streams are non-equilibrium systems that have considerable influence on the attributes of riparian communities. Due to the seasonal variations in discharge, even the most tolerant species are challenged by the environmental conditions created. Accordingly, riparian plant communities tend to be composed of specialized and disturbance-adapted species, with morphological and physiological adaptations to floods and droughts (Naiman and Decamps 1997; Naiman *et al.* 2005). Most riparian species are categorized as either resisters (ability to withstand flooding) or endurers (ability to resprout after breakage) in response to specific riparian disturbances. For example water can reach up to 10 m on the central Amazon Basin floodplains and remain submerged for about 50 to 270 days yearly, and riparian plant species show strong morphological, phenological, and physiological adjustments to the low oxygen wet conditions (Naiman *et al.* 2005). In Australia, paper bark tree (*Melaleuca* sp.) are successful because they have characteristics that allow them to bend in floods, thereby reducing the shear stress they must withstand (Naiman *et al.* 2005). *Breonadia salicina* grows on bedrock core bars of South African rivers in the Savanna Biome and is adapted to withstand substantial flooding, like many other species living in high energy environments (van Coller *et al.* 1997).

Riparian plant species are also resilient to fire (Naiman *et al.* 1998). In the Western Cape, *Brabejum stellatifolium, Metrosideros angustifolia*, and *Brachylaena neriifolia* are able to resist fire; if burnt they regenerate quickly from canopy or soil-stored seeds, or by re-sprouting (Holmes 1998). Similarly, Sitka and Scouler willows are adapted to many disturbances including fire, their seeds germinate and establish post-fire, individuals have the ability to resprout following light intensity fires, and adventitious roots appear when the stems are fragmented by fires, floods or herbivory (Naiman and Decamps 1997).

The width of the riparian zone varies greatly according to stream size, local geomorphology, and hydrological regime (Naiman *et al.* 2005). In most headwater streams this zone is narrow and in some cases can be a closed canopy. For mid-sized streams, the riparian zone is wider and almost always represented by a distinct band of vegetation. Large rivers usually have complex floodplains, lateral channel migration and a diverse vegetative community (Naiman and Decamps 1997), particularly in their lower reaches. The boundary of the riparian area can be demarcated using changes in soil conditions, vegetation, and bank topography (Naiman *et al.* 2000).

The diversity in riparian characteristics is a result of the complex interactions between hydrology, lithology, topology, climate, natural disturbances, as well as the life history characteristics of riparian organisms (Poff and Ward 1989; Naiman and Decamps 1997; Naiman *et al.* 2005). The occurrence of patterns in the riparian community is a reflection of the physical template and the dynamics of individuals, as well as modifications to the physical environment; thus integrating these interactions provides insights into understanding the biotic dynamics of riparian zones (Naiman *et al.* 2005).

The presence of lateral zonation in riparian vegetation has been well documented and clear patterns are formed by riparian communities around the world (Naiman *et al.* 2005). Distinct zonation patterns are exhibited by vegetation on lateral banks (Ward 1998), this reflects the ability of plants colonising the riparian and aquatic zones to cope with frequent flood disturbances, intense droughts and riverine sediments that are low in organic matter and free-draining (Gurnell *et al.* 2011). An example of lateral zonation of riparian vegetation is shown by *Rumex* spp. in the Netherlands. Of the seven species of the riparian plant *Rumex* (sorrel) along the banks of Rhine River; *Rumex acetosa* and *R. thyrsiflorus* are sensitive to floods and occur high up the bank, *R. obtusifolius*, *R. crispus*, and *R. conglomeratus* find optimal conditions in the midbank area, which is relatively wetter, while *R. maritimus* and *R. palustris* prefer the wet marginal zone directly or even in the water (Naiman *et al.* 2005).

Although the naming may differ, the existence of lateral zones is usually defined using four factors: (i) periodicity of hydrological influence, (ii) marked changes in lateral elevation or moisture gradients, (iii) changes in geomorphic structure and (iv) changes in plant species distribution or community composition along lateral gradients, (Boucher 1999; Boucher 2002; Kleynhans *et al.* 2007; Reinecke e*t al.* 2007). In South Africa, Boucher (2002) recognized three principal zones (aquatic, wet bank and dry bank), which were shown to be consistently present on rivers in the Western Cape and Lesotho. Kleynhans *et al.* (2007) also identified three general zones for South African rivers; the marginal, lower and upper zones, based on changes in lateral elevation and/or moisture gradients. Boucher (2002), also recognized a transition zone between the dry and wet bank zone, which was called the lower dynamic subzone, this is an area of deposition or erosion. Recently, Reinecke and Brown (2013) included this sub-zone in their four-zone classification of South African riparian areas and showed that the two main areas and all four zones are characterised by functional and species differences.

- Wet Bank
  - Marginal zone - situated on the edge of the active channel and includes the area from the low-flow water level to the lower dynamic zone. It is dominated by obligate riparian (wet) species.
  - Lower dynamic zone - separates the marginal from the lower zone and serves as a transitional area between the wet and dry bank as it contains species from these two neighbouring zones.
- Dry Bank
  - Lower zone - extends from the lower dynamic to the upper zone and is characterised by facultative riparian (wet/dry) species.
  - Upper zone - extends from the lower zone to the terrestrial area forming the outer boundary of the riparian areas. This zone is dry for most of the year and is characterised by a mixture of riparian and incidental terrestrial species (dry).

Of the four zones, the marginal is the most consistently present across all river types and settings (Kleynhans *et al.* 2007).

In the Western Cape, the marginal zone is dominated by *Prionium serratum* and *Isolepis prolifera,* the lower dynamic zone by *Calopsis paniculata* and *Morella serrata*, the lower zone by *Metrosideros angustifolia* and *Elegia capensis* and the upper zone by *Pteridium aquilinum* and *Diospyros glabra* (Reinecke and Brown 2013). Reinecke and Brown (2013) also showed that for Fynbos Rivers, the wet bank occurs within 1.5 m of the water's edge (the marginal and lower dynamic zone), and that for South African rivers in general the wet bank and dry bank may be separated using the stage of the 1:2 year flood (a flood magnitute that has a two years recurrence interval) on a cross-section.

2.1.1 Links between lateral zonation and river flow

In streams, the primary source of environmental variability and disturbance is the flow regime (Poff and Ward 1989), which controls the abundance and spatial arrangement of individuals and the dispersal of vegetative propagules (e.g seeds, stem fragments), and thus successional dynamics (Tuner 1998). Disturbance (floods and intermittency) and flow variability act on the physical template (Poff and Ward 1989): floods act as a transport mechanism exporting and importing plant propagules, sediments and nutrients, which impose both negative and positive effects on growth and survival of riparian vegetation (Friedman and Auble 2000). The temporal variability in river bank wetting results in the development of zones occupied by species with different moisture tolerances and adaptations to the frequency and duration of flood pulses (del Tánago and de Jalón 2006). Most plants occurring in the riparian zone are specially adapted to cope with conditions associated with flood events such as sediment deposition, physical abrasion, and stem breakage (Busch and Smith 1995; Naiman *et al.* 2005). Nonetheless, different riparian species have different tolerances to floods and droughts and growth responses to inundation (Friedman and Auble 2000; Pettit *et al.* 2001). In the absence of flooding, rates of river meandering and channel realignment often decrease, potentially causing a narrowing of the riparian zone and a decrease in the patchiness as well as diversity of the riparian habitat (Stromberg 1993). For instance, scouring floods may increase species diversity as they prepare sites for primary succession by pioneering species (Naiman *et al.* 2005). Thus, stream-flow can be considered a "master variable" that controls the distribution and abundance of riverine species and balances the ecological integrity of flowing water systems (Poff and Ward 1989; Poff *et al.* 1997; Friedman and Auble 2000; Pettit *et al.* 2001; Bunn and Arthington 2002; Richter *et al.* 2003; Gurnell *et al.* 2011; Reinecke and Brown 2013).

The links between zone pattern and flow have been well documented. In ecology the critical aspects of a flow regime are; magnitude, frequency, seasonal timing, predictability, duration and rate of change of flow condition (Poff *et al.* 1997; Richter *et al.* 1997; Naiman *et al.* 2008). The interaction of these components helps in the maintenance of the in-channel dynamics that are essential to aquatic and riparian species (Poff *et al.* 1997). Low and high flows at different time intervals are widely used in the characterization of a rivers natural hydrology, these and other aspects of flow regime dynamics are important because they often act as ecological "bottlenecks" (i.e. critical stresses or opportunities) for aquatic species (Poff and Ward 1989).

The timing of flows is critical for riparian vegetation dynamics (Pettit *et al.* 2001). Plants are adapted to the seasonal timing of flow events through "emergence phenologies" that determine the sequence of a plant life from flowering, seed dispersal, and seedling growth (Lyte and Poff 2004; Poff *et al.* 1997). Seasonal variations in the timing and pattern of high flows have a huge impact on seedling survival and the subsequent plant community structure. For example Naiman *et al.* (2005) recorded a 100-fold range in seedling density among years and a different dominant species each year depending on interactions between summer flow conditions, species-specific dispersal and germination phenology, together with sediment characteristics on the Wisconsin River. Along the San Miguel River in Colorado, USA, plant communities are arrayed along the hydrologic gradient, and riparian zones can be estimated using the frequency of floods (Friedman *et al.* 2006). A *Salix exigua* community dominated areas that have a less than 2.2 years flooding interval. Another, *Alnus incana* and *Betula occidentalis,* peaked on sites that were inundated every 2.2 to 4.6 years (Friedman *et al.* 2006).

Although both low and high flows are important for the maintenance of a riparian community (King *et al.* 2003b), the intensity and duration of the flows still plays an important role in their survival and growth. Varied flows (disturbances) impose both negative and positive effects on growth and survival of riparian vegetation (Friedman and Auble 2000). Prolonged inundation is an important source of mortality among riparian plants (Boucher 2002). In an extreme case, continual flooding on the Bill Williams River from 1978 to 1980 (as a result of dam releases) caused death of nearly all of the cottonwoods (99%) and most of the willows (64%) in some areas (Stromberg 1993). Bunn and Arthington (2002) suggest that stable water levels reduce growth and survival of native riverine macrophytes and encourage the invasion of water hyacinth and a *Typha* spp. in Australia.

The effects of a regional drought on riparian vegetation were studied in the Colorado River delta in Mexico from 2002 to 2007; this was a time of notably reduced surface flows when compared with the previous seven years. It was found that reduced surface flows led to a reduction in native tree cover but an increase in shrub cover, mostly due to an increase in *Tamarix* spp., an exotic halophytic shrub, and a reduction in *Populus fremontii* and *Salix gooddingii* trees. Overall the abundance of riparian obligate species decreased, and generalist (facultative) species increased (Hinojosa-Huerta *et al.* 2013). Reduced flows can give way for invasive species to dominate while not necessarily changing the total vegetation percentage cover at a site. Droughts and low flow events are also likely to limit overall habitat availability (Bunn and Arthington 2002). However, according to Gasith and Resh (1999) if the rate of drying is slow and with presence of isolated pools, the overall species abundance can remain high

Temporary periods of low or no flow releases from impoundments may also cause tree death. For example, at a site along the Verde River, 46 - 84% of the Fremont cottonwoods died during a dry period in the 1970's. This was due to a combination of low flow releases from the Bartlett Dam and groundwater pumping from the Verde River Infiltration Gallery and Well Facility (Stromberg 1993). Extreme events such as uncommon floods or droughts are of importance as they either reset or alter physical and chemical conditions that influence the long-term development of biotic communities. Although such disturbances are catastrophic/ disastrous and costly to human life, they are ecologically important. In rivers, for example, extreme droughts and floods are crucial for maintaining common biological, physical characteristics and ecological vitality (Naiman *et al.* 2008).

A flow regime regime that mimics natural variations, rather than just a minimum low flow, is required to sustain freshwater ecosystems (Naiman *et al.* 2005; King *et al.* 2003b; Richter *et al.* 2003; Naiman *et al.* 2008). Different flow regimes are important for the maintenance of a river including: the dry-season low flows; the small floods that occur every year; the intermediate floods with occurrence intervals of two to about five years, larger floods that can be catastrophic for the system; and natural flow variability at daily, monthly annual and inter-annual levels (King *et al.* 2003b). According to Bunn and Arthington (2002) the loss of wet-dry cycles often has drastic ecological impacts that favour exotic species. Rising and falling water levels transport and deposit sediments, vegetation debris and vegetative propagules to downstream locations (Goodson *et al.* 2001). This process may play an important role in structuring plant communities (Merrit and Wohl 2002) and maintaining high species richness in riparian ecosystems (Richardson *et al.* 2007; Chambert 2006).

2.1.2 Links between zonation and geomorphology

2.1.2.1 Influences of geomorphology on the structure of riparian vegetation

Together with the fluvial regime, the fluvial processes and channel form of a river have major influences on the spatial and temporal structure of riparian vegetation (Pettit *et al.* 2001). Site-specific erosion and deposition together with lateral channel migration are the two geomorphological aspects important for understanding patterns and processes in riparian vegetation (Naiman and Decamps 1997). The general patterns of community structure and succession are also dependent on the responses of riparian vegetation to soil conditions such as organic matter content, moisture content, nutrient availability and mycorrhizal associations (Naiman *et al.* 2005). Naiman and Decamps (1997) point out that vegetation distribution is also determined by soil-water retention and that groundwater flows are important to consider.

Just like varied flows, geomorphic instability often creates sites that are most favourable for germination (Hinojosa-Huerta *et al.* 2013). Disturbance frequency and moisture gradients on riparian zones determine vegetation composition and are usually associated with riparian landforms. Distinctive plant communities occupy floodplain, low-terrace, and high-terrace landforms along smaller channels (Naiman *et al.* 2000). Bendix and Hupp (2000), explain that the likelihood of a given species to robustly grow on a particular landform is a function of (i) the suitability of the site for germination and establishment, and (ii) the surrounding environmental conditions at the site that permit persistence at least until reproductive age. Thus, the presence of a given species on a particular landform may allow for considerable inference regarding the hydro-geomorphological conditions characteristic of the landform (Hupp and Bornette 2005).

Different landforms may be likely to support different vegetation by virtue of either the processes that are active on them (principally flooding) or their physical characteristics such as substrate type (Bendix and Hupp 2000). Rivers with unstable substrates usually have low species diversity (Bunn and Arthington 2002) as substrate type has an influence on soil-water retention, aeration, resistance to penetration by roots, and availability of nutrients (Sher and Marshall 2003). It is clear that the distribution of plant species within watersheds is not random, and is linked to the distribution of hydro-geomorphological processes and landforms (Bendix and Hupp 2000).

Multiple scales of environmental interactions complicate the recognition and analysis of hydro-geomorphological impacts on riparian vegetation (Bendix and Hupp 2000). Naiman *et al.* (2000) explains how the structure and dynamics of the riparian zones are a result of the interaction between biophysical factors acting at different scales. At the largest scales, the form of the valley influences alluvial landform development and pattern (such as high and low terrace). At small to medium scales, the arrangement of the physical environment and the characteristics of the riparian forest vary with spatial and temporal scale. At the smallest scale, alluvial landforms of different height above the channel mediate the impact of fluvial disturbance on riparian zones, thus influencing the composition of vegetation. Integration of these biophysical factors across all scales, with the disturbance regime, determines channel type and channel shape.

2.2 Recruitment and mechanisms for seed dispersal

Environmental heterogeneity of riparian plant communities (species richness) is ultimately constrained by dispersal (Merritt and Wohl 2002). Hydrochory, the dispersal and transport of seeds by flowing water, is an effective means of seed dispersal and may be a key factor in controlling the position of species along rivers and laterally up river banks (Merritt and Wohl 2000; Andersson *et al.* 2000; Pettit and Froend 2001; Merritt and Wohl 2002; Reinecke *et al.* 2007), and also enables new plant populations to become established at great distances from parent populations. Dispersal of seeds by animals (zoochory) and by wind (anemochory) may also be of importance, but few empirical data exist for comparison (Naiman and Decamps 1997).

Bendix and Hupp (2000) suggest that riparian communities should be considered compositionally stable, maintained by periodic flooding, rather than successional, recovering from floods. They describe three important roles of floods in the establishment and survival of riparian vegetation:

- Most riparian plants seeds germinate in alluvium that is deposited during floods, fresh deposits provide sites for colonization, and the energy conditions of the floods determine the texture of the new substrate. The reproductive biology of Fremont cottonwoods and Goodding willows is strongly tied to fluvial processes; seedling recruitment of both species is dependent upon periodic flood flows to deposit and moisten alluvial sediment bars (Stromberg 1993).
- Floods create colonization sites by removing existing vegetation. A change in habitat from riverine plants to large woody debris was reported after the Sabie River floods in February 2000, where large woody debris occupied about 2 to 11% area of the riverine landscape. Large woody debris acts as localized focal points for accumulating fine sediments, nutrients and moisture, which then results in patchy resource availability. Favourable microclimates (increased soil moisture, reduced summer soil temperatures) and soil nutrients within large wood piles remained evident for years afterward (Naiman *et al.* 2008).
- The occurrence or lack of floods after germination may determine whether seedlings will survive to maturity. In some cases, floods play a significant role in dispersing vegetative propagules to colonization sites. Vegetative propagules may be clonal segments or seeds, including some that are more often thought of as wind-dispersed (Bendix and Hupp 2000).

For seeds to successfully recruit during the post-flood period, the plants reproductive phenology must synchronize with the flooding pattern, if not, the species will require a propagule bank, such as a persistent soil-stored seed bank which may be triggered to germinate after a flood (or rain) event (Richardson *et al.* 2007). Naiman and Decamps, (1997) noted a positive relationship between floating capacity of diaspores and species occurrence in the riparian vegetation in Sweden.

Most riparian species have evolved life history strategies whereby seeds are produced during a specific season synchronized with the timing of hydrological events for successful dispersal (Bunn and Arthington 2002; Chambert 2006). Merrit and Wohl (2002) argue that the final location of hydrochorous seeds along riparian strips is a result of at least three interacting; factors: (1) the hydrological regime during seed release and transport, as defined by the timing and magnitude of peak flows together with the rate and direction of change in discharge, (2) channel morphology and hydraulics, and (3) the phenology of seed release as it relates to hydrologic regime.

Gurnell *et al.* (2011) suggested that the potential of the deposited propagules to survive is hydrologically controlled by the flood stage, which determines deposition site, and the depth to the alluvial water table, which controls after deposition survival and growth. The higher they are deposited within the active corridor, the less likely that they will be disturbed as they sprout and establish.

Seedlings are the most sensitive stage of a plant life cycle (Eriksson and Ehrlen 2008). A recent review concluded that the most common causes of seedling mortality, as percentages, were herbivory (38), drought (35) and fungal attack (20); less frequent were physical damage (4.6) and seedling to seedling competition (1.3) (Eriksson and Ehrlen 2008). Survivorship is thus highly regulated by substrate texture and soil moisture, with the pattern of river discharge playing a key role in the establishment of saplings (Naiman *et al.* 2005; Eriksson and Ehrlen 2008). Once a seedling's roots reach the water table, aeration and penetration of the substrate may become more important for growth than soil-water retention (Sher and Marshall 2003). In the Ord and Blackwood River in Australia, a higher density of seedlings were found to have established in wet and moist riparian vegetation sites than in the dry sites (Pettit and Froend 2001). Also an investigation into the relationship between bank elevation and seedling density showed a strong negative relationship between bank elevation and seedling density, with most seedlings occurring at lower elevations of the bank (Pettit and Froend 2001).

Although plants may initially establish at different sites, they are only successful on "safe sites". Safe sites have suitable conditions for germination such as adequate water and oxygen, also environmental conditions compatible with life history requirements (Naiman *et al.* 2005). Bank length, bank stability and bank undercut are variables that have influences on the establishment, growth and distribution of riparian vegetation (del Tánago and de Jalón 2006). Seasonal variations in the timing and pattern of flooding have profound effects on seedling survival and subsequent plant community structure. In the Western Cape mountain streams, however, Galatowitsch and Richardson (2005) reported that seedlings are not found on recent (new) deposition along channels, but rather on stable banks and along rock fractures. This was because headwater streams tend to be erosional, not depositional and are not prone to frequent overbank flooding. Consequently, seedling recruitment as a response to flooding disturbance may not be an adaptive advantage.

Substrate particle size is among the key environmental variables for determining seedling survival and growth, therefore potentially competitive success (Sher and Marshall 2003). In the Middle Rio Grande of New Mexico both *Populus* sp. and *Tamarix* sp. had greater germination and early growth densities on clay than in sand, but during the following year saplings grew better in sandier substrates. This may relate to abiotic demands differing at these growth stages (Sher and Marshall 2003).

2.3 Effects of flow modification on riparian community structure

Human influences have substantially changed the natural flow of rivers around the world, disrupting the dynamic equilibrium between the movement of both water and sediment (Poff *et al.* 1997) with cascading effects on the physical and ecological integrity of rivers including the riparian area (Stromberg *et al.* 1996; del Tánago and de Jalón 2006). Downstream effects of modified flow include altered river discharge, decreased suspended sediment, channel incision, flooding, floodplain and channel narrowing, stream meandering, and a decrease in diversity of the riparian habitat; accompanying such changes are shifts in riparian plant community composition (Stromberg 1993; Nilsson *et al.* 1991; Busch and Smith 1995; Gilvear *et al.* 2002). The extent of manipulations is expected to continue to increase with growth in human population and demand for energy, irrigation and industrial activities (Poff *et al.* 1997).

With this comes a need to predict the biological impacts that are associated with water management activities and setting water management targets that maintain riverine biota (Resh *et al.* 1988). Sustained flooding cause damages that may lead to mortality of riparian communities, death by inundation is also common for riparian species that grow in or near new or expanded reservoirs (Stromberg 1993). Prolonged drought or flow reductions of any kind can lead to a lowering of riparian water tables and ultimately mortality in riparian trees (Richardson *et al.* 2007).

According to Merritt and Wohl (2000) alteration of the natural flow regime is an inescapable consequence of water development that influences both the temporal availability and suitability of stream-side habitat and the dynamics of seed delivery to sites that are suitable for establishment. Resh *et al.* (1988) contend that once the environment is pushed outside the range of its natural variability the potential for native species and natural communities to survive is reduced. However Richter *et al.* (2003) argued that certain alterations do not threaten the viability of native species and the ability of an ecosystem to provide valuable products and services for society.

In many rivers flow modifications are responsible for increases in riverine plant abundance. Excessive growth of submerged aquatic macrophytes in a regulated Norwegian river was caused by reduced summer floods and increased winter flows (i.e., a relatively stable flow throughout the year). Up to 55% of the tail water surface area and slow-flowing reaches further downstream in the River Otra were covered with prolific growths of the submerged phenotype of *Juncus bulbosus* (Bunn and Arthington 2002).

The effects of flow modification on riparian vegetation may lead to competition in plant communities and may give way to plant invasions, where it is frequently assumed that the exotic species have invaded a habitat through competitive exclusion of native species, however often invaders are competitively weak and therefore depend on disturbance to remove the competitively superior native species (Sher and Marshall 2003). After clearing invasive species along selected headwater streams in the Cape Floristic Region (South Africa), small tree species (indigenous) became typically dominant in riparian scrub (*Brabejum stellatifolium, Brachylaena neriifolia, Erica caffra and Metrosideros angustifolia*), suggesting that these species may find suitable conditions for establishment in cleared sites that are free from competition (Galatowitsch and Richardson 2005). Plants that are stressed by floods will also be placed at a competitive disadvantage (Bendix and Hupp 2000), which makes a river's hydrological regime a main driving force of the out-come of species interactions. As flow modification continues the most successful invaders will be those that are adapted to the modified flow regime (Bunn and Arthighton 2002).

As river margin communities are dependent on river hydrology (Naiman and Decamps 1997), a change in river flow causes change in the riparian community (Jansson *et al.* 2000). It takes a long time for an ecosystem to change; the transition to a new, altered ecosystem state can take tens to hundreds of years as chain reactions cascade through second and third order effects within an ecosystem (Richter *et al.* 2003). However the specific changes that come with flow regulation on streams are difficult to predict due to complexity of rivers. To understand the combined and ultimate effects of river regulation, a combination of long-term studies for post regulation conditions are required.

2.4 Environmental flows and adaptive management

Environmental Flows (EFs) have been defined as the water that is left in a river system, or released into it, for the specific purpose of managing the ecological condition of that river (King *et al.* 2003a). Methods to estimate environmental flow requirements for rivers focus primarily on one or a few species that live in the wetted river channel. Most of these methods have the narrow intent of establishing minimum allowable flows (Poff *et al.* 1997). Brown and King (2006) acknowledge that there is no single method, approach or framework that is perfect to determine an EF and in most cases holistic methodologies are considered. There are four main types of flow-assessment approaches (King *et al.* 1999); (i) hydrological data are essentially desktop methods and were among the earliest, (ii) hydraulic rating methods use field measurements to describe channel-discharge relationships, (ii) habitat rating approaches, the best known of which is the Instream Flow Incremental Methodology and (iv) holistic approaches such as the Building Block Methodology in South Africa (Tharme and King 1998), Holistic Approach (Arthington and Zaluski 1998) and the Expert Panel Assessment Method (Swales and Harris, 1995 in King *et al*. 2003a). Recognition of the natural flow variability and careful identification of key processes that are linked to various components of the flow regime are critical to making these judgments.

Although there is little functional information of river system to place much confidence on the recommendations made; when EFs are set the changes on the riverine ecosystems are predicted, there after a monitoring process is put in place to provide feedback on the effects of the recommendations nearly enough information on the functioning of the system to place confidence on the recommendations that were made. In the process of monitoring if it is realised that the changes in the ecosystem are not those predicted by the ecologists, then an adaptive management strategy is applied.

Strategic adaptive management has been simply defined as the adjustment of management plans which are informed by monitoring results (King *et al.* 2003a; Brown and King 2006). According to Poff *et al.* (2010), an effective adaptive management means "designing, implementing and interpreting research programs to refine flow alteration-ecological response relationships, and ensuring that this new knowledge translates into updated, implemented flow standards”. Moore *et al*. (2011) stated that the focus of adaptive management is not research, although the main objective is the accumulation of knowledge for improving decision making. Adding to this Gunderson (1999) indicates that it is called ‘adaptive’ because it acknowledges that managed resources will keep changing as a result of human intervention, that surprises are inevitable, and that new uncertainties will emerge. Nonetheless active learning is the way in which the uncertainty is dealt with.

3 Physical influences of recruitment on the structure of the lateral riparian zone

3.1 Introduction

Riparian zones occupy a three-dimensional transitional area between aquatic and terrestrial ecosystems and serve as conduits for the exchange of materials and energy between these systems (Naiman and Decamps 1997; Richardson *et al.* 2007). The structure of riparian zones consists of three essential components. The first is a longitudinal continuity from river source to mouth, which comprises a continuous vegetated strip along the channel that contributes to the control of the flow or movement of water, nutrients, sediment and species through the landscape. Secondly, the lateral dimension (width) of the channel and floodplain containing natural riparian vegetation defines the riparian area where hydrological and ecological processes and functions take place, and influences the heterogeneity of the riparian zone (del Tánago and de Jalón 2006). Thirdly, the species composition and structure of the riparian vegetation which reflects species responses to prevailing abiotic controls (van Coller 1992).

Riparian vegetation exhibits distinct lateral zonation patterns from the channel outwards up the banks, resulting in broad-scale spatial segregation of species along an elevation gradient (Ward 1998). The presence of lateral zonation in riparian vegetation has been well documented: flooding events shape the vegetation on riverbanks and the zones that are inundated annually (wet bank) have different vegetation from those that are inundated inter-annually (dry bank) (Sieben and Reinecke 2007). Zones of different plant communities have been recognized laterally up the river bank from the water's edge to outer edge of land influenced by the occurrence of small to medium floods, and the duration of inundation when flooded intra-annually (Reinecke and Brown 2013). These lateral zones are defined based on; periodicity of hydrological changes in lateral elevation or moisture gradients, and or changes in plant species distribution or community composition along lateral gradients.

The flow regime of a river is a primary determinant of the structure and function of aquatic and riparian ecosystems (Poff and Ward 1989, Gurnell *et al.* 2011), and is considered to be a "master variable" that influences the distribution and abundance of riverine species (Richter *et al.* 2003). According to Mahoney and Rood (1998), different stages of river flows affect seedling recruitment within lateral zones: (i) high flows drive geomorphological processes that create suitably moist sites (nursery sites); (ii) receding flows expose the favorable nursery sites; (iii) a gradual decline in flow after germination permits the growing roots to maintain contact with the receding moisture levels; and (iv) sufficient flows through the low flow period provide seedlings with a favourable water balance to withstand the winter season. For successful recruitment in the post-flood period, flowering and seed set should take place during the flooding season as this will disperse seeds into nursery sites. Failing this, plants will have to depend on a persistent seed bank in the soil that is triggered to germinate by flood (or rain) events (Richardson *et al.* 2007). Successful seedling recruitment on the riparian zone depends mainly on suitable conditions created by flow events at specific times. However changes in flow patterns often shift the timing of preferred conditions (Naiman *et al.* 1998). Once plants have passed the seedling stage, water availability may be the dominant factor controlling their survival (Reinecke 2013).

3.1.1 Seed set and flow

Most riparian species synchronize seed production with the timing of hydrological events as these enhance their chances of dispersing successfully (Chambert 2006). For instance seed dispersal linked to fluctuating water levels is a major factor in determining zonation of willow and poplar species (Naiman *et al.* 1998). During low flows seeds are deposited lower down the bank, close to the wetted channel, while during high flows they are deposited further up the bank. Naiman *et al.* (1998) points out that the timing of germination may be partially responsible for the ability of different species to survive flooding.

Figure 3.1 illustrates the differences in the seasonal variation of selected species' seed release with the corresponding flow in the Molenaars River, which displays a flow regime typical of rivers in the Western Cape, South Africa. Flows peak during mid- June, persist through July and start to recede in August. Thereafter, river flows gradually decrease through the summer, with February having the lowest flow, before rising again between March and April.

Suggested seed and flower release periods of the selected species in the Western Cape are as follows; according to Reinecke (2013), *Salix mucronata* prefers year-round waterlogged conditions and releases seeds during January coinciding with the summer low flows, which allows the seeds to establish closer to the dry season water's edge. For many species of Salicaceae, abundant seeds are produced in spring and early summer (which are low flow periods). Seed dispersal is by means of air and water, and seedlings establish only if the soil on which the seeds are deposited is moist and remains undisturbed through germination and establishment (Karrenberg *et al.* 2002).

Metrosideros angustifolia releases its seeds over the four months from the peak of winter high flows (June) to the beginning of the low flow period in September (Reinecke 2013). This allows the seeds to be deposited down the river banks as the flows recedes. *Brabejum stellatifolium* seeds are released during autumn (April to May) during the approach of the wet season, in the Western Cape area. As a result *Brabejum stellatifolium* recruits more on the upper portions of the riverbank as the seeds are deposited by the rising flows. *Brachylaena neriifolia* flowers in summer and sets seed in autumn; January to March (Goldblatt and Manning 2000). This disperses seeds closer to the wetted channel where they germinate before the high flow season arrives. *Morella serrata* flowers from August to December and the fruits ripen in January (Goldblatt and Manning 2000). It is a typical lower dynamic species occurring closer to the water's edge. *Freylinia lanceolata* flowers during high-flow summer periods from June to August (Pitta 2002). Although the understanding of timning of seed production in the Western Cape is limited in scope,a general cinception is illustrated.

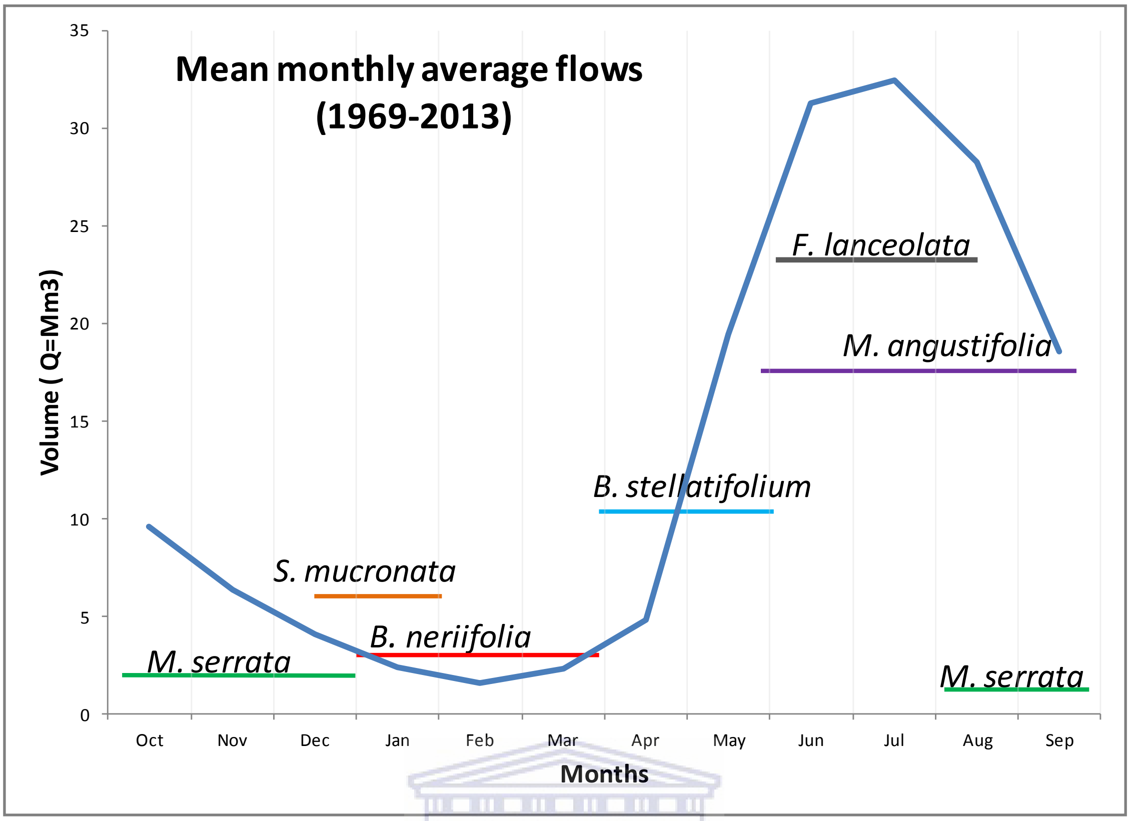


Figure 3.1 **Seed release of species with relation to the seasonality of flows**

3.1.2 Lateral zonation in the Western Cape

The riparian zone is divided into a number of lateral zones that are characterized by their species composition. According to Reinecke (2013), various descriptions of zonation along the riparian bank assume that lateral zones exist and closely link them to changes in bank topography, aspects of the flow regime or rather their interaction thereof. Although the actual number of lateral zones that occur along river banks may differ, the Wet and Dry banks are always defined. Boucher (2002) introduced a classification system with seven zones that were distinguished on the basis of their species composition and flood recurrence intervals. Three principal zones were recognized (Aquatic, Wet bank and Dry bank), which he showed were consistently present on rivers in the Western Cape and Lesotho. For South African rivers, Kleynhans *et al.* (2007) described three lateral zones (Marginal, Lower and Upper zone) characterised by flood recurrence and bank shape. Although lateral zonation for Western Cape Rivers has not been intensively studied until recently with no formal classification (Prins *et al.* 2004), some authors have acknowledged their presence and defined them. In the Western Cape Fynbos Riparian Vegetation Community, seven lateral zones were recognized by Reinecke *et al.* (2007) consisting of wet bank (made of Wet Edge and Channel Fringe) and dry bank (made of the Tree Shrub, Outer Transitional and the Non Riparian), while the aquatic vegetation zone was not addressed. Reinecke and Brown (2013) reported evidence of four lateral zones distinguished by plant species (Marginal, Lower dynamic, Lower and Upper zone). Indicator plant species (Table 3.1) were identified for the four lateral zones (Reinecke and Brown 2013) in Fynbos Riparian Vegetation community (Mucina and Rutherford 2006).

Table 3.1 Indicator species for each lateral zone (Reinecke and Brown 2013).

	Lateral zone	Indicator species
1	Marginal	*Prionium serratum* and *Isolepis prolifera*
2	Lower dynamic	*Calopsis paniculata* and *Morella serrata*
3	Lower	*Metrosideros angustifolia* and *Elegia capensis*
4	Upper	*Pteridium aquilinum* and *Diospyros glabra*

This chapter focuses on temporal changes in fynbos riparian systems of the Western Cape to assess the possible influences of flow on the recruitment pattern of plants communities on the riparian lateral zones. The key research question was: Are the physical influences of flow (drought and floods) on riparian communities exerted before or after recruitment? The working hypothesis was that the structure of plants on lateral zones will be determined by factors that are exerted post-recruitment. The aim is to study if the structure of the riparian vegetation is determined by other influences before recruitment (pre-recruitment) or by influences that affect them after recruitment or establishment (post recruitment). Sites where riparian vegetation communities were sampled in 2004 (Reinecke 2013) and 2011 (Otto 2014) were re-sampled in 2013. Changes in population structure of undisturbed riparian zones on two rivers were assessed over a period of nine years. Attention was paid to the distribution of saplings and seedlings in order to determine preferred recruitment location and survival post recruitment.

3.1.3 Location of study sites

The location of the study sites within the Western Cape Province is shown in Figure 3.2.

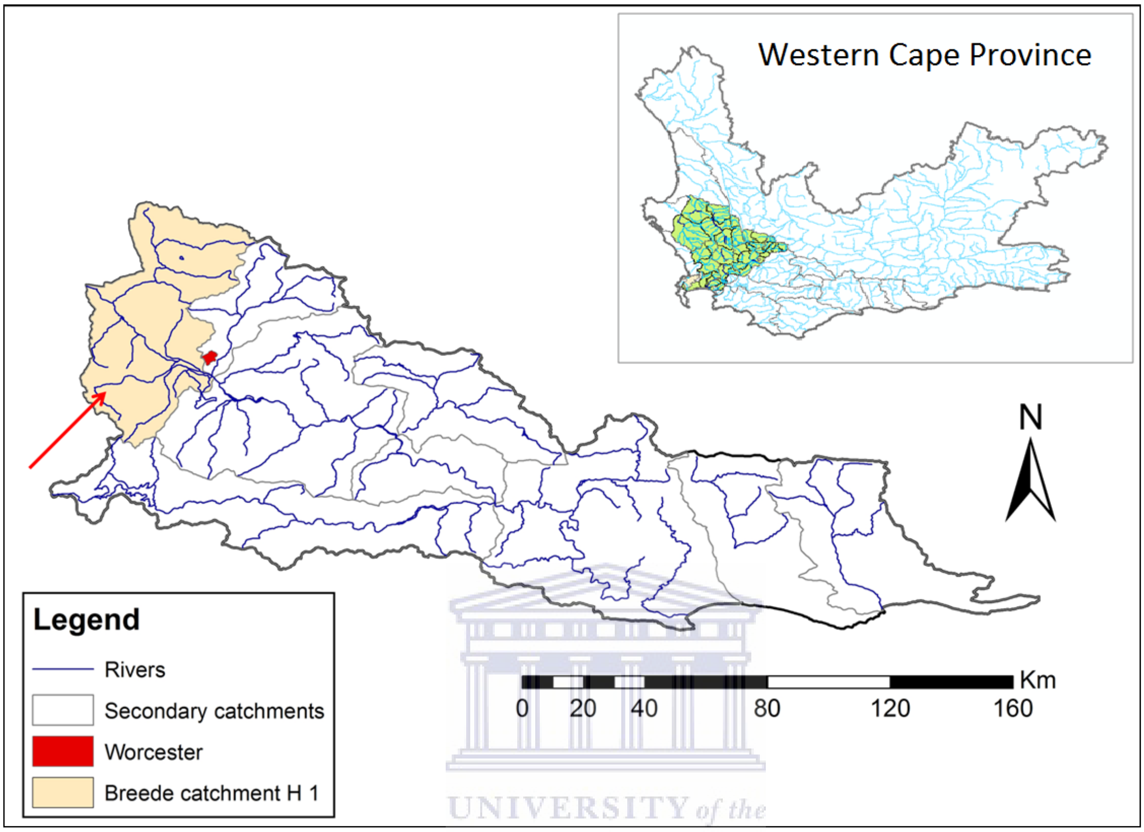


Figure 3.2 The location of the study catchments within the Western Cape Province. The arrow points to the approximate location of study sites.

3.2 Methods

3.2.1 Data collection

River cross sections were surveyed from Elands (Ela) and Molenaars (Mol) Rivers. Moreover, vegetation transects were sampled and hydrological data were collated from nearby gauging stations.

3.2.1.1 Cross section data

The variation in elevation across cross-sections of the channel at each site was surveyed in 2011 and again in 2013 to establish whether there were any major changes in bank shape that may have influenced the distribution of riparian vegetation. Two cross-sections were surveyed at each site, except for Mol 2 where the repeat surveys did not overlap the original cross-sections. Two cross sections that were 10 m apart were surveyed to give the overall shape of the river channel at sample sites. A control point which was permanently marked in 2004 at each site was used as a reference starting point thereafter taking a reading for the horizontal distance and elevation at vegetation sample plots which were one meter apart from each other. The naming of the cross-sections at sites was done using the distance from the river (meter number) at its location. The locations of the surveys are given in Table 3.2.

Table 3.2 Location of cross-sections on sampling grid in 2011 and 2013.

	Cross-section 1	Cross-section 2	Cross-section 3	Cross-section 4	Cross-section 5
Transect at site :	0 m	5 m	10 m	15 m	20 m
Ela 3	√		√		√
Ela 4		√		√	
Mol 2 (Only in 2013)		√		√	
Mol 5		√		√	

3.2.1.2 Vegetation data

A long term data set was constructed using data collected at permanently marked plots on the Elands and Molenaars Rivers in the Breede River Catchment (Figure 3.2). Sampling was conducted during the low flow season during 2004 (Reinecke *et al.* 2007), 2011 (Otto 2014) and 2013 (this study). Vegetation data were collected in permanently marked vegetation transects centered on sample grids adopted from Reinecke *et al.* (2007). Two suitable sites were selected for each river, the four sites were sampled in 2004 (Reinecke *et al.* 2007) and 2011 (Otto 2014) using whole community sampling as part of different studies, and then resampled in 2013 for this study, except for one site (Mol 5), which was only sampled in 2011 and 2013.

The sites were named using the first three letters of the river name and a numeric code that corresponds to the original (2004) study, namely: Ela 3, Ela 4 on the Elands River and Mol 2, Mol 5 on the Molenaars River. The numeric code is according to the location of one site relative to the other; with the more upstream site having the smaller number, i.e., Ela 3 is upstream of Ela 4.

3.2.1.3 Sample plot design

At each site four vegetation transects were laid out on one bank. Each transect was 20 m long along the wetted edge of the river, and several meters wide laterally up the bank dictated by the width of the riparian zone (Figure 3.3). Each transect was divided into contiguous 1 x 5 m sample plots. Sample plot labeling was done by number (1 to 'n') to indicate distance from the water in metres, and by letter A to D to indicate the four different transects. Vegetation in the wetted channel (part of the channel with flowing water) was also sampled using the same layout, however negative numbers were used in the naming of these sample plots; i.e. the one metre distance from 0 m into the channel was -1 m.

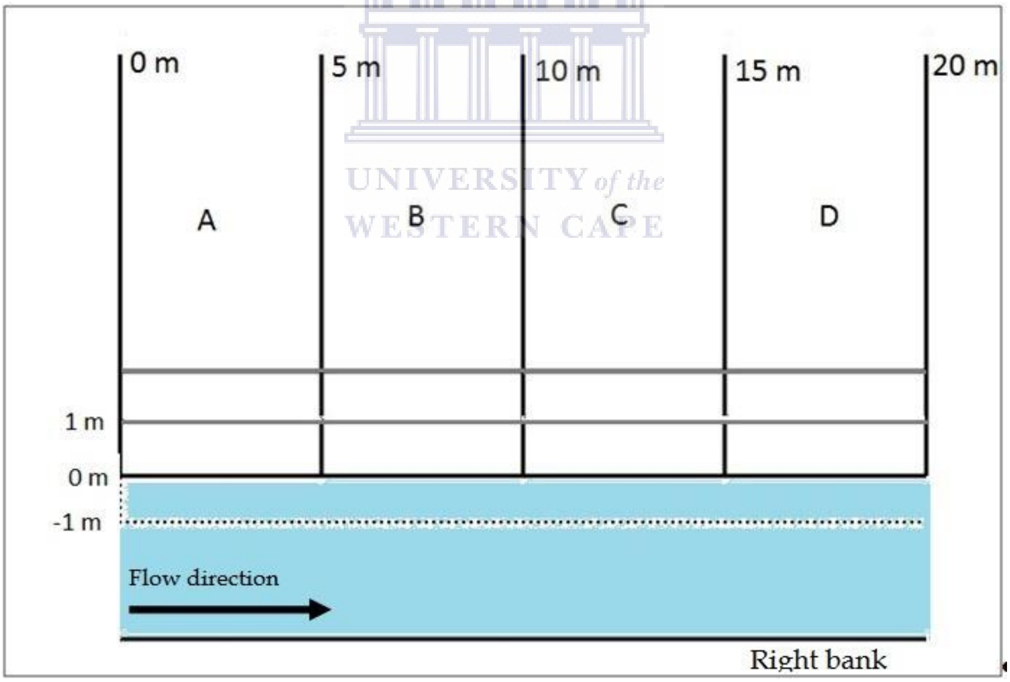


Figure 3.3 Vegetation transects A – D, showing sample plot layout

The number, height, and contribution to canopy cover of each species were recorded for every species rooted in every 5 m^2 plot in order to describe the abundance and distribution of the plant species. The same sample plots used in 2004 and 2011 were re-sampled. The rooted position of each plant was recorded i.e., the position at which the roots of the plant were located in the sample plot. The number of tree individuals was recorded in three height classes (Table 3.3) per sample plot. These three height classes were selected according to plant life history stages for growth. Two specimens of each plant species were collected, pressed, dried and catalogued into two separate herbaria: one for field reference and another for identification. Identification of plant species was done by plant specialists from the Compton Herbarium at Kirstenbosch National Botanical Gardens in Cape Town, the two historical data sets (2004 and 2011) were also identified at this place. Six indicator species that are common to the Western Cape were used: *Salix mucronata, Metrosideros angustifolia, Brabejum stellatifolium, Morella serrata, Freylinia lanceolata* and *Braclylaena neriifolia*.

Table 3.3 Three height classes used for division of the vegetation canopy (Reinecke *et al.* 2007)

Growth stage	Height (m)
Seedlings	< 0.3
Saplings (juveniles)	0.4 – 1.9
Adults	> 2

Cover was estimated visually as a percentage of the cover canopy for each plant species in every sample plot. Cover percentages of woody plants were recorded for every individual plant observed while for graminoids and groundcovers (non-woody) a percentage was given as a total for that species in that sample plot.

3.2.2 River flow data

Flow data were obtained from the South African Department of Water Affairs website (http://www.dwaf.gov.za/Hydrology/). For each river, daily and monthly flow data were downloaded for the flow gauging station closest to the sample sites (Table 3.4). These data were used to study the flow patterns in each river in an effort to relate them to the vegetation structure.

Table 3.4 Gauging stations on each river

River	Used for sites	Gauge station number	Location co-ordinates
Elands	Ela 3 and Ela 4	H1H033	33.73667 S 19.11472 E
Molenaars	Mol 2 and Mol 5	H1H018	33.72472 S 19.16972 E

3.3 Data analysis

3.3.1 Comparing cross-sections

The variation of elevation with distance across the channel at each cross-section in 2011 and 2013 were compared to establish possible changes in the channel profile. Survey data were plotted against one another (horizontal distance and elevation difference between points across a river) in Microsoft Excel in order to produce graphs depicting channel shapes. Cross-sections surveyed at sites in 2011 and 2013 were overlaid to determine whether significant changes had taken place to the river's cross-section profile between years.

3.3.2 Analysis of vegetation data

This was done in separate sub-sections for the purposes of identifying the lateral zonation patterns and observing the distribution of different plant species at different life stages (seedlings, saplings and adults) on the lateral zone.

3.3.2.1 Analysis of hydrological data

A full data set of available daily flows for each gauging station at the Elands and Molenaars River were plotted together with average monthly flow data for each year sampled. This was done to deduce if the pattern of flow for the sampled years followed overall seasonal pattern of flows received at each station.

3.3.2.2 Lateral zonation

Everitt (1979) describes classification as a process of allocating entities to initially undefined classes so that individuals in the same class are, in some sense, similar to one another. Cluster analysis aims to partition a set of objects into similar sub-sets. For clusters, the within-group dissimilarity should be minimised while maximizing dissimilarity between clusters (Everitt 1993; Gordon 1999). Sample plots were partitioned using plant species so that sample plots that contain similar species were allocated to one of the clusters. Multivariate analyses were used to discern patterns of zonation based on species level similarities. Data were 4th root transformed in order to boost the presence of smaller species at lower covers. Bray-Curtis similarity coefficients were calculated between sample plots. Cluster analysis and non-metric multi-dimensional scaling (MDS) ordinations were used to determine similarity coefficients between sites and sample plots within sites. Groups of sample plots with greater than 40% similarity were recognized, along with a few clusters of plots with lower similarity but obvious cohesion as a group. According to the resulting groupings, sample plots were allocated to one of four zones (Marginal, Lower dynamic, Lower and Upper zone) based on the habitat characteristics of dominant species. The lateral zones were compared within sites for the three years (2004, 2011 and 2013) to establish whether there was a shift in zones over time. Once a sample plot had been allocated to a zone, the frequency of species occurrence at a zone was calculated relative to a category of growth stage. With these the plant assemblages for the site under study was defined.

There is no completely satisfactory method that can be used for testing the significant number of clusters (Everitt 1979; Mazvimavi 2003). Several methods have been tested and weaknesses shown, however Everitt (1993) and McGarigal *et al.* (2000) recommended the use of a visual inspection of fusion levels displayed on a dendogram. The union or joining of clusters at shorter distances suggests a strong similarity between samples tested. Therefore an examination of distance at which clusters join was used in this study to assist in determining the number of clusters, and then allocate lateral zones to each.

Lateral zonation was studied in two ways, using a combination of groundcover and tree data, and later by separating the two plant types. This was done to investigate whether the usage of data differently would still suggest the same lateral zonation patterns at sites.

3.3.2.3 Vegetation assemblages

Species composition of each zone was determined using the total cover percentage and the frequency of occurrence of individual species within the lateral zone. This was done to identify the dominant species at lateral zones of each site.

3.3.2.4 Distribution of trees

To show the overall distribution of tree species on the lateral zone, the number of individuals for all life stages (seedling, sapling and adults) were summed together for each species represented at all sites. These results were presented graphically showing the abundance of common of species along the lateral zone.

The progression from seedlings to saplings to adults at each bank position at each site was examined. To do this it was inferred that the saplings found in 2013 in the same positions as seedlings in 2011 were probably the same plant. Similarly adults were considered to be later life stages of the saplings or seedlings found in the same position in previous years.

3.4 Results

3.4.1 Flow data analysis

At the Elands River (Figure 3.4) daily flows for 1969 - 2013 (red) were presented to show the average flows for each month. The pattern of flow for each sampled year was compared to that of the long term data to observe if the vegetation at sites was influenced by the same pattern of flow. During data analysis, the sample year for this study (2013) did not have a full flow data (January to June) on for the Elands River (Figure 3.4). A gradual rise in flows was noted from April, the highest peak was in June, which was followed by a sudden fall in July then a gradual fall from August. The summer months (November to March) show flows that are lower than 1 Mm^3/month. The river receives lowest flows between January to March. Distinguished high flows are noted during the month of June at all cases except for 2004 that had its highest flow in August.

For the Molenaars, (Figure 3.4) the monthly average flows were generally lowest from December to end of March, flows start increasing from April peaking in June followed by a slight decrease from July and then after August there was a noticeable gradual decrease. During 2004 and 2013, the largest peak flow occurred in the month of August wherease in 2011 the highest flow came through in June. For all the three years there are noticeable rises in flows during June and August. During 2004 the lowest flow occurred in February (0.429 Mm^3/month) and the highest flow was 82.203 Mm^3/month recorded in August. In 2011, the lowest flow occurred in March (0.348 Mm^3/month) and the highest was in June with a volume of 74.299 Mm^3. In 2013 the lowest flow occurred in March (0.380 Mm^3/month) and the highest was in August with a volume of 1118.273 Mm^3/month. Overall the three years followed the pattern of flow illustrated by the average flows from the full data available (1969 to 2013).

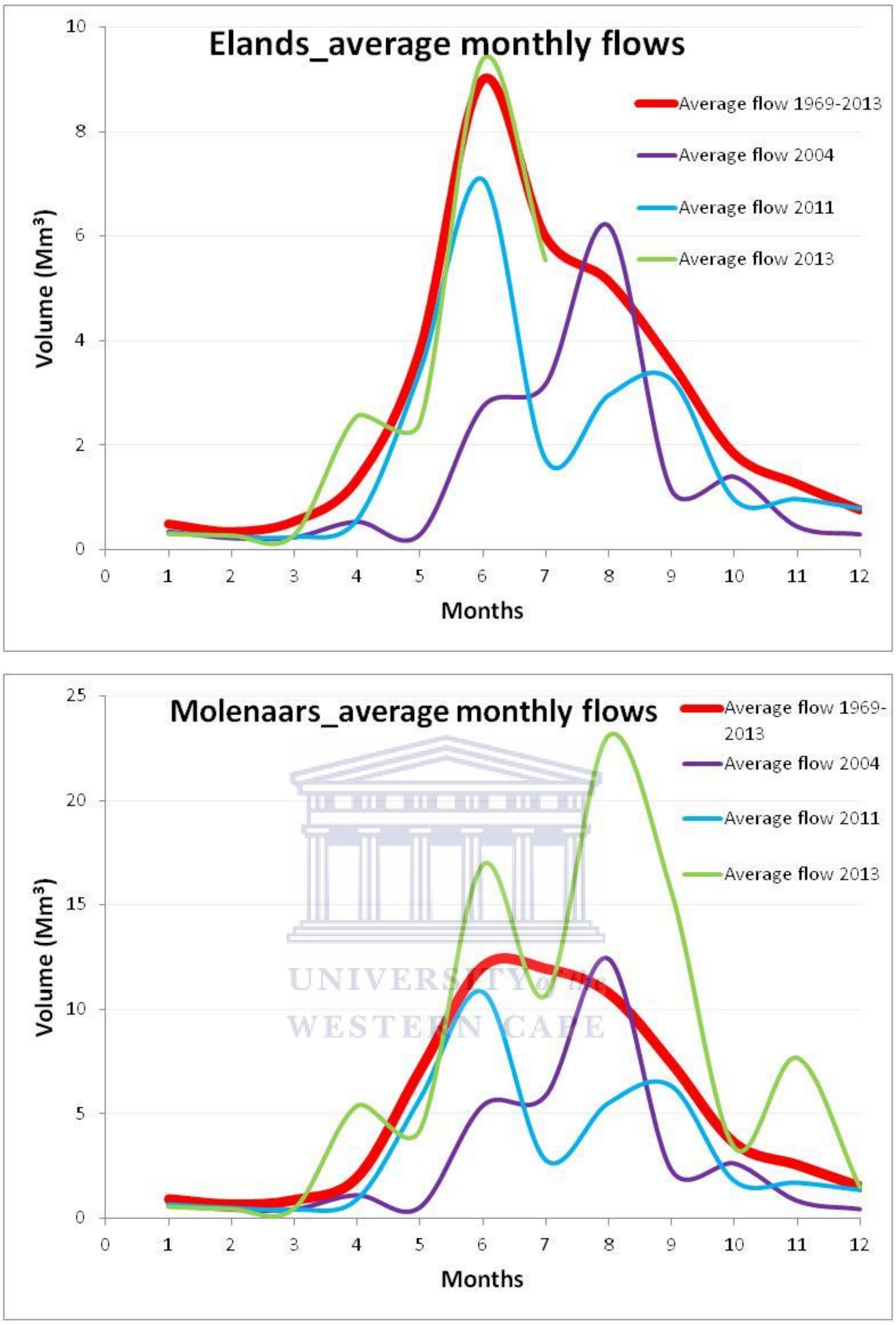


Figure 3.4 Monthly flows 1969 - 2013 for the Elands and Molenaars Rivers, averaged for the whole record and plotted individually for the sample years: 2004; 2011 and 2013.

It was also evident on all graphs that after flows drop in July it was followed by a short period of high flow between August and September. In general, the year 2004 had delayed events of low and high flows as compared to the other years, the first peak flow occurred in August while the second small one arrived in October. The record shows slight rise and fall of flows between March and May at both 2004 and 2013, although it was fairly flat in 2011.

3.4.2 Horizontal distance and elevation (river morphology)

The cross-sectional profiles surveyed in 2011 and 2013 are provided (Figure 3.5). Vegetation samples were taken on the right bank of the Elands River, while the left bank was sampled at the Molenaars River. There were no major differences in the cross-sections at any of the sites, although there were some small changes.

At the 10 m transect (as shown in Figure 3.3) at Ela 3, the shape of the channel in 2011 and 2013 is much the same, however the 20 m transect shows a rise on the left and right bank. This could have been caused by a boulder surveyed on the right bank in 2011 at the 0 m transect which was then missing in 2013. At Ela 4, both transects show similar shapes for both years. The cross-sections at Ela 3 and Ela 4 show a gently sloping river bank with the latter being slightly narrower than the former and deposition taking place on the right bank at Ela 3 while erosion was taking place on the right bank at Ela 4. At Mol 2, transects at 5 and 15 m were only surveyed in 2013, the site has a wide wetted channel accompanied by a gradually rising right bank and a gentle rising left bank. On the left bank the wet bank was 3 m in width and behind this there was a side channel 2 m in width, after which there was a sudden increase in on bank slope. At Mol 5, both cross-sections showed slight changes on the shape of the wetted channel. Mol 5 was a pool and characterised by steeper channel banks when compared to Mol 2.

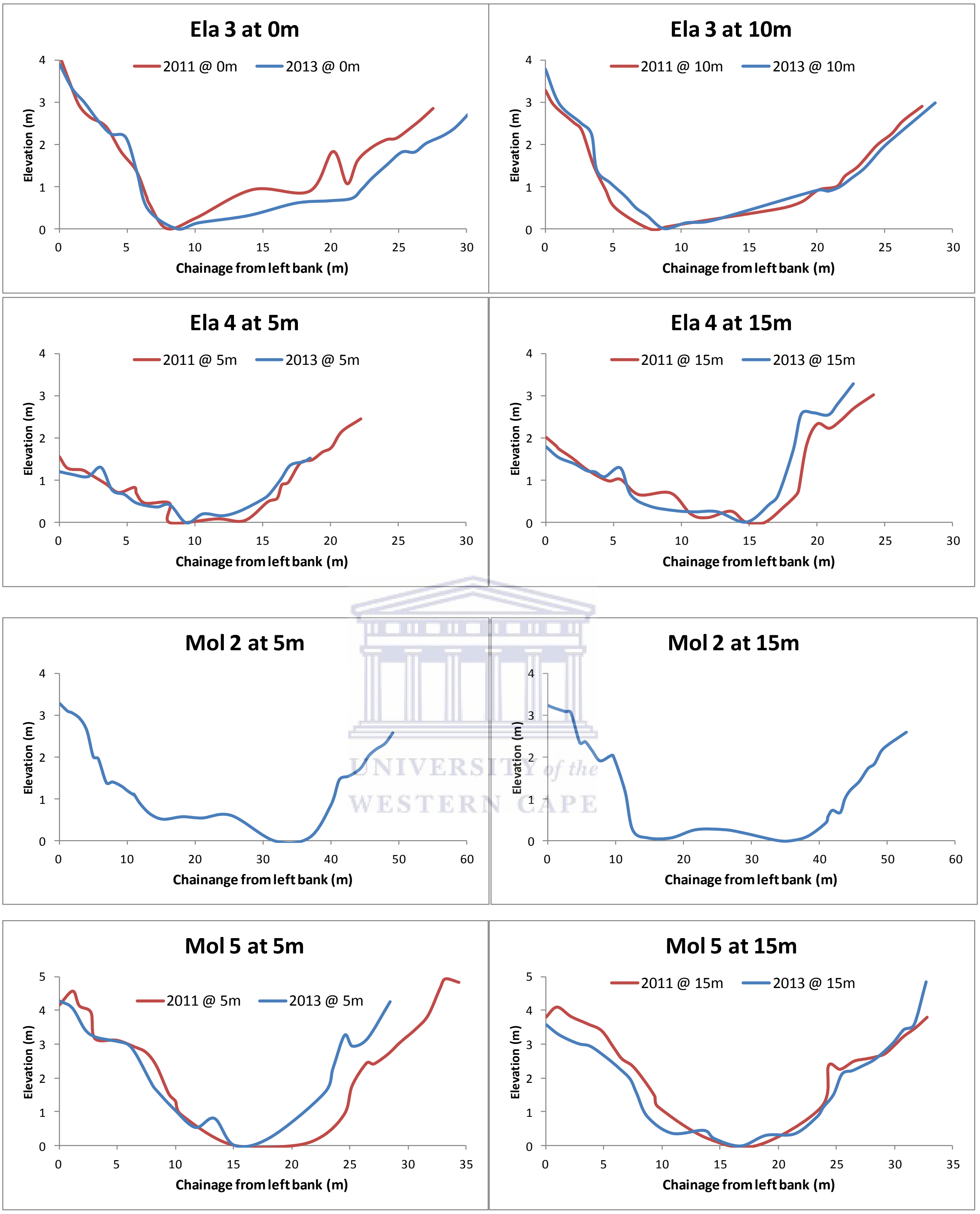


Figure 3.5 Cross-sectional profiles for the Elands and Molenaars River sites in 2011 and 2013. Chainage is from the left bank

The variation in channel cross-sections between years (2011 and 2013) was presumably a result of different points being surveyed along the transects at which the level staff was placed as the readings were being taken. The Molenaars River sites, in the upper foothills, are fairly wider than the Elands River sites. Although there was not a perfect overlap of the cross sections (2011 and 2013), the basic bank shape suggests that there were no major changes in the cross-section with exception to Ela 3 at transect 20m.

3.4.3 Lateral zonation

Lateral zonation was studied in two ways, first using a combination of both ground cover and tree (woody plants) data and then using separate data sets. This was done to investigate whether the usage of data differently would still suggest the same lateral zonation patterns at sites.

3.4.3.1 Zonation using all species

All species collected are listed in Appendix Table 1. Non-metric MDS ordinations and cluster diagrams constructed using a combination of the rooted cover percentage of groundcover and woody plants within each 1 m^2 sample plot in 2013 were used to identify the lateral riparian zones. The allocation of lateral zones was done according to the type species contained within each sample plot, the indicator species in Table 3.1 were used to guide these decisions. The results are presented in Figure 3.6, Figure 3.7, Figure 3.8 and Figure 3.9 for Ela 3, Ela 4, Mol 2 and Mol 5, respectively.

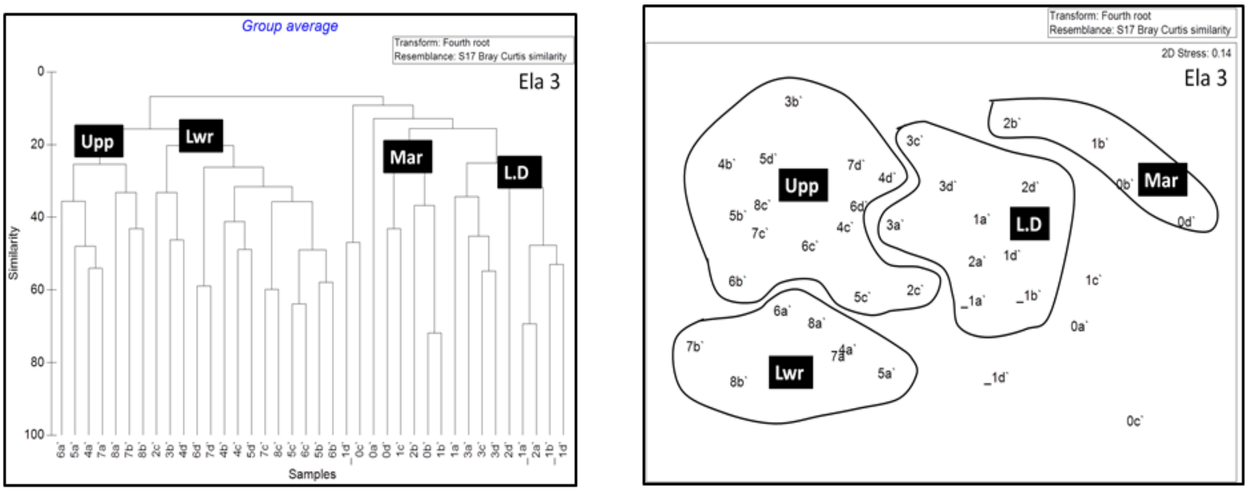


Figure 3.6 Cluster and MDS ordinations for 2013 at Ela 3. Sample plots (indicated as samples) are indicated within Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp.= upper zone

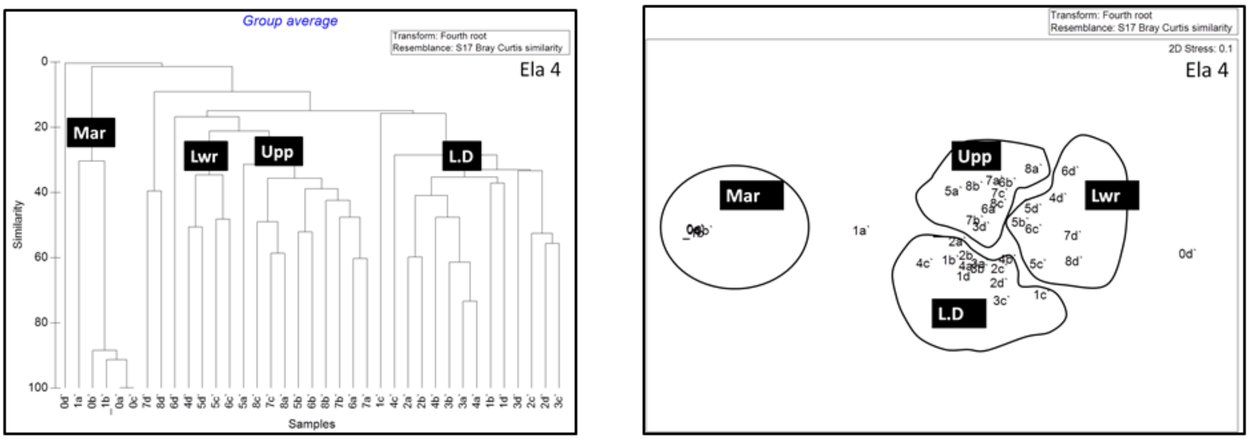


Figure 3.7 Cluster and MDS ordinations for 2013 at Ela 4. Sample plots (indicated as samples) are indicated within Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp.= upper zone

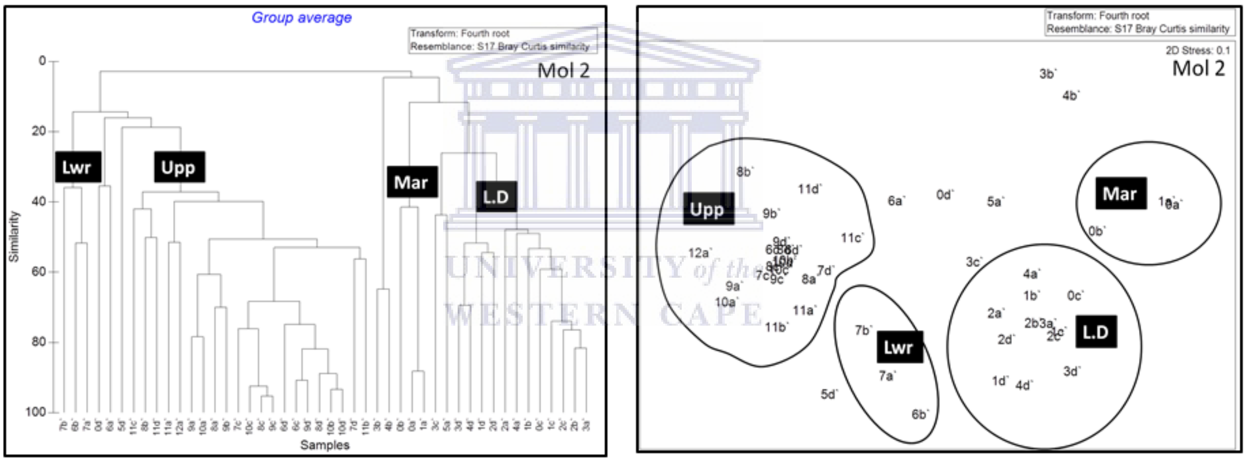


Figure 3.8 Cluster and MDS ordinations for 2013 at Mol 2. Sample plots (indicated as samples) are indicated within Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp.= upper zone

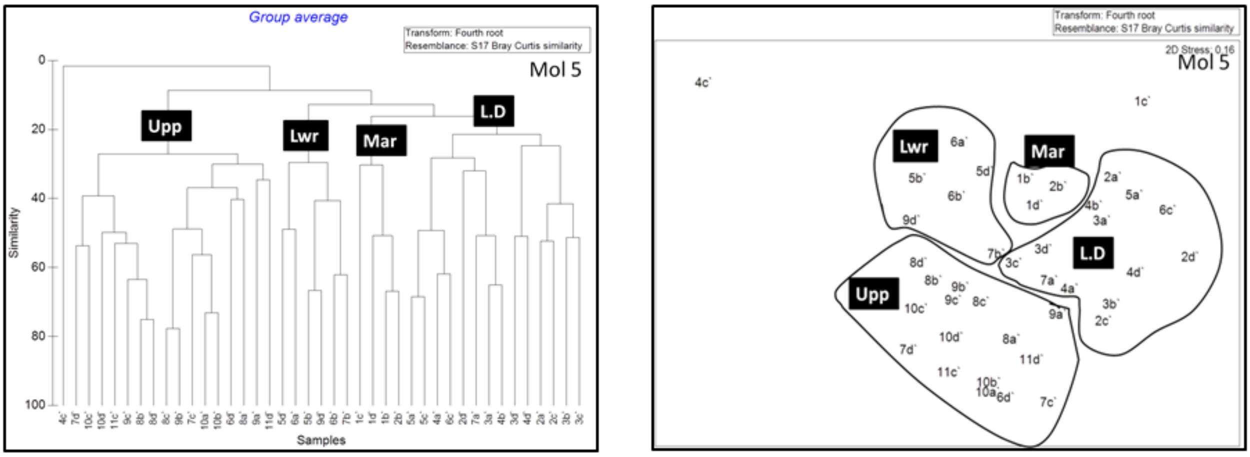
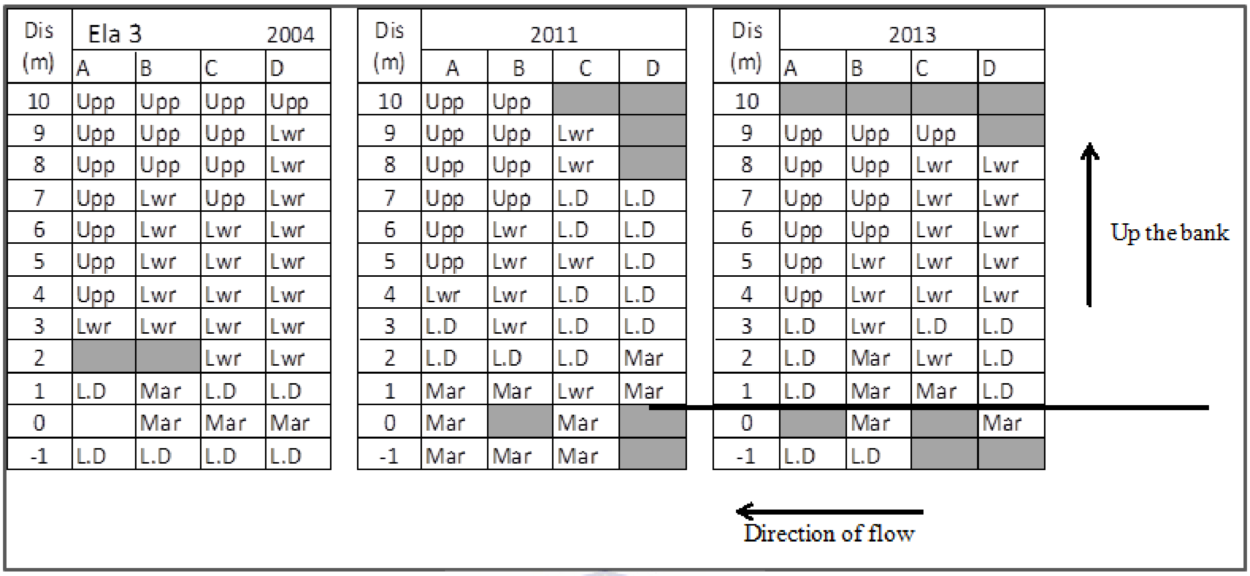


Figure 3.9 Cluster and MDS ordinations for 2013 at Mol 5. Sample plots (indicated as samples) are indicated within Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp = upper zone

At all sites four lateral zones were evident from the data collected; the marginal zone and lower dynamic zone that make up the wet bank, the lower zone and upper zone that make up the dry bank (after Reinecke and Brown 2013). The marginal zone was situated at the edge of the wetted channel, followed by the lower dynamic, which separated the marginal from the lower zone. The lower dynamic zone was a transitional zone and contained similar species to those from the neighbouring zones. The lower dynamic zone was followed by the dry bank zones, which formed the outer boundary of the riparian zone and comprised lower zone and the upper zone. At all the sites, the bigger portion (several metres) of the riparian bank was comprised the lower and upper zones.

The overall distribution of lateral zones at each site was also studied. The distribution of lateral zones within sample plots in 2013 was compared with that of 2004 and 2011. This was done in order to determine if there were temporal changes in lateral zonation between years (Figure 3.10 to Figure 3.13). The figures below show, for each site, a lateral zone that was allocated to each sample plot for the three years studied.

At Ela 3 (Figure 3.10), there were more similarities in the marginal and lower dynamic zones (-1 and 1 m) between 2004 and 2013, than between these years and 2011. Similarly, the dry bank started at 4 m in 2004 and 2013, but in 2013 2 - 7 m was a mixture of lower dynamic, lower and the upper zone. The upstream transect (A) of this site appeared to be drier than the more downstream transects. For instance, in 2004 and 2011, the upper zone on Transect A starts at 4 m, while on the other transects (B, C and D) the upper zone starts at 7 m.



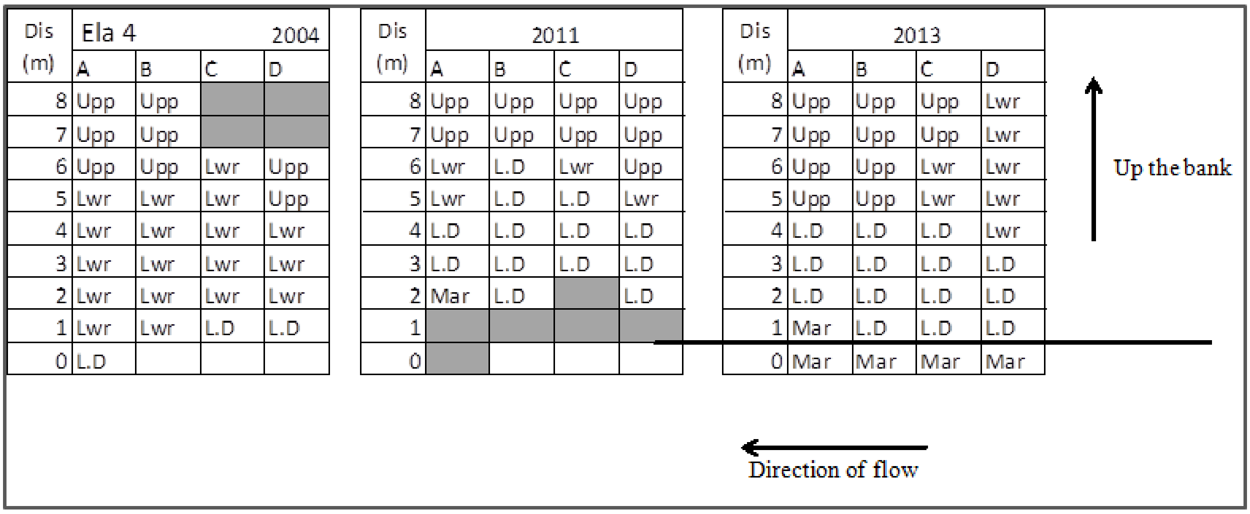
Dis (m)	Ela 3 A	B	C	2004 D
10	Upp	Upp	Upp	Upp
9	Upp	Upp	Upp	Lwr
8	Upp	Upp	Upp	Lwr
7	Upp	Lwr	Upp	Lwr
6	Upp	Lwr	Lwr	Lwr
5	Upp	Lwr	Lwr	Lwr
4	Upp	Lwr	Lwr	Lwr
3	Lwr	Lwr	Lwr	Lwr
2	▨	▨	Lwr	Lwr
1	L.D	Mar	L.D	L.D
0		Mar	Mar	Mar
-1	L.D	L.D	L.D	L.D

Dis (m)	2011 A	B	C	D
10	Upp	Upp	▨	▨
9	Upp	Upp	Lwr	▨
8	Upp	Upp	Lwr	▨
7	Upp	Upp	L.D	L.D
6	Upp	Lwr	L.D	L.D
5	Upp	Lwr	Lwr	L.D
4	Lwr	Lwr	L.D	L.D
3	L.D	Lwr	L.D	L.D
2	L.D	L.D	L.D	Mar
1	Mar	Mar	Lwr	Mar
0	Mar	▨	Mar	▨
-1	Mar	Mar	Mar	▨

Dis (m)	2013 A	B	C	D
10	▨	▨	▨	▨
9	Upp	Upp	Upp	▨
8	Upp	Upp	Lwr	Lwr
7	Upp	Upp	Lwr	Lwr
6	Upp	Upp	Lwr	Lwr
5	Upp	Lwr	Lwr	Lwr
4	Upp	Lwr	Lwr	Lwr
3	L.D	Lwr	L.D	L.D
2	L.D	Mar	Lwr	L.D
1	L.D	Mar	Mar	L.D
0	▨	Mar	▨	Mar
-1	L.D	L.D	▨	▨

Figure 3.10 **Ela 3 lateral vegetation zones lateral zones 2004 (left) 2011 (middle) and 2013 (right). Dis= distance from the water's edge and vegetation transects (A, B, C and D). Lateral riparian zones are indicated using Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp = upper zone. The gray boxes are outliers or where no vegetation was recorded**

At Ela 4 (Figure 3.11), there were noticeable shifts in lateral zones between 2 - 6 m over the period 2004 to 2013. For instance in 2004, the sample plots at 2 and 6 m were classified as lower zone, in 2011 they were lower dynamic zone, and in 2013 2 - 4 m were lower dynamic, and 5 – 6 were upper zone.



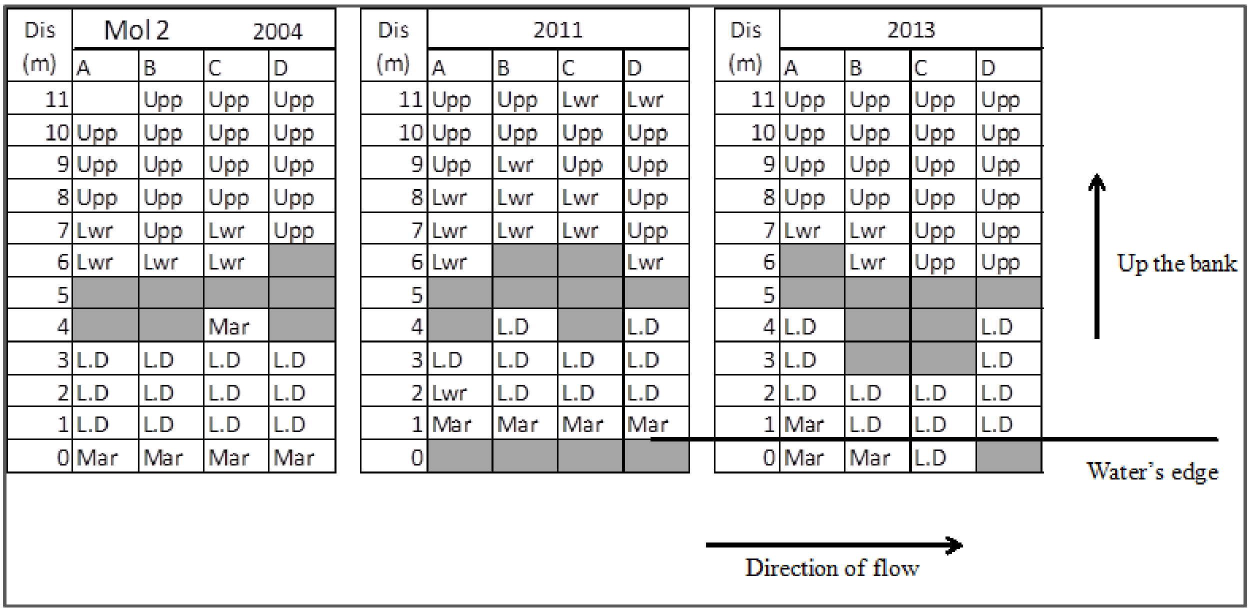
Dis (m)	Ela 4 2004			
	A	B	C	D
8	Upp	Upp	▨	▨
7	Upp	Upp	▨	▨
6	Upp	Upp	Lwr	Upp
5	Lwr	Lwr	Lwr	Upp
4	Lwr	Lwr	Lwr	Lwr
3	Lwr	Lwr	Lwr	Lwr
2	Lwr	Lwr	Lwr	Lwr
1	Lwr	Lwr	L.D	L.D
0	L.D			

Dis (m)	2011			
	A	B	C	D
8	Upp	Upp	Upp	Upp
7	Upp	Upp	Upp	Upp
6	Lwr	L.D	Lwr	Upp
5	Lwr	L.D	L.D	Lwr
4	L.D	L.D	L.D	L.D
3	L.D	L.D	L.D	L.D
2	Mar	L.D	▨	L.D
1	▨	▨	▨	▨
0	▨			

Dis (m)	2013			
	A	B	C	D
8	Upp	Upp	Upp	Lwr
7	Upp	Upp	Upp	Lwr
6	Upp	Upp	Lwr	Lwr
5	Upp	Upp	Lwr	Lwr
4	L.D	L.D	L.D	Lwr
3	L.D	L.D	L.D	L.D
2	L.D	L.D	L.D	L.D
1	Mar	L.D	L.D	L.D
0	Mar	Mar	Mar	Mar

Figure 3.11 Ela 4 lateral vegetation zones lateral zones 2004 (left) 2011 (middle) and 2013 (right). Dis= distance from the water's edge and vegetation transects (A, B, C and D). Lateral riparian zones are indicated using Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp = upper zone. The gray boxes show outliers or where no vegetation was recorded.

There were some shifts in zone boundaries at Mol 2 (Figure 3.12). This may be partly because the wet bank and dry bank were divided by a side channel. For all three years, the wet bank was located between 0 and 3 m, with the marginal zone between 0 and 1 m. There was a side channel about 2 m wide at a distance of 3 m form the main channel, which is shown by the grey boxes in Figure 3.12, where after the dry bank communities start.



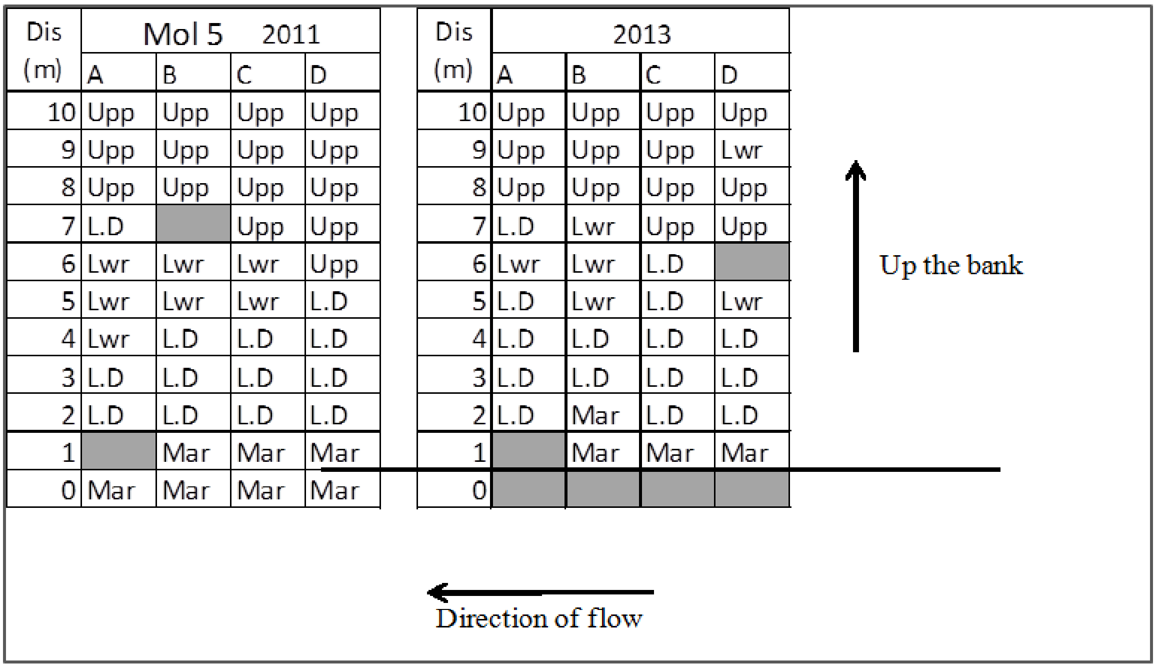
Dis (m)	Mol 2 2004			
	A	B	C	D
11		Upp	Upp	Upp
10	Upp	Upp	Upp	Upp
9	Upp	Upp	Upp	Upp
8	Upp	Upp	Upp	Upp
7	Lwr	Upp	Lwr	Upp
6	Lwr	Lwr	Lwr	▨
5	▨	▨	▨	▨
4	▨	▨	Mar	▨
3	L.D	LD	L.D	L.D
2	L.D	LD	L.D	L.D
1	L.D	LD	L.D	L.D
0	Mar	Mar	Mar	Mar

Dis (m)	2011			
	A	B	C	D
11	Upp	Upp	Lwr	Lwr
10	Upp	Upp	Upp	Upp
9	Upp	Lwr	Upp	Upp
8	Lwr	Lwr	Lwr	Upp
7	Lwr	Lwr	Lwr	Upp
6	Lwr	▨	▨	Lwr
5	▨	▨	▨	▨
4	▨	L.D	▨	L.D
3	L.D	L.D	L.D	L.D
2	Lwr	L.D	L.D	L.D
1	Mar	Mar	Mar	Mar
0	▨	▨	▨	▨

Dis (m)	2013			
	A	B	C	D
11	Upp	Upp	Upp	Upp
10	Upp	Upp	Upp	Upp
9	Upp	Upp	Upp	Upp
8	Upp	Upp	Upp	Upp
7	Lwr	Lwr	Upp	Upp
6	▨	Lwr	Upp	Upp
5	▨	▨	▨	▨
4	L.D	▨	▨	L.D
3	L.D	▨	▨	L.D
2	L.D	L.D	L.D	L.D
1	Mar	L.D	L.D	L.D
0	Mar	Mar	L.D	▨

Figure 3.12 **Mol 2 lateral vegetation zones lateral zones 2004 (left) 2011 (middle) and 2013 (right). Dis= distance from the water's edge and vegetation transects (A, B, C and D). Lateral riparian zones are indicated using Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp = upper zone. The gray boxes show outliers or where no vegetation was recorded.**

At Mol 5 (Figure 3.13) data were only collected for 2011 and 2013. As was the case for Mol 2, there were only minor changes in the locations of the lateral zones. Plots identified as the lower dynamic (between 2 - 4 m) and the lower zone (5 - 6 m) in 2011 mostly remained the same in 2013. The marginal (between 0 and 1 m) and upper (> 7 m) remained unchanged.



Dis (m)	Mol 5 2011			
	A	B	C	D
10	Upp	Upp	Upp	Upp
9	Upp	Upp	Upp	Upp
8	Upp	Upp	Upp	Upp
7	L.D	▨	Upp	Upp
6	Lwr	Lwr	Lwr	Upp
5	Lwr	Lwr	Lwr	L.D
4	Lwr	L.D	L.D	L.D
3	L.D	L.D	L.D	L.D
2	L.D	L.D	L.D	L.D
1	▨	Mar	Mar	Mar
0	Mar	Mar	Mar	Mar

Dis (m)	2013			
	A	B	C	D
10	Upp	Upp	Upp	Upp
9	Upp	Upp	Upp	Lwr
8	Upp	Upp	Upp	Upp
7	L.D	Lwr	Upp	Upp
6	Lwr	Lwr	L.D	▨
5	L.D	Lwr	L.D	Lwr
4	L.D	L.D	L.D	L.D
3	L.D	L.D	L.D	L.D
2	L.D	Mar	L.D	L.D
1	▨	Mar	Mar	Mar
0	▨	▨	▨	▨

Figure 3.13 Mol 5 lateral vegetation zones lateral zones 2011 (left) with 2013 (right). Dis= distance from the water's edge and vegetation transects (A, B, C and D). Lateral riparian zones are indicated using Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp = upper zone. The gray boxes show outliers or where no vegetation was recorded

In general for all four sites, the transition between the wet (marginal and lower dynamic zones) and dry (lower and upper zones) banks occurred at around 6 m from the water's edge. There were some shifts in zones but these were mainly associated with the boundary between the marginal and lower dynamic zones. Overall, the dry bank (lower and upper zones) did not change markedly at any of the sites.

3.4.3.2 Zonation using groundcover and trees separately

Using the 2013 vegetation data, two sets of MDS ordinations and cluster diagrams were generated; one using only groundcover species and the other using only tree species. The zonation pattern obtained using groundcovers was similar to that obtained using all species presented above and are presented in Appendix Figure 2. However, where only trees were used, the wet and dry banks were not easily separated (Figure 3.14 and Figure 3.15). In most cases, only the lower dynamic zone and the lower zone were distinguishable. In Ela 4 and Mol 5, the marginal zone was not identified, the reason could be that the cover percentage of the indicator tree species was less than cover percentages of other species (that are of other zones) that were present. At Mol 5 the *S. mucronata* species, which is mostly a marginal zone species was not present, whilst in Ela 4 it was present but in minimal amounts.

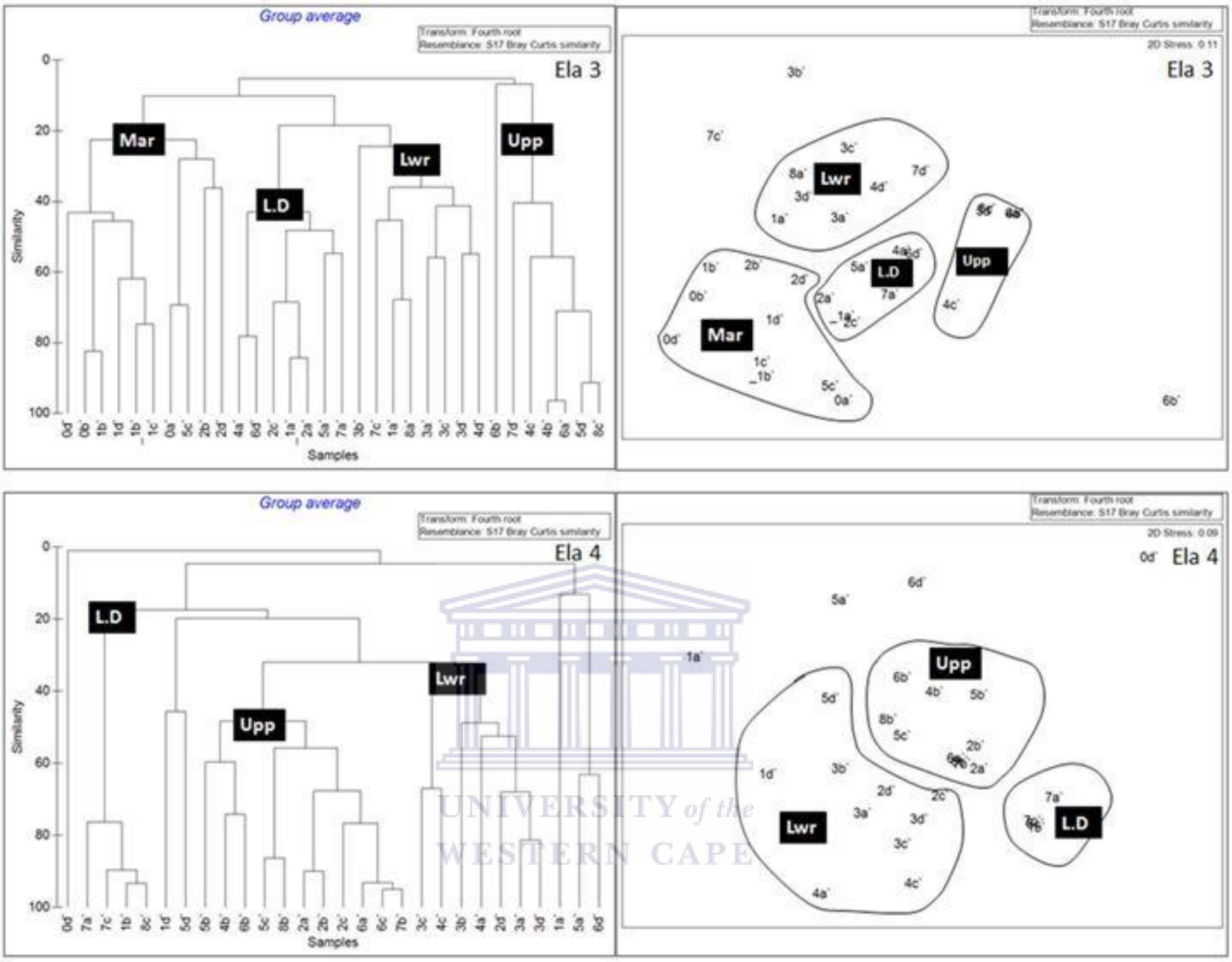


Figure 3.14 Cluster and MDS ordinations for 2013 tree data at Ela 3 and Ela 4. Sample plots (indicated as samples) are indicated within Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp =upper zone

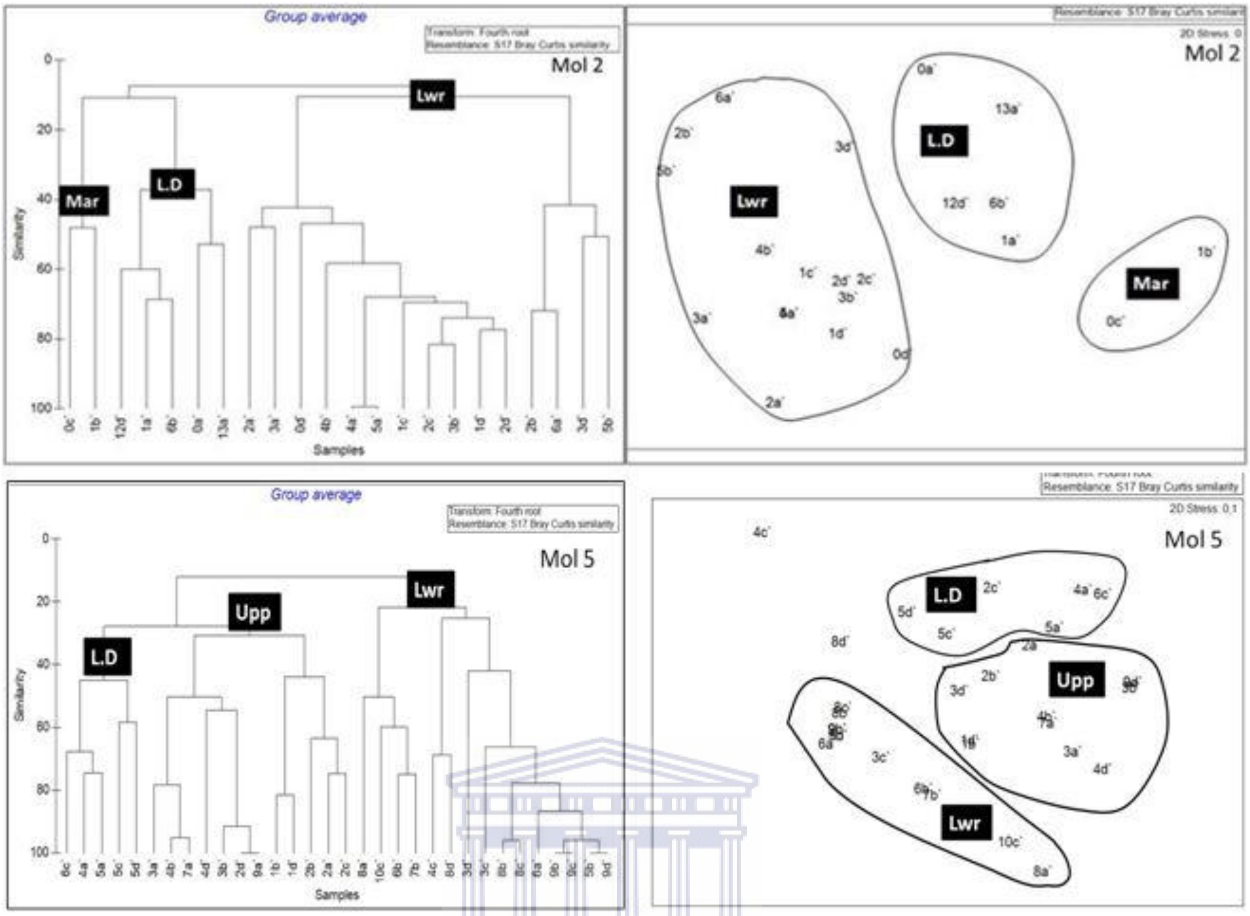


Figure 3.15 Cluster and MDS ordinations for 2013 tree data at Mol 2 and Mol 5. Sample plots (indicated as samples) are indicated within Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp =upper zone

3.4.4 Vegetation assemblages in the lateral zones

The percentage cover of individual species in the riparian zones ranged from as little as 0.15 to 57%, reflecting a wide variation in the distribution of plants between lateral zones and between sites (refer to Table 3.5 to Table 3.8). The assemblage analyses revealed that at all sites the marginal zones comprised mainly *Isolepis prolifera*, *Salix mucronata*, *Prionium serratum* and *Metrosideros angustifolia* seedlings.

At Ela 3 (Table 3.5) and Ela 4 (Table 3.6), the lower dynamic zone was characterised by *Elegia capensis* and saplings of *Salix mucronata*, *Brachylaena neriifolia* and *Brabejum stellatifolium*, with a number of *Metrosideros angustifolia* and *Salix mucronata* seedlings.

At Mol 2 (Table 3.7) and Mol 5 (Table 3.8), this zone was dominated by the trees *Morella serrata* and *Metrosideros angustifolia*.

Table 3.5 Species composition of each zone at Ela 3 with respectivetrees heights in meters. Column T shows the total cover percentage of a species and column F is the frequency of occurrence of the species within the lateral zone

Ela 3

Marginal	T	F	Lower dynamic	T	F
Metrosideros angustifolia seedling	26	2	*Metrosideros angustifolia seedling*	34	2
Salix mucronata 2-5	25	2	*Salix mucronata 0.3-2*	26	4
Salix mucronata 0.3-2	20	4	*Salix mucronata seedling*	13	2
Salix mucronata seedling	10	2	*Isolepis prolifera*	12	3
Isolepis prolifera	9	3	*Brabejum stellatifolium seedlings*	6	1
Brabejum stellatifolium seedlings	5	1	*Platylophus trifoliatus 0.3-2*	3	1
Moss	2	1	*Moss*	3	1

Lower	T	F	Upper	T	F
Elegia capensis	11	8	*Schizaea tenella*	12	4
Pteridium aquilinum	8	8	*Aristea sp.*	10	6
Brabejum stellatifolium 0.3-2	6	5	*Pteridium aqualinum*	7	6
Schizaea tenella	5	2	*Moss*	6	2
Diospyros glabra	5	7	*Capeochloa cincta*	6	4
Brabejum stellatifolium 2-5	5	4	*Cyperaceae sp.*	5	3
Morella serrata 0.3-2	3	3	*Metrosideros angustifolia 2-5*	4	1
Ilex mitis 2-5	3	1	*Calopsis paniculata*	3	2
Moss	3	5	*Morella serrata 0.3-2*	2	4
Metrosideros angustifolia 2-5	3	1	*Brabejum stellatifolium 2-5*	2	1
Aristea sp.	2	2	*Elegia sp.*	2	2
Drosera capensis	2	3	*Drosera capensis*	2	3
Metrosideros angustifolia 0.3-2	2	2	*Elegia capensis*	2	1
Podalyria sp.	1	2	*Morella serrata 2-5*	1.4	1
Psoralea cf. affinis	1	2	*Brabejum stellatifolium 0.3-2*	1.4	1
Brachylaena neriifolia 2-5	1	1	*Cyperaceae sp.12*	1.4	1
Platylophus trifoliatus 0.3-2	1	1	*Metrosideros angustifolia 0.3-2*	0.9	1
Platylophus trifoliatus 2-5	1	2	*Lycopodiella caroliniana*	0.9	1
Capeochloa cincta	1	1	*Diospyros glabra*	0.5	1
Brachylaena neriifolia 0.3-2	1	2	*Pentameris (Pentaschistis) sp.*	0.5	1
Todea babara	1	1	*Podalyria sp.*	0.5	1
Metrosideros angustifolia seedling	1	3	*Osmitopsis*	0.3	1
			Morella serrata seedlings	0.2	1
			Ehrharta ramosa	0.2	1
			Stoebe sp.2	0.2	1

Table 3.6 Species composition of each zone at Ela 4 with respectivetrees heights in meters. Column T shows the total cover percentage of a species and column F is the frequency of occurrence of the species within the lateral zone

Ela 4

Marginal	T	F
Isolepis prolifera	57	5
Morella serrata 2-5	17	1
Metrosideros angustifolia seedling	11	1
Brabejum stellatifolium seedlings	6	1
Moss	6	1
Morella serrata seedlings	3	1

Lower dynamic	T	F
Moss	12	8
Elegia capensis	11	7
Brachylaena neriifolia 0.3-2	9	7
Brabejum stellatifolium 0.3-2	9	9
Metrosideros angustifolia 2-5	7	4
Calopsis paniculata	7	7
Morella serrata 0.3-2	6	5
Metrosideros angustifolia 0.3-2	6	5
Erica caffra	5	5
Diospyros glabra	5	5
Stoebe sp.	4	6
Pseudobaeckia africana	3	2
Aristea sp.	2	3
Platycaulos sp.	2	1
Schizaea tenella	1.4	1
Erica pinea	0.9	1
Psoralea cf. affinis	0.9	1
Metrosideros angustifolia seedling	0.7	1
Ilex mitis 0.3-2	0.5	1
Heeria argentea 0.3-2	0.2	1
Drosera capensis	0.2	1
Ischyrolepis subverticillata	0.2	1

Lower	T	F
Erica pinea	23	5
Cliffortia strobilifera	13	2
Brabejum stellatifolium 2-5	9	1
Brabejum stellatifolium 0.3-2	8	3
Hymenolepis parviflora	7	2
Hackea sericia	6	2
Cymbopogon marginatus	5	2
Ischyrolepis subverticillata	5	1
Erica caffra	4	1
Diospyros glabra	4	4
Ilex mitis 0.3-2	3	1
Brachylaena neriifolia 2-5	3	1
Morella serrata 0.3-2	1.2	1
Aristea sp.	0.6	1
Cf. Heliophila sp.	0.6	1

Upper	T	F
Cyperaceae sp.	19	9
Pentameris (Pentaschistis) sp.	10	8
Cliffortia strobilifera	8	5
Brabejum stellatifolium 0.3-2	8	5
Erica pinea	7	5
Morella serrata 0.3-2	6	6
Ilex mitis 0.3-2	4	3
Aristea sp.	4	4
Moss	4	6
Stoebe plumosa	3	3
Hymenolepis parviflora	3	5
Ischyrolepis subverticillata	3	3
Calopsis paniculata	2	1
Stoebe sp.	2	3
Diospyros glabra	2	3
Pseudobaeckia africana	1	1
Askidiosperma paniculatum	1	1
Brabejum stellatifolium seedlings	1	1
Todea barbara	1	1
Metrosideros angustifolia 0.3-2	0.3	1
Elegia capensis	0.3	1
Ehrharta ramosa	0.3	1
Lobelia jasionoides	0.3	1
Morella serrata 2-5	0.1	1

Table 3.7 Species composition of each zone at Mol 2 with respectivetrees heights in meters. Column T shows the total cover percentage of a species and column F is the frequency of occurrence of the species within the lateral zone.

Mol 2

Marginal	T	F
Isolepis prolifera	24	3
Hemarthria altissima	13	3
Metrosideros angustifolia 0.3-2	11	2
Morella serrata 0.3-2	7	2
Platycaulos sp.	6	3
Prionium serratum	5	2
Capeochloa cincta	5	4
Brabejum stellatifolium 0.3-2	4	1
Salix mucronata 0.3-2	4	2
Freylinia lanceolata 0.3-2	3	1
Holcus lanatus L.	3	2
Acacia mearnsii 0.3-2	2	2
Pentameris (Pentaschistis) sp.	2	1
Sesbania punicea	1.2	3
Moss	1.0	1
Morella serrata seedlings	0.4	1
Acacia mearnsii seedling	0.2	1

Lower dynamic	T	F
Restionaceae sp.	25	12
Morella serrata 2-5	21	11
Platycaulos sp.	13	9
Metrosideros angustifolia 2-5	11	8
Ischyrolepis subverticillata	6	4
Salix mucronata 2-5	5	3
Brabejum stellatifolium 0.3-2	4	6
Freylinia lanceolata 0.3-2	3	4
Moss	2	2
Metrosideros angustifolia 0.3-2	2	1
Isolepis prolifera	2	2
Morella serrata 0.3-2	1	3
Holcus lanatus L.	1	1
Anthospermum spathulatum	0.5	1
Capeochloa cincta	0.5	1
Pycreus polystachyos	0.3	1
Sesbania punicea	0.2	2
Prionium serratum	0.15	1
Hemarthria altissima	0.15	1
Freylinia lanceolata seedlings	0.10	1
Acacia mearnsii 0.3-2	0.10	1
Salix mucronata seedling	0.10	1
Metrosideros angustifolia seedling	0.05	1
Morella serrata seedlings	0.05	1

Lower	T	F
Morella serrata 0.3-2	15	1
Prionium serratum	15	1
Fuirena hirsuta	10	1
Elegia capensis	6	1
Holcus lanatus L.	5	2
Platycaulos sp.	5	3
Stoebe plumosa	4	2
Searsia angustifolia	4	4
Acacia mearnsii 0.3-2	4	2
Brabejum stellatifolium 0.3-2	4	2
Restionaceae sp.	4	1
Salix mucronata 0.3-2	3	1
Freylinia lanceolata 0.3-2	3	1
Acacia mearnsii seedling	2	2
Anthospermum spathulatum	1.5	1
Pseudobaeckia africana	1.5	1
Ehrharta ramosa	1.5	1
Erica sp.	1.2	1
Pteridium aqualinum	0.9	1
Asteraceae sp.	0.9	1
Hemarthria altissima	0.6	1

Upper	T	F
Stoebe plumosa	30	17
Searsia angustifolia	25	15
Pteridium aqualinum	20	19
Cliffortia strobilifera	7	5
Diospyros glabra	5	4
Ischyrolepis subverticillata	3	3
Pentameris (Pentaschistis) sp.	3	2
Brabejum stellatifolium 0.3-2	1.4	1
Fuirena hirsuta	1.4	1
Erica sp.	1.4	2
Acacia mearnsii 0.3-2	0.9	2
Hymenolepis parviflora	0.4	1

Table 3.8 Species composition of each zone at Mol 5 with respectivetrees heights in meters. Column T shows the total cover percentage of a species and column F is the frequency of occurrence of the species within the lateral zone.

Mol 5

Marginal	T	F
Morella serrata 0.3-2	22	3
Ehrharta ramosa	22	4
Prionium serratum	9	2
Calopsis paniculata	7	1
Brabejum stellatifolium 0.3-2	7	1
Isolepis prolifera	7	3
Metrosideros angustifolia seedling	6	3
Metrosideros angustifolia 0.3-2	4	2
Morella serrata seedlings	4	1
Acacia mearnsii 0.3-2	4	3
Holcus lanatus	4	1
Platycaulos sp.	4	1
Moss	1.2	1

Lower dynamic	T	F
Brabejum stellatifolium 0.3-2	25	11
Morella serrata 0.3-2	14	6
Metrosideros angustifolia 2-5	14	4
Erica caffra	12	5
Metrosideros angustifolia 0.3-2	6	3
Cyperaceae sp.	5	2
Calopsis paniculata	5	2
Ischyrolepis subverticillata	4	4
Freylinia lanceolata 2-5	4	1
Moss	3	2
Acacia mearnsii 0.3-2	2	3
Acacia longifolia 0.3-2	2	3
Searsia angustifolia	0.8	1
Stoebe plumosa	0.4	1
Diospyros glabra	0.4	1
Morella serrata seedlings	0.4	1
Fuirena hirsuta	0.4	1
Metrosideros angustifolia seedling	0.16	1

Lower	T	F
Metrosideros angustifolia 2-5	25	1
Acacia mearnsii 0.3-2	22	6
Metrosideros angustifolia 0.3-2	18	2
Cyperaceae sp.	16	2
Ischyrolepis subverticillata	7	1
Brabejum stellatifolium 2-5	5	1
Acacia longifolia 0.3-2	4	1
Calopsis paniculata	2	1
Diospyros glabra	2	1

Upper	T	F
Searsia angustifolia	36	15
Diospyros glabra	13.1	6
Ischyrolepis subverticillata	7.3	8
Fuirena hirsuta	5.6	6
Acacia mearnsii 0.3-2	4.6	5
Stoebe plumosa	4.4	3
Calopsis paniculata	4.1	3
Brabejum stellatifolium 2-5	3.6	2
Morella serrata 2-5	2.1	1
Metrosideros angustifolia 0.3-2	1.8	2
Elegia capensis	1.5	2
Hemarthria altissima	1.3	2
Brabejum stellatifolium 0.3-2	1.03	1
Prionium serratum	1.03	1
Cliffortia sericea	0.77	1
Pentameris (Pentaschistis) sp.	0.77	2
Anthospermum spathulatum	0.51	1
Thesium juncifolium	0.36	1
Peucedanum galbanum	0.26	1
Elytropappus scaber	0.26	1
Platycaulos sp.	0.26	1
Brabejum stellatifolium seedlings	0.05	1

The lower zone comprised some species that also belonged to the lower dynamic and upper zone. The lower zone at Ela 3, Ela 4 and Mol 2 was dominated by *Brabejum stellatifolium* and *Morella serrata*, with the latter being typical of the lower dynamic zone. Similarly, at Ela 3 and Ela 4, *Pteridium aquilium*, an upper zone plant, occurred in the lower zone and at Mol 2 *Prionium serratum*, which is a marginal species occured in the lower zone. At the Elands sites, there was a high percentage of *Diospyros glabra* in the lower zone while on the Molenaars River much this species was mostly in the upper zone.

At Ela 3 and Ela 4, the upper zone was dominated by the fern species *Schizaea tenella*, and some species of *Cyperaceae* and *Pentameri*s. The upper zone at the Mol 2 and 5 was dominated by bushes of *Searsia angustifolia*, *Diospyros glabra* and *Stoebe plumosa*. *Calopsis paniculata* appears in this zone at all sites but in small amounts.

3.4.5 Distribution of trees in the lateral zones

The distributions of five common trees were compared across the lateral zones at all sites: *Salix mucronata*, *Morella serrata*, *Metrosideros angustifolia*, *Brabejum stellatifolium* and *Brachylaena neriifolia* (Figure 3.16). These were selected based on their common occurrence in the Western Cape area and because they are members of the Fynbos Riparian Vegetation community.

Different species were more numerous at different distances up the bank (Figure 3.16 and Figure 3.17). *S. mucronata* was dominant at 0 to 1 m, *M. angustifolia* was found all the way up the bank but numbers peaked at 1 m from the water’s edge. *B. stellatifolium* also occurred throughout the riparian zone, but the number of individuals peaked at 3 m. *B. neriifolia* did not occur within the channel, but from 1 m, numbers gradually increased to a peak at 5 m. There was a mixture of species in the wetted channel and on the water’s edge, with *M. serrata, S. mucronata* and *M. angustifolia* being most abundant.

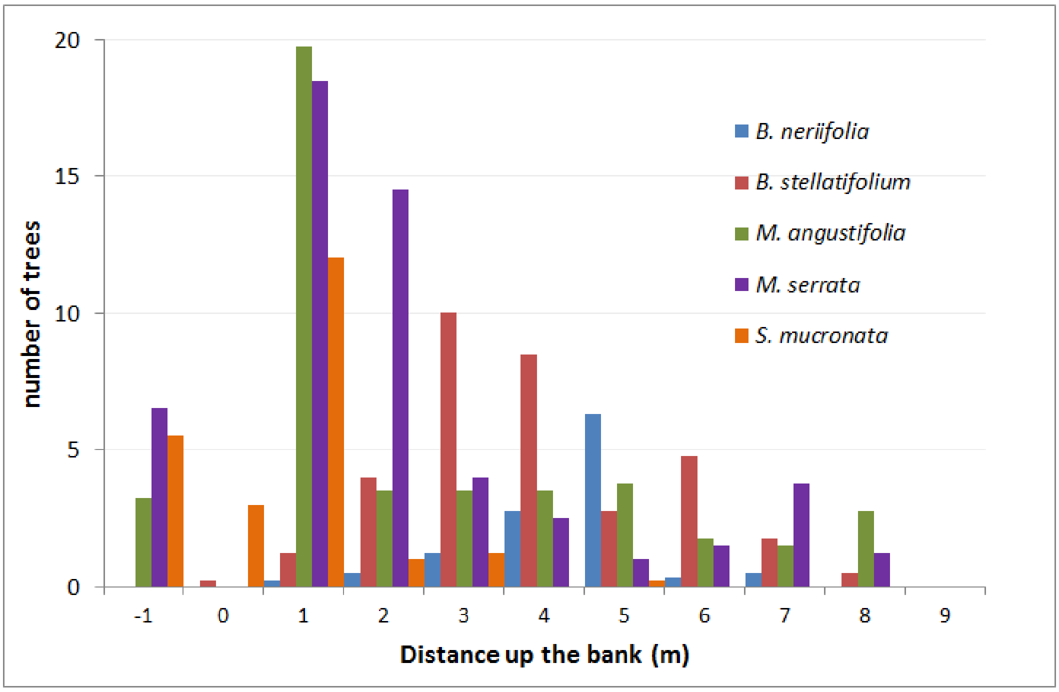


Figure 3.16 The mean number of individuals per species up the bank at the four study sites in 2013

Wet bank species tended to have the highest abundance at distances that are closer to the water's edge whilst the dry bank species peaked after this distance. For instance, *S. mucronata*, *M. serrata* and *M. angustifolia* all peaked at 1 m from the water's edge then gradually decreased up the bank (Figure 3.17). On the other hand the dry bank species, *B. stellatifolium* and *B. neriifolia*, gradually increased to 3 m and then declined again after 6 m. *M. serrata* (lower dynamic zone), *M. angustifolia* (lower zone) and *B. stellatifolium* (upper zone) have multiple peaks at different positions up the bank. This is a different behaviour from the *S. mucronata* (marginal zone) which only have one high peak followed by a sudden fall. Thus the wet bank species possibly occur as groups and populate the same area whilst the dry bank species are usually well spread laterally on bank.

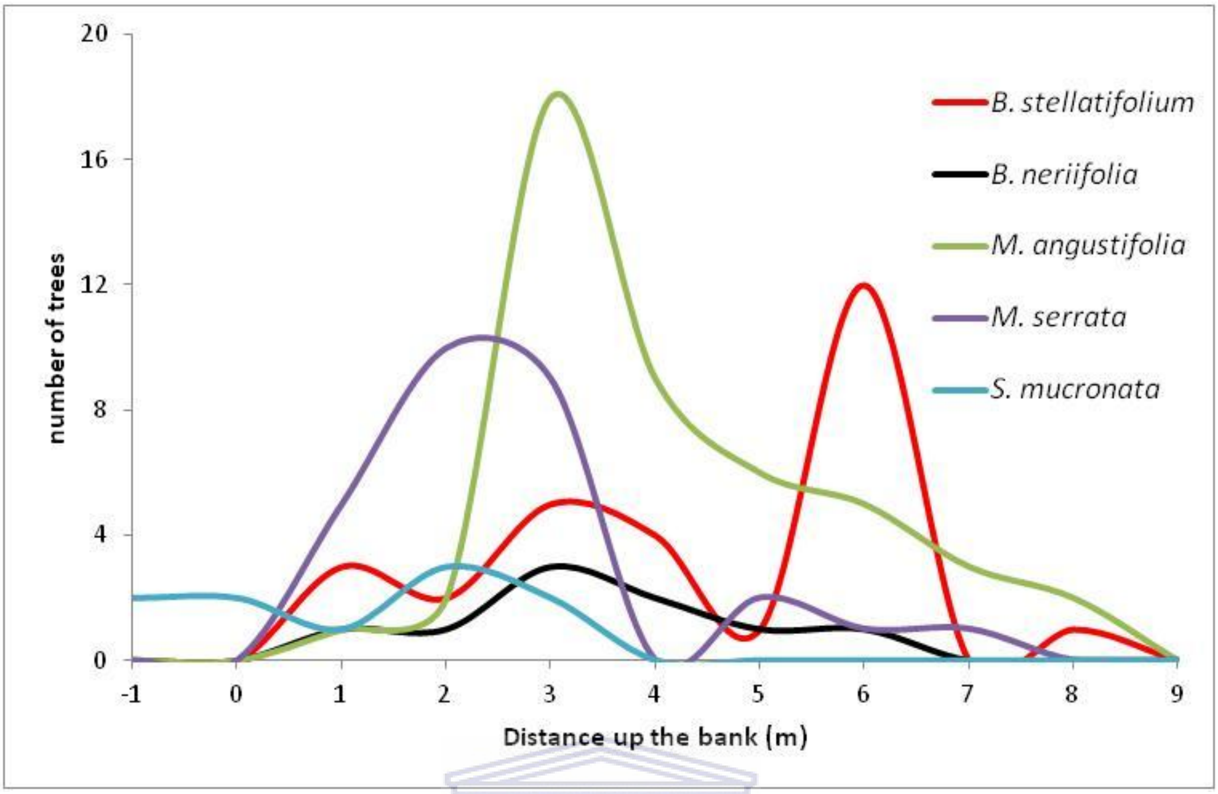


Figure 3.17 An illustration of the distribution of species abundance up the bank

3.4.6 Distribution of life stages of trees

Trees were categorized into three life stages based on height; seedlings (<0.3 m tall), saplings (0.4 to 1.9 m tall) and adults (>2 m tall). Thereafter, the number of seedlings, saplings and adults in 2004, 2011 and 2013 were examined (Figure 3.18). For the most part, regardless of the date of collection, there were more seedlings than saplings and adults, and again more saplings than trees, except in 2004, where there were more adults than saplings (114 saplings and 128 adults).

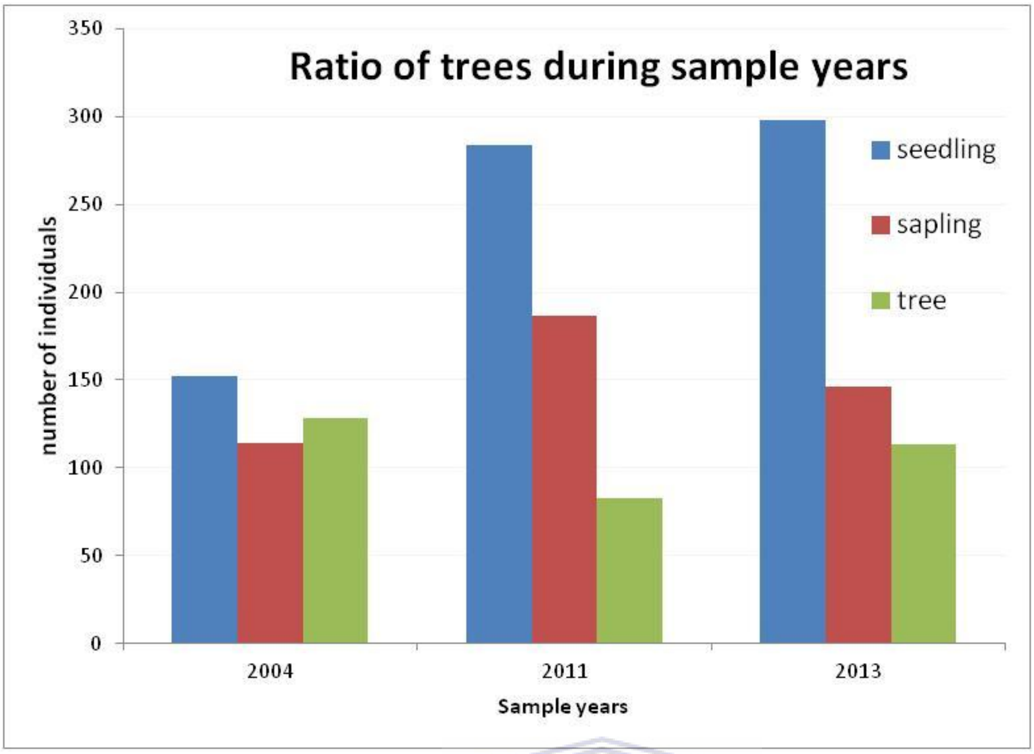
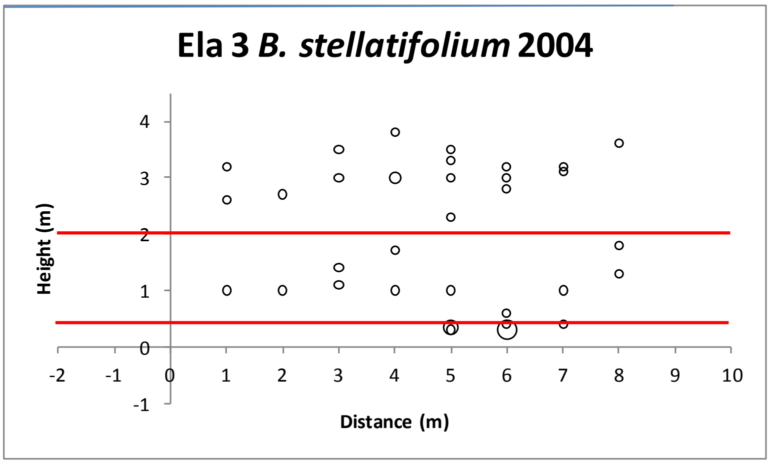
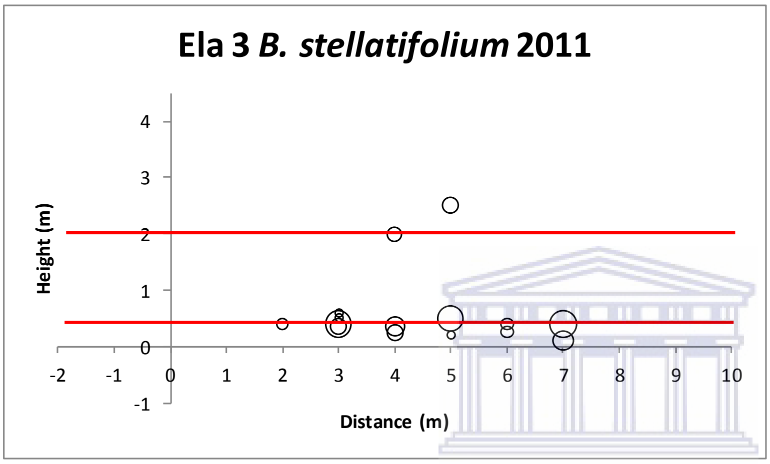


Figure 3.18 Number of seedlings, saplings and adults for all sites in 2004, 2011 and 2013

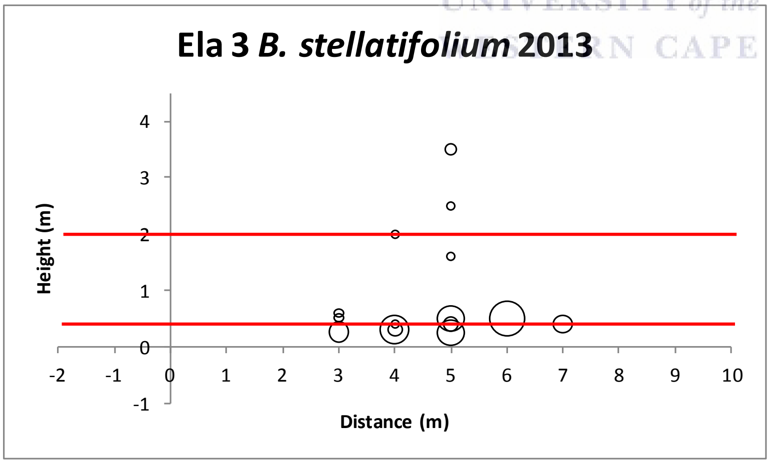
A comparison of plant life stages that occurred at distances up the bank at each site was done for the three sample periods. The distributions of seedlings, saplings and adults for each species at each site in each year are provided in Figure 3.19 to Figure 3.34. The size of the circle is proportional to the number of individuals of the same height occurring at a particular distance up the bank. The table alongside each graph gives the actual count of trees of different height at distances (Dis) from the water's edge.



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1			1			1		1
2			1			1		
3			1	1		1	1	
4			1	1			1	1
5	4		1		1		2	1
6	6	1				1	3	
7	1		1				2	
8			1	1				1
9								
10								

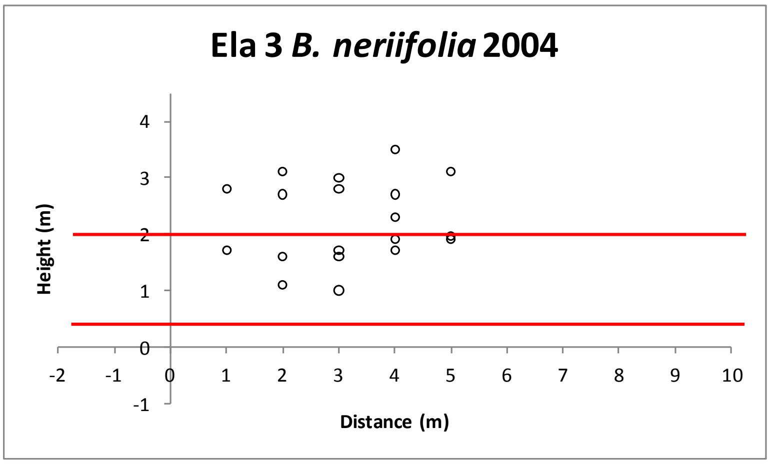


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2	3							
3	5	14						
4	8				1			
5	10	4		1		2		
6	8							
7	33							
8								
9								
10								

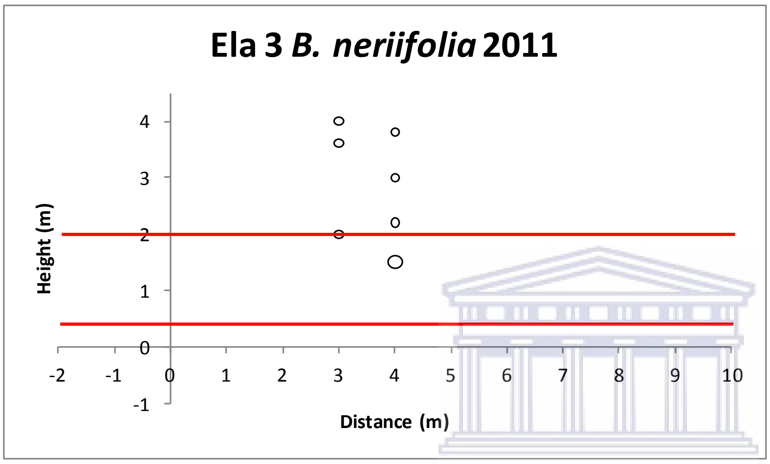


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2								
3	6	2						
4	16			1				
5	23			1			2	
6		18						
7	5							
8								
9								
10								

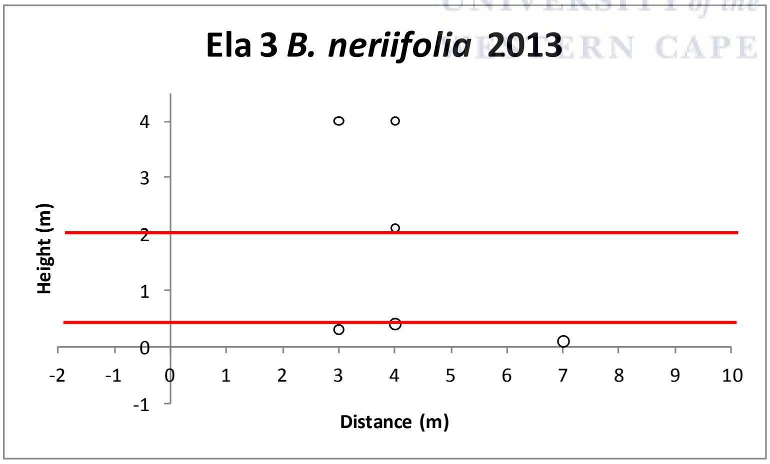
Figure 3.19 The number of individuals of *B. stellatifolium* in the three life stages at Ela 3. Red lines separate the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank, reflected by the size of the circles on the graph



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1				1		1		
2			1	1		1	1	
3			1	2		1	1	
4				2	1	1		1
5				2			1	
6								
7								
8								

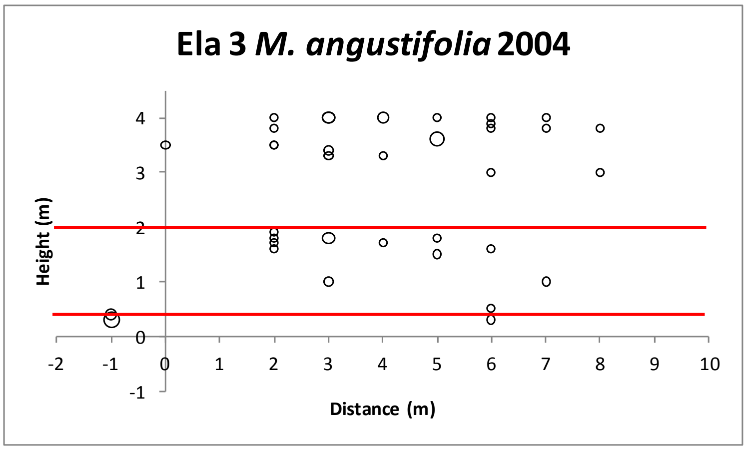


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2								
3					1			2
4				3	1			1
5								
6								
7								
8								

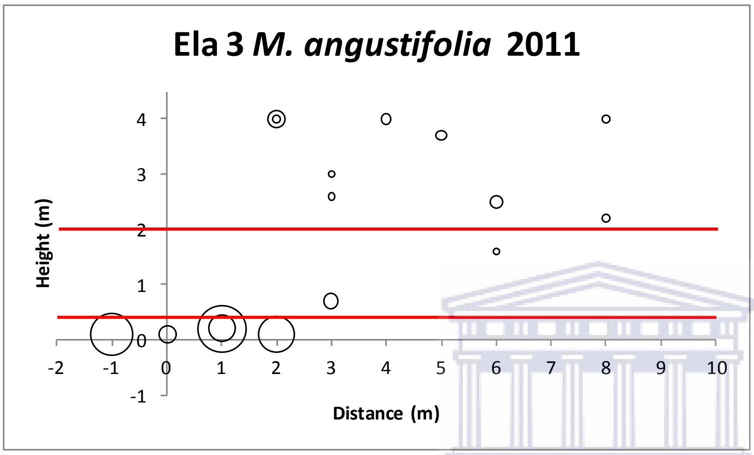


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2								
3	1							1
4	2				1			1
5								
6								
7	2							
8								

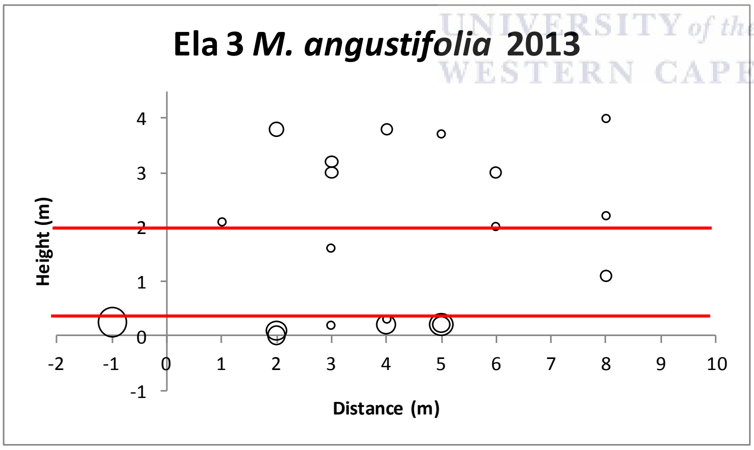
Figure 3.20 The number of individuals of *B. neriifolia* in the three life stages at Ela 3. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
-1	6							
0								1
1				3				
2					4			4
3			1					
4				1			2	2
5				2				2
6	1	1		1			1	2
7			1					2
8							1	1

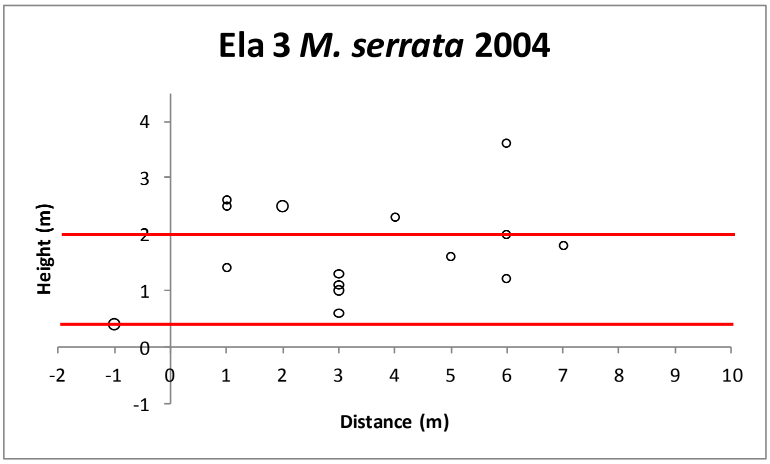


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
-1	35							
0	6							
1	59							
2	26							7
3		4				2		
4								2
5								2
6				1		3		
7								
8					1			1



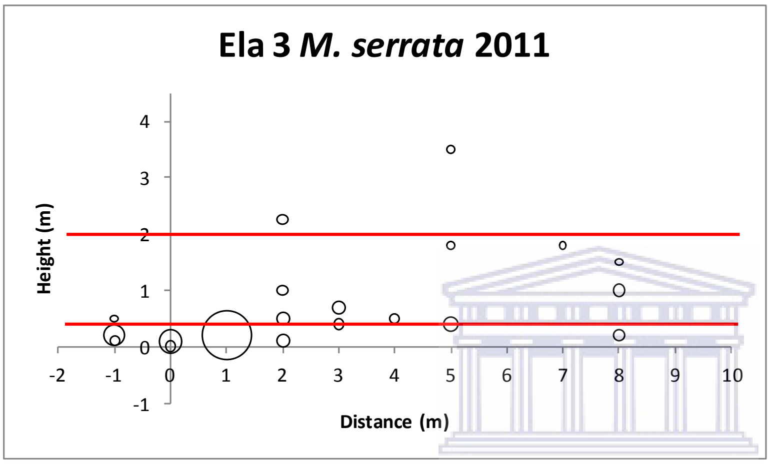
Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
-1	13							
0								
1					1			
2	5							3
3	1		2			2		
4	7							2
5	11							1
6				1		2		
7								
8			2		1			1

Figure 3.21 The number of individuals of *M. angustifolia* in the three life stages at Ela 3. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph



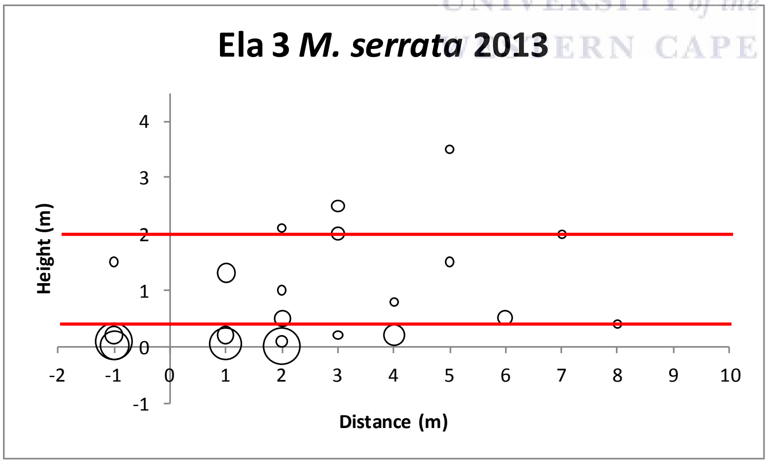
Ela 3 *M. serrata* 2004

Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
-1	2							
0								
1			1			2		
2						2		
3		1	3					
4					1			
5				1				
6					2			1
7				1				
8								



Ela 3 *M. serrata* 2011

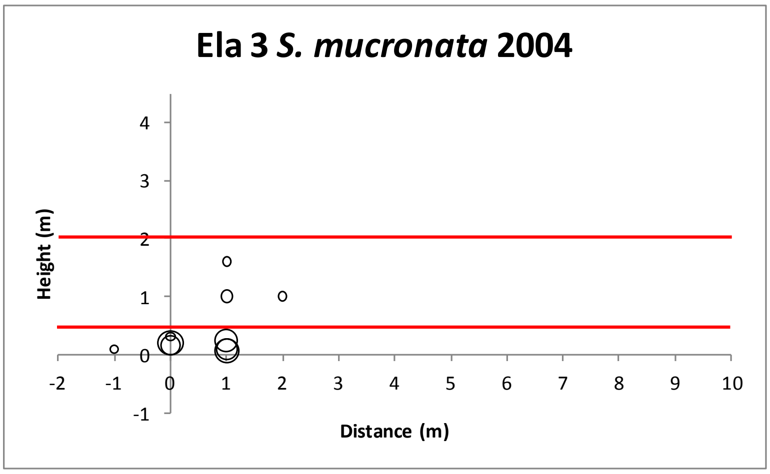
Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
-1	11							
0	13							
1	46							
2	3	3	2		2			
3	2	3						
4		2						
5	4			1			1	
6								
7				1				
8	3	1	2					



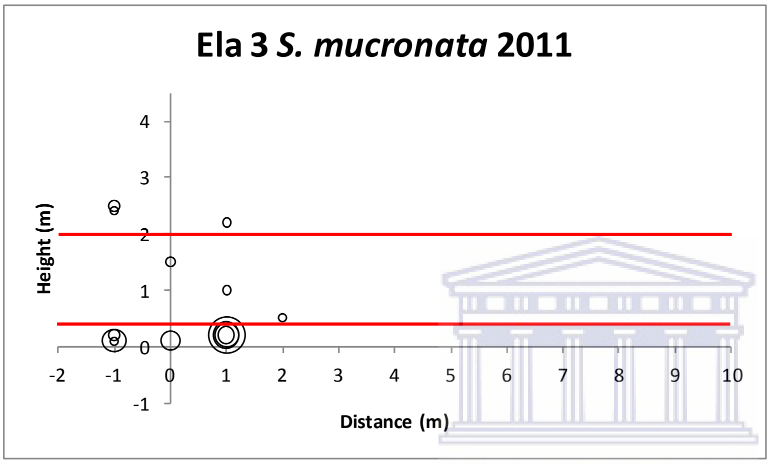
Ela 3 *M. serrata* 2013

Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
-1	37		1					
0								
1	19		5					
2	22	4	1		1			
3	1				2	2		
4	6	1						
5			1				1	
6		3						
7				1				
8	1							

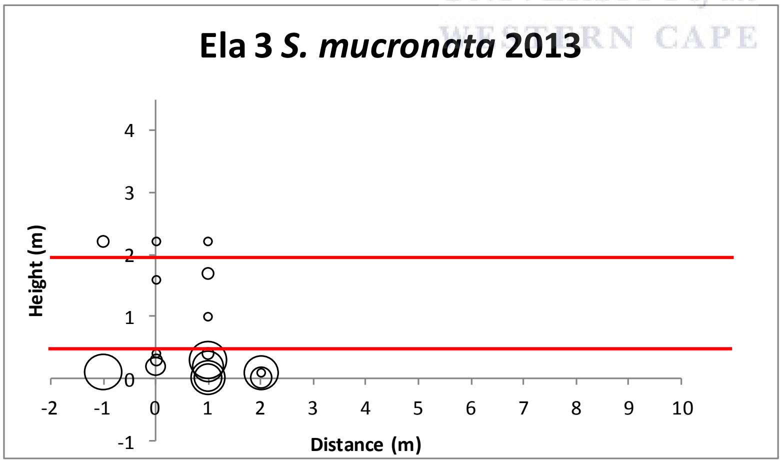
Figure 3.22 The number of individuals of *M. serrata* in the three life stages at Ela 3. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
-1	1							
0	15							
1	8	8	2	1				
2			1					
3								
4								
5								
6								
7								
8								

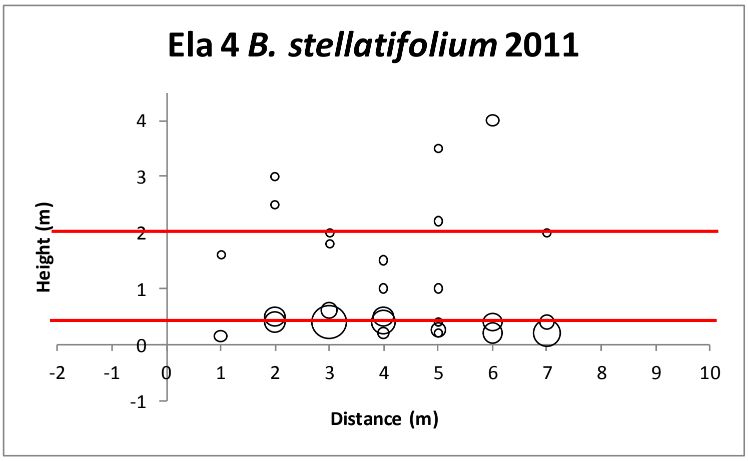


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
-1	11				1	2		
0	6			1	1			
1	39		1					
2		1						
3								
4								
5								
6								
7								
8								



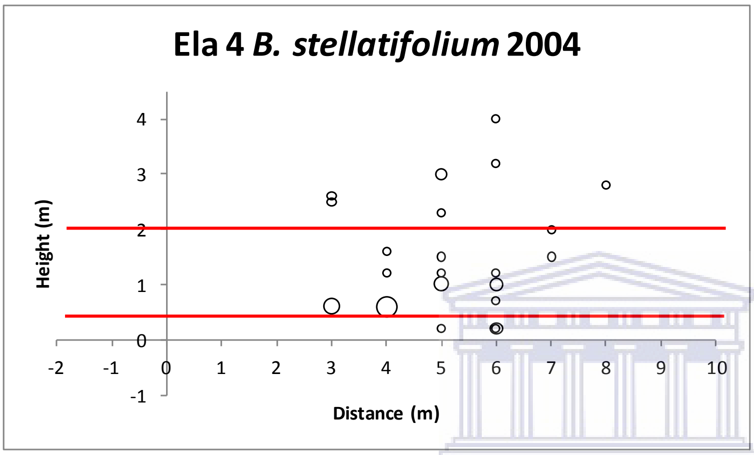
Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
-1	20				2			
0	8			1	1			
1	65	1			1			
2	25							
3								
4								
5								
6								
7								
8								

Figure 3.23 **The number of individuals of *S. mucronata* in the three life stages at Ela 3. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph**



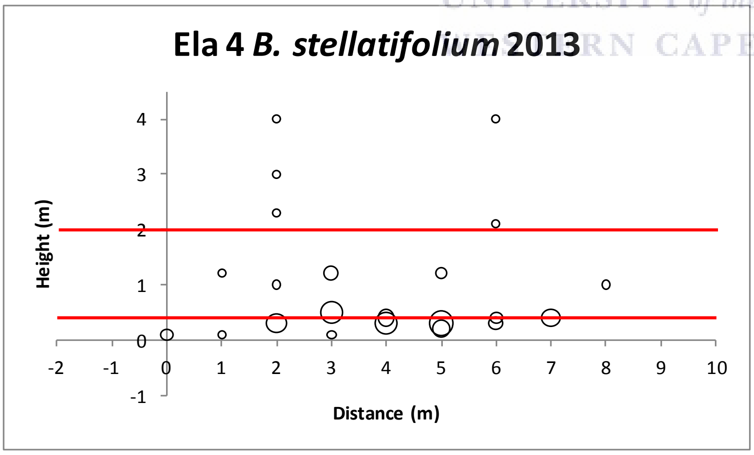
Ela 4 *B. stellatifolium* 2011

Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	2			1				
2	7				1	1		
3	18	4		1	2			
4	11	6	1	1				
5	6		1		1		1	
6	11							2
7	13				1			
8								
9								
10								



Ela 4 *B. stellatifolium* 2004

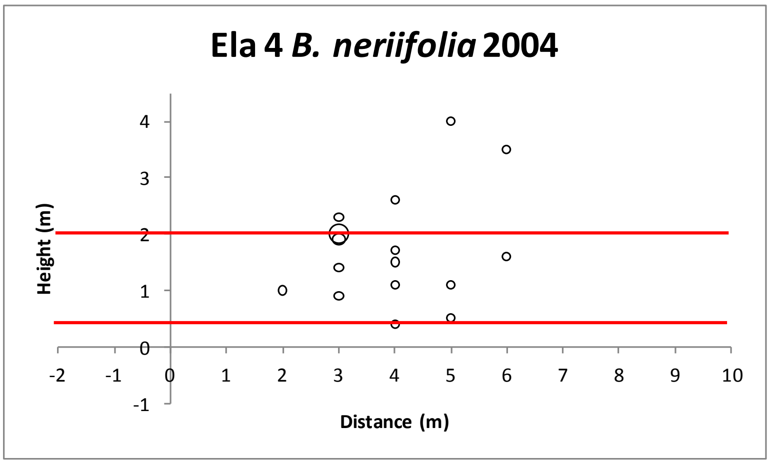
Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2								
3		4			1	1		
4		6	1	1				
5	1		5		1	2		
6	3	1	2				1	1
7			1	1				
8						1		
9								
10								



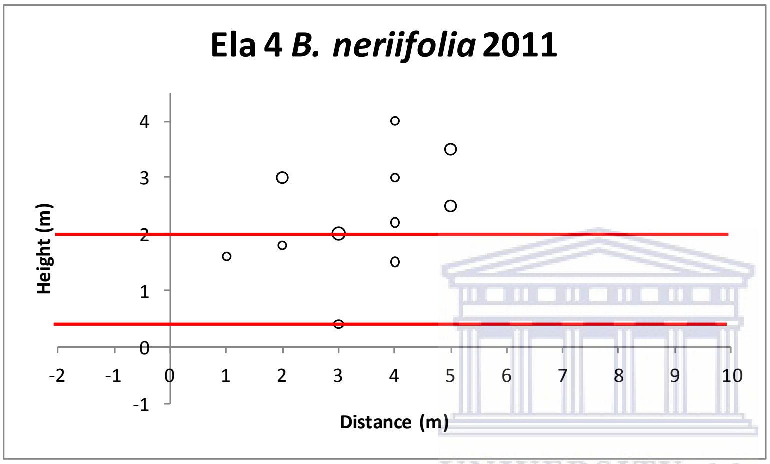
Ela 4 *B. stellatifolium* 2013

Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
0	2							
1	1		1					
2	6				1	1		1
3	1	8	3					
4	11							
5	13		2					
6	5				1			1
7	5							
8			1					
9								

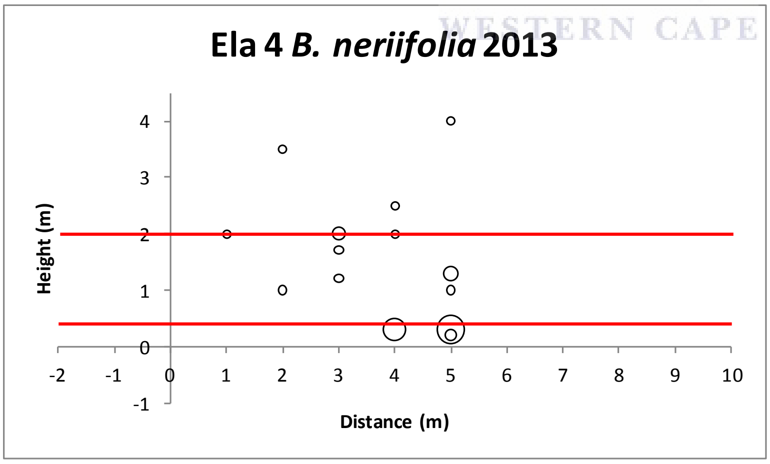
Figure 3.24 The number of individuals of *B. stellatifolium* in the three life stages at Ela 4. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2			1					
3		1	1	2	6			
4	1		1	2	1			
5		1	1					1
6				1				1
7								
8								
9								
10								

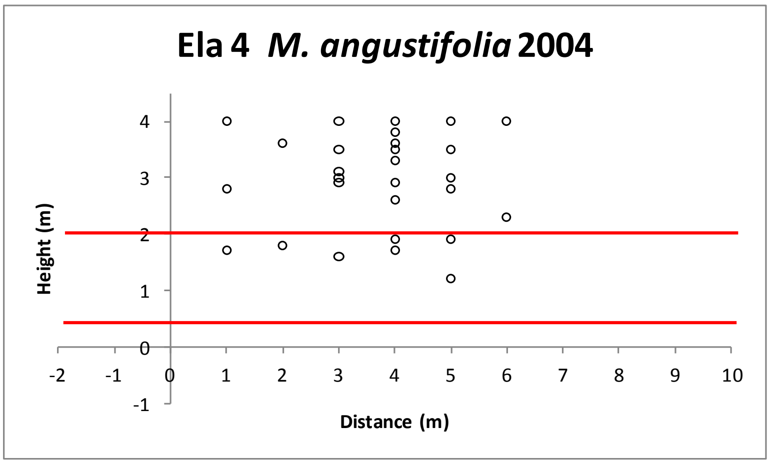


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1				1				
2				1		2		
3	1			2				
4			1		1	1		1
5					2		2	
6								
7								
8								
9								
10								

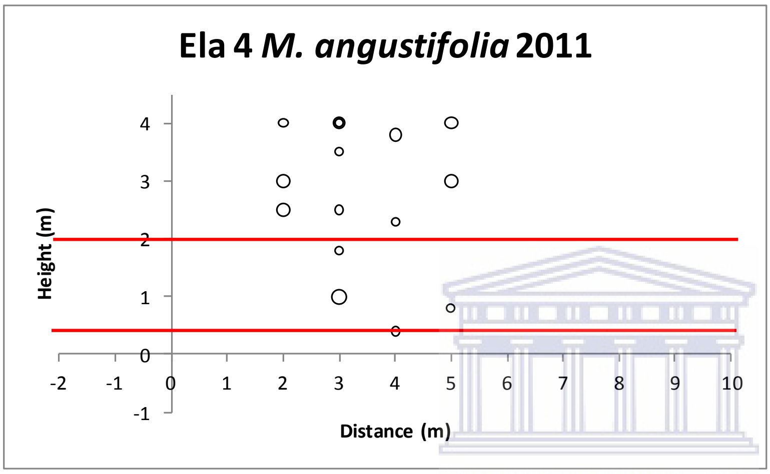


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1					1			
2			1				1	
3			1	1	2			
4	7				1	1		
5	14		4					1
6								
7								
8								
9								
10								

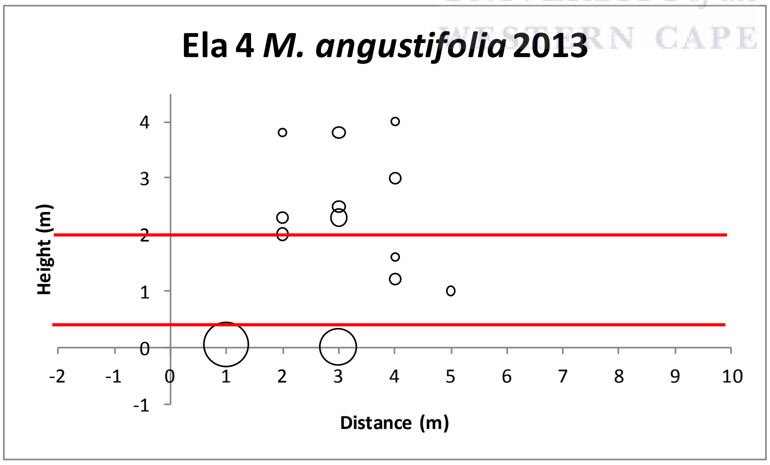
Figure 3.25 The number of individuals of *B. neriifolia* in the three life stages at Ela 4. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1				1		1		1
2				1				2
3				1		1	3	1
4				2		2	1	2
5			2	1		1	1	1
6					2			1
7								
8								
9								
10								

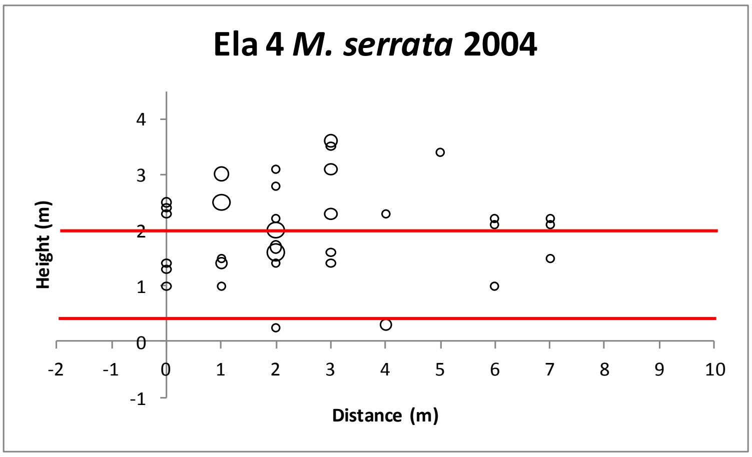


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2						2	2	1
3			1	1		1		3
4	1				1			2
5		1					2	2
6								
7								
8								
9								
10								

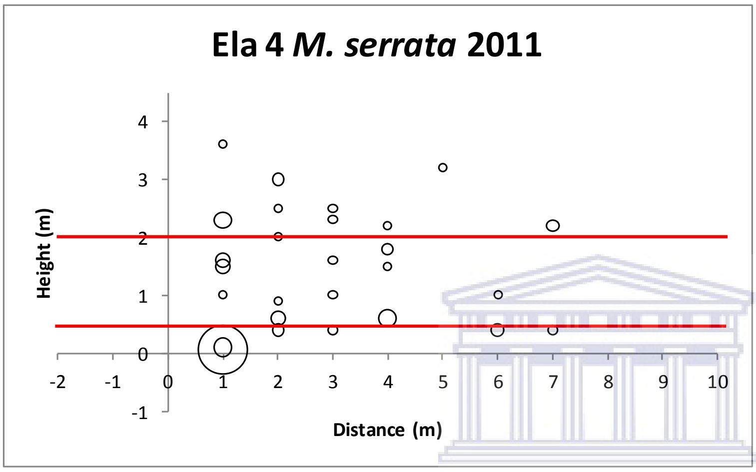


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	30							
2					2			1
3	20				4	1		2
4			2	1			2	1
5		1						
6								
7								
8								
9								
10								

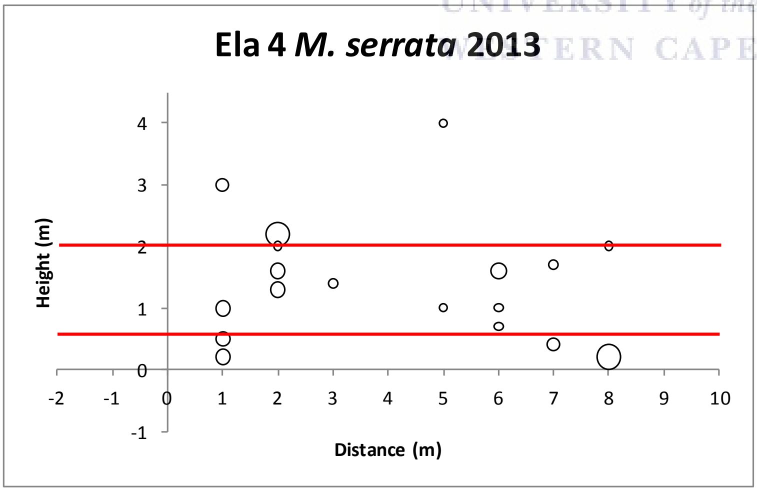
Figure 3.26 **The number of individuals of *M. angustifolia* in the three life stages at Ela 4. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph**


Ela 4 *M. serrata* 2004

Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
0			3		3			
1		1	3		4	3		
2	1		1	7	5	1		
3			1	1	2		5	
4	2				1			
5							1	
6		1			2			
7			1		2			
8								
9								
10								

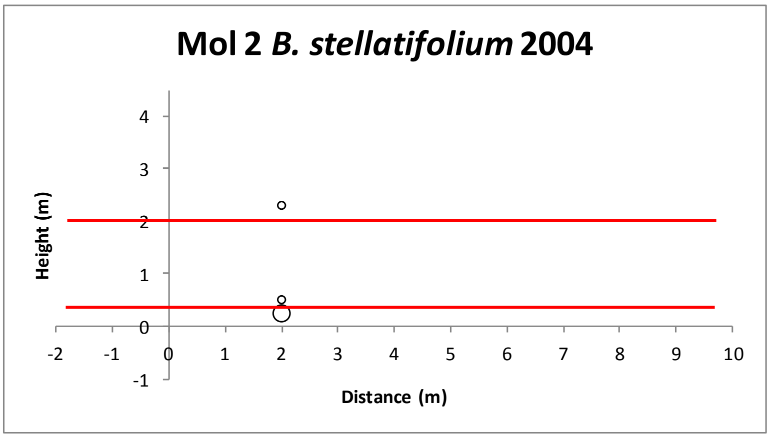

Ela 4 *M. serrata* 2011

Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	40	1	3	3				1
2	2	4		1	1	2		
3	1	1		1	1	1		
4		4	1	2	1			
5							1	
6	2	1						
7	1				2			
8								
9								
10								

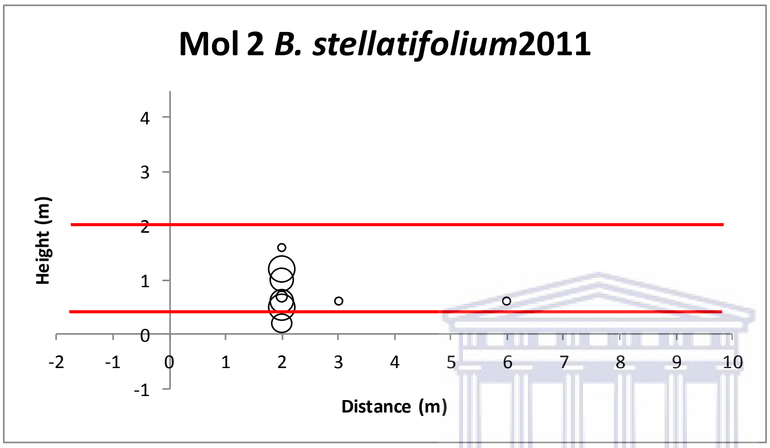

Ela 4 *M. serrata* 2013

Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	6	3				2		
2			3	4	7			
3			1					
4								
5		1						1
6		2		3				
7	2			1				
8	8			1				
9								
10								

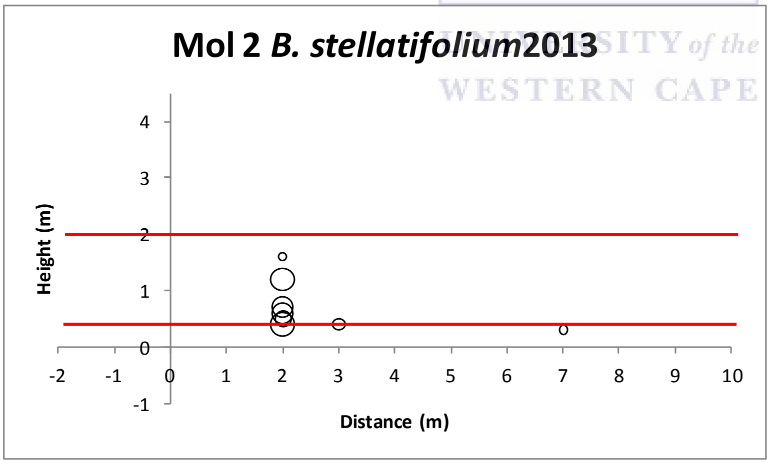
Figure 3.27 The number of individuals of *M. serrata* in the three life stages at Ela 4. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2	5	1			1			
3								
4								
5								
6								
7								
8								

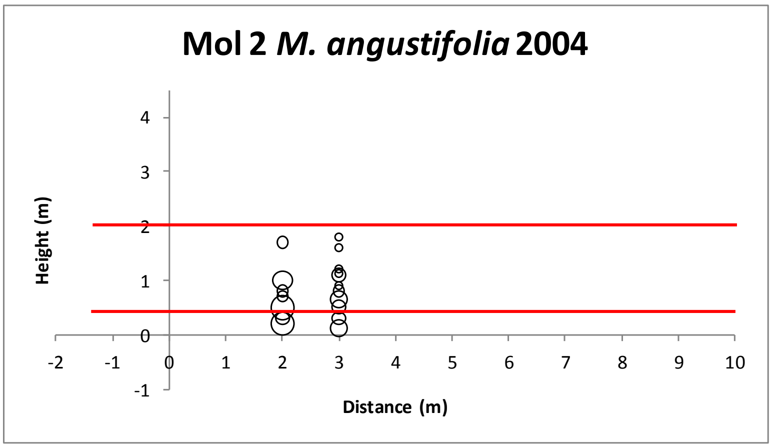


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2	6	22	13	1				
3		1						
4								
5								
6		1						
7								
8								

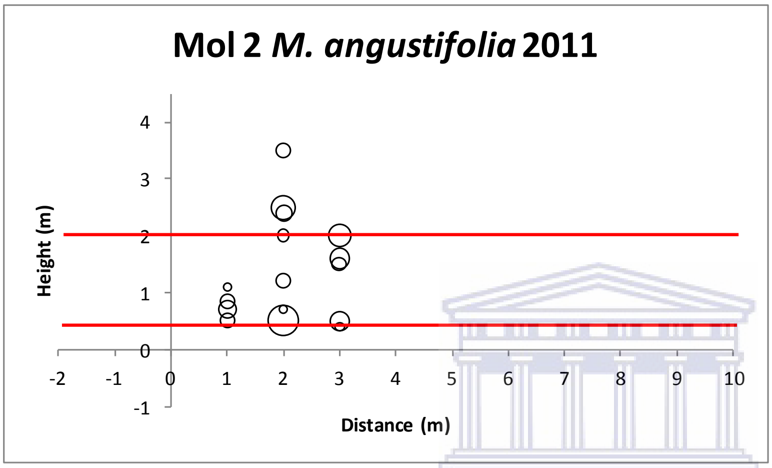


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2	12	7	8	1				
3	2							
4								
5								
6								
7	1							
8								

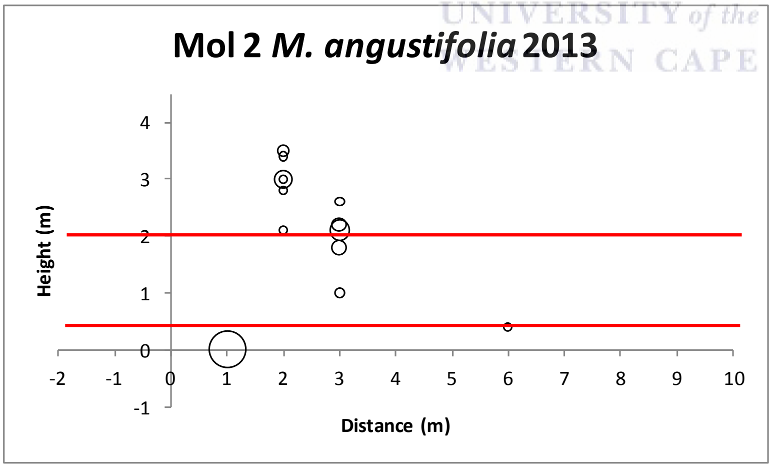
Figure 3.28 The number of individuals of *B. stellatifolium* in the three life stages at Mol 2. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2	11	13	6	2				
3	8	10	5	2				
4								
5								
6								
7								
8								

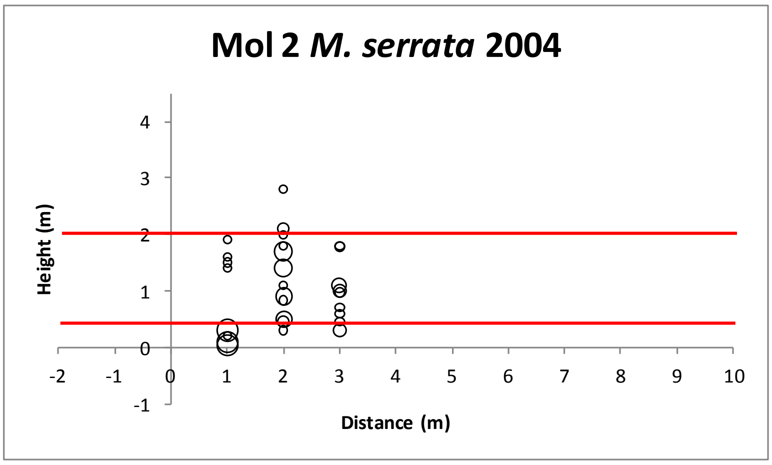


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1		11	1					
2	14	1	3	2	13		3	
3	6		9	8				
4								
5								
6								
7								
8								

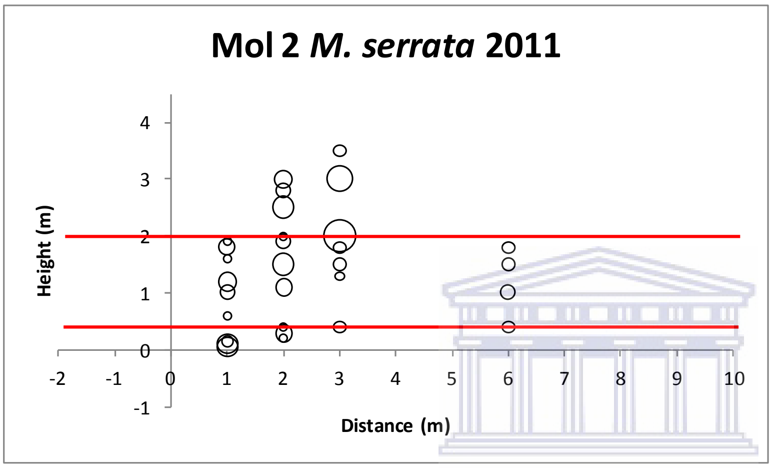


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	20							
2					1	5	3	
3		1		6	3			
4								
5								
6	1							
7								
8								

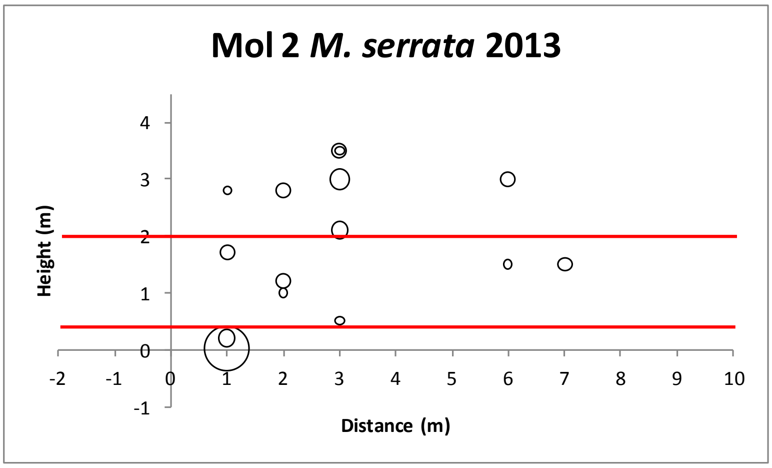
Figure 3.29 The number of individuals of *M. angustifolia* in the three life stages at Mol 2. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	20		2	2				
2	8	5	6	6	3	1		
3	1	3	5	2				
4								
5								
6								
7								
8								

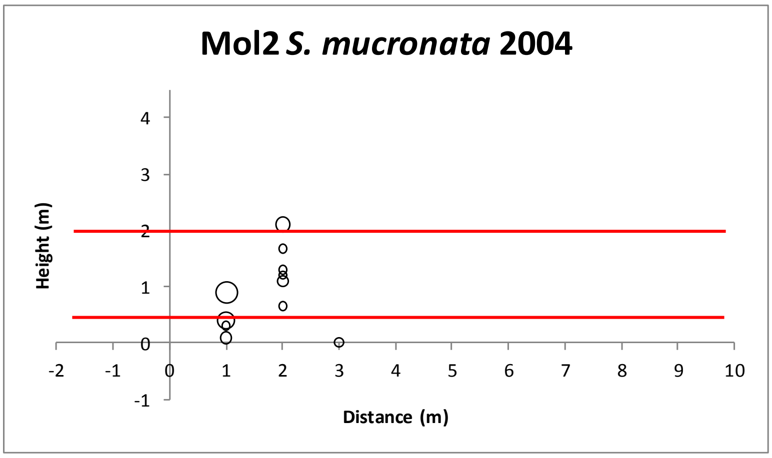


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	14	3	5	6				
2	6		11	3	7	6	1	
3	2		3	18		10	2	
4								
5								
6	2	3	2	2				
7								
8								

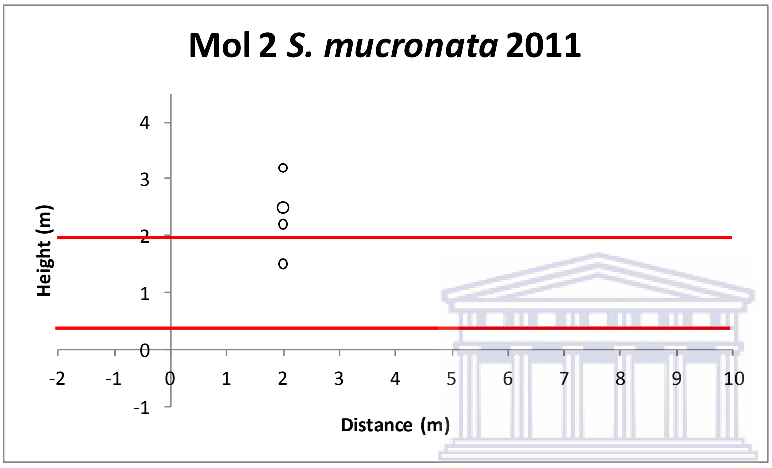


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	34			3		1		
2			3			3		
3	1			4		6	4	
4								
5								
6			1			3		
7			3					
8								

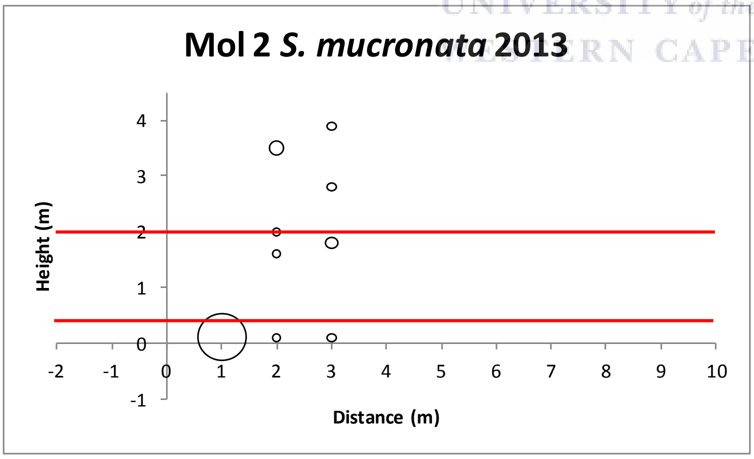
Figure 3.30 The number of individuals of *M. serrata* in the three life stages at Mol 2. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	12	4			1			
2		1	4	1				
3	1							
4								
5								
6								
7								
8								

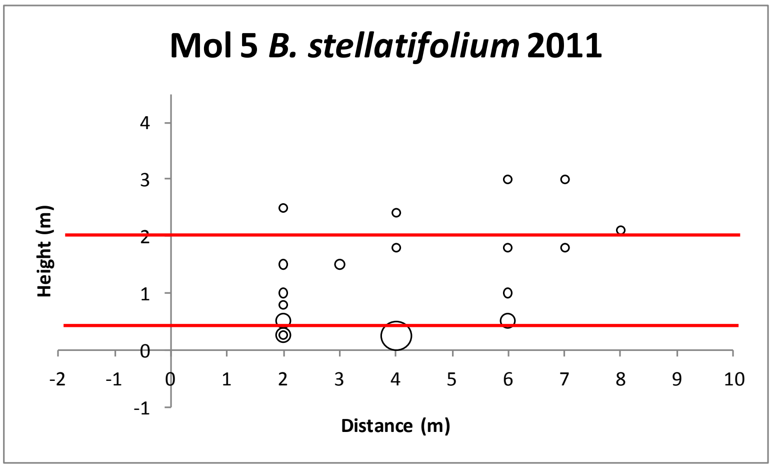


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2				1	1	3	1	
3								
4								
5								
6								
7								
8								

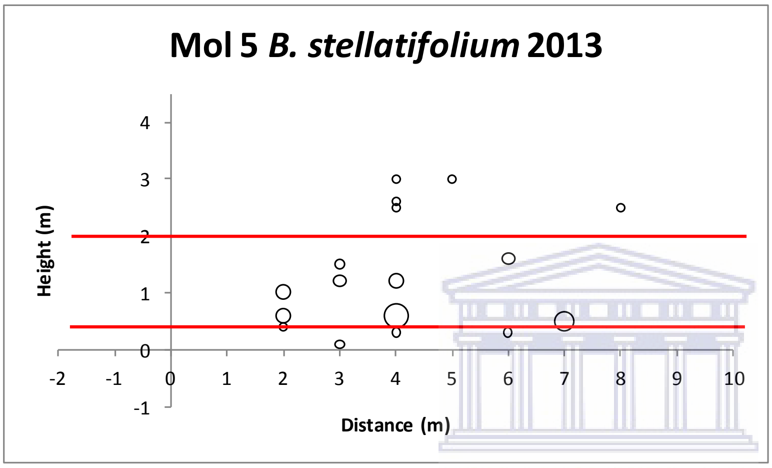


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	35							
2	1			1	1			
3	1			2		1		1
4								
5	1							
6								
7								
8								

Figure 3.31 **The number of individuals of *S.mucronata* in the three life stages at Mol 2. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph**

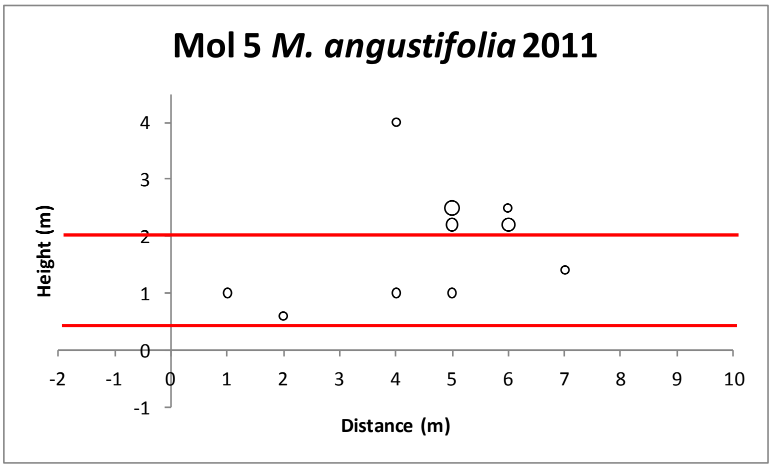


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2	7	2	1		1			
3			1	1	1			
4	13							
5								
6	3	1		1		1		
7				1		1		
8					1			

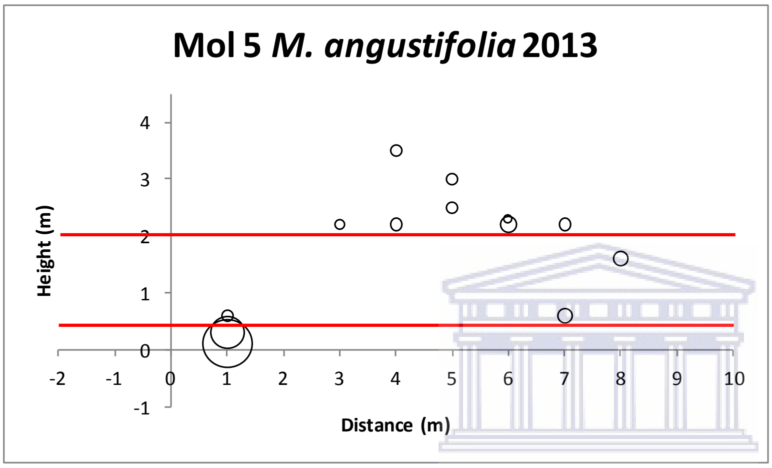


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1								
2	1	4						
3	1		3					
4	1	8	3		1	1		
5						1		
6	1			2				
7	5							
8					1			

Figure 3.32 The number of individuals of *B. stellatifolium* in the three life stages at Mol 5. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph

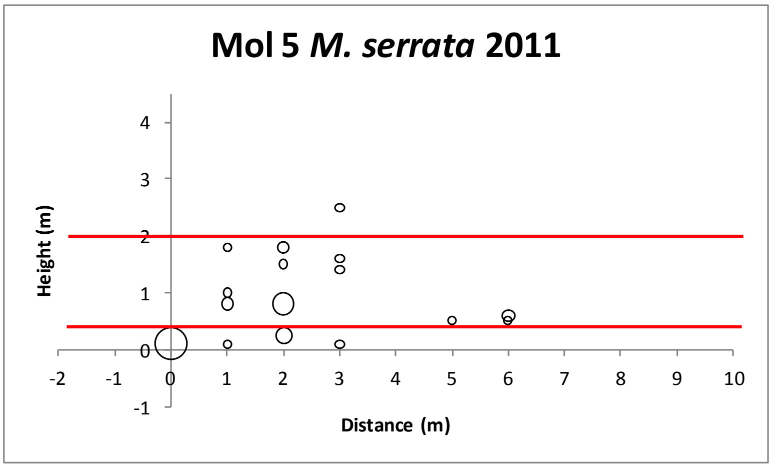


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1			1					
2		1						
3								
4			1					1
5			1			3		
6					2	2		
7			1					
8								

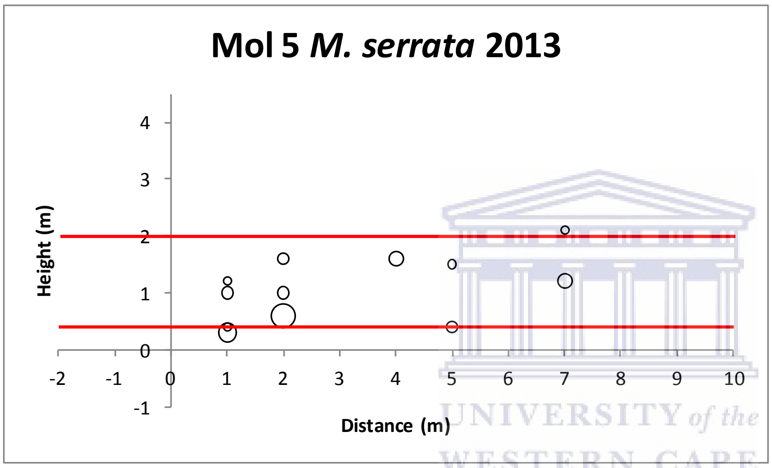


Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	47	2						
2								
3					2			
4					2			2
5						2	2	
6					5			
7		3			2			
8				3				

Figure 3.33 The number of individuals of *M. angustifolia* in the three life stages at Mol 5 Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
0	15							
1	1	2		1				
2	4	7		3				
3	1		1	1		1		
4								
5		1						
6		3						
7								



Dis	<0.5	<1.0	<1.5	<2.0	<2.5	<3.0	<3.5	<4.0
1	6		3					
2		8	2	2				
3								
4				2				
5	2			1				
6								
7			3		1			
8								

Figure 3.34 The number of individuals of *M. serrata* in the three life stages at Mol 5. Red lines separates the three height classes, below 0.3m=seedling, below 2m=saplings and above 2m=adults. The tables show the number of individuals in relation to distance up the bank reflected by the size of the circles on the graph

At Ela 3, *B. stellatifolium* recruited away from the water's edge, while saplings and trees were mostly found beyond 4 m from the water's edge, except in 2004, when *B. stellatifolium* was spread throughout the riparian zone with several saplings and adults at the 1, 2 and 3 m mark (Figure 3.19). However, by 2011 these individuals were no longer present. *B. neriifolia* tended to dominate positions at distances between 3 to 5 m from the water's edge and is one of the dominant plants of the lower dynamic zone at the Elands River sites (Figure 3.20).

At Ela 4, in 2004 all life stages of *B. stellatifolium* were concentrated between 3 and 6 m (Figure 3.24). In 2011 and 2013, however, there were many *B. stellatifolium* seedling and saplings between 1 and 7 m. There were no *B. neriifolia* seedlings in 2004 and 2011, but in 2013 they were at 4 and 5 m (Figure 3.25). Saplings were mainly between 2 and 5 m in 2004 and 2013, but were situated lower down the bank in 2011. Adults were present between 3 and 6 m. *M. angustifolia* adults are mostly distributed between 2 and 5 m up the bank (Figure 3.26). For all the three years *M. serrata* saplings and adults were densely spread between 1 and 7 m from the water's edge (Figure 3.27).

At Mol 2, all plant species of all life stages mostly occurred clustered at certain positions, this was evident especially for *B. stellatifolium, M. angustifolia* and *M. serrata.* For *B. stellatifolium* seedings, saplings and adults were concentrated at 2 m (Figure 3.28, Figure 3.29 and Figure 3.30, respectively). In 2004 and 2013, *S. mucronata* seedlings were abundant at 1 m but there were no seedlings in 2011 (Figure 3.31). The progression from seedling (2004), to saplings and adults (2011 and 2013) at 2 m suggests preferable conditions for growth of seedlings into adults over time.

At Mol 5, *B. Stellatifolium* (Figure 3.32) seedlings recruited between 2 and 4 m, but saplings were spread between 2 and 7 m. Adults were fewer than saplings and did not occur in clusters like those of seedlings and saplings. Positions that had *M. angustifolia* adults in 2011 also had adults in 2013, indicating that some saplings had grown into adults (Figure 3.33). There was a marked paucity of saplings in 2013 relative to 2011. *M. serrata* seedlings and saplings were clustered at metres 1, 2 and 3 but adults (>2 m) took up an arrangement that is different from that of the other life stages (Figure 3.34). This arrangement may have been due to the landscape of the site, which has a 2 m wide side channel at 4 to 5 m, it separates the wet and dry banks.

3.4.7 Temporal shifts in life stages at site scale

To get an overview of the progression of plants from seedlings to saplings and adults the following analyses were done:

- the number of seedlings at each position in 2011 were compared with the number of sapling in that position in 2013;

- the number of sapling at each position in 2011 were compared with the number of adults in that position in 2013;
- the number of sapling at each position in 2004 were compared with the number of adults in that position in 2011; and
- the number of adults in at each position in 2004 were compared with the number of adults in that position in 2011 and 2013.

3.4.7.1 The number of seedlings in 2011 compared to saplings in 2013

The comparison of seedling loss and success (survival) was carried out based on the total number of trees of a given life stage at a site. Seedlings that were recorded in 2011 were not marked so they could not be traced to establish if they had become saplings, however this study seeks to describe (estimate) the ability of different species to survive (in this case by passing on to the next life stage to become saplings or adults) or withstand the conditions at the position on which they recruit at. This has been done by inferring that the saplings that were found in 2013 at the exact same positions (sample plot) as seedlings during 2011 were probably the same plant (Figure 3.35 to Figure 3.38), the same applied in case of saplings to adults (Figure 3.39 to Figure 3.45). The total number of seedlings (2011) and saplings (2013) were compared at each site graphically. Note: Graphs are plotted at different scales of the y-axis.

At Ela 3, none of the seedlings recorded between -1and 0 m in 2011 were present in 2013 (Figure 3.35). Between 0 and 1 m there were 27 seedlings in 2011 and five saplings in 2013. The *M. angustifolia* seedlings that occurred at -1 to 2 metres in 2011 were no longer present in 2013. At -1 m there were eight *M. serrata* seedlings in 2011, but only one sapling was recorded in 2013. Half of the total *B. stellatifolium* seedlings that recruited at 5 m in 2011 survived to saplings stage in 2013. In addition, there was some recruitment subsequent to the 2011 sample because there were saplings present in 2013 where there were no seedlings in 2011.

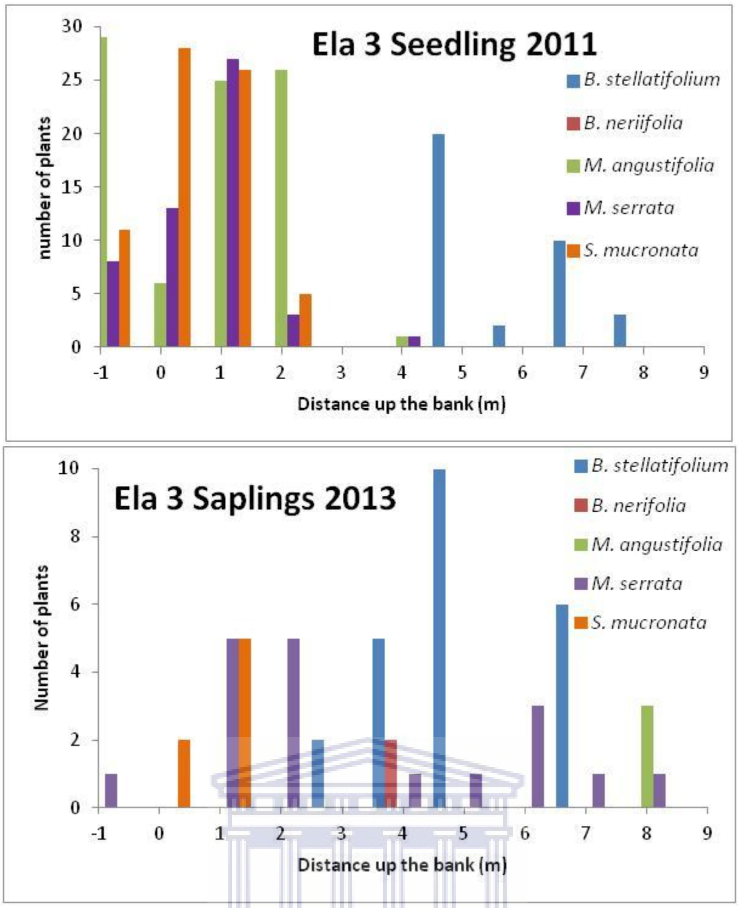


Figure 3.35 The number of seedlings in 2011 versus saplings in 2013 at Ela 3

At Ela 4 (Figure 3.36) there is a shallow pool and due to the boulder edge between -1 and 0 m there was no recruitment recorded in both years. There was one *B. stellatifolium* seedling between 0 and 1 m, in 2011 and the same position had two saplings in 2013. It is a possible that they are both new recruits since their height was less than 1 m. The number of *B. stellatifolium* saplings that were recorded in 2013 between 0 and 3 m was greater than the seedlings recorded in the same position in 2011 while fewer saplings than seedlings were recorded between 3 and 6 m. Saplings of different species (*B. stellatifolium, M. serrata* and *M. angustifolia*) were recorded in 2013 up the bank although there were no seedlings at those positions in 2011. There were 29 *M. serrata* seedlings in 2011 and, only nine saplings in the same position during 2013; all the other saplings that were recorded beyond 1 m were not found as seedlings in 2011.

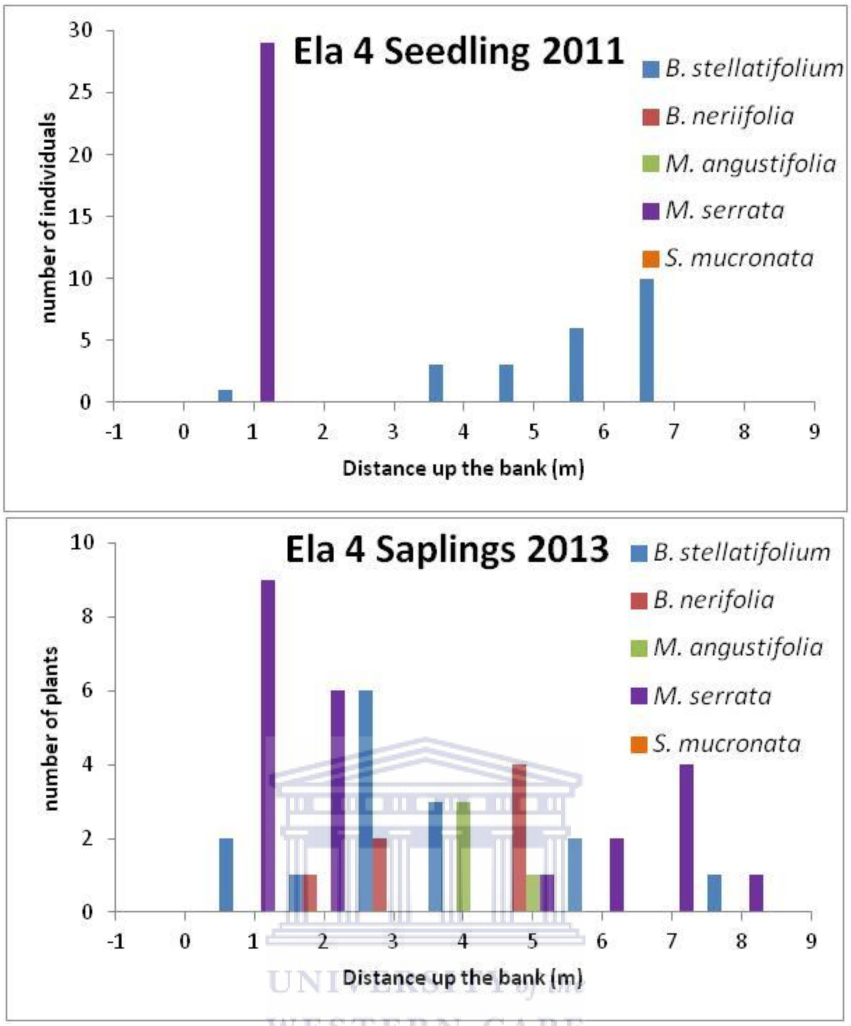


Figure 3.36 The number of seedlings in 2011 versus saplings in 2013 at Ela 4

At Mol 2 (Figure 3.37) there were fewer *B. stellatifolium* saplings in 2013 than seedlings in 2011 at 2 m and new saplings were established at 3 m in 2013 that were not present as seedlings in 2011. Out of 14 *M. angustifolia* seedlings at 1 and 2 m, only two survived and became saplings in 2013 at metres 1 and 2 respectively. One seedling that had recruited at 6 m was not found in 2013. *M. serrata* saplings that occurred at 3 and 7 m were not recorded as saplings in 2011, only five of the fifteen *M. serrata* and two of the *M. angustifolia* seedlings that were on metre 1 in 2011 survived. *M. serrata* saplings were dominant at distances between 1 and 3 m from the water's edge while new *S. mucronata* saplings were recorded between 1 and 2 metres.

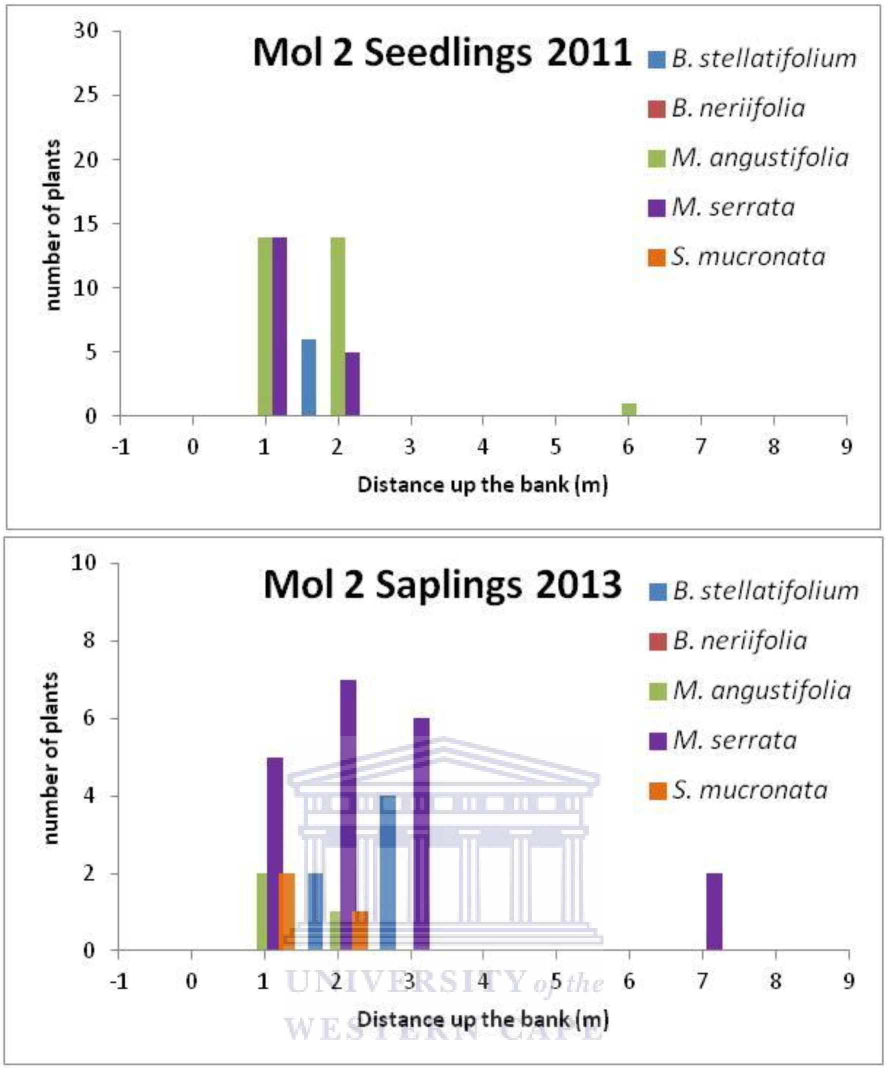


Figure 3.37 The number of seedlings in 2011 versus saplings in 2013 at Mol 2

At Mol 5 (Figure 3.38) there were more saplings of *M. serrata* at positions 1, 2 and 3 m in 2013 than seedlings recorded in 2011 and new saplings were recorded at 4, 7 and 8 m in 2013 despite the absence of seedlings at these positions. The three *B. neriifolia* seedlings did not survive to be saplings. There were no *M. angustifolia* seedlings in 2011, the saplings present must have recruited after the 2011 sampling. There were 13 *B. stellatifolium* seedlings at 4 m in 2011 and only 3 of those were saplings during 2013. There were more saplings at positions in 2013 as compared to the number of seedlings, at 1 m there was only one *M. serrata* seedling while in 2013 the same position had five saplings, 2 m had four seedlings while in 2013 the same position had six saplings. Positions where more saplings were recorded when compared with seedlings were 4, 7 and 8 m containing species of *M. angustifolia* and *M. serrata*.

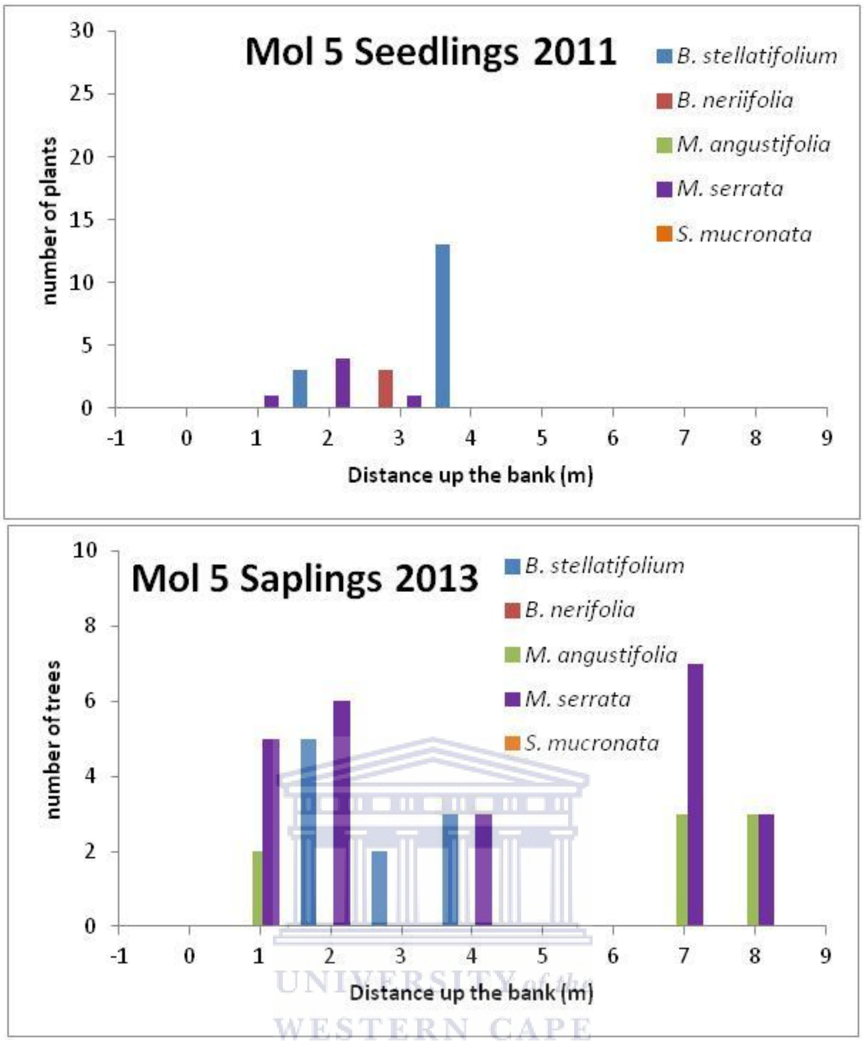


Figure 3.38 The number of seedlings in 2011 versus saplings in 2013 at Mol 5

In general, there were more saplings present in 2013 at positions where seedlings were present during 2011. These are possibly plants that recruited (established) after the 2011 sampling was done. However recruitment of saplings was also recorded at all sites in 2013 where no seedlings were present in 2011 and this did not appear to be related to bank position.

3.4.7.2 The number of saplings in 2011 compared to adults in 2013

Few sapling individuals grew on to become adults. The distribution of saplings does not relate well to that of the adults, thus the dominance of saplings at specific locations is not the same as that of adults.

At Ela 3 (Figure 3.39), there were a greater number of sapling individuals in 2011 than adults in 2013. *M. serrata* saplings were well spread throughout the site, from -1 to 9 m up the bank, in 2013 while adults only occurred at 2, 3 and 5 m. The pattern was the same for *B. stellatifolium* with adults found between 3 and 6 m in 2013. For both *B. stellatifolium* and *M. serrata*, the number of sapling individuals peaked between 2 and 5 m. *B. neriifolia* recruited at 3 and 4 m after the 2011 sampling period. At -1 and 0 m there was only one *S. mucronata* sapling in 2011 and in 2013 they were two adults at each of these positions.

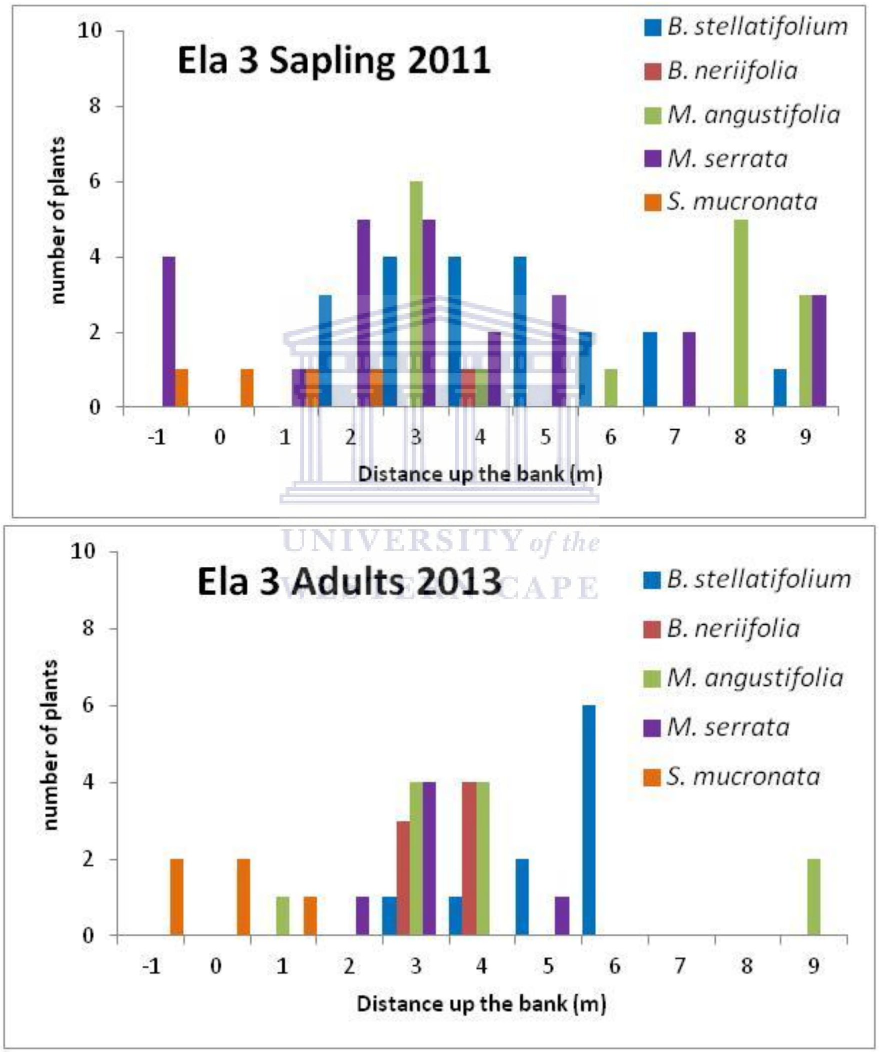


Figure 3.39 The number of saplings in 2011 versus adults in 2013 at Ela 3

At Ela 4 (Figure 3.40), the same number of *B. neriifolia* saplings and adults was found between 2 and 3 m, while there was a greater number of saplings than adults beyond 4 m. There was an increase in the number of *M. angustifolia* adults in 2013 when compared to saplings of 2011. Saplings of *B. stellatifolium* and *M. serrata* at Ela 3 and Ela 4 both peaked at similar positions up the bank (1 to 4 m for Ela 4 and 2 to 5 m for Ela 3).

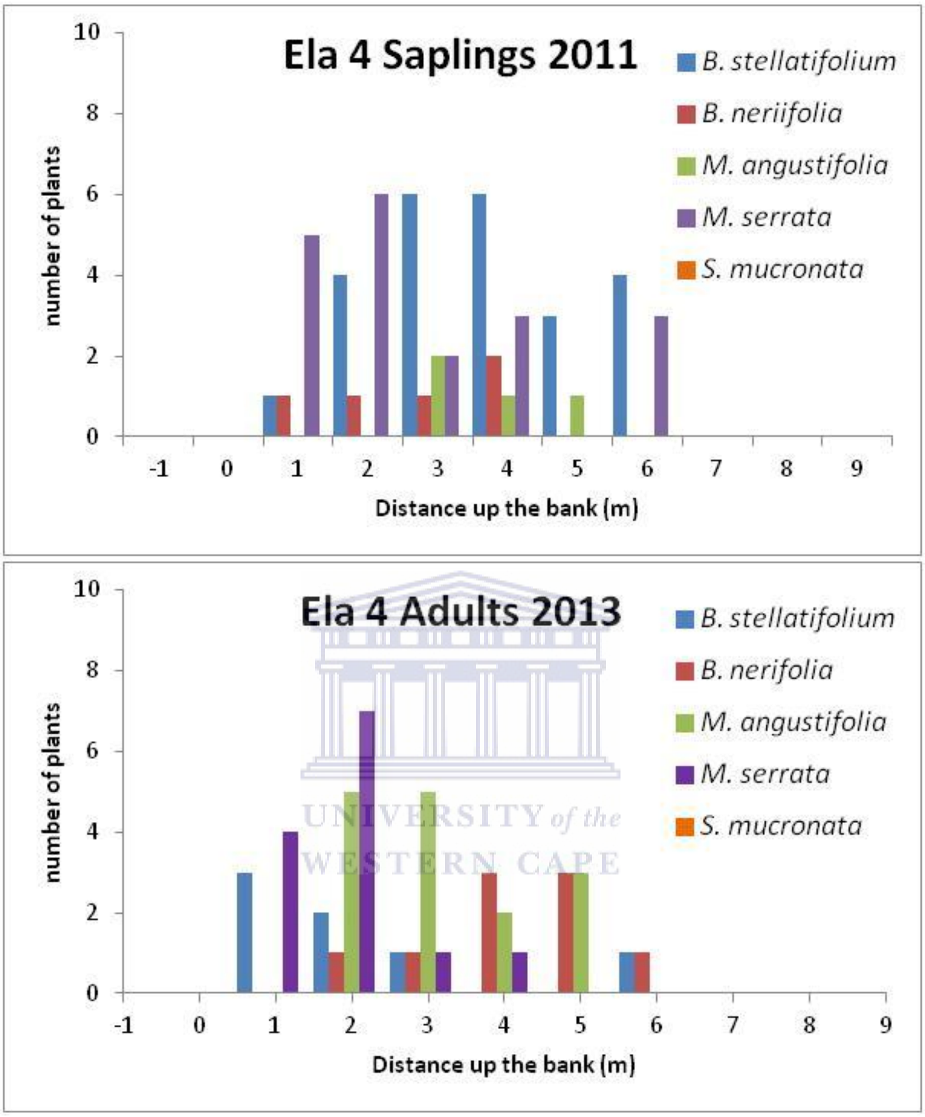


Figure 3.40 The number of saplings in 2011 versus adults in 2013 at Ela 4

At Mol 2 (Figure 3.41), there were fewer adults in 2013 than saplings recorded in 2011 for all species except for *S. Mucronata* . Both saplings and adults were concentrated between 1 and 3 m, while some saplings of *M. serrata* grew on to become adults beyond 3 m.

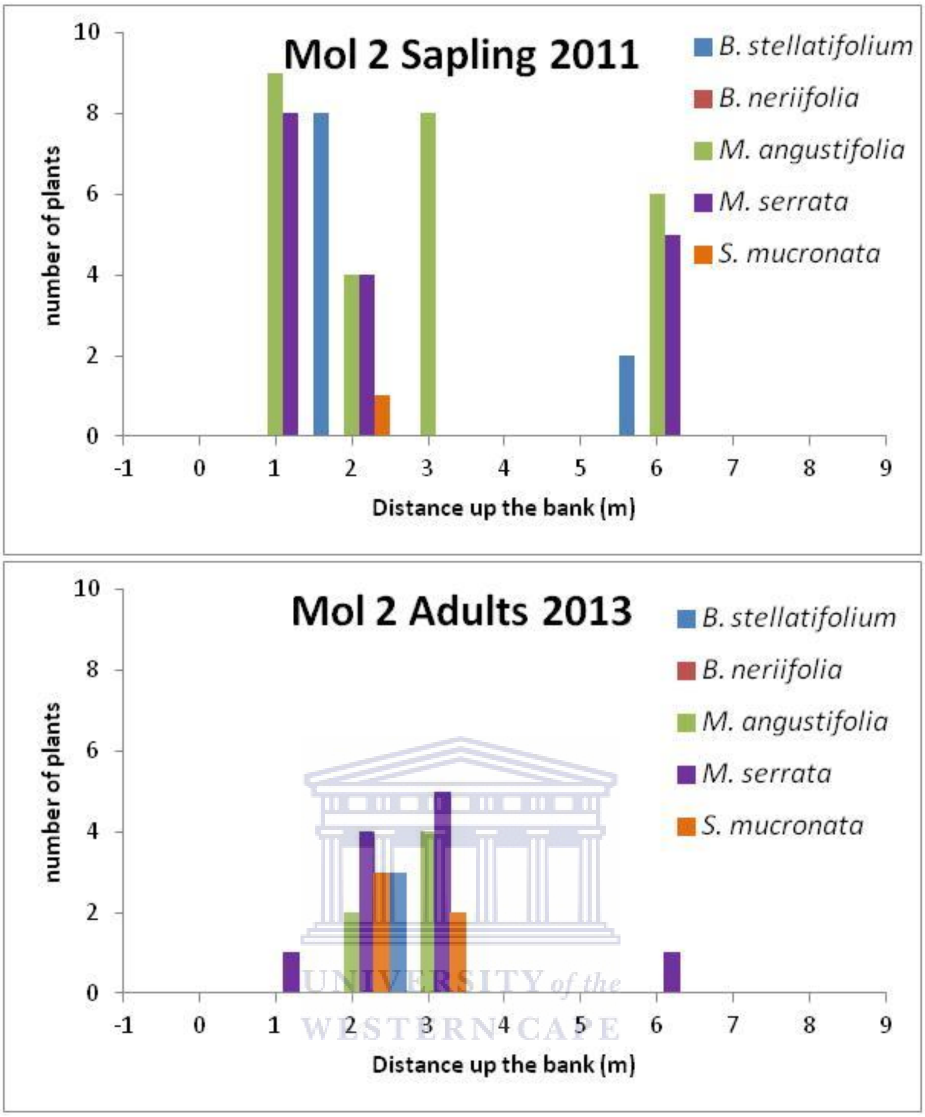


Figure 3.41 The number of saplings in 2011 versus adults in 2013 at Mol 2

At Mol 5 (Figure 3.42), all *B. neriifolia* and *S. mucronata* saplings that were sampled in 2011 between 1 – 6 m were not present as trees during 2013. There were a greater number of *M. angustifolia* trees between 3 and 7 m in 2013 when compared to saplings in 2011. The reason for this increase could be that, there were some trees already present at 2011.

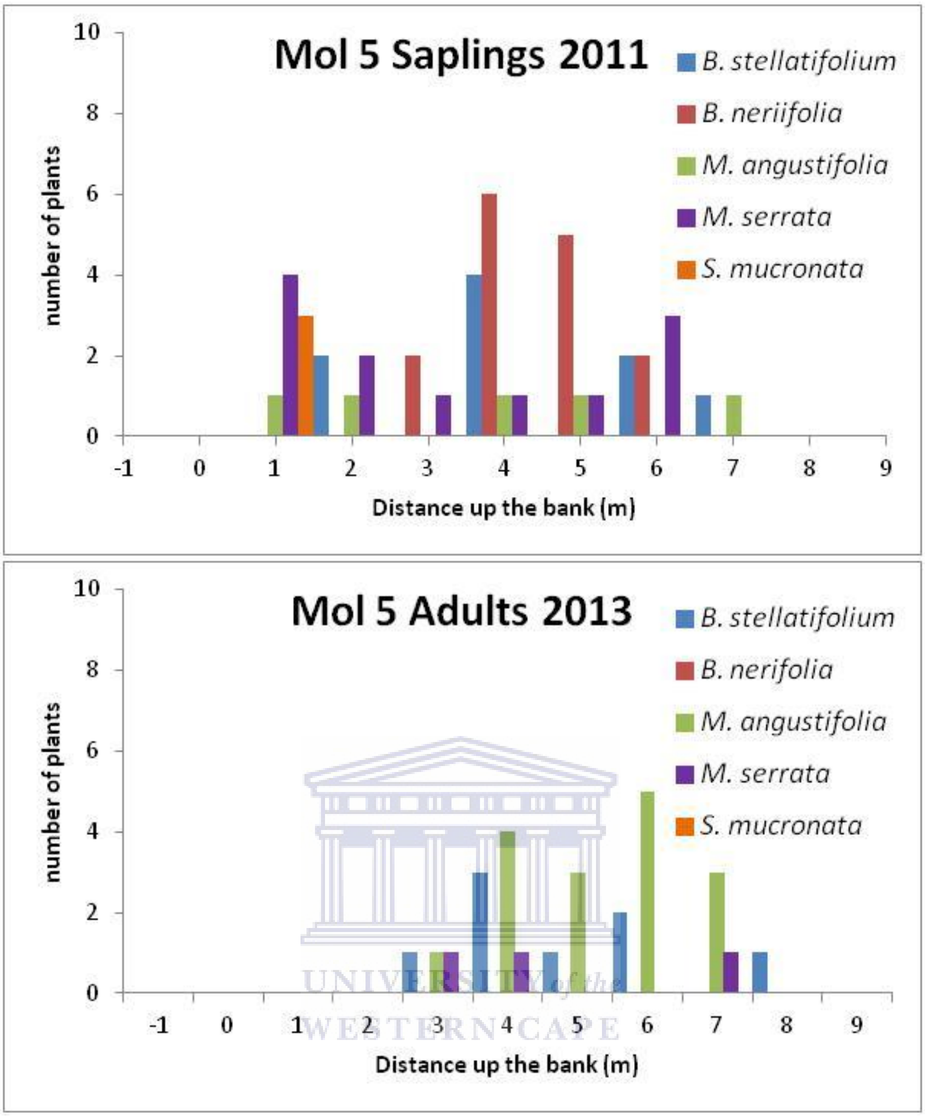


Figure 3.42 The number of saplings in 2011 versus adults in 2013 at Mol 5

During the comparison of saplings to adults for each site there was no obvious pattern in how the number of saplings related to that of the adults between 2011 and 2013. Overall there were a greater number of saplings recorded in 2011 than there were adults in 2013 and saplings and adults of the same species were located near one another. There were more saplings recorded in 2013 when compared to 2011, probably because many 2011 seedlings had grown on to become saplings by 2013 while younger 2011 saplings had not grown sufficiently in height to become trees.

3.4.7.3 The number of saplings in 2004 compared to adults in 2011

The number of saplings in 2004 was compared to adults in 2011, and the results are shown in Figure 3.43 and Figure 3.45.

At Ela 3 (Figure 3.43), there were five *S. mucronata* saplings at -1, 0 and 1 m during 2004, and of which 3 adults remained at -1 m, none at 0 m and one at 1 m. A mixture of *B. stellatifolium*, *B. neriifolia*, *M. angustifolia* and *M. serrata* saplings occurred between 2 and 7 m, and by 2013 different species had taken root as adults at different positions.

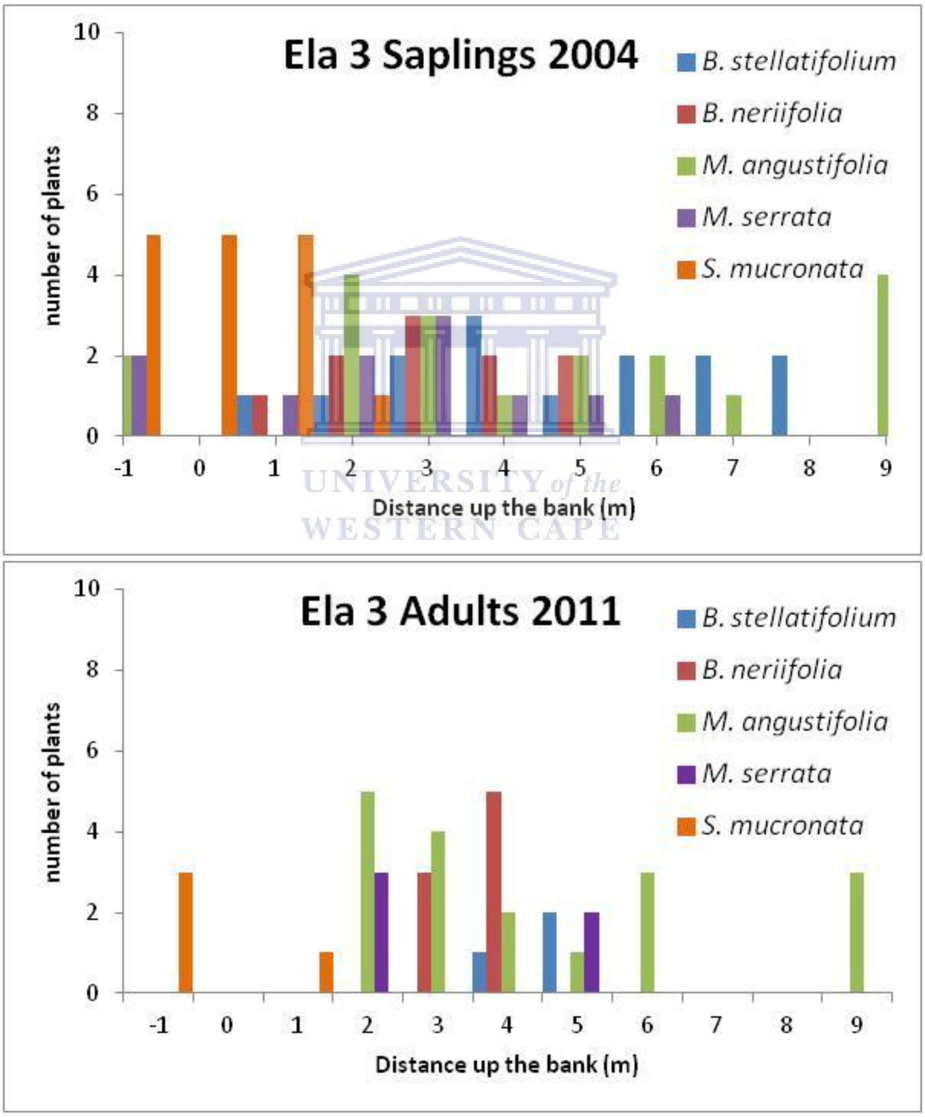


Figure 3.43 The number of saplings in 2004 versus adults in 2011 at Ela 3

At Ela 4 (Figure 3.44), in 2004, *B. stellatifolium* saplings occur between 3 and 8 m, while adults were found between 2 and 7 m in 2011. Increased numbers of *M. angustifolia* adults at 2 to 5 m were recorded in 2013. *B. neriifolia* adults occurred at same positions in 2004 as saplings in 2011. Adults of *M. serrata*, which is a lower dynamic species, occurred as far up as 6 and 7 m on the bank.

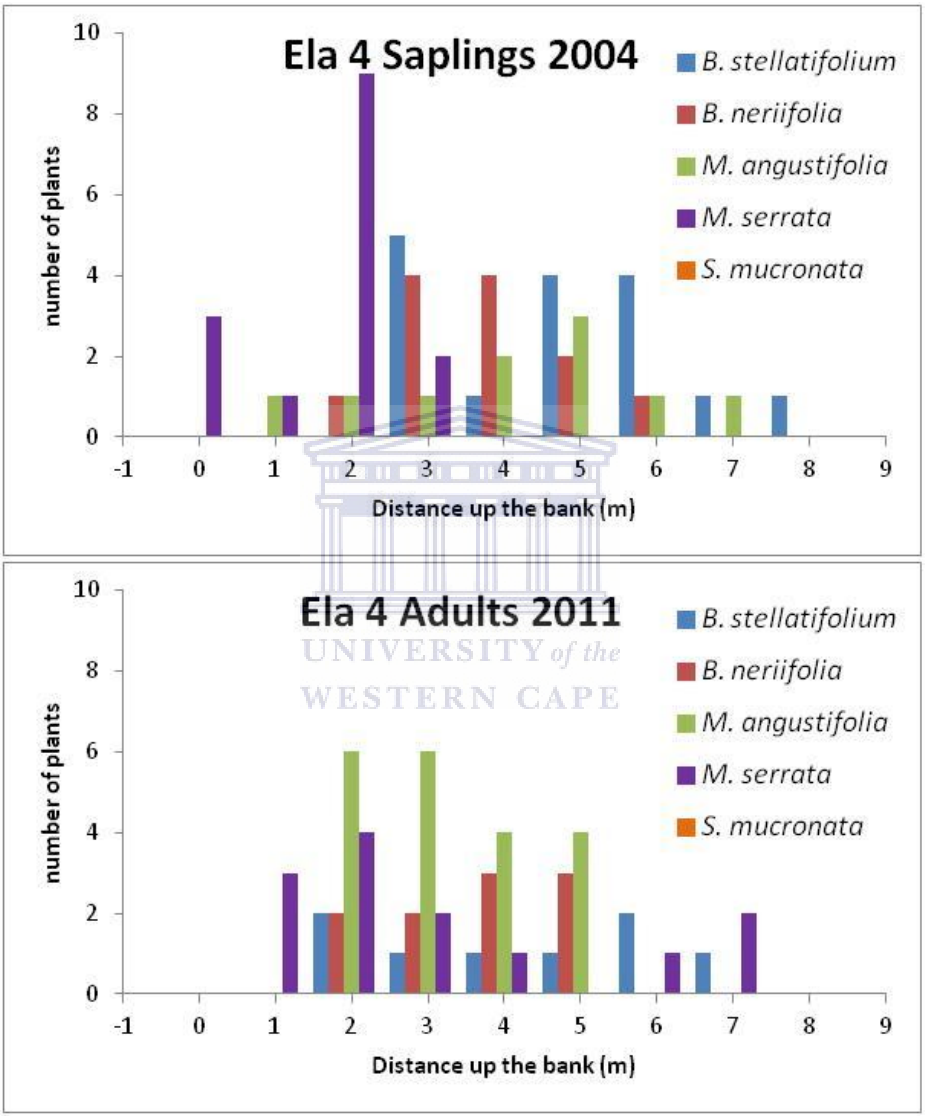


Figure 3.44 The number of saplings in 2004 versus adults in 2011 at Ela 4

At Mol 2 (Figure 3.45), in 2004, saplings of *S. mucronata* occurred between 0 and 2 m, but in 2013 adults were only recorded at 2 m. In 2004 there were no *M. serrata* saplings but by 2011 there were adults at 2 and 3 m.

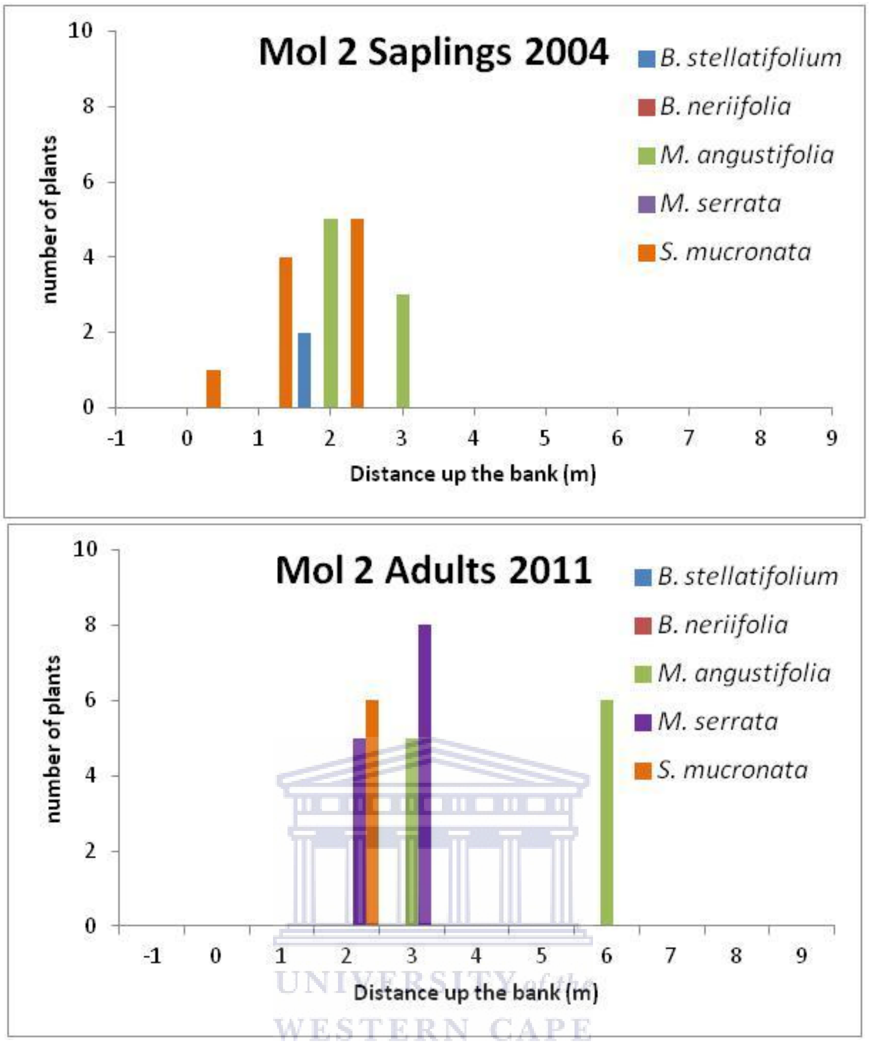


Figure 3.45 The number of saplings in 2004 versus adults in 2011 at Mol 2

Over the six year period, new adults of different species occurred at positions where no saplings were previously recorded and positions where saplings were recorded were more likely to grow on to adults for each species.

3.4.7.4 The number of adults in 2004, 2011 and 2013

A comparison of the adults between 2011 and 2013 showed that adults still occupied the same position in most cases. In some cases a tree was recorded in an adjacent sample plot between the sample years, especially if the tree was at a sample plot boundary as it may have grown or indeed have been knocked over during a flood and resprouted a new canopy from a shifted position. The sample plots positions were realigned accordingly using the bigger adult trees greater than 2.5 m tall that were recorded both in 2011 and 2013. As was seen for saplings, the number of adults at Ela 4 and Mol 5 increased suggesting that some saplings had grown to become adults. Figure 3.47 below is an example of the structure of adults at Ela 4 that were recorded in 2004, 2011 and in 2013. In this case the same arrangement of adults was maintained.

At Ela 3 (Figure 3.46) all *B. stellatifolium, M. serrata* and *B, neriifolia* adults at metres 0, 1, 7, 8 and 9 m were removed over time. Between 2 to 5 m, *M. angustifolia* adults persisted over the years. At 4 and 5 m there were three *B. stellatifolium* adults in 2011 which were still present in 2013.

At Ela 4 (Figure 3.47), at 3, 4 and 5 m, there were the same species although the number of adults varied each year. *B. neriifolia, M. angustifolia* and *M. serrata* dominated this site and occupied similar positions (metres that are closer to each other) during all three years. In 2004 there were five *B. neriifolia* at 3 m and one at 4 to 6 m, during 2011 and 2013 there were two at 3 m and three at 4 to 5 m. The number of *M. angustifolia* peaks from 2 to 5 m across all years.

At Mol 2(Figure 3.48), during 2011 and 2013 there were plenty *M. serrata* adults at this site whilst in 2004 there were none. The *B. stellatifolium* adults that were at positions 0 and 2 m in 2004 were not recorded in 2011; however in 2013 metre 2 had three adults of this species. Even though the same number of individuals occurred at this position these could be new plants and not necessarily the same ones that were there in 2004. This site was mainly dominated by adult species of *M. angustifolia* and *S. mucronata.*

The Mol 5 site (Figure 3.49) was only established in 2011, so there were no 2004 data for this site. The *B. neriifolia* adults recorded at 3 and 4 m in 2011 were not present in 2013. The total number of *B. stellatifolium, M. serrata* and *M. angustifolia* adults at the site was higher in 2013 than in 2011.

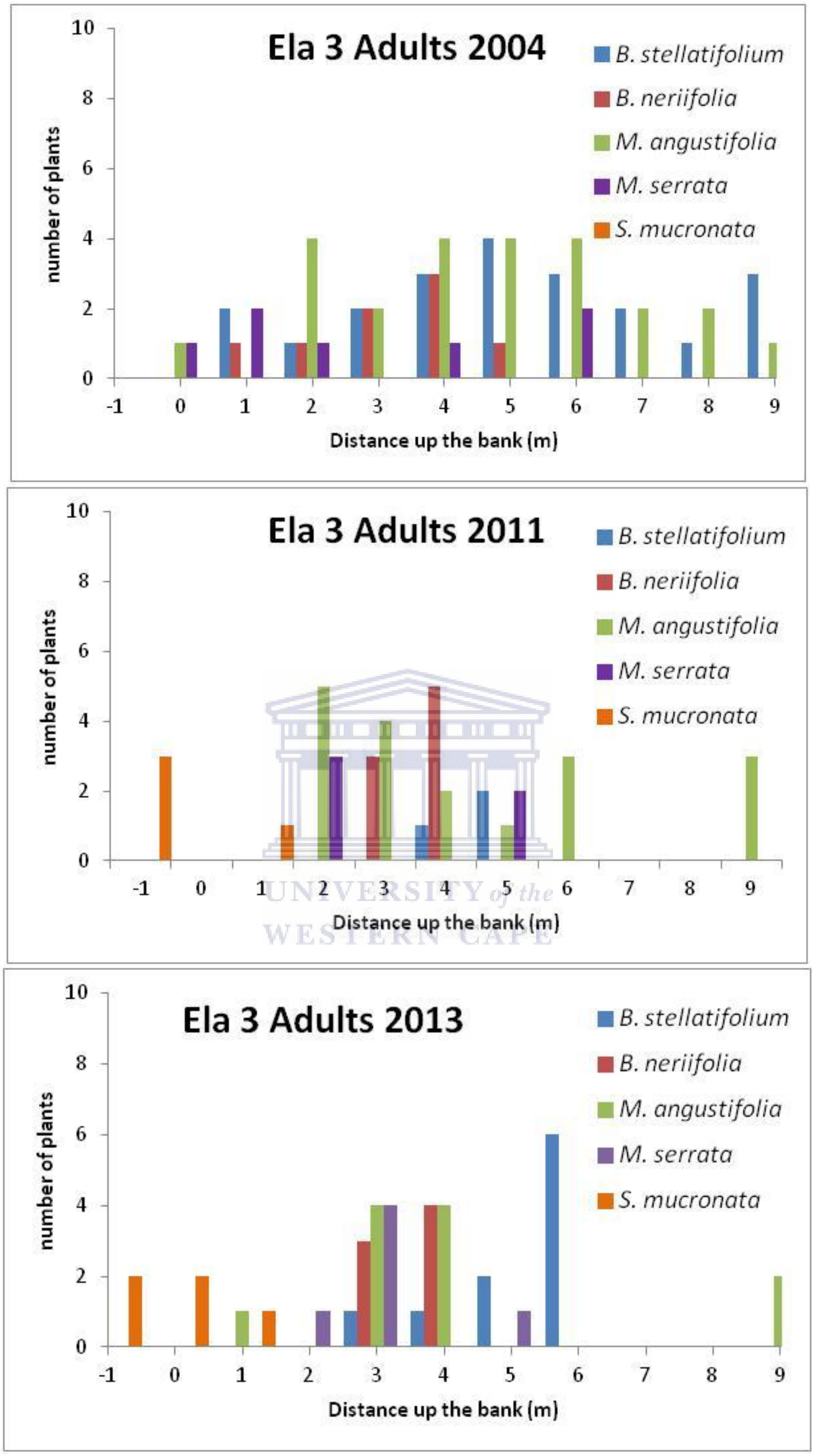


Figure 3.46 The number of adults in 2004, 2011 and 2013 at Ela 3

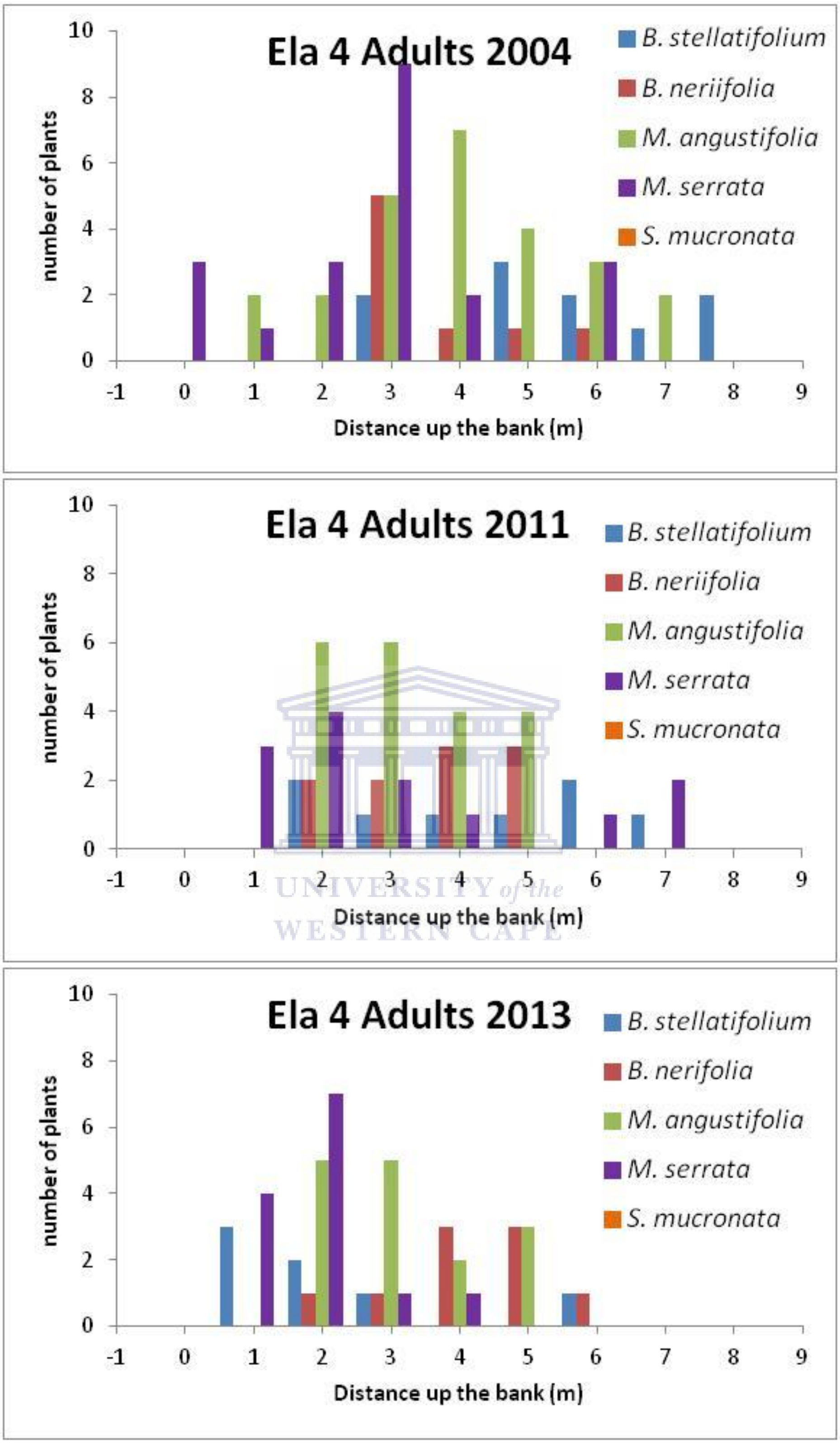


Figure 3.47 The number of adults in 2004, 2011 and 2013 at Ela 4

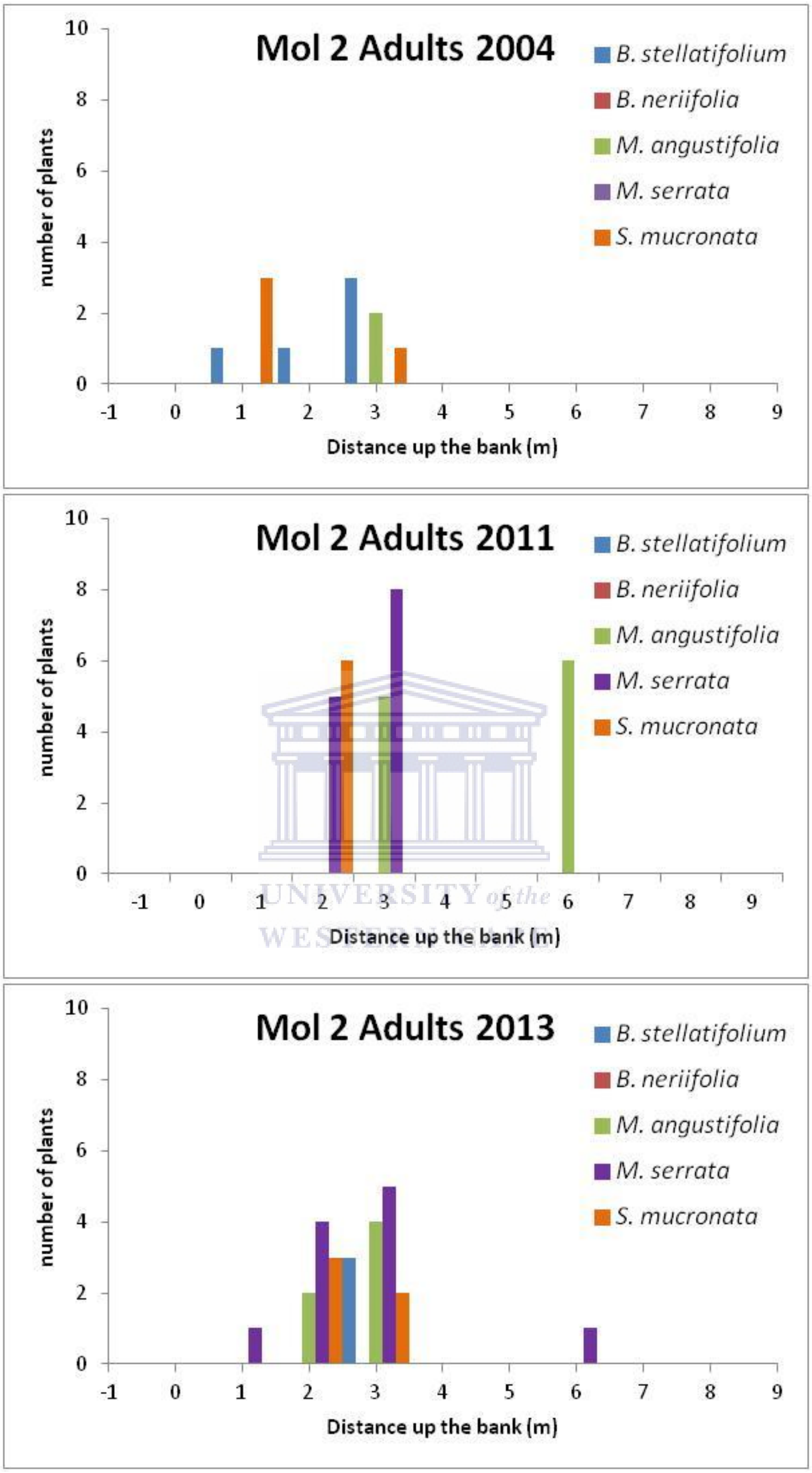


Figure 3.48 The number of adults in 2004, 2011 and 2013 at Mol 2

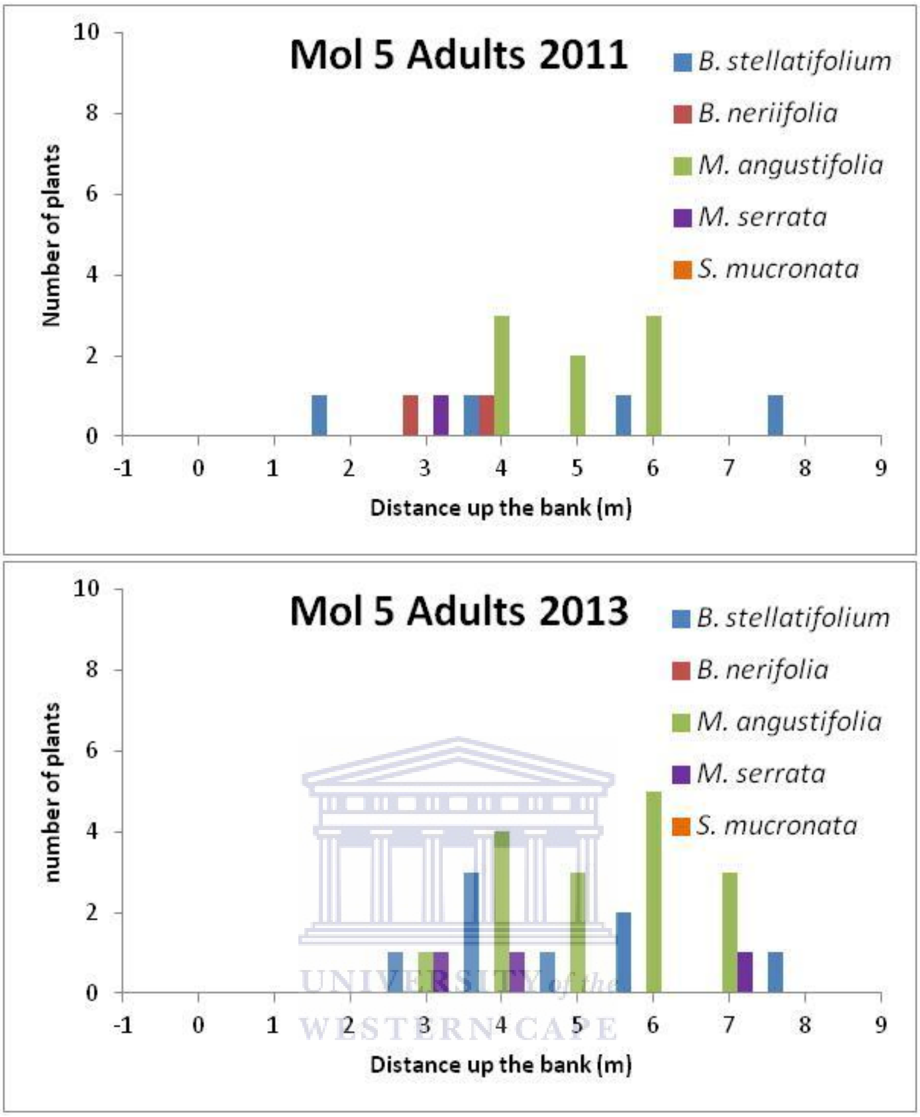


Figure 3.49 **The number of adults in 2011 and 2013 at Mol 5**

At Ela 3 and Ela 4, the same adults of *B. stellatifolium*, *B. neriifolia M. serrata* and *M. angustifolia* species were present at the same positions over the 9 year period. At all sites the number of adults in 2004 was much higher than those in 2011 and 2013. The species distribution however was similar for all the years, with *B. stellatifolium* mostly dominated between 3 and 6m. *M. angustifolia* was dominant between 1 and 5 m up the bank, with *M. serrata* mostly populating distances that are 1 to 3 m from the water's edge. *S. mucronata* remained in the wetted channel and just up to 2 m from the water's edge.

Even though the adults sampled during the three years could not be retraced the presence of the same species of a certain life stage at similar positions suggests that the adults are able to withstand the conditions at the particular lateral zone they occupy. The individuals however keep getting replaced by newer adults. However, for saplings this happens faster and more often than for the adult trees. As for seedlings, seeds of all species get deposited at different positions on the lateral zones where they recruit and can only grow to the next life stage if they are able to withstand the conditions at site. The presence of a nursery area that has enough water is important at all growth stages of a species. For this study across all sites, more than half of the total number of seedlings did not become saplings; this reduction of the number of individuals is noticeable across all species. The seedlings that recruit much closer to the wetted channel (mostly at -1 and 0 m) did not seem to be able to grow into saplings. These positions were mainly occupied by seedlings, sedges and other groundcover species. Only at the Elands River sites were all life stages of *M. serrata* and *S. mucronata* found closer to the water's edge (positions -1 and 0 m).

3.5 Discussion

The profile of a river changes as it moves from the upper to lower course as a result of changes in the river's energy and other processes associated with the river channel (Naiman and Decamps 1997). These changes in the cross-sectional profile of a river also have implications for plant survival and growth (Naiman and Decamps 1997). In this study, between 2011 and 2013, alternate banks at both sites were subject to deposition and erosion. Erosion and deposition at the sites possibly contributed to the differences in survival of seedlings and saplings that progressed to the next life stage, thus affecting plant distributions at a site. In this study, however, despite slight changes on cross-sections between 2011 and 2013, there was not much change to the number and distribution of trees greater than 2.5 m tall.

Four lateral zones, marginal, lower dynamic, lower and upper zones were identified at each study sites. A clear distinction between the dry and wet bank zones was shown using a combination of both groundcovers and tree cover percentage data. In general the transition between the wet (marginal and lower dynamic zones) and dry (lower and upper zones) banks occurred at distances of about 6 m from the water's edge. There were some shifts in lateral zones but these were mainly associated with the boundary between marginal and lower dynamic zones. When comparing the number of individuals at different life stages for the three years, it was evident that regardless of year of collection, there were more seedlings than saplings and adults, and again more saplings than adults. An exception to this was the 2004 period, when there were more adults than saplings.

Species that are found closer to the water's edge and in the wet bank in general, such as *S. mucronata, M. serrata* and *B. neriifolia* release their seeds during the summer low flow period. Within this period water levels are low allowing the seeds to establish closer to the water's edge. *M. angustifolia* release its seeds over a period of four months starting during the winter high flow to the beginning of the low flow period (Reinecke 2013). This allows the *M. angustifolia* seeds to be deposited throughout the lateral bank as flow recedes. *B. stellatifolium* seeds are released at the approach of the wet season, which could explain why it recruits more on the upper bank as the seeds are deposited by the rising flows.

With exception to *S. mucronata,* the other indicator species recruited throughout the riparian zone, despite their saplings and trees being concentrated in particular lateral zones. Only *S. mucronata* showed zone specific recruitment, with seedlings, saplings and adults all restricted within two metres of the water's edge. For the other species new recruits established at different positions on the bank, with plants shorter than 1 m showing less pattern than larger individuals. For instance, at the Ela 3 and Ela 4, plants shorter than 1 m were evenly spread between 3 and 7 m, and those taller than 1 m were restricted to positions between 2 – 5 m up the bank. Zonal patterns started to emerge for plants that were taller than 1.5 m, and trees greater than 2 m tall have a fairly distinct zonal arrangement and tended to dominate more or less the same positions up the bank in all three years. This suggests that as plants establish there is no clear lateral zonation that is presented but as they grow and withstand the conditions at site positions a pattern of plant arrangement then emerges.

The areas of most recruitment differed between species. For instance, *M. angustifolia* seedlings were mostly concentrated at 1 to 3 m, while those of *B. stellatifolium* were most dense at 3 to 5 m. However, at all sites *M. angustifolia* and *B. stellatifolium* adults were most common in the dry bank and their seedlings equally common in the wet and dry banks. The seedlings that recruited close to the wetted edge (mostly at -1 and 0 m) tended not to grow to become saplings, either because they were washed out or because they were out-competed by marginal zone specialists such as sedges and other groundcovers. That said, *S. mucronata* also showed a fairly high failure rate of seedlings becoming saplings and adults. This was true for all sites, even though *S. mucronata* is a well-adapted marginal zone species. In this case seedlings established at a site, but their survival at particular positions of recruitment was not guaranteed. This suggests that even though plants are well adapted to a specific zone their survival could still be affected by other factors, which were not investigated in this study.

Across all sites, seedling establishment was plentiful and widely distributed through the lateral zones. A high turnover of seedlings was recorded but there was a clear decline in the number of individual seedlings that developed to saplings and grew on to become adults. This suggests that the lateral zonation seen in the riparian vegetation community is at least partly determined by factors exerted after recruitment, and that the zonation is dictated by the ability of different species to withstand floods and zonal perturbations of different magnitudes. This is clearly shown by the fact that the distribution pattern of seedlings of a species differs from that of individuals taller than 1.5 m. It suggests that, for some reason, seedlings do not always survive the conditions at a given lateral zone and thus do not make it to the next life stage. For an individual to grow into mature adults, they must withstand the conditions that prevail at positions of recruitment. The results obtained in this study agree with those of Mahoney and Rood (1998), who showed poor seedling survival outside of the optimal zone for survival. Mahoney and Rood (1998) suggested that most seedlings die from drought-stress, and those individuals that survive do so because they are able to maintain a functional root contact with the moisture zone.

Findings from this study suggest that seedlings and saplings prefer different bank position for colonisation. Thus the positions where seedlings dominate are not necessarily the positions where saplings will dominate. Although the focus of this study differs from that conducted by Sher and Marshall (2003), which looked at competition between seedlings across substrate types the findings are in agreement. Sher and Marshall (2003) illustrated that seedlings and saplings show a substrate preference. For instance, *Populus deltoides* and *Tamarix ramosissima* seedlings grew best in clay, while their saplings grew better in sandier substrates. The suggestion given was that this could be due to differing abiotic demands.

4 The effects of diminished dry season low flows on riparian vegetation communities

4.1 Introduction

Aquatic ecosystems require a certain amount of water be purposefully left in or released to maintain conditions that will support direct and indirect use values of these systems (King *et al.* 2003a). The flows left or maintained in a river so that the system remains in a state considered desirable are referred to as environmental flows. Other terms used to refer to these flows are ecological or instream flow requirements. Failure to manage the condition of the ecosystem leads to decline in the health of water resources around the world (Poff *et al.* 1997; Richter *et al.* 2003; Postel and Richter 2003; Brown and King 2003). In efforts to prevent future ecological damage, there is increasing awareness of the need to provide for the water needs of river ecosystems proactively by reserving a portion of river flows for ecosystem support (Tharme and King 1998; Richter *et al*. 2006).

The provision of EFs has become one of the priorities of the South African water resource governance through the National Water Act (NWA, 1998). Prior to the enactment of this legislation, aquatic ecosystems were generally perceived as a competing for water use (King *et al.* 2003a). The NWA makes provision for the Reserve, which is comprise allocation of water for the human basic need and an allocation of water for the aquatic environment. The establishment of the Ecological Reserve in NWA introduces direct competition between the aquatic ecosystem and the needs of humans (van Wyk *et al.* 2006) and, as such, decisions on the volumes of the original flow regime, that should be left or released downstream to maintain the aquatic ecosystem of the river system (Yang *et al.* 2009) are often highly contested and difficult to make. In South Africa, the level of use (and conversely it protection) of any water resource is decided by first identifying the condition in which it should be maintained (Ecological Category; after Kleynhans *et al*. 1999), and then setting the Reserve Quality Objectives (RQOs; including the volume and timing of flows required for the Ecological Reserve) in accordance with the chosen category (King and Pienaar 2011). These provisions are then incorporated into any licences (Section 29 of NWA) to use water which control the extent to which the resource can be used (King and Pienaar 2011).

Regions with mediterranean climate are generally water-stressed (Gasith and Resh 1999), because high temperatures in summer result in high evaporation and transpiration rates and at the same time having low to no rainfall during this season. This results in a drying up of those rivers with no significant groundwater contributing to flows, and hence aquatic ecosystems become stressed (Moor and Day 2013). When complete drying of the river beds occurs, taxa lacking desiccation-resistant stages or those unable to find refugia are eliminated (Gasith and Resh 1999). In the Western Cape Province of South Africa, the abstraction of water for irrigating crops in summer coincides with the occurrence of low river flows. Moor and Day (2013) have suggested that direct water abstractions are the biggest threat to riverine biodiversity in the Western Cape. Streams in mediterranean climate regions are shaped by sequential seasonal events of flooding and drying over an annual cycle (Gasith and Resh 1999). Diversions of water from the stream may change a perennial river to an intermittent one (Gasith and Resh 1999). Such changes may alter the distribution of the biota, life history cues and overall structure of the riparian community. According to Gasith and Resh (1999) during the dry season habitat conditions become harsher, with more water abstracted during low flow periods, it leaves less for the biota at the time when they need the water most. A major but rarely discussed consequence of water diversions is the change in salinity that puts the biota of mediterranean-type streams at risk (Gasith and Resh 1999). Boucher (2002) states that drying of stream banks without compensatory releases leads to an increase in fire temperatures.

Riparian vegetation is sensitive to changes in minimum and maximum flows (NRC 1992; Stromberg 1993) and low flows have long been thought to be crucial for maintaining riparian vegetation during dry conditions (Boucher 1999), although there are very few studies that address this directly. A study by Boucher and Rode (2001) in the Breede River, Western Cape, showed that plants that were closer to the water developed faster than those on dry parts of the bank. Typically plants that occur in or near the wetted channel are influenced by hydro-geomorphological factors while those that grow higher up the bank are mainly influenced by plant-induced (autogenic) factors (Francis 2006). Many marginal zone species are soft-stemmed or fleshy and thus may easily suffer stem break, be uprooted or broken into fragments during periods of high flow (Reinecke 2013). Also on the Breede River, the effect of summer abstraction for agriculture and resultant low summer flows were shown to promote invasion and establishment of alien species (*Eucalyptus camaldulensis* and *Sesbania punicea.*) on the transitional area between the wet (see Sections 2.1 and 3) and dry bank zones

(DWAF 2002). Indeed, in the Western Cape alien-invaded rivers typically have reduced summer flow due to abstractions (Sieben and Reinecke 2008). Boucher and Rode (2001) stated that the migration of typical dry bank species into wet bank zone intensifies flooding. A study of the Breede River and its tributaries by (Boucher and Rode 2001) revealed that following the closure of Theewaterskloof Dam there was been a considerable reduction in both the magnitude and variability of summer flows which has had a major influence on the riparian vegetation along the river. On the Riviersonderend the wet bank zone was poorly-developed and the drybank was dominated by woody aliens. On the Baviaans River, also downstream of a long-standing abstraction reservoir, there were changes in lateral vegetation zones had migrated to lower levels on the banks relative to where they were found in unimpacted rivers. Prolonged low flow periods also resulted in the invasion of the stream bed by wet bank zone vegetation such as *Prionium serratum* and *Paspalum distichum* (Boucher and Rode 2001). Changes to the riparian vegetation will have knock-on effects for the whole ecosystem as riparian vegetation helps to shape aquatic habitats for aquatic ecosystems such as fish and macroinvertebrates (Stromberg 2001). In the McKenzie River lowered flows caused a reduction in channel movement, which led to a loss of spawning gravel and a loss of habitat for juvenile salmon and a reduced average population size (Ligon *et al.* 1995). In Mediterranean streams, benthic macroinvertebrate assemblages that are flow-dependent taxa (such as filter feeders) are affected when flow into pools is eliminated, when isolated pools are formed this may increase predation (Gasith and Resh 1999). Riparian vegetation also affects sediment supply and movement, lowering of flows may lead to a reduction in the river's efficiency to transport incoming sediment, which may result in the build up of sediment deposits in the wetted channels and the covering of the exposed bedrock to form sand sheets and alluvial anastomising bars (Van Coller 1997). Conversely, an increase in sediment transport potential through channel narrowing may result in armouring, and a loss of important gravel and cobble habitat (Gilvear *et al.* 2002; Rowntree 1990; Kleynhans 1996).

This study focused on the links between summer low flows and the population structure of selected plant species along river banks on four mountain streams in the Western Cape, South Africa. The objective was to determine whether long-term abstraction of dry season low flows has had an influence on the recruitment success of selected (common) riparian species. To address this objective, recruitment patterns were recorded upstream and downstream of abstraction points that remove most or all of the dry season low flows. Differences in recruitment success within the wetted channel under two different flow regimes, viz. near-natural versus the absence of dry season low flows, were compared for six common species of Fynbos Riparian Vegetation (*Salix mucronata; Morella serrata, Metrosideros angustifolia; Brachylaena neriifolia; Freylinia lanceolata* and *Brabejum stellatifolium*). The key research question was "What are the influences of the lack of dry season low-flows on the lateral distribution of riparian vegetation communities?"

The working hypotheses of this chapter were as follows:

- The downstream sites have less clear zonation than the upstream sites.
- There are more seedlings in the channel downstream than upstream, and the marginal zone is narrower in response to abstraction.

4.2 Study sites

Data were collected from eight paired sites on four rivers during the summer of 2012/2013. The four rivers were the Sanddrifskloof, the Morraineskloof, the Keurhoek and the Jonkershoek Rivers (Figure 4.1). Each pair was situated upstream and downstream of an abstraction point (Figure 4.2), which diverted the bulk of the summer base flow leaving the channel downstream dry or with standing pools for the summer months (December to March in the Western Cape). Three of the abstraction points were situated downstream of a flow gauging station. The exception was the Sanddrifskloof River where the abstraction point was located downstream of the gauging weir (Figure 4.2). Site locations and flow gauge numbers are provided in Table 4.1. At the time of sampling, surface flow at the upstream sites was strong, and at the downstream sites was negligible, although there were small, isolated, shallow pools and a thin section of the channel remained wet. Replicate samples of the riparian vegetation were collected on opposing banks and were named as follows using the Sanddrifskloof River as an example: San1 LB (left bank) and San1 RB (right bank).

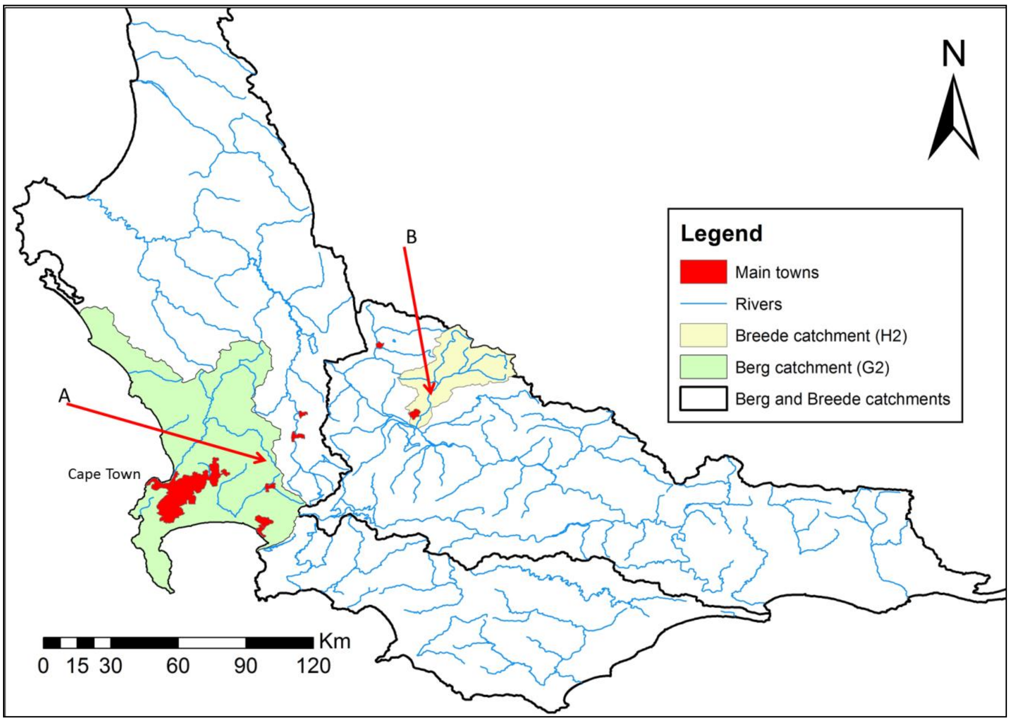


Figure 4.1 Map showing the location of the study sites, arrow A showing the location of river sites in the Breede catchment and B points at river sites on the Berg catchment

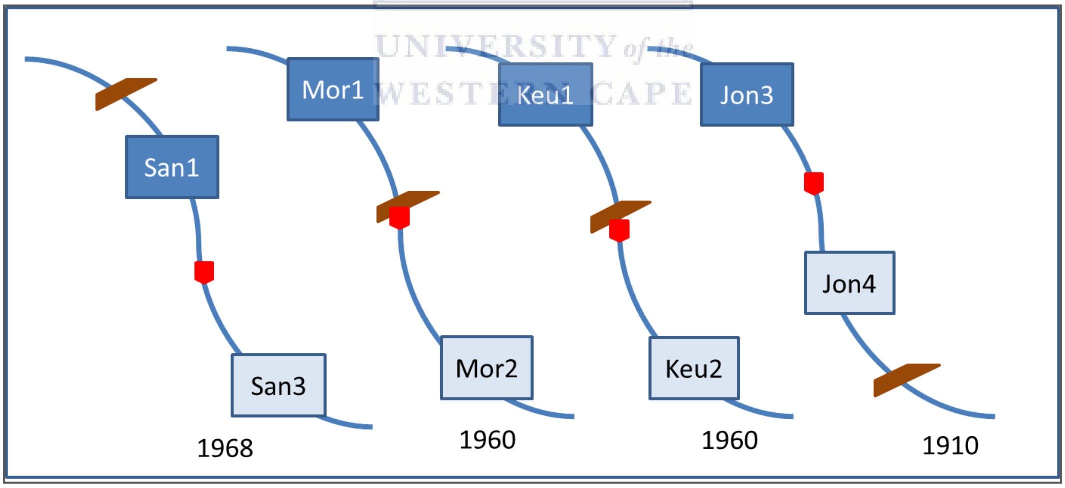


Figure 4.2 Schematic diagram showing sample site orientation in relation to the abstraction points (red) and the flow gauging stations (brown). The year that abstraction began at each river is also shown

Table 4.1 Details of study sites and DWA flow gauges at each river

Catchment	River	Site Code	Gauge	Month of no flow	Co-ordinates
Breede	Sanddrifskloof	San1 LB San1 RB San3 LB San3 RB	H2L004	February to April	33.48556S 19.52917E
Breede	Morraineskloof	Mor1 LB Mor1 RB Mor2 LB Mor2 RB	H2L001	December to March	33.49722S 19.49444E
Breede	Keurhoek	Keu1 LB Keu1 RB Keu2 LB Keu2 RB	H2L003	January to April	33.52083S 19.48750E
Berg	Jonkershoek	Jon3 LB Jon3 RB Jon4 LB Jon4 RB	G2H037	December to March	33.98472S 18.95333E

4.2.1.1 Study site descriptions

Sanddrifskloof River

Abstraction of water from the Sandrifskloof has been taking place since *c*. 1968, i.e., for more than 45 years. At the time of sampling there was no flow downstream, the wetted channel comprised stagnant pools. The riparian vegetation at both the upstream and downstream sites was relatively undisturbed. At the upstream sites the left bank was steep and had little vegetation on it. The right bank was of a shallower gradient and there were many Cape willows (*Salix Mucronata*) and lance-leaf waxberries (*Morella serrata*) recruiting into the wetted channel. At the downstream sites both left and right margins of the river were dominated by the restio *Ischyrolepis subverticillata* as well as Palmiet (*Prionium serratum*) in the wetted channel.

Morraineskloof River

Abstraction of water from the Morraineskloof has been taking place since *c*. 1960, i.e., for more than 50 years. At the time of sampling the upstream site comprised shallow pools of water and at the downstream site there was a narrow strip (1 m) of very low flow. The sites were fairly flat and characterised by sandy banks, particularly upstream. The downstream sites had more cobbles and boulders. The riparian vegetation at both the upstream and downstream sites was relatively undisturbed. The upstream site was dominated by saplings of *Morella serrata* and *Freylinia lanceolata* situated close to the water's edge while the downstream site was dominated by *Pelargonium scabrum* and *Brabejum stellatifolium* adults mainly.

Keurhoek River

Abstraction of water from the Keurhoek River has been taking place since *c.* 1960, i.e., for more than 50 years. At the time of sampling, the upstream site comprised pools on the left and right banks, which could make it difficult for the seedlings to establish on the margins of the channels. The downstream site did not have flowing water but there were small pools of shallow stagnant water between rocks, the channel was populated by grasses and shrubs. The left bank of both up- and downstream sites had a steep cliff and comprised a very narrow marginal area and a mountain of boulders; the right banks were however, fairly flat with loose sand. A thick bush of *Ischyrolepis subverticillata* and shrubs of *Pteridium aquilinum* at the back dominated upstream sites. The downstream sites were characterized by a strip of *Morella serrata* and *Metrosideros angustifolia* saplings in the wetted channel extending outwards.

Jonkershoek River

Abstraction of water from the Jonkershoek River has been taking place since c. 1910, i.e., for more than 100 years. At the time of sampling, the upstream sites had a mixture of pools and riffles while on the downstream sites there was no flow but the middle section of the channel was wet with a few pools. The upstream sites were characterized by gently sloping banks with sand covered by old tree residues just outside the channel. The right bank at the downstream sites was similar to those at the upstream site, but the left bank was steeper. A lot of *Freylinia lanceolata* and *Brachylaena neriifolia* saplings had established closer to the wetted channel at upstream sites while *Brabejum stellatifolium* and *Ilex mitis* adults dominate the margins of the downstream sites. Both sites lacked the characteristic Western Cape riparian species *Salix mucronata*.

4.3 Methods

4.3.1 Data collection

4.3.1.1 Flow data

Average daily discharge records for the gauging weirs at each of the sites were obtained from the Department of Water Affairs website: www.dwa.gov.za. Information about the volume of water abstracted from the Morraineskloof, Keurhoek and Sanddrifskloof Rivers was obtained from the chairperson of the Hex Valley Water User Association, Mr Christiaan Olivier. Information for the Jonkershoek River was obtained from Dr Joan Barnes, an independent consultant.

4.3.1.2 Vegetation data

Vegetation data were collected in replicate transects on opposing banks at each site. Transects were arranged in the same way as those of the previous chapter (Figure 3.3). Each transect was 10 m wide, along the wetted edge of the river, and stretched several metres up the bank. The length of each transect was dictated by the width of the riparian area (Figure 4.3). Each transect was divided into two bands 5 m in width and into contiguous sample plots 1 m in length. Sample plot labeling was done by number (1 to 'n') to indicate distance from the wetted edge in metres, and by letter A and B for the two bands. In cases where plant species were rooted on islands or cobble bars in the wetted channel, or where the edge of channel was not straight, the vegetation transect was extended into the channel and numbered in a negative direction. The maximum height and percentage cover of all species present in each sample plot was recorded as well as the number of individuals and relative positions of trees to 1-m accuracy.

Trees were separated into two life stages (Chapter 3): juveniles (height < 2 m); and adults (height > 2 m). These data were collected for six small trees that are common along fynbos rivers (Sieben and Reinecke 2008): *Salix mucronata; Morella serrata, Metrosideros angustifolia; Brachylaena neriifolia; Freylinia lanceolata* and *Brabejum stellatifolium*. Five of these species were present at every site and *Salix mucronata* was absent from the Jonkershoek River. The different plants establish at different lateral zones of the riparian bank, the favourable conditions allow them to survive in their respective zones.

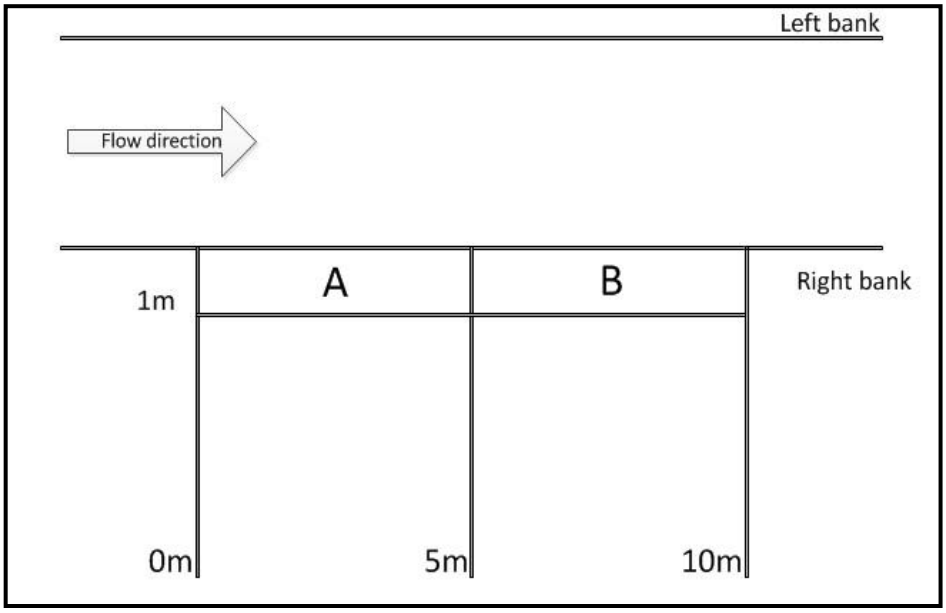


Figure 4.3 Sample grid showing the matrix and numbering of sample plots

4.4 Data analysis

4.4.1 Flow data

Time series of daily average flows were obtained from DWA (2012) for the gauging stations near each site (Table 4.1). The mean monthly flow for each site was calculated and plotted on graphs to show high and low flow periods for each river.

4.4.1.1 Vegetation data

The data were analysed at two scales: across rivers (at a river scale) and between sites (at a sample plot scale). Sites on different rivers represented replicates of the upstream and downstream conditions, with two sites on the up and downstream of the abstraction point. This was done in order to compare sites on different rivers and catchments at some level. The plants within sample plots were used to identify the lateral zones at site scale; this was also done to give a glimpse into the difference in zonation at disturbed (downstream) and undisturbed (upstream) sites.

River comparisons: Species abundances at each site, as percentage cover, of all sample plots at each site were summed and standardised to give a single value per species. Data were 4th root transformed in order to boost the presence of smaller species at lower percentage covers.

Bray-Curtis similarity coefficients were calculated in PRIMER between rivers and the results were displayed using cluster analyses (Clarke and Gorley 2006). Following the MDS and cluster analysis, dissimilarities between rivers and river sites were then studied by using species composition. A global nested pair-wise ANOSIM routine (PRIMER V6, Clarke and Warwick 2006) of species abundance between sites was used. ANOSIM is a method that allows testing for significant differences in species composition between a priori identified groups, in this case upstream and downstream sites.

Measures of species diversity were calculated between sites using the DIVERSE routine in PRIMER V6, (Clarke and Gorley 2006). Paired and unpaired T-tests were used to discern differences between rivers (four replicates, hereafter referred to as river-scale) and/or sites (eight replicates, hereafter referred to as site-scale). After testing species diversity, further tests were done examining possible differences at species level. Differences at river scale were studied, using different growth forms and riparian factors (Appendix Table 3) for each plant. There were six growth form types as shown in Appendix Table 3, i.e. tree, shrub, herbaceous perennial, restio, sedge, and grass. Species habitats were assigned according to habitat preference for each species using three categories (referred to as riparian factors; Goldblatt and Manning 2000), as follows:

- Obligate riparian - plant species that are common on or near streamsides, seeps, rivers and watercourses (wet species),
- Incidental terrestrial - plant species occurring on rocky slopes and outcrops or mountain slopes (dry species) and
- Facultative riparian - plant species that occur in bush, woodland or forests and/or associated with water courses (wet/dry species). The species in this group are associated with wet conditions but their survival is not entirely dependent on the water.

Not all plants could be identified to species level, and almost half were only identified to genus. Plants that were not identified to species level were left out of the riparian factor analysis as they could not be allocated to a specific factor. Thus, for analysis for the riparian factor section, only data for the plants that were known to the species level were used (Appendix Table 3). The unidentified species were however used for the comparison on growth forms.

Testing for significant differences between up and downstream sites was done by comparing:

- the number of individuals at different life stages (seedling, sapling and adults);
- the number of individuals of different growth forms;
- the number of species in each growth form category;
- the number of individuals in each riparian category; and,
- the number of species in each riparian category.

After testing for significant differences between sites, the SIMPER routine (PRIMER v6, Clarke and Gorley 2006) was used to identify typical and indicator species for each group (up/downstream sites). SIMPER identifies the taxa that are responsible for similarities and dissimilarities between and within prior defined groups (in this case up and downstream sites). The percentage dissimilarity between the upstream and downstream sites was also calculated, and the characteristic species that contributed to the dissimilarity between the two groups were identified (Table 4.11).

The number of individuals of typical wet and dry bank species was then compared in bar graphs at a site-scale. Finally, the relative positions of wet and dry bank juveniles were compared between sites. A combination of seedlings and saplings was used to study the positions at which recruitment at downstream sites is more probable, as the main aim of the chapter was to study the effects of the absence of flows on recruitment. The sum of saplings and seedlings (juveniles) at each site was then plotted against the lateral distance on the bank.

4.5 Results

4.5.1 River flows

The monthly hydrographs for each of the sites are provided in Figure 4.4. An increase in average flow is observed between April and May for all sites. The high flows persist for about seven months followed by a sudden decrease of flows in October. The period from December to March has the lowest flows for all sites: this is the dry summer period in the Western Cape.

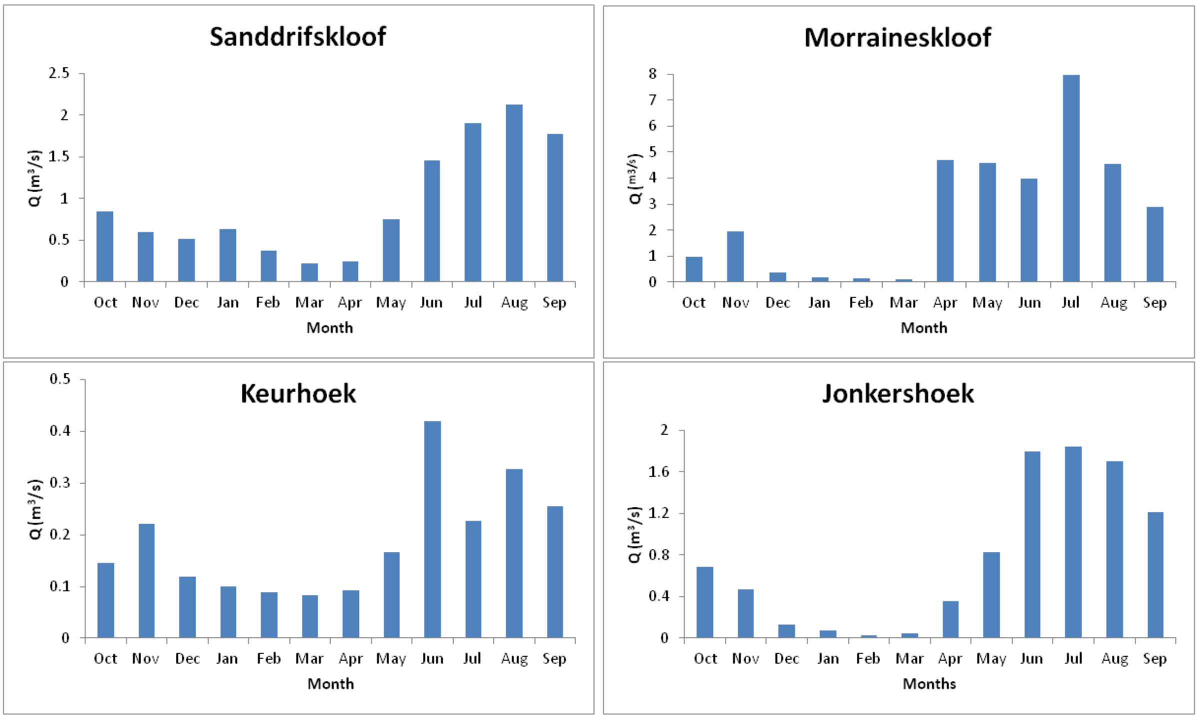


Figure 4.4 Mean monthly flows for a hydrological year at each site

4.5.2 River comparisons

The results of the MDS and cluster analysis are shown in Figure 4.5. The 16 sites grouped according to catchment. The three rivers in the Hex valley (Breede River catchment; Sanddrifskloof, Morraineskloof and Keurhoek) were more closely related to one other than to the Jonkershoek River (Berg River) catchment, which grouped on its own (Figure 4.5). Within these catchment groups the sites at each river separated from those at other rivers. Within each river, upstream sites separated from the downstream except for the Keurhoek River, where Keu1 LB was an outlier, possibly because of the left bank being a sparsely vegetated near vertical cliff (see Section 4.2.1.1).

The Morraineskloof sites were most similar to the Keurhoek sites, and Mor2 LB and Mor2 RB paired with Keu2 LB and Keu2 RB, Mor1 LB and Mor1 RB sites paired with Keu1 RB. The Sanddrifskloof upstream and downstream sites were most strongly related to one another at a 60% similarity between sites, while the Morraineskloof and Keurhoek sites exhibited 50% similarity and the Jonkershoek sites a less than 40% similarity (Table 4.2).

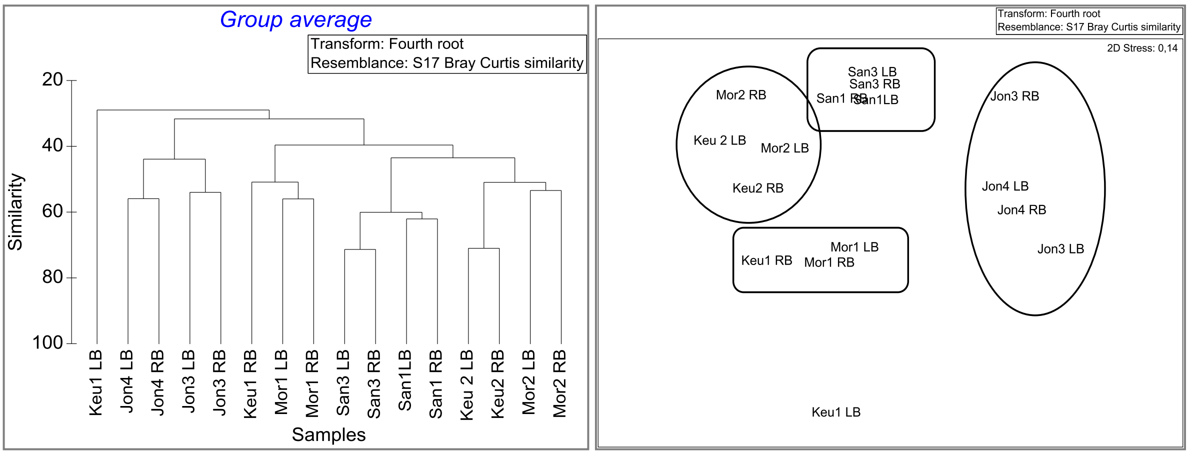


Figure 4.5 A Cluster and MDS ordination of Bray Curtis similarity between species composition of sites. Site codes as per Table 4.1

Table 4.2 Similarity coefficients between upstream and downstream sites

	San1 LB	San1 RB	San3 LB	San3 RB	Mor1 LB	Mor1 RB	Mor 2 LB	Mor2 RB	Keu1 LB	Keu1 RB	Keu2 LB	Keu2 RB	Jon3 LB	Jon3 RB	Jon4 LB	Jon4 RB
San1 LB																
San1 RB	62.0															
San3 LB	57.5	57.0														
San3 RB	63.7	61.7	71.3													
Mor1 LB	46.7	41.4	43.7	38.1												
Mor1 RB	39.1	37.9	34.7	40.8	55.9											
Mor2 LB	41.6	51.5	39.8	41.4	40.2	41.9										
Mor2 RB	50.1	49.6	47.0	44.7	37.0	41.1	53.4									
Keu1 LB	22.0	30.6	20.5	23.7	33.2	35.8	34.2	22.1								
Keu1 RB	37.6	37.5	33.1	36.9	51.0	50.7	34.6	44.5	37.5							
Keu2 LB	39.1	49.5	38.2	37.9	34.0	33.3	54.8	50.2	29.9	45.2						
Keu2 RB	41.2	44.7	39.1	39.6	35.4	42.1	50.6	48.0	34.4	52.7	70.9					
Jon3 LB	31.6	30.3	26.6	30.7	29.9	34.5	32.1	21.5	30.0	25.2	24.1	26.8				
Jon3 RB	41.5	45.9	36.7	41.4	30.1	31.3	34.4	26.4	22.7	26.8	26.5	28.2	53.9			
Jon4 LB	39.8	31.3	35.2	35.5	35.2	27.7	33.6	26.3	27.7	30.1	31.6	35.9	41.1	41.7		
Jon4 RB	40.0	33.1	40.0	36.0	36.0	32.5	28.5	18.0	29.6	30.7	23.2	28.3	52.4	40.2	55.8	

The left bank at Keu1 was an outlier (Figure 4.5), which showed that this site was different from all the other sites (including the other sites from the same river), however, the general pattern of Keu1 LB relative to Keu2 samples was similar to that between Keu1 RB and Keu2 samples.

Dissimilarities in species composition between rivers and between sites were investigated. A global nested pair-wise ANOSIM of species abundance between sites showed that rivers were significantly different from one another (Global R = 0.896). Overall the species composition between upstream and downstream sites was also significantly different (Global R =0.813).

4.5.2.1 Lateral zonation

The analysis of lateral zone pattern between upstream and downstream sites did not show a conclusive result. At most sites all lateral zones were present, although at the downstream sites had some dry bank species on their marginal and lower dynamic zones. The results for the lateral zonation within sites did not show major dissimilarities between the upstream and downstream sites. Some of the downstream sites had all the four lateral zones.

All sites on the Sanddrifskloof River had the marginal zone, all of which were 3 m wide except for San1 LB which was 2 m in width (Table 4.3). At upstream sites, the wet bank width (all wet bank zones combined) was 2 m on the left bank and 3 m on the right bank, while at the downstream sites they were 5 m on both banks (Figure 4.6).

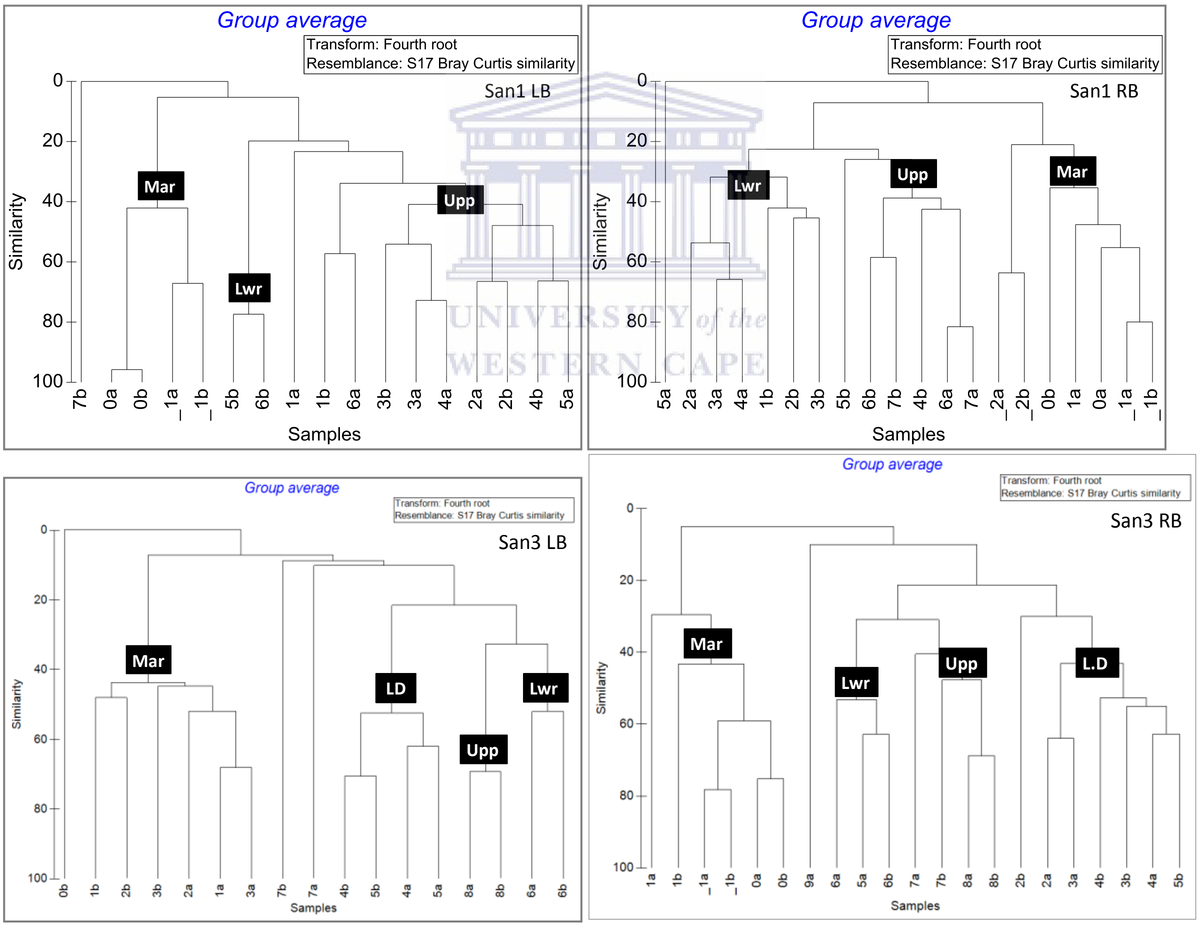


Figure 4.6 MDS ordinations for the Sanddrifskloof River sites. Sample plots (indicated as samples) are indicated within Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp.= upper zone

Sites at Morraineskloof River did not have the marginal zone except for Mor2 RB which was 1 m in width (Table 4.3). The upstream sites comprised pools at the water's edge, which could explain the absence of the marginal zone. For the upstream sites, the total width of the wet bank was 1 m on the right bank while on the left bank it was not represented. At downstream sites the wet bank was 2 m wide on both banks (Figure 4.7).

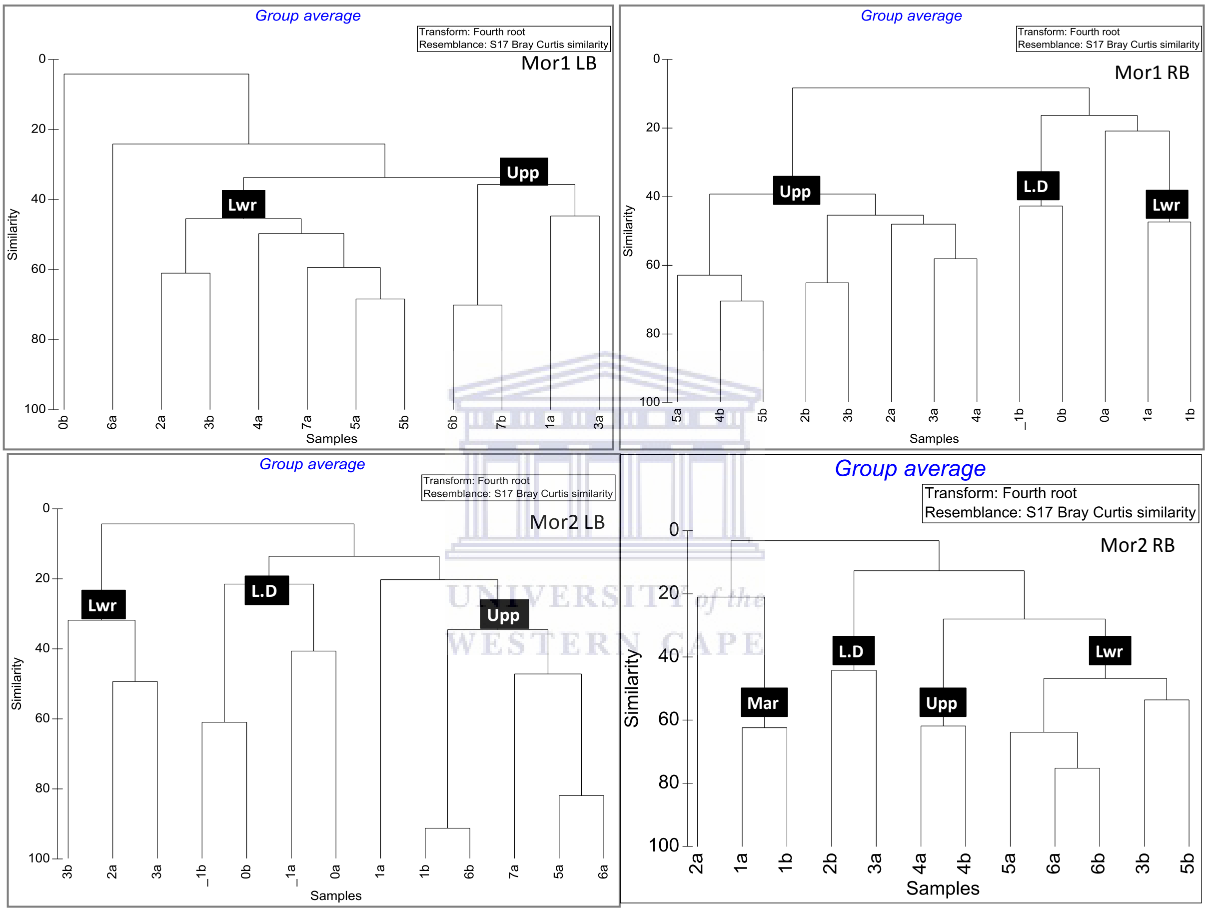


Figure 4.7 MDS ordinations for the Morraineskloof River sites. Sample plots (indicated as samples) are indicated within Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp.= upper zone

At the Keurhoek River, Keu1 RB and Keu2 LB did not have the marginal zone. The upstream left bank marginal zone was 1 m thick, while the downstream right bank was 2 m (Table 4.3). The width of the wet bank area of upstream sites was 3 m on the left bank and 1 m on the right bank. At downstream sites the right bank was 1.5 m wide while on the left bank it was 4 m in width (Figure 4.8).

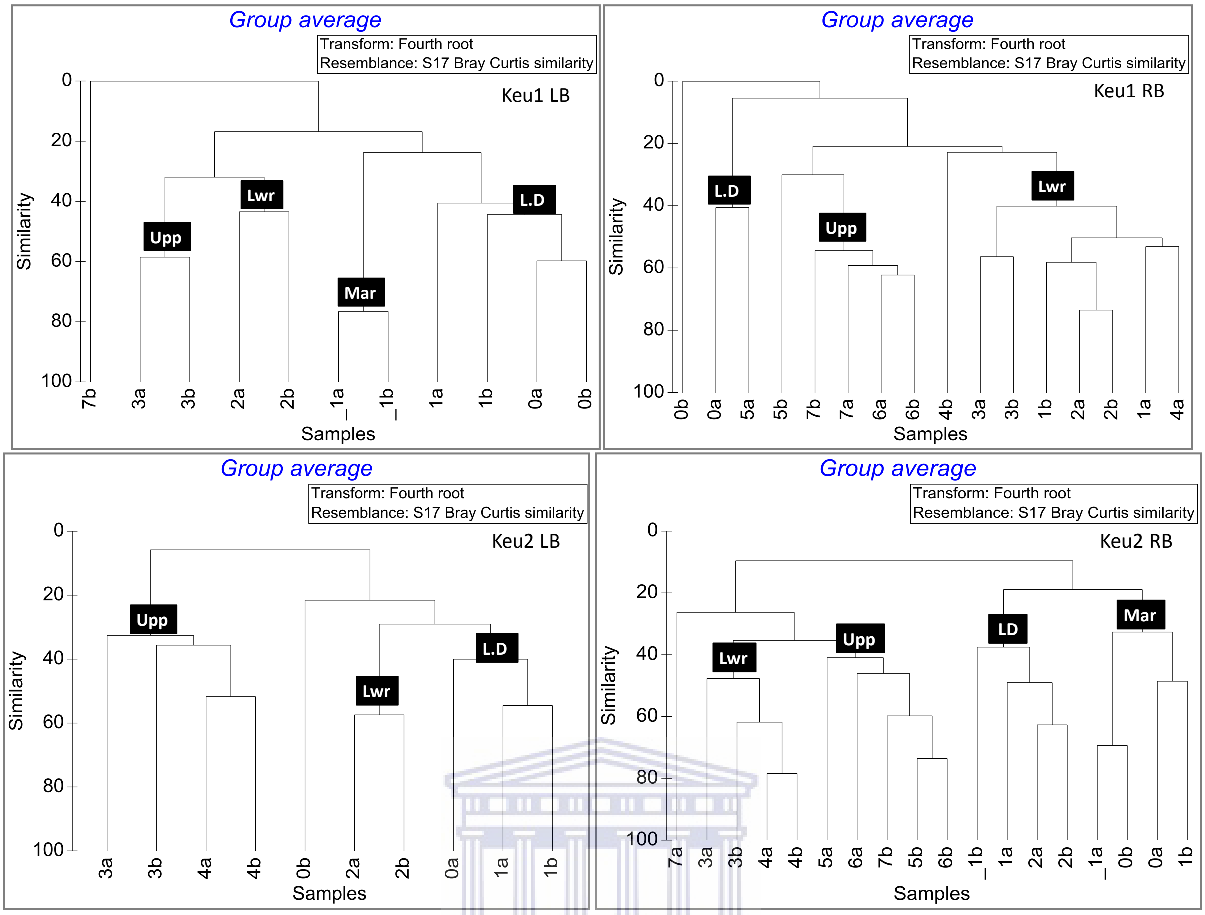


Figure 4.8 **MDS ordinations for the Keurhoek River sites. Sample plots (indicated as samples) are indicated within Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp.= upper zone**

At the Jonkershoek River, the marginal zone was absent at all sites (Table 4.3). The entire wet bank width for downstream sites (1 m) was smaller than that of the upstream (2 m) (Figure 4.9).

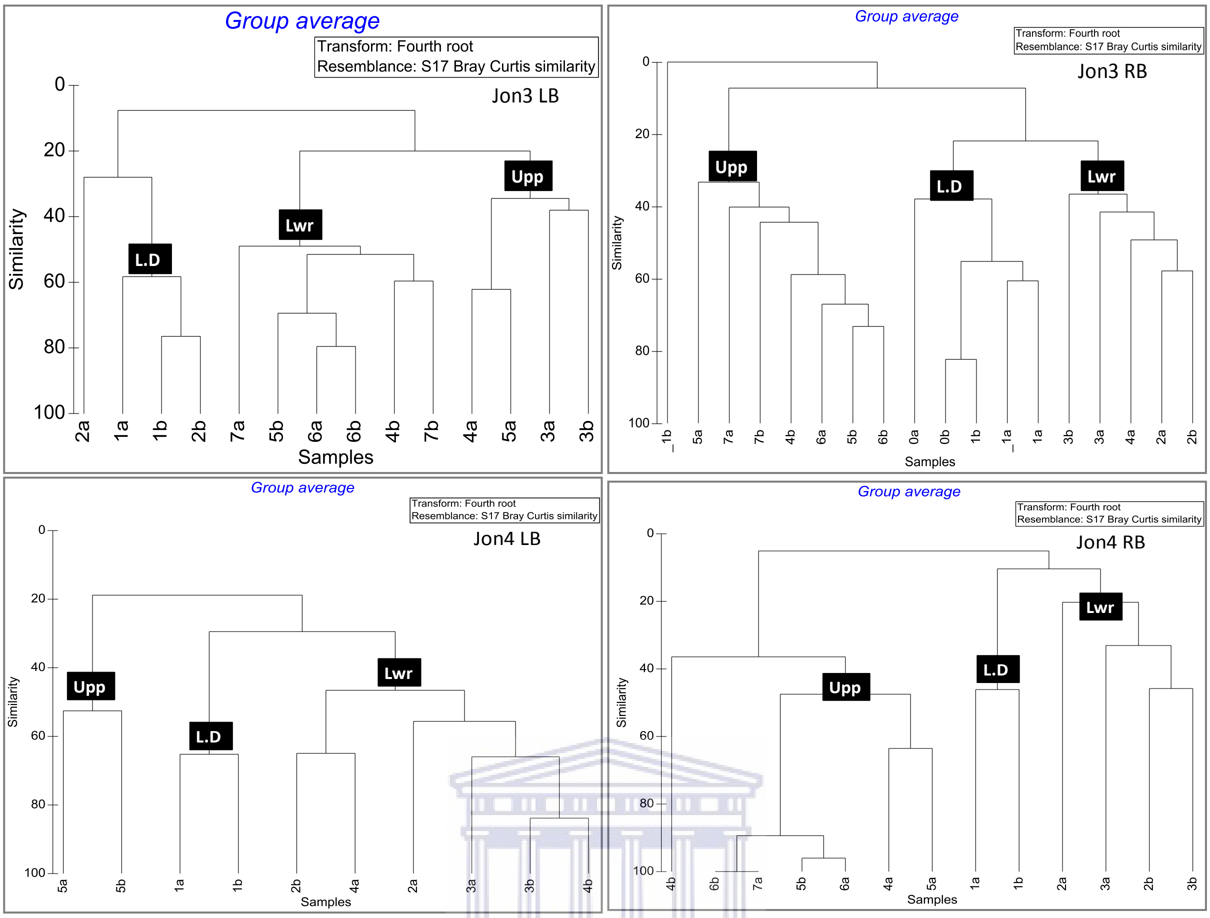


Figure 4.9 MDS ordinations for the Jonkershoek River sites. Sample plots (indicated as samples) are indicated within Mar = marginal zone, L.D = lower dynamic, Lwr = lower zone and Upp.= upper zone

4.5.2.2 Width of riparian zone

Overall, the width of the entire wet bank zone (marginal and lower dynamic zones) at upstream sites was smaller than that of the downstream sites at Jonkershoek and Keurhoek River. At Sanddrifskloof, the wet bank of the downstream sites was wider than that of the upstream sites. However, there was no definite reduction on the marginal zones at downstream sites, instead the marginal zone is represented by similar widths at both up and downstream sites for each river. Although at downstream sites the marginal zone had extended into the channel, most marginal zones are -1 to 0 m positions.

Table 4.3 Width of the marginal zone at sites

Site	Bank	Marginal zone width	
		Upstream (m)	Downstream (m)
San	Left	2	3
	Right	3	3
Mor	Left	0	0
	Right	0	2
Keu	Left	1	0
	Right	0	3
Jon	Left	0	0
	Right	0	0

4.5.2.3 Species diversity

Five measures of species richness were calculated and compared using t-tests: 1. total number of species; 2. Margalef's species richness (d, Margalef 1972 in Magurran 2004); 3. Shannon Weiner equitability (H; Shannon and Weaver 1949 in Magurran 2004); 4. Pielou's relative diversity (J; Pielou 1975 in Magurran 2004) and 5. Simpson's index (ƛ, Simpson 1949 in Magurran 2004). There were no significant differences between sites for any of the diversity measures tested for either the paired or the unpaired test (Table 4.4). Following this, further analysis sought to identify the characteristics responsible for group separations.

Table 4.4 Different univariate diversity measures used to test for significance between river sites. S = Total species, d = species richness (margalef), J` = Pielou’s evenness, H=.Shannon Weiner and Lambda= Simpson’s index

Sites	Diversity measures				
	S	d	J'	H'($\log_e$)	1-Lambda'
San1 LB	18	3.69	0.98	2.82	0.95
San1 RB	21	4.34	0.98	2.99	0.96
Mor1 LB	15	3.04	0.98	2.65	0.94
Mor1 RB	17	3.47	0.99	2.79	0.95
Keu1 LB	11	2.17	0.98	2.36	0.91
Keu1 RB	15	3.04	0.99	2.67	0.94
Jon3 LB	15	3.04	0.98	2.65	0.93
Jon3 RB	19	3.91	0.99	2.91	0.95
Mean	**16.38**	**3.34**	**0.98**	**2.73**	**0.94**
SD	**3.07**	**0.67**	**0.00**	**0.20**	**0.01**
San3 LB	15	3.04	0.97	2.64	0.93
San3 RB	18	3.69	0.98	2.85	0.95
Mor2 LB	19	3.91	0.98	2.89	0.95
Mor2 RB	22	4.56	0.98	3.03	0.96
Keu 2 LB	19	3.91	0.98	2.90	0.95
Keu2 RB	18	3.69	0.98	2.85	0.95
Jon4 LB	12	2.39	0.97	2.42	0.92
Jon4 RB	7	1.30	0.99	1.92	0.86
Mean	16.25	3.31	0.98	2.69	0.93
SD	4.77	1.04	0.01	0.36	0.03
Paired P-value	**0.96**	**0.96**	**0.49**	**0.80**	**0.66**
Unpaired P-value	**0.95**	**0.95**	**0.76**	**0.77**	**0.61**

4.5.2.4 Life stages

There were no significant differences between the number of individuals of different life stages of the six species of trees tested (seedlings, saplings and adults) at upstream and downstream sites (Table 4.5).

Table 4.5 Number of plants in each life stage for each site

	Sites	Life stage		
Upstream sites		Seedling	Sapling	Adult
	San1LB	12	41	44
	San1 RB	70	56	55
	Mor1 LB	26	2	7
	Mor1 RB	27	71	13
	Keu1 LB	41	5	7
	Keu1 RB	76	13	32
	Jon3 LB	37	12	3
	Jon3 RB	46	19	14
	Mean	**27.38**	**41.88**	**21.88**
	SD	**25.54**	**21.92**	**19.38**
Downstream sites				
	San3 LB	18	16	31
	San3 RB	49	31	51
	Mor2 LB	85	15	5
	Mor2 RB	73	28	13
	Keu 2 LB	18	35	15
	Keu2 RB	48	2	6
	Jon4 LB	18	7	6
	Jon4 RB	13	16	7
	Mean	**18.75**	**40.25**	**16.75**
	SD	**11.63**	**27.88**	**16.29**
T-test	**Unpaired**	**0.39**	**0.89**	**0.57**
	Paired	**0.32**	**0.9**	**0.21**

This led to an investigation of whether there were differences between growth forms and/or between the riparian factors (Appendix Table 3) at up and downstream sites.

4.5.2.5 Growth form

The number of species (Table 4.7) and individuals (Table 4.6) in each growth form were tested to see if they differed significantly between upstream and downstream sites. Six categories of growth forms were used as shown in Appendix Table 3: tree, shrub, herbaceous perennial, restio, sedge and grass. There were significant differences at the 5 and 10% level between the number of individuals making up the herbaceous perennials and sedges with p-value = 0.025 and 0.095 respectively.

The number of species within the sedges were also significantly different at the 5 and 10% level with p-value =0.09 (Table 4.7).

Table 4.6 Number of individuals for each growth form at sites. Asterisked values are significant. Herb = herbaceous perennial

Site	Growth form					
	Grass	Herb	Restio	sedge	Shrub	Tree
San1 LB	2	2	2	4	8	93
San1 RB	3	2	3	1	8	181
Mor1 LB	0	1	2	1	7	37
Mor1 RB	0	1	3	2	11	111
Keu1 LB	0	2	2	4	5	53
Keu1 RB	1	1	4	1	9	122
Jon3 LB	3	2	2	4	6	52
Jon3 RB	2	0	2	2	7	79
Mean	**1.38**	**1.25***	**2.5**	**1.25***	**7.63**	**91**
SD	**1.3**	**0.71***	**0.76**	**0.46***	**1.85**	**47.04**
San3 LB	1	7	2	1	4	65
San3 RB	2	9	3	2	5	131
Mor2 LB	1	2	1	1	4	105
Mor2 RB	1	1	3	0	13	114
Keu 2 LB	2	2	5	0	10	68
Keu2 RB	2	7	5	1	13	56
Jon4 LB	1	2	2	0	5	31
Jon4 RB	0	6	2	0	4	36
Mean	**1.25**	**4.5***	**2.88**	**0.63***	**7.25**	**75.75**
SD	**0.71**	**3.07***	**1.46**	**0.74***	**4.06**	**36.88**
Paired P-value	**0.826**	**0.025***	**0.401**	**0.095***	**0.773**	**0.348**
Unpaired P-value	**0.814**	**0.011***	**0.528**	**0.063***	**0.815**	**0.482**

Table 4.7 Number of species of different growth forms at upstream and downstream sites. Asterisked values show significant differences. Herb = herbaceous perennial

Sites	Growth form					
	Tree	Shrub	Herb	Restio	Sedge	Grass
San1LB	12	8	2	2	2	2
San1 RB	14	8	2	3	1	3
Mor1 LB	10	7	1	2	1	0
Mor1 RB	11	11	2	3	1	0
Keu1 LB	5	5	2	2	2	0
Keu1 RB	7	9	1	4	1	1
Jon3 LB	8	6	5	2	1	3
Jon3 RB	12	7	6	2	1	2
Mean	**9.88**	**7.63**	**2.63**	**2.50**	**1.25***	**1.38**
SD	**3.00**	**1.85**	**1.85**	**0.76**	**0.46***	**1.30**
San3 LB	12	8	1	2	1	1
San3 RB	13	7	2	3	2	2
Mor2 LB	9	11	2	1	1	1
Mor2 RB	12	13	1	3	0	1
Keu 2 LB	9	10	2	5	0	2
Keu2 RB	6	13	2	5	1	2
Jon4 LB	10	5	2	2	0	1
Jon4 RB	8	4	2	2	0	0
Mean	**9.88**	**8.88**	**1.75**	**2.88**	**0.63***	**1.25**

Sites	Growth form					
	Tree	Shrub	Herb	Restio	Sedge	Grass
SD	**2.36**	**3.44**	**0.46**	**1.46**	**0.74***	**0.71**
Paired P-value	**1.00**	**0.26**	**0.21**	**0.40**	**0.09***	**0.83**
Unpaired P-value	**1.00**	**0.38**	**0.21**	**0.52**	**0.063***	**0.81**

4.5.2.6 Riparian factors

The number of species (Table 4.8) and individuals (Table 4.9) in each riparian factor category were tested to see if they differed significantly between upstream and downstream sites. There were significant differences between upstream and downstream sites between the number of individuals in the facultative category, with p-value = 0.01 (Table 4.8).

Table 4.8 Number of individuals belonging to each riparian category at upstream and downstream sites. Asterisked values show significant differences

Sites	Riparian factor			Sites	Riparian factor		
	Obligate	Incidental	Facultative		Obligate	Incidental	Facultative
San1 LB	93	2	1	San3 LB	65	1	0
San1 RB	181	2	1	San3 RB	131	1	0
Mor1 LB	36	5	1	Mor2 LB	105	8	1
Mor1 RB	111	3	1	Mor2 RB	114	9	0
Keu1 LB	53	6	1	Keu2 LB	68	5	1
Keu1 RB	121	5	1	Keu2 RB	56	9	1
Jon3 LB	52	4	2	Jon4 LB	31	3	0
Jon3 RB	79	2	2	Jon4 RB	36	1	1
Mean	**90.75**	**3.63**	**1.25**	**Mean**	**75.75**	**4.63**	**0.5***
SD	**47.11**	**1.6**	**0.46**	**SD**	**36.88**	**3.62**	**0.53***
Paired P-value					**0.357**	**0.358**	**0.019***
Unpaired P-value					**0.489**	**0.486**	**0.009***

When data for species composition were tested, once again the facultative riparian factor showed that the upstream sites were significantly different from those downstream. The mean value for the upstream sites was 1.25 while for the downstream sites was 0.5 (Table 4.9). The probability (p-value) for this riparian factor was 0.01.

Table 4.9 Number of species belonging to each riparian category at the upstream and downstream sites. Asterisked values show significant differences

Sites	Factor			Sites	Factor		
	Obligate	Incidental	Facultative		Obligate	Incidental	Facultative
San1LB	17	2	1	San3 LB	16	1	0
San1 RB	22	2	1	San3 RB	21	1	0
Mor1 LB	13	3	1	Mor2 LB	15	5	1
Mor1 RB	16	3	1	Mor2 RB	18	6	0
Keu1 LB	8	3	1	Keu2 LB	16	3	1
Keu1 RB	13	3	1	Keu2 RB	13	5	1
Jon3 LB	12	2	2	Jon4 LB	12	3	0
Jon3 RB	18	1	2	Jon4 RB	9	1	1
Mean	**14.88**	**2.38**	**1.25***	**Mean**	**15**	**3.13**	**0.5***
SD	**4.29**	**0.74**	**0.46***	**SD**	**3.7**	**2.03**	**0.53***
Paired P-value					**0.940**	**0.190**	**0.019***
Unpaired P-value					**0.950**	**0.340**	**0.009***

The SIMPER routine (PRIMER v6, Clarke and Gorley 2006) was used to identify typical and indicator species for the upstream and downstream communities. The dissimilarity percentage between the upstream and downstream sites was also calculated, and the characteristic species that contributed to the dissimilarity identified. In general, the similarity between upstream sites was driven by wet bank species and that between the downstream sites was driven by dry bank species (Table 4.10).

Table 4.10 Similarity percentages for species at the upstream and downstream sites

Site dominant	Species	Sim/SD	Growth form	Riparian factor factor
Upstream	*M. angustifolia* juveniles	6.10	Tree	Obligate
	Pteridium aquilinum	2.73	Herbaceous perennial	Facultative
	B. lanceolata juveniles	5.37	Tree	Obligate
Downstream	*M. angustifolia* juveniles	5.51	Tree	Obligate
	Diospyros glabra	3.53	Shrub	Incidental
	F. lanceolata saplings	1.59	Tree	Facultative

The upstream sites were 43.66% similar to one another, this group of sites was characterised by species of *M. angustifolia* juveniles (16.98%), *Pteridium aquilinum* (13.58%) and *B. neriifolia* juveniles (12.04%), which together contributed 42.60% of the total similarity of 43.66%. Downstream sites were 43.87% similar to each other and were characterised by two species: *M. angustifolia* juveniles (13.88%), *Diospyros glabra* (13.72%) and *F. lanceolata* juveniles (10.91%). Together these contributed 38.52% of the total similarity of 43.87%.

The dissimilarity between the upstream and downstream sites was 58.18% (Table 4.11). The species that were mainly responsible for this were juveniles of the trees *B. stellatifolium, B. neriifolia, F. lanceolata,* a shrub, *Pteridium aquilinum* and a restio, *Ischyrolepis subverticillata*. Overall the contribution of adult trees to the dissimilarities between the up/downstream sites was weak (Table 4.11). *M. angustifolia* was a dominant species at both up and downstream sites.

Table 4.11 Dissimilarities between upstream and downstream sites calculated from SIMPER, with average cover of each species upstream and downstream. The blue shading shows typical wet bank species and brown shows the dry bank species

Groups: Upstream and downstream sites						
Average dissimilarity = **58.18**						
Species	Upstream	Downstream				
	Average cover	Average cover	Av.Diss	Diss/SD	Contrib%	Cum.%
B. stellatifolium juvenile	4.64	7.15	3.07	1.17	5.29	5.29
Pteridiun aquilinum	7.78	3.9	2.95	1.55	5.07	10.35
Diospyros glabra	3.33	7.54	2.55	1.45	4.38	14.73
B. neriifolia juvenile	6.05	5.14	2.39	1.59	4.12	18.85
Ischyrolepis subverticillata	5.82	4.67	2.26	1.29	3.89	22.74
M. serrata juvenile	5.47	3.62	2.15	1.31	3.7	26.44
Prionium serratum	2.46	3.57	2.13	1.12	3.66	30.1
Searsia angustifolia	2.83	6.07	2.11	1.4	3.62	33.72
F. lanceolata juvenile	2.84	6.09	2.05	1.62	3.52	37.24
Erica cafra	2.75	4.17	1.95	1.4	3.35	40.59
Stoebe plumosa	3.66	1.44	1.88	1.07	3.24	43.83
Isolepis prolifera	3.89	1.08	1.86	1.15	3.2	47.03
Notobubon galbanum	2.47	2.86	1.7	1.14	2.92	49.95
Cliffortia strobilifera	1.35	2.82	1.5	1.03	2.58	52.53
Stoebe cinerea	2.01	1.64	1.45	0.78	2.49	55.03
Calopsis paniculata	1.62	2.3	1.4	1.08	2.4	57.43
Blechnum capense	1.62	1.42	1.36	0.68	2.33	59.76
M. angustifolia juvenile	8.38	7.66	1.35	1.3	2.32	62.09
B. stellatifolium adult	1.35	1.96	1.34	0.81	2.31	64.4
S. mucronata juvenile	1.22	2.4	1.34	1.03	2.3	66.7
Elegia capensis	2.39	0.99	1.34	0.94	2.3	69
Psoralea aphylla	2.4	0	1.2	0.77	2.07	71.06
M. angustifolia t	2.15	2.66	1.15	1.35	1.97	73.04
Pelargonium scabrum	0.93	1.68	1.11	0.84	1.9	74.94
M. serrata adult	2.48	2.01	1.1	1.14	1.89	76.82
B. neriifolia adult	1.67	1.43	1.1	0.96	1.88	78.71
Dodonaea viscosa	0.48	1.99	1.07	0.84	1.84	80.54
Rhus crenata	0.67	1.8	1.03	0.82	1.76	82.31
Acacia longifolia	1.19	1.15	0.93	0.79	1.59	83.9
F. lanceolata t	0.88	1.22	0.87	0.72	1.5	85.4
S. mucronata adult	1.3	1.41	0.86	1.13	1.48	86.88
Anthospermum spaculata	0.66	1.26	0.82	0.67	1.41	88.29
Ehrharta ramosa	1.45	0	0.73	0.53	1.25	89.54
Heeria argentea	1.42	0	0.71	0.38	1.22	90.76

The cover of dry bank trees (*B. stellatifolium*, *F. lanceolata*, *M. angustifola*) all increased downstream. Apart from *S. mucronata* the wet bank (*M. serrata* and *B. neriifolia*) had a consistently less cover downstream.

4.5.2.7 Bank position

The positions on the lateral bank of the juveniles (seedlings and saplings) of six common trees (wet bank species: *S. mucronata; M. serrata, B. neriifolia*; and dry bank species: *B. stellatifolium*, *F. lanceolata, M. angustifola*) were then investigated for differences in the recruitment patterns upstream and downstream of the abstraction points. To do this, the number of juveniles for the typical dry bank species was plotted against their positions on the bank (Figure 4.10).

There were no marked differences for the wet bank trees. However, for the dry bank species, the results showed that the juveniles established closer to the water's edge (0 m) at the downstream sites than at the upstream sites (Figure 4.10). There were also very few individuals further than 3 m from the water's edge at the downstream sites. *B. stellatifolium* juveniles occurred in similar numbers at the up and downstream sites for all rivers but that at the upstream sites they occurred 2 - 5 m from the water's edge, whereas downstream they were most abundant 1 to 3 m from the water's edge. There were fewer *F. lanceolata* juveniles at the upstream sites than at downstream sites, and most occurred 2-3 m from the wetted channel, while at the downstream sites they were concentrated much closer to the wetted channel (at 0-2 m). At the upstream site on the Keurhoek River there were no *F. lanceolata* juveniles. There were numerous *M. angustifola* at all sites, but there were considerably more downstream than upstream at Morraineskloof and Keurhoek. The positioning of *F. lanceolata* juveniles at downstream sites was similar to that of in the upstream, the *M. angustifolia* juveniles were spread out between 3 - 7 m from the water's edge, and while downstream they occurred at distances 0 - 2 m. Indeed, *M. angustifolia* established in the wetted channel on Mor2 LB and Keu2 RB.

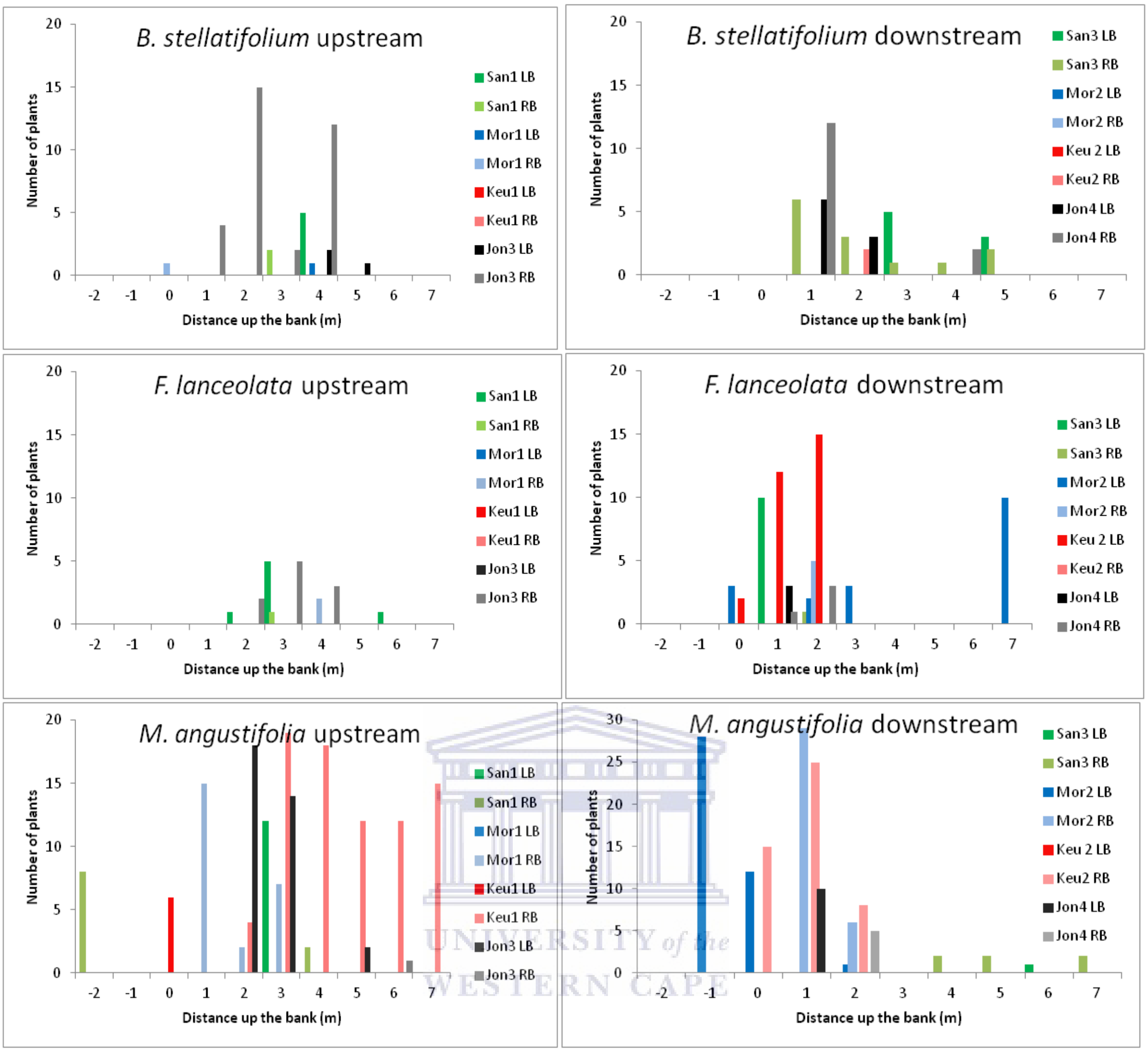


Figure 4.10 The number of juvenile individuals for three dry bank species that were most abundant in the wet bank zone of the downstream sites

4.6 Discussion

The flow regimes at the downstream sites are distinguished from their upstream counterparts by an almost complete lack of summer surface flows. They are virtually identical in all other respects. In all cases the abstractions that remove the summer flow have been in place for more than 40 years. Thus, if the absence of summer flow from a naturally perennial river does have an influence on riparian vegetation community structure it is reasonable to assume that this would be evident at the downstream sites. Disruption of any of vegetation zones implies that their function is impeded and that ecological processes associated with a particular zone are affected (Boucher and Rode 2001). As expected from the onset, the data gathered in this study showed differentiation between rivers on the basis of catchment and within each catchment, sites were further separated into different rivers. Catchments were shown to differ in species composition although they were located on rivers with the same vegetation community. This agrees with the findings of Reinecke (2013) and Otto (2014), and has been attributed to a riparian-based river signature. These data also showed significant differences between the communities upstream and downstream of the abstraction points, however, discerning the exact nature of these differences was difficult.

The first hypothesis that the downstream sites would have less clear zonation than the upstream sites did not hold. All lateral zones were present at most downstream sites, and it was possible to distinguish between them at both upstream and downstream sites. There was also no significant difference in species diversity upstream versus downstream. The second hypothesis that there would be more seedlings in the channel downstream than upstream, with a shrinking marginal zone in response to abstraction, was less clear. There were no significant differences in the diversity or abundance of different life stages of trees, and no difference in the position of wet bank juveniles. Instead the differences were more subtle and were shown as significant differences in the abundance of sedges and herbaceous perennials and in the diversity and abundance facultative riparian plants.

The changes between upstream and downstream can be described as functional adjustments. In the absence of dry season flows, the seedlings of dry bank trees species recruited closer to the channel than when summer flows were present, similar to that shown by Boucher and Rode (2001). There is a relationship that emerges with the timing of recruitment for plants and locations/positions of juvenile trees. With the absence of summer flows the plants that are known to recruit during the summer period are in lower quantities at the downstream sites (Figure 3.1; Goldblatt and Manning 2000). The opposite case can be made for the recruitment and distribution of plants that are reliant on the winter flows: these floods still occur and thus the seeds of species are able to get to the site and, once there, they arguably have less competition from the summer recruiting plants than would be the case upstream. So the hypothesis that there would be more seedlings in the channel downstream than upstream is partially supported in that dry bank species have moved closer to the channel and some recruited into the channel (*F. lanceolata and M. angustifolia*). However, what is more interesting is that these species have essentially replaced the wet bank species. This is also evident with the loss of herbaceous plants and sedges at downstream sites, both of which are favoured by moist conditions. A similar behavior was observed in Boucher (1999) when the dry bank vegetation was observed on the wet bank zone position. In the south-western Cape and Lesotho, the aquatic zone was invaded by herbaceous plants during the dry periods (Boucher 2002). This suggests that there is a gradual drying out of the riparian zone as a result of the summer abstractions, as these plants are usually not found in the wetted channel (Reinecke 2013, Reinecke unpublished data). The drying out of the wet bank zone is also supported by the increase in facultative species downstream.

The second part of the second hypothesis pointed to a shrinking marginal zone in response to abstraction. The results do not show a noticeable reduction on the width of the marginal zone, although a shrinking of the wet bank zone is evident at downstream sites relative to their upstream partners. The narrowing of the riparian vegetation distribution is usually associated with more constant flows rather than reduced flows (Kleynhans 2007). There may be some growth factors at play as some data suggest that the herbaceous perennials and sedges were fewer downstream than upstream, but this was not explored further here. With increasing aridity, riparian vegetation becomes more restricted closer to the wetted channel (Gasith and Resh 1999), and may result to a loss of a major proportion of plants such as grasses, sedges and willows (Boucher 1999). As wet banks gets dry, obligate species are subject to change as they depend on shallow water tables or perennial streamflow for their survival. On the other hand facultative species may remain unaffected or move into areas that were once occupied by riparian obligates (Stromberg 2001).

Plants that grow closer to flowing water tend to be composed of specialized and disturbance-adapted species, with morphological and physiological adaptations to floods and droughts (Naiman and Decamps 1997; Naiman *et al.* 2005). For instance in Australia paperbark (*Melaleuca*) are successful close to the river channel because they have characteristics that allow them to bend in floods, thereby reducing the shear stress they must withstand (Naiman *et al.* 2005). In South African rivers, *Breonadia salicina* living in high energy environments is adapted to withstand substantial flooding (van Coller *et al.* 1997; Reinecke 2013). In this study at downstream sites, the position usually occupied by wet bank species (wetted channel and marginal zone) was dominated by dry bank species, which tend to be less flexible and more resistant to floods, and thus increase the sheer stress on the banks. The colonization of dry bank species on the wet bank zone thus intensifies the problems of flooding (Boucher and Rode 2001).

The interaction between large volumes of fast moving water and non-flexible trees may focus flows more into the channel, leading to an increase in in-channel erosion and a change in instream habitats. For instance, it is conceivable that smaller sediment size such as silt, mud, sand and gravel, which are critically important components of aquatic habitat (Sher and Marshall 2003; Gurnell *et al*. 2011), would be flushed more effectively downstream than upstream (Gordon *et al*. 2004).

There were no significant differences in species richness between up- and downstream sites. The findings of this study agrees with those presented in Nilsson *et al*. (1999), for two rivers: the natural Vindel River and the regulated Ume River in northern Sweden, there were no significant difference on the number of species found but the frequency distributions (abundance) of species were largely different between rivers (this abundance was also not related to plant life stage), the Ume had lower species than the Vindel. It was reported that the perennials and the natural vegetation were responsible; again the zonation of plants was not clear on the regulated stream. In Gasith and Resh (1999) it was found that provided isolated pools remain, the overall species richness at a site can remain high. There are however significantly fewer herbaceous perennial plants and sedges at the downstream sites. The reasons for this could be that they were eliminated by the drying or that they have been out-shaded by the large dry bank species that have colonised their area. A reduction in biodiversity is expected following reduced transport of silt and clay, for instance herbaceous riparian plants tend to increase on fine soil textures (Stromberg 2001). All this gives a possible increase in the scour which in turn affects the whole riverine ecosystem including riparian vegetation. Therefore it is vital that river management processes are to consider the effects of river flow alteration on common plants at sites as this could lead to a total change in the river ecosystem and functional dynamics if not carefully managed. According to Stromberg (1993), Environmental Flows are relatively high for riparian trees, implying that even partial diversions of flow can result in riparian vegetation decline. In the Western Cape this situation gets to be more adverse as the province does not receive summer low flows and remains dry for most of the season.

5 Conclusion

Understanding the functional responses of riparian species to flow regime is necessary for restoration, conservation planning, and to inform environmental flow studies (Reinecke 2013) and adaptive management. Making precise predictions of ecosystem response to disturbance is difficult, although it is possible to use historical studies to see what has happened in the past and then use that knowledge to predict what will happen in the future. Nonetheless, riverine ecosystems are characterised by complex and simultaneous physical, chemical and ecological interactions (Thoms 2006) and Poff *et al*. (2010) suggest that the development of strong relationships of flow-ecology needs to take into consideration the role that other environmental factors play in shaping ecological patterns in streams.

Evaluation of the recruitment phase of plants' lifecycles is particularly useful for understanding functional changes in riparian vegetation in response to flow change. In riparian vegetation, recruitment is closely linked to the flow regime of a river and tends to have both a temporal (seasonal) and a spatial component that can be related to different parts of the hydrograph. The seasonal component defines the time when each species flowers, seeds, fruits and recruit (Lyte and Poff 2004; Poff *et al.* 1997) and the spatial component determines the location or position on the river bank where it establishes (Reinecke and Brown 2013).

An added benefit is that changes in recruitment occur far more rapidly than do changes in the adult population. Once a tree is established it can withstand a wide array of climatic and other impacts to which recruiting individuals are far more vulnerable. The recruiting life stage of any species is highly affected by many factors, and is the most sensitive stage of a plant life cycle (e.g., Eriksson and Ehrlen 2008). Thus, if a dam is constructed on a river, changing the downstream flows, the effects of these changes are more likely to be reflected in the behavior and survival of recruiting plants than of adults. Thus, changes shown by the young plants are important not only for predicting EFs but are also useful for monitoring purposes and adaptive management.

This study illustrated that the factors controlling seedling and adult positions are fairly complex. Although fruiting, flowering and the release of seeds of different species is timed to link with different flow conditions (Chapter 3), these do not ultimately define the position of these species on the bank. Spatial arrangement in the riparian zone has as much to do with flow conditions post recruitment as it does with conditions during recruitment. Seedlings were found throughout the riparian zones but adults were positioned in clear lateral zones. This implies that the structure of riparian vegetation is probably determined not only by whether or not the minimum flows are met but also the larger floods that deposit seeds at different zones and small to medium floods that remove seedlings before they can become established. Thus, for instance, *Salix mucronata* release their seeds during summer low flow periods and grow immediately adjacent to the wetted channel (Chapter 3; Section 3.1.1). Thus, if summer low flows do not come through, *Salix mucronata* may not recruit or recruiting individuals may dry out and die (Table 4.11), and/or dry bank species will migrate to this zone (Section 4.5.2.7 and Figure 4.10). However, it is also clear from the results that if the large floods do not occur then *Salix mucronata* could be out-competed by other - more robust - dry bank species as these would not be removed post-recruitment (Figure 4.10). Thus, although *Salix mucronata* does not have a direct phenological link to large floods it is indirectly dependent on them to establish the conditions it requires to thrive

The result presented in this study also suggested that plant recruitment is substrate specific (Chapter 3; Otto 2014). Sediments deposited by floods of different magnitude vary in depth, texture, and nutrient content, and support different assemblages of plants (Marks 1950 in Stromberg *et al*. 2001). This suggests that if sediment supply or transport conditions were to change through land-use changes, construction of an upstream reservoir or through changes in the flow regime (van Wyk 1987; Ligon *et al.* 1995; Bunn and Arington 2002), that recruitment, and presumably the whole structure of the riparian zone, would also change (Stromberg 2001), and emphasizes the importance of an holistic approach to environmental flow studies, and catchment and river management. Consideration of drought, low-flows and floods are crucial as together they maintain biological, physical characteristics and ecological vitality (Naiman *et al.* 2008), not only one part of the flow regime can be focused on while the others are neglected. Even for a species that is obviously being driven by one part of the flow regime, competitors of that species may be driven by the other part of the flow regime.

The importance of mimicking the natural annual and intra-annual variability of a flow regime, rather than just a minimum low flow, in sustaining freshwater ecosystems has been recognised by many different authors (King *et al.* 2003a; Richter *et al.* 2003; Naiman *et al.*

2005; Naiman *et al.* 2008). Shortening of the natural flood peaks can prevent recruitment of native riparian vegetation and allow alien invasion (Stromberg *et al.* 2001), and alteration of flood patterns in the western United States and Canada has reduced recruitment rates of *Populus* and *Salix* trees (Poff *et al*. 1997; Stromberg *et al.* 2001). Long term studies of naturally variable systems show that dry periods favour some species while the wet periods favour other species and that overall biological diversity and ecosystem function benefit from these variations in species success (Tilman *et al.* 1994 cited in Poff *et al.* 1997). The loss of wet-dry cycles often has drastic ecological impacts that favour exotic species (Bunn and Arthington 2002). Stromberg *et al*. 2001 calls for a restoration of water and sediment of flows in sufficient quantities and with appropriate temporal and spatial patterns

There will always be some uncertainty in the understanding of functional relationships between flow alteration and ecological responses (King *et al*. 2003a; Poff *et al*. 2003; Richter 2003; Brown and King 2006; Poff *et al.* 2010). However to be able to maintain and restore the integrity of river ecosystems, it is required that the conservation and management actions be strongly grounded on scientific understanding (Poff *et al.* 1997). Long term data are needed to study the natural flow regime of a river, this is described by the characteristic pattern of a river's flow quantity, timing, and variability; this flow patterns vary during seasons and over years.

In South Africa, a four-part strategy is being adopted in environmental flow assessments: (i) more research on environmental flows to increase the knowledge base; (ii) moving ahead with limited knowledge (taking decisions based on limited knowledge); (iii) monitoring the outcomes of the management actions (learning by doing); and (iv) strategic adaptive management. Thus, although there is a dearth of historic data for many (most) of our riverine species (Brown and King 2006), functional information is gradually being developed to predict how the ecosystems will respond. This study illustrates some of the finer building blocks of lateral zonation in vegetation and specifically riparian vegetation recruitment dynamics in Western Cape streams that are subject to high levels of abstraction particularly in the summer low flow month, and shows that such information is available, even in rivers with highly variable, and fairly unpredictable, flow regimes. Although the ecosystems are complex, the accumulation of knowledge on individual aspects of their functionality can, and will eventually, build up to a more complete picture and a better understanding of how these systems are likely to respond to outside pressures. Thus, studies such as this one add to the body of knowledge that is needed to make recommendations and take decisions in environmental management. Despite the complexity of system, it is possible to break it into smaller fractions to study separately.

It also illustrates the importance of a holistic approach to understanding rivers and river management. Poff *et al*. (1997) suggest that incorporating the five critical components of the natural flow regime (i.e., magnitude, frequency, duration, timing, and rate of change) into a broader framework for ecosystem management would constitute a major advance in contribute to the developing science of stream restoration. Focusing on just one or a few species and on minimum flows fails to recognize that what is good for individual species may not be of benefit to the ecosystem (Poff *et al.* 1997). The use of holistic methods on the other hand makes use of different species and how they respond to different kinds of flow then use the information to build up a recommendation. For a long time in environmental flow management focused on minimum flows for key species, but the results for this study show that for riparian vegetation, concentrating on only one species can lead to incorrect recommendations, not the least because the behavior of that species is affected by the behavior with the other species.

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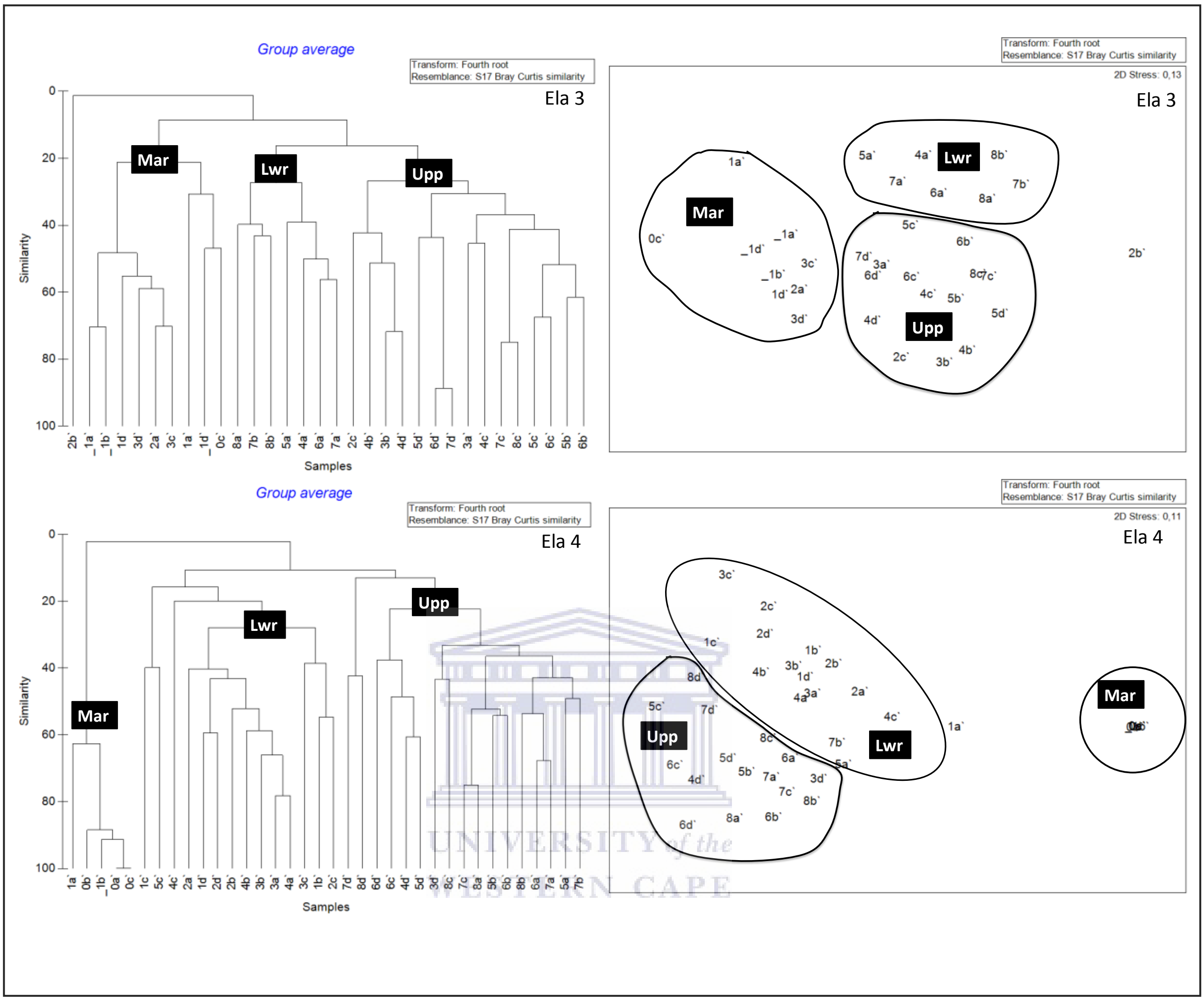
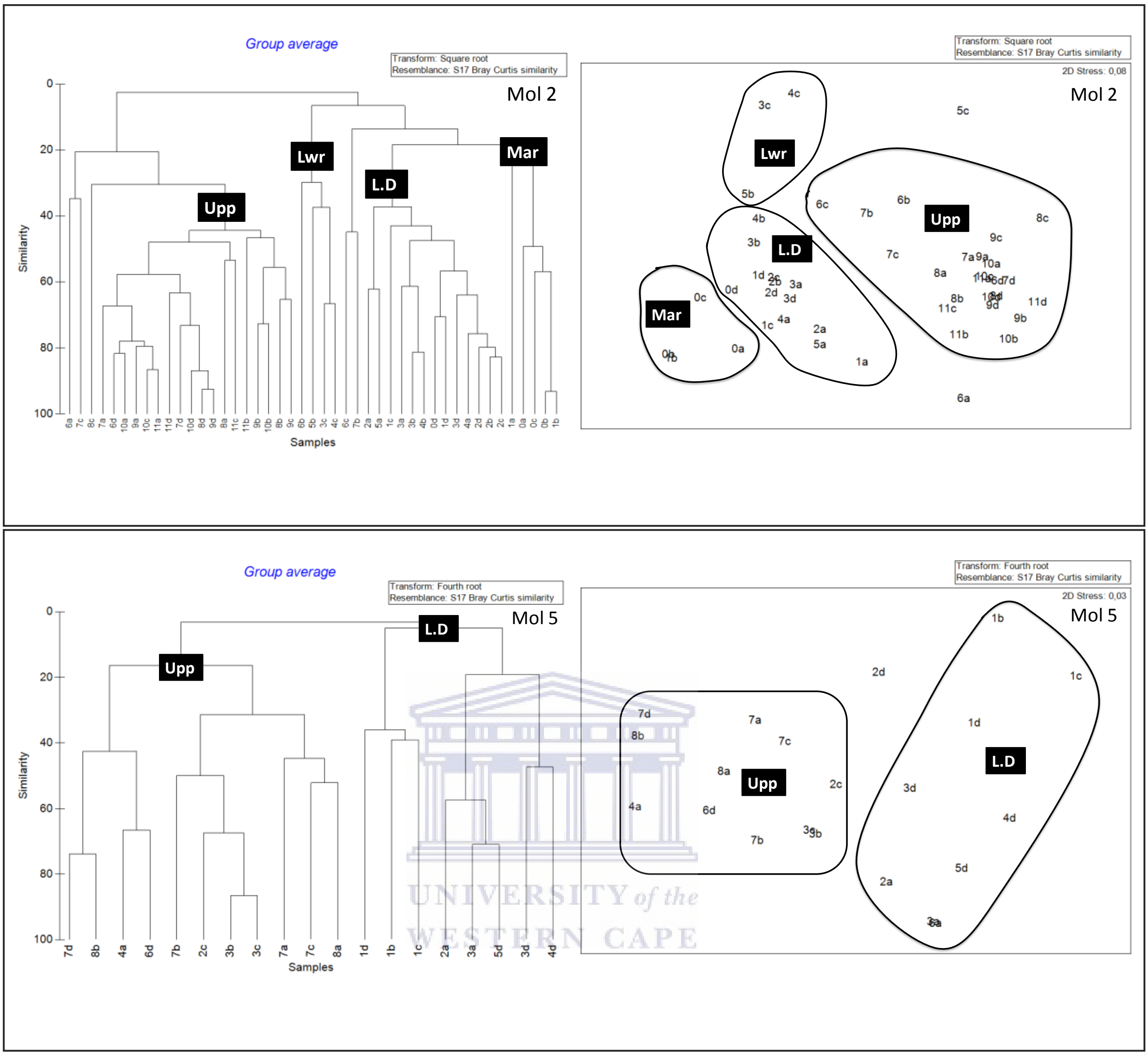
Appendices

Appendix A. Additional figures referred to in the text



Appendix Figure 1 Lateral zones formed using groundcovers only (2013) at Elands River sites



Appendix Figure 2 Lateral zones formed using groundcovers only (2013) at Molenaars River sites

Appendix B. Additional tables referred to in the text

Appendix Table 1 Presence and absence of species at sites 2013

Species (tree height in metres)	Sites sampled			
	Ela 3	Ela 4	Mol 2	Mol 5
Acacia longifolia 0.3-2			*	*
Acacia longifolia 2-5				
Acacia longifolia seedlings			*	
Acacia mearnsii 0.3-2			*	*
Acacia mearnsii 2-5				
Acacia mearnsii seedlings			*	
Anthospermum spaculata			*	*
Aristea sp.	*	*		
Askidiosperma paniculatum		*		
Asteraceae sp.15			*	
Brabejum stellatifolium 0.3-2	*	*	*	*
Brabejum stellatifolium 2-5	*	*		*
Brabejum stellatifolium seedlings	*	*		*
Brachylaena neriifolia 0.3-2	*	*		
Brachylaena neriifolia 2-5	*	*		
Brachylaena neriifolia seedlings				
Calopsis paniculata	*	*		*
Cannamois sp.				
Capeochloa cincta	*		*	
Cf. Heliophila sp.		*		
Cliffortia sericea				*
Cliffortia strobilifera		*	*	
Cyclopia maculata				
Cymbopogon marginatus		*		
Cyperaceae sp.11	*			*
Cyperaceae sp.12	*			
Diospyros glabra	*	*	*	*
Drosera capensis	*	*		
Ehrharta ramosa	*	*	*	*
Elegia capensis	*	*	*	*
Elegia sp.1	*			
Elytropappus scaber				*
Erica caffra	*	*		*
Erica pinea		*		
Erica sp.			*	
Erica sp.1				
Freylinia lanceolata 0.3-2			*	*
Freylinia lanceolata 2-5			*	*
Freylinia lanceolata seedling				
Fuirena hirsuta			*	*
Hackea sericia		*		
Halleria olyphia				

Species (tree height in metres)	Sites sampled			
	Ela 3	Ela 4	Mol 2	Mol 5
Heeria argentea 0.3-2		*		
Heeria argentea 2-5				
Heeria argentea seedlings				
Hemarthria altissima			*	*
Holcus lanatus L.			*	*
Hymenolepis parviflora		*	*	
Ilex mitis 0.3-2		*		
Ilex mitis 2-5	*			
Ilex mitis seedlings				
Ischyrolepis fraterna				
Isolepis digitata				
Isolepis prolifera	*	*	*	
Lobelia jasionoides		*		
Lycopodiella caroliniana	*			
Metrosideros angustifolia 0.3-2	*	*	*	*
Metrosideros angustifolia 2-5	*	*	*	*
Metrosideros angustifolia seedling	*	*	*	*
Morella serrata 0.3-2	*	*	*	*
Morella serrata 2-5	*	*	*	*
Morella serrata seedlings	*	*	*	*
Osmitopsis	*			
Osmitopsis osmitoides			*	
Osteospermum spinosum				
Pennisetum macrourum	*			
Pentameris (Pentaschistis) sp.	*	*	*	*
Pentameris sp.1				
Peucedanum galbanum				*
Phylica axillaris				
Phylica sp.1				
Platycaulos sp.1		*	*	*
Platylophus trifoliatus 0.3-2	*			
Platylophus trifoliatus 2-5	*			
Platylophus trifoliatus seedlings				
Podalyria sp.5	*			
Prionium serratum			*	*
Protea soft	*			
Pseudobaeckia africana		*	*	
Pseudoselago sp.3				
Psoralea aphylla				
Psoralea cf. affinis	*	*		
Pteridium aqualinum	*		*	
Pycreus polystachyos			*	
Ischyrolepis subverticillata		*	*	*
Rubus fruiticosus				
Salix mucronata 0.3-2	*		*	

Species (tree height in metres)	Sites sampled			
	Ela 3	Ela 4	Mol 2	Mol 5
Salix mucronata 2-5	*		*	
Salix mucronata seedlings	*		*	
Schizaea tenella	*	*		
Searsia angustifolia			*	*
Senecio sp.				
Sesbania punicea			*	
Stoebe aethiopica				
Stoebe plumosa		*	*	*
Stoebe sp.1		*		
Stoebe sp.2	*			
Thesium juncifolium				*
Todea babara	*	*		

Appendix Table 2 Presence and absence of species at sites referred to in chapter 4.

Species tree height (m)	Sites sampled															
Acacia longifolia 0.3-2	*		*	*		*										
Acacia longifolia seedling																
Acacia longifolia 2-5																
Anthospermum sp.			*	*												
Anthospermum spaculata						*	*	*								
Aristea sp.													*	*		
Aspalathus rugosa							*	*								
Asparagus rubicundus															*	
Asteraceae sp.											*	*				
Athanasia dentata								*								
Blechnum capense													*	*	*	
Lobostemon sp.						*	*					*				
Calopsis paniculata				*		*		*		*	*	*				
Cannamois sp.											*	*				
Carpha glomerata										*						
Cliffortia strobilifera	*	*	*					*			*	*				
Cyclopia maculata														*		
Diospyrus glabra	*	*	*	*	*		*	*		*	*	*			*	*
Dodonaea viscosa		*	*	*			*									
Drosern capensis				*												
Ehrharta ramosa	*	*														
Ehrharta sp.	*	*	*	*			*	*		*	*	*				
Elegia capensis		*								*	*	*		*		
Elegia sp.													*		*	*
Erica cafra	*	*		*			*	*			*	*	*	*	*	
Heeria argentea									*							
Isolepis prolifera		*		*	*	*	*		*				*			
Isolepis sp.									*			*				
Moss	*	*	*	*		*	*	*	*		*	*	*	*	*	*
Notobubon galbanum					*	*	*	*		*	*	*				
Olea africana Mill.															*	
Osmitopsis osmitoides						*										
Osteospermum spinosum							*	*	*							
Pelargonium scabrum							*		*		*	*				
Pentameris (Pentaschistis) sp.													*	*		
Phylica sp.															*	
Platycaulos sp.	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Pleopeltis macrocarpa													*	*		
Podalyria sp.														*		
Prionium serratum	*	*	*	*									*	*		*
Psoralea aphylla					*	*				*						
Pteridium aquilinum	*	*			*	*	*		*	*	*	*	*	*		*
Ischyrolepis subverticillata	*	*	*	*	*	*		*	*	*	*	*				
Rhus crenata					*		*				*	*				
Schizaea tenella Kauf.														*		

Species tree height (m)	Sites sampled															
Searsia angustifolia 0.3-2	*	*	*	*			*	*		*	*	*		*	*	
Searsia angustifolia seedling																
Searsia angustifolia 2-5																
Senecio sp.	*			*												
Stoebe cinerea								*	*	*		*				
Stoebe plumosa					*	*		*		*		*	*			
Stoebe sp.														*		
Thesium juncifolium													*	*		
Brabejum stellatifolium 0.3-2	*		*	*	*	*						*	*	*	*	*
Brabejum stellatifolium 2-5		*											*	*	*	*
Brabejum stellatifolium seedling	*		*	*	*			*		*				*	*	*
Brachylaena neriifolia 0.3-2	*	*		*		*				*		*	*	*	*	*
Brachylaena neriifolia 2-5		*					*	*	*		*			*		
Brachylaena neriifolia seedling					*	*			*	*	*		*		*	*
Freylinia lanceolata 0.3-2		*	*	*		*	*	*			*	*		*	*	*
Freylinia lanceolata 2-5		*					*				*			*		
Freylinia lanceolata seedling	*	*			*		*	*			*	*			*	
Metrosideros angustifolia 0.3-2	*	*		*		*	*	*		*	*		*	*		*
Metrosideros angustifolia 2-5			*			*	*	*	*	*	*	*	*		*	
Metrosideros angustifolia seedling	*	*	*	*	*	*	*		*	*		*	*	*	*	*
Morella serrata 0.3-2	*	*	*	*	*	*	*	*					*	*		
Morella serrata 2-5	*	*	*	*	*	*	*	*						*		
Morella serrata seedling	*	*	*	*	*	*		*						*		
Salix mucronata 0.3-2	*	*		*				*								
Salix mucronata 2-5	*	*	*	*	*			*			*					
Salix mucronata seedling		*	*	*							*					
	* shows species occurs at site															

Appendix Table 3 **A list of plants known to species level that were used with their associated riparian factor and specified growth forms.**

	Species	Habitat characteristic	Riparian factor	Growth form	Lateral zone
1	*Acacia longifolia*	Riverine, Exotic	Obligate	Tree	Wet
2	*Anthospermum spathulatum*	Clay slopes, DRY	Incidental	Shrub	Dry
3	*Aspalathus rugosa*	Mountain fynbos, DRY	Incidental	Shrub	Dry
4	*Asparagus rubicundus*	Sandy and granite slopes, DRY	Incidental	Shrub	Dry
5	*Athanasia dentata*	Sandy coastal slopes, DRY	Incidental	Shrub	Dry
6	*Blechnum capense*	Riverine, WET	Obligate	Herbaceous perennial	*Dry*
7	*Brabejum stellatifolium*	Riverine, WET	Obligate	Tree	Dry
12	*Brachylenea seedling*	Riverine, WET	Obligate	Tree	Wet
13	*Calopsis paniculata*	Riverine, WET	Obligate	Restio	Wet
14	*Carpha glomerata*	Riverine, WET	Obligate	Sedge	Wet
15	*Cliffortia strobilifera*	Moist sandstone flats and lower slopes, WET	Obligate	Shrub	Wet
16	*Cyclopia maculata*	Streamside lowland (Riverine, WET)	Obligate	Shrub	Dry
17	*Diospyros glabra*	Sandy flats and slopes, DRY	Incidental	Shrub	Dry
18	*Dodonaea viscosa*	Riverine thicket and rocky outcrops, WET	Obligate	Tree	Dry
19	*Drosera capensis*	Marshy sandstone, WET	Obligate	Herbaceous perennial	Wet
20	*Ehrharta ramosa*	Mountain slopes, DRY	Incidental	Grass	Dry
21	*Elegia capensis*	Riverine, WET	Obligate	Restio	Dry
22	*Erica cafra*	Riverine, WET	Obligate	Shrub	Wet
23	*Freylinia lanceolata*	Riverine, DRY	Facultative	Tree	Dry
26	*Heeria argentea*	Rocky forest and bush, DRY	Incidental	Tree	Dry
27	*Ischyrolepis subverticillata*	Riverine, WET	Obligate	Restio	Wet
28	*Isolepis prolifera*	Riverine, WET	Obligate	Sedge	Wet
29	*Metrosideros angustifolia*	Riverine, WET	Obligate	Tree	Dry
34	*Morella serrata*	Rocky streamsides, WET	Obligate	Tree	Wet
35	*Notobubon galbanum*	Moist rocky and sandy soils, WET	Obligate	Shrub	Dry
36	*Olea africana*	Rocky sandstone/ granite slopes, DRY	Incidental	Tree	Dry
37	*Osmitopsis osmitoides*	Moist slopes and forest margins, WET	Obligate	Shrub	Dry
38	*Osteospermum spinosum*	Gravelly slopes and flats, DRY	Incidental	Shrub	Dry
39	*Pelargonium scabrum*	Rocky sandstone slopes, DRY	Incidental	Shrub	Dry
40	*Pleopeltis macrocarpa*	Forest	Facultative	Herbaceous perennial	Dry
41	*Prionium serratum*	Riverine, WET	Obligate	Shrub	Wet
42	*Psoralea aphylla*	Mountain and lowland fynbos, streambanks, WET	Obligate	Shrub	Wet
43	*Pteridiun aquilinum*	Fynbos, forest	Facultative	Herbaceous perennial	Dry
44	*Rhus crenata*	Sandy coastal slopes, DRY	Incidental	Shrub	Dry
45	*Salix mucronata*	Riverine, WET	Obligate	Tree	Wet
48	*Schizaea tenella*	Riverine, WET	Obligate	Shrub	Dry
49	*Searsia angustifolia*	Riverine, WET	Obligate	Tree	Dry
50	*Stoebe cinerea*	Rocky slopes, DRY	Incidental	Shrub	Dry
51	*Stoebe plumosa*	Rocky flat and slopes, DRY	Incidental	Shrub	Dry
52	*Thesium juncifolium*	Sandstone slopes, DRY	Incidental	Shrub	Dry