Regeneration Dynamics of Natural Forest Species within a Stand of the Invasive Alien *Acacia mearnsii* along the Buffeljagsrivier, Swellendam, South Africa

by

Angeline Atsame-Edda

Thesis presented in partial fulfilment of the requirements for the degree of Master of Science in Forestry (Forest Science) in the Faculty of AgricSciences at Stellenbosch University

Supervisor: Prof. Coert Johannes Geldenhuys
Co-Supervisor: Prof. Thomas Seifert

April 2014

Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own original work, that I am the sole owner thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

Abstract

Several studies have shown that stands of invasive alien plants in the natural forest environment can facilitate the rehabilitation and recovery of such forests and challenged the general and global perception that such invasive species threaten the biodiversity and functioning of natural vegetation systems. The aim of this study was to develop an understanding of the dynamics of the spread and establishment of natural forest species in a large stand of the invasive alien plant species *Acacia mearnsii* (Black wattle) along the Buffeljagsrivier, Western Cape, South Africa. Several patches of Moist forest, Dry forest and Riparian forest occur along the Buffeljagsrivier, above the Buffeljagsrivier dam. The stand of Black wattle consists of 90 ha for a distance of 3.12 km. The main objective was pursued through four specific objectives: (i) to map and assess the patterns in the distribution, size and species composition of the natural forest clusters within the Black wattle stand; (ii) to determine the relationship between natural forest clusters establishing within the Black wattle stand and the neighboring natural forest patches as potential seed sources for the developing forest clusters; (iii) to determine the subsequent spread of natural forest species from the developing forest clusters into the rest of the Black wattle stand; and (iv) to synthesize the information on the dynamics of the spread and establishment of natural forest species into the Black wattle stand as a basis for developing general guidelines for the conversion of invasive alien plant stands in the forest environment towards regrowing natural forest.

In total, 329 clusters of natural forest species were GPS recorded and mapped (Arc-GIS) in three zones (Proximal, Intermediate and Distant in relation to the forest patches) within the Black wattle stand: 266 small clusters (one to three reproductively mature trees), 36 medium-sized clusters (four to nine trees) and 27 large clusters (more than 10 trees). Large clusters were abundant in the zone close to the natural forest patches and the number of small clusters increased with increasing distance from the forest patches. A total of 28 species of 20 families were recorded. Natural forest species are therefore able to establish within a Black wattle stand.

The relationship between natural forest clusters establishing within the Black wattle stand and the natural forest patches as potential seed sources was studied by sampling the stand composition along transects through the stands. A total of 55 rectangular plots (20 m x 10 m, 200 m^2) were sampled across forest patches and forest clusters. Hierarchical clustering analysis, using number of stems of a species per plot, identified three main groups and 10 sub-groups. All the sampled forest clusters were included in four of the five Riparian forest sub-groups. Most Moist and Dry forest species were absent from the forest clusters. The three main forest types differed in their general characteristics and site conditions, and this was supported by the ordination analyses: aspect, slope and canopy closure. The developing forest clusters within the Black wattle stand related more to the Riparian forest in terms of similar very gentle south-westerly slope and mean stem diameter. This suggested Riparian forest to be the primary seed source of the establishing forest clusters within the Black wattle stand. However, the large-sized stems of common species were not significantly different between Riparian forest patches and forest clusters, suggesting that large-sized stems in the forest clusters could be part of remnant forest patches, which could act as local seed sources. Detailed evaluation of species importance values and stem diameter distributions showed that some important Moist and Dry forest species are present in the forest clusters. The conclusion was that every type of forest patch contributes to a greater or lesser degree to the development of forest clusters within the Black wattle stand.

Seven large clusters were selected to sample the regeneration of natural forest species within 18 m from the forest cluster boundary. Two species lists were generated; one of species from adjacent natural forest patches, and another from 59 forest clusters of all sizes sampled throughout the wattle stand. The results indicated that (1) Mature trees of well-established forest clusters were the main seed sources for the cluster expansion in all directions; (2) Three different patterns were observed in terms of the distance of expansion of regeneration from the clusters: a decrease in regeneration with increasing distance from the cluster margin; increasing regeneration with increasing distance from the cluster; and no distinct pattern with a lack of regeneration of the dominant species of a forest cluster. The 40 species recorded within the Buffeljagsrivier site include a wide range of fruit and seed characteristics. Four main groups of woody species were identified, based on their presence/absence in forest patches and forest clusters. The presence/absence of most species can be explained in terms of their fruit/seed characteristics and dispersal mechanisms. The majority of recorded woody species were most likely dispersed by birds and mammal, particularly Rameron pigeons and baboons.

In conclusion, a conceptual framework was developed to guide the rehabilitation of stands of light demanding invasive stands in the forest environment. Several topics for further research were identified.

Keywords: *Acacia mearnsii stand*, Forest cluster, Neighboured natural forest, Invasive species, Forest succession, Regeneration, Expansion, Seed sources, MIPS, Forest rehabilitation, Black wattle.

Opsomming

Verskeie studies het gewys dat opstande van uitheemse indringerplante in die woudomgewing kan die rehabilitasie en herstel van sulke woude fasiliteer, en daag die algemene en globale persepsie uit dat sulke indringerplantspecies die biodiversiteit en funksionering van natuurlike plantegroeisisteme bedreig. Die doel van hierdie studie was om ‘n beter begrip te ontwikkel van die dinamika vir die verspreiding en vestiging van inheemse woudspesies binne ‘n omvangryke opstand van die uitheemse indringerplant, *Acacia mearnsii* (swartwattel), langs die Buffeljagsrivier, Wes-Kaap, Suid Afrika. Verskeie kolle (‘patches’) van Vogtige, Droë- en Oewerwoud kom langs die Buffeljagsrivier voor. Die *swartwattel* opstand van ongeveer 90 ha groei langs die Buffeljagsrivier oor ‘n afstand van 3.12 km, tussen die dam en die woudkolle aan die stroom-op kant van die swartwattelopstand. Die hoofdoel is nagevolg deur vier spesifieke doelwitte: (i) om die groepies (‘clusters’) vestigende inheemse houtagtige plantsoorte binne die swartwattelbos te karteer en die patrone in hul verspreiding, grootte en spesies samestelling binne die swartwattelopstand te evalueer; (ii) om die verwantskap tussen natuurlike woudgroepies wat binne die swartwattelopstand vestig en die aangrensende woudkolle as potensiële saadbronne vir die ontwikkelende woudgroepies te bepaal; (iii) om die daaropvolgende verspreiding van inheemse woudspesies vanaf die ontwikkelende woudgroepies binne die res van die swartwattelopstand te bepaal; en (iv) om die inligting oor die dinamika van die verspreiding en vestiging van die woudspesies binne-in die swartwattelopstand saam te vat as ‘n basis vir die ontwikkeling van algemene riglyne vir die omskepping van uitheemse indringerplantopstande in die woudomgewing na hergroeiende inheemse woud.

In totaal is 329 groepies van inheemse woudspesies aangeteken (via GPS) en gekarteer (Arc-GIS) in drie sones (nabygeleë, intermediêre en afgeleë) binne die *swartwattel* opstand: 266 klein groepies (een tot drie voortplantingsvolwasse bome), 36 medium-grootte groepies (vier tot nege bome) en 27 groot groepies (10 of meer bome). Groot groepies was volop in die sone naby aan die woudkolle en die aantal klein groepies het toegeneem met toenemende afstand vanaf die woudkolle. ‘n Totaal van 28 species van 20 families is aangeteken, en spesies soos *Canthium inerme, Celtis africana, Gymnosporia buxifolia, Rapanea melanophloeos* en *Vepris*

lanceolata was algemeen binne die swartwattelopstand. Dit is daarom moontlik vir inheemse woudspesies om binne die swartwattelopstand te vestig.

Die verhouding tussen inheemse woudgroepies wat binne die swartwattelopstand vestig en die woudkolle as potensiële saadbronne is bestudeer deur die opstandsamestelling langs transekte deur die opstande te bemonster. ‘n Totaal van 55 reghoekige persele (20 x 10 m, 200 m^2) is opgemeet: nege in Droeëwoudkolle, 17 in Vogtige woudkolle, 20 in Oewerwoudkolle, en nege in die woudgroepies binne the swartwattelopstand. Hiërargiese Groeperingsanalise, gebaseer op aantal stamme van ‘n spesies per plot, het drie hoofgroepe en 10 sub-groepe ge-identifiseer: Vogtige woud met drie sub-groepe, Oewerwoud met vyf sub-groepe, en Droeëwoud met twee sub-groepe. Al die gemete woudgroepies is in vier van die Oewerwoud sub-groepe ingesluit. Die meeste Vogtige en Droeëwoud spesies was afwesig van die woudgroepies. Die hoof woudtipes (Droog, Vogtig, Oewer) verskil in hul algemene eienskappe en groeiplektoestande, en dis ondersteun deur die ordinasie-analises: aspek, helling en kroonsluiting. Die ontwikkelende woudgroepies binne die swartwattelopstand was nouer verbonde met Oewerwoud in terme van soortglyke baie geleidelike suid-westelike helling en gemiddelde stamdeursneë. Dit veronderstel dat Oewerwoud is die primêre saadbron van die vestigende woudgroepies binne die swartwattelopstand. Baie inheemse woudspesies kom egter oor die verskillende groepe en sub-groepe voor, met goeie verjonging oor die gemeenskappe. Die stamdeursneë van goter stamme van algemene spesies was nie-beduidend verskillend tussen die Oewerwoudkolle en die woudgroepies, en dit veronderstel dat die groter stamme in die woudgroepies kan deel wees van oorblywende woudkolle, wat as plaaslike saadbronne kan dien. Gedetaileerde ontleding van spesies belangrikheidswaardes en stamdeursneëklasverdelings het getoon dat sommige belangrike Vogtige en Droeëwoud spesies is wel teenwoordig in die woudgroepies. Die gevolgtrekking was dat elke tipe woudkol in a mindere of meerdere mate bydra tot die ontwikkeling van die woudgroepies binne die swartwattelopstand.

Sewe groot woudgroepies is geselekteer om die woudverjonging binne 18 m vanaf die woudgroepierand te bemonster. Twee spesieslyste is saamgestel; een van spesies van die aangrensende woudkolle, en een van spesies van 59 woudgroepies van alle groottes wat deur die hele swartwattelopstand aangeteken is. Die resultate het aangetoon dat (1) volwasse bome van goed-gevestigde woudgroepies was die hoof saadbronne vir die uitbreiding van die woudgroepies in all rigtings; (2) drie verskillende patrone is waargeneem in terme van die afstand van uitbreiding van verjonging weg vanaf die woudgroepies: ‘n afname in verjonging met toenemende afstand vanaf die groepierand; toenemende verjonging met toenemende afstand vanaf die woudgroepie; en geen beduidende patroon met ‘n gebrek aan verjonging van die dominante spesies van die woudgroepie. Die 40 spesies wat binne die Buffeljagsrivierstudiegebied aangeteken is het ‘n wye reeks vrug- en saadeienskappe ingesluit. Vier hoofgroepe van houtagtige spesies is geïdentifiseer, gebaseer op hul aan- of afwesigheid in die woudgroepies and woudkolle: spesies algemeen in die woudkolle en teenwoordig in die woudgroepies; spesies spesifiek to bepaalde woudkolle en teenwoordig in die woudgroepies; spesies teenwoordig in die woudkolle maar afwesig van die woudgroepies; en spesies afwesig van die woudkolle maar teenwoordig in die woudgroepies. Die aan- of afwesigheid van die meeste spesies kan verduidelik word in terme van hul vrug/saadeienskappe en verspreidingsmeganismes. Die meerderheid van aangetekende houtagtige spesies was meeswaarskynlik deur voëls en soogdiere versprei, veral Geelbekbosduiwe en Bobbejane.

Ten slotte, ‘n konsepsuele raamwerk is ontwikkel om die rehabilitasie van opstande van ligafhanklike indringerspesies in die woudomgewing te rig. Verskeie onderwerpe vir verdere navorsing is geïdentifiseer.

Résumé

Plusieurs études ont montré que les peuplements de plantes exotiques envahissantes dans le milieu de forêt naturelle peuvent favoriser la réhabilitation de ces forêts contestant par-là, la perception générale et globale que ces espèces envahissantes menacent la biodiversité et le fonctionnement des systèmes de végétation naturelle. L'objective de cet étude était de mieux comprendre le dynamisme d'établissement et de propagation dans une forêt naturelle des espèces forestières au sein d'un large peuplement de l'espèce de plantes exotiques envahissantes *Acacia mearnsii* (acacia noir) le long de Buffeljagsrivier, Western Cape, en Afrique du Sud afin d'élaborer des axes directives de réhabilitation relative aux recouvrements d'espèces invasive. La forêt de Buffeljagsrivier s'étale sur un gradient de petites parcelles de forêt allant de forêt sèche, humide et marécageux. Au milieu de ces parcelles de Buffeljagsrivier, on circonscrit un peuplement d'acacia noir estimé à 90 ha sur une distance de 3,12 km. L'objective principal s'est poursuit à travers quatre sous objectives à savoir: (i) cartographier et évaluer les formes d' invasions dans la distribution, la taille et la composition des recouvrements des espèces de forêt naturelle à l'intérieur du recouvrement *d'*acacia noir servant comme preuve possible de l'existence et établissement des espèces de forêt naturelle sous un recouvrement d'une espèces invasive; (ii) de déterminer la relation entre les recouvrements de forêt naturelle s'établissant á l'intérieur du peuplement d'a*cacia noir* et ceux de la forêt naturelle avoisinante humide, sèche et marécageuse pouvant être considéré comme sources potentiel de semences conduisant au développement des premiers recouvrement cités; (iii) de déterminer l'étalement subséquent des espèces de la forêt naturelle à partir des recouvrements d' *acacia noir* se développant à l'intérieur du reste du peuplement de l'*Acacia* noir*;* (iv) Synthétiser les informations sur la dynamique de la propagation et l'établissement d'espèces forestières naturelles dans l'acacia noir comme une base pour l'élaboration des lignes directrices générales pour la conversion de peuplements de plantes exotiques envahissantes se trouvant dans l'environnement de la forêt vers des repousses des forêts naturelles.

Au total, 329 recouvrements d'espèces forestières naturelles ont été GPS enregistrées et cartographiées (Arc -GIS) dans trois zones (Proximale, Intermédiaire et Eloignée par rapport aux parcelles de forêt avoisinantes) dans le peuplement de l'acacia noir: 266 petits recouvrements avaient un à trois arbres matures, 36 recouvrements de taille moyenne avaient

quatre à neuf arbres matures et 27 larges recouvrements avaient plus de 10 arbres matures. La visualisation de la carte a révélé que les larges recouvrements de forêt mature étaient abondant dans la zone proche des parcelles de forêt naturelle avoisinantes et que de petits recouvrements de jeunes arbres de forêt naturelles croissaient en nombre à mesure que la distance depuis les parcelles de forêts naturelles adjacentes s'élargissait. Un total de 28 espèces appartenant à 20 familles a été répertorié. Deux familles, *Rubiaceae* suivit de *Anacardiaceae* ont dominé l'echantillon. Les espèces forestières naturelles sont donc en mesure de s'établir dans un peuplement d'acacia noir.

L'échantillon qui a servi à l'évaluation des sources de semences pour le développement des recouvrements de forêt naturelle à travers l'investigation de la relation entre les recouvrements de forêt naturels qui s'établissent à l'intérieur du peuplement d'acacia noir et les parcelles de forêt avoisinantes humide, sèche et marécageuse était constitué de 55 placettes rectangulaires de $200m^2$ le long de layons à travers le site d'étude. Une analyse hiérarchique des recouvrements réalisée sur la composition des espèces de l'échantillon a révèle que la forêt marécageuse concentre les espèces les plus fréquentes des recouvrements de forêts, et que la majorité des espèces présentes sur les parcelles des forêts sèches et humides étaient absente dans l'ensemble des recouvrements des forêts de l'acaci noir. Les trois principaux types de forêts différaient dans leurs caractéristiques générales et les conditions du site, et cela a été appuyé par l'analyse d'ordinants à partir de trois facteurs environnementaux, la pente, l'angle d'inclinaison par rapport au soleil, et la fermeture de la canopée. Les recouvrements de foret en développement au sein de l'acacia noir se sont trouvés davantage liés à la forêt marécageuse en termes de pente plate orientée sud-ouest et en diamètre moyen des arbres. Ces résultats ont désigné la forêt marécageuse comme la première source potentielle de semences permettant l'établissement des recouvrements de forêt à l'intérieur des peuplements d'acacia noir. Cependant, les souches d'arbres de grande taille des espèces communes entre les parcelles de forêts marécageuses et les recouvrements de forêt dans l'acaci noir n'étaient pas significativement différents, suggérant ainsi que ces arbres de grande taille trouves dans les recouvrements de foret pourraient faire parties des parcelles de forêt subsistantes de la dernière turbulence. Elles pourraient constituer des sources locales de semences. Par ailleurs, une évaluation détaillée des valeurs d'importance des espèces et des distributions des diamètres des souches d'arbres a montré que certaines espèces importantes de forêts humides et sèches sont présentes dans les recouvrements de

foret. Finalement l'on conclue que chaque type de parcelles de forêt contribue plus ou moins à l'établissement des recouvrements de forêt dans le peuplement de l'acacia noir.

Sept grands recouvrements de foret ont été sélectionnés pour étudier la régénération des espèces forestières naturelles sur un rayon de 18 m depuis la limite du recouvrement de foret. Deux listes d'espèces ont été générées, l'une des espèces de parcelles de forêt naturelle adjacentes, et une autre venant des 59 recouvrements de foret, toutes tailles confondues le long de l'acacia noir. Les résultats ont indiqué que (1) Les recouvrements de forêts, lorsque bien matures et bien établies devenaient les principales sources de semences pour leur expansion sur toutes les directions; (2) Trois allures différentes ont été observées en fonction de la distance de l'expansion de la régénération autour des recouvrements: une diminution de la régénération avec l'augmentation de la distance; une croissance de la régénération avec une distance croissante depuis les revcouvrements de foret, et pas d'allure particulaire voire une absence de régénération de certaines especes pourtant dominant dans les recouvrements de foret. Les 40 espèces recensées sur le site deBuffeljagsrivier comprennent un large éventail de caractéristiques de fruits et de graines. Quatre principaux groupes d'espèces ligneuses ont été identifiées, en fonction de leur présence / absence dans des parcelles de forêt et les recouvrements de forêt. De façon générale, la présence / absence de la plupart des espèces a pu être expliquée en termes de caractéristiques de leur fruits/graines et les mécanismes de dispersion. La majorité des espèces ligneuses enregistrées sont susceptibles d'être dispersées par les oiseaux et les mammifères, en particulier les pigeons rameron et les babouins vues sur le terrain.

En conclusion, un cadre conceptuel a été élaboré pour guider la réhabilitation de peuplements envahissants de lumière en milieu forestier. Plusieurs sujets pour des recherches plus poussées ont été identifiés.

Mots clés: Peuplement d'*Acacia mearnsii,* Recouvrement de foret, Forêt naturelle avoisinante, Espèce invasive, Succession de forêt, Expansion, Sources de semences, MIPS-Réhabilitation, Acacia noir.

Acknowledgements

Such a great goal cannot be achieved alone; it takes support and collaboration. I would like to show my gratitude to everyone who, at different levels, has contributed so that you can read this thesis today. My thanks go particularly to:

Prof Coert Geldenhuys, for being there at every moment of the journey. You have shown trust and support when all I yet had was potential. Thanks for your leadership, and for letting me sharing your passion for Natural Forest over the past four years; I have learnt a lot.

Prof Thomas Seifert, you have been so encouraging; your leadership makes everyone count.

The Gabonese Government through CENAREST for giving its employees the opportunity to fulfill their purpose and for funding my studies and my stay of four years in South Africa. I would like to mention here the International Office, Linda, Carmien, Dorothy for managing the link between Gabonese Government and me.

The Water Resources Commission (WRC) for funding my research project. I am grateful for having been able to attend the 2013 annual meeting near Pietermaritzburg. Thank you, Colin.

To the Gabonese community, thank you for being there when my daughter and I missed home, your support all along the way from the English Language Centre to that very last step in this journey you have been there. I would like to name here Patricks Voua, the Idima's, Blanche Assame, Blanchard, Emmanuel, Pavlick, Robert, all my kids Liron, Fidel and Audry, your love has powered me.

I would not forget my spiritual family; our God has done amazing things: The Gules, the Huili's, Hillsong Church, my spiritual kids Dan, Emile, William, Clemensia, Katy and Solange. South Africa has been my "Rehoboth".

Finally I would like to express my sincere gratitude to all the members of staff and postgraduate students of the Department of Forest and Wood Science for providing me with necessary assistance: Anton for my GIS needs, Ben for positive criticisms, and Christian for abstract translation.

To you who show interest by reading this thesis, I give many thanks.

Dedications

God, for you have formed plans to prosper and to give me a future, to you goes the glory!

TABLE OF CONTENTS

List of Figures

List of Tables

List of Abbreviations & Acronyms

ANOVA	Analysis of Variance
CCA	Canonical Correspondence Analysis
CENAREST	Centre National de Recherches Scientifiques et Technologiques
DAFF	Department of Agriculture, Forestry and Fisheries
DBH	Diameter at Breast Height, 1.3m from the ground
DWAF	Department of Water Affairs and Forestry
DWA	Department of Water Affairs
FAO	Food and Agriculture Organization
GPS	Global Positioning System
IAPs	Invasive Alien Plant stands
IUCN	International Union for Conservation of Nature
IVs	species Importance Values
MIPS	Manipulation of Invasive Plant Stand
WfW	Working for Water
WRC	Water Research Commission

Chapter 1:
General Introduction

1.1 Background

There is evidence that stands of Invasive Alien Plant species (IAPs) can facilitate the rehabilitation and recovery of natural evergreen forests in contrast to the global concern that IAPs generally threaten the biodiversity and functioning of natural vegetation (**Geldenhuys & Bezuidenhout, 2012)**. There are several questions around this observation that need to be addressed: What are the underlying processes of natural forest species spreading into the IAP stands? Can such invasion of invader plant stands by natural forest species be managed to facilitate natural forest recovery?

IAPs are considered as one of the major threats to biodiversity, on a similar level as global warming and the destruction of life-support systems. "Invasive alien organisms come in the form of plants, animals and microbes that have been introduced into an area from other parts of the world, and have been able to displace indigenous species" (**Preston & Williams, 2003**). It is important to note that biological invasions are a fundamental and integral part of nature and have always been present in the history of life on earth. What is of concern, is the extraordinary rate at which the invasions are now taking place (**IUCN, 2000**) and requires global attention and action.

In South Africa, invasive alien trees are a concern for many people and cause conflicting approaches to their management. Introduced tree species forms the backbone of the commercial forestry industry and takes the pressure away from the natural forests to supply in the wood and fibre needs (**Geldenhuys, 1986; Richardson & van Wilgen, 2004**). At the same time the conversion of natural grasslands to commercial plantations destroyed the grassland biodiversity, and several of the introduced tree species has become invasive (**Richardson & van Wilgen, 2004**). There is a high public awareness of the impact of IAPs, partly due to the existing legislation, the large number of publications on the topic of invasive alien species in South Africa and notably to the large contribution of the WfW programme.

The different perceptions developing around some invasive species very often constitute the sources of conflict of interest. Many introduced species can be both a high value species, such as industrial timber, and at the same time pose a threat of becoming, or being an aggressive and harmful invasive species (**Geldenhuys, 1986; Armstrong, 1992**; **Preston & Williams, 2003**). The diverse perceptions often lead to conflicting management approaches, some of which may not be appropriate for the control of specific invasive species (**Geldenhuys, 2008**). However, management concepts should rather be based on a sound scientific concept than on perceptions, which could be misleading. Scientific studies could lead to a comprehensible, even sustainable, and cost-effective management of invasive alien species in South Africa.

Wide field observation, a survey of the role of introduced species in the natural forest environment (**Geldenhuys *et al*., 1986**), and participation in a worldwide study on the facilitated recovery of natural forest species under planted tree stands (**Geldenhuys, 1997**), led **Geldenhuys (2008)** to argue that light-demanding invasive species such as Black wattle can facilitate the rehabilitation and recovery of natural forest species. In such areas it is not necessary to clear the IAP stands, but rather to manipulate them to facilitate natural forest recovery. The question is how do the natural forest species spread into the IAP stands and then become redistributed from the developing clusters within extensive areas of IAPs? How could such information help us to improve the conversion of such IAPs towards forest rehabilitation?

The extensive narrow strip of 90 ha of young, dense Black wattle growing along the Buffeljagsrivier near Swellendam, Western Cape Province, provided an opportunity to study the potential answers to the posed questions. Moist, dry and riparian forest patches near the upstream end of the Black wattle stand covered a total natural forest area of 3 ha. Clusters of natural forest species started to establish within the wattle stand.

1.2 Literature review

This literature review covers three broad topics: the concepts of succession versus invasion in natural forests; a brief overview of the history and management of invasive trees in South Africa; and the ecology and management of invasive alien trees.

1.2.1 Forest invasion and forest succession: from introduced commercial to invasive trees

Not all introduced tree species become invasive. A successful invader has these principal attributes: a short juvenile phase, good annual and long–lived sturdy seed crops and small seed size that can be dispersed easily (**Geldenhuys, 1996**). It is evident that the extent to which introduced species may proliferate and spread, is affected by the state of the receiving ecosystem. An alien species may find a vacant niche and spread, or it may compete for one already occupied by a native species. The lack of natural competitors and natural pathogens in this new ecosystem allows invasive species to be successful and resistant enough to survive in a foreign environment (**Rejmanek & Richardson, 1996**).

The light requirements of an introduced species, for example intolerant to shade or strongly light demanding, is one of the factors that would determine the probability that a species would or would not establish and colonize a certain type of ecosystem (**Geldenhuys, 2004**). Thus some introduced species might be invasive in one biome and non-invasive in another biome (**Geldenhuys *et al.*, 1986; Macdonald *et al.*, 1986**). Fynbos shrubland in the south-western Cape are more susceptible to be invaded than the natural evergreen forest biome, which is not very prone to invasion (**Macdonald *et al.*, 1986**). Only a few alien species are true invaders into the natural evergreen forest; 80% of a total of 82 species recorded as invasive in the literature, were reported to be opportunistic invaders because they occur in large forest gaps and along the forest margin (**Geldenhuys *et al.*, 1986**). They are driven by disturbance that would open the canopy and allows light infiltration.

Identification and understanding of the ecological drivers that favour the invasion in a certain ecosystem are critical to set up an approach of management for the invasive alien species present in a particular ecosystem **(Geldenhuys, 2011**).

Disturbance is one of the main drivers of this process. In forest ecology it induces visible changes in a relative stable ecosystem. In case of moderate disturbance such as forest clearing or superficial fire, the changes are visible in terms of open canopies. With time, forest would tend to recover naturally through the process of forest succession. The theory of the process has been well-developed but is also the subject of controversial issues (**Clements, 1916; Connell & Slatyer, 1977; Pidwirny, 2006**). In the context of this study, the presence of a dense stand of a fast-growing, light-demanding, and also relatively short living invasive species in the forest environment is part of the forest succession process after a disturbance. In such a situation, the stand can rather be considered as a facilitative stage that can be used to rehabilitate forests through natural processes.

1.2.2 History of introduced invasive tree species in South Africa

The history of introduction of invasive tree species in South Africa is well documented (**Phillips, 1963**; **Campbell, 1987**; **Geldenhuys, 1986; 1997; Geldenhuys *et al*., 1986**). The establishment of introduced tree species in all parts of the country began immediately after European colonization (**Phillips, 1963**). Commercial afforestation started in 1890 to provide resources in order to meet the increasing demand for timber. Timber demands could not be met from the small area of indigenous forest, which was less than 1% of the country (**Geldenhuys, 1986, 1997; Geldenhuys *et al*., 1986; Bink & van der Zel, 2004)**
Introduced tree species were planted in overexploited portions of the Eastern Grootvadersbosch near Swellendam (**Campbell, 1987**). In a few cases, small areas of indigenous forest were cleared to plant fast-growing introduced tree species (**Geldenhuys *et al*., 1986**). Afforestation with introduced tree species were initially believed to have several benefits to the environment and such species were often planted to repair damaged ecosystems (**Adair, 2002**; **Richardson, 2008**). They were planted in forest gaps to aid regeneration, to build up the humus content of the soil, and to assist in raising the forest canopy, and along the forest margin for protection against fire. Many species were selected for more extensive planting in the country (**Geldenhuys, 1986; Geldenhuys *et al*., 1986**).

About 180 species of invading introduced plants cover 10 million hectares of land (8% of the total land area in South Africa), especially in the wetter regions (mainly grassland and Fynbos Biomes ***Appendix I***) (**Phillips, 1931**; **Richardson & van Wilgen, 2004; FAO, 2005).** The invasive introduced species were not only found to be threatening biodiversity by displacing indigenous vegetation; they were also recognised to consume much more water compared to the indigenous vegetation, especially in riverine areas **(Binns *et al*., 2001)**. As response, a governmental programme called Working for Water (WfW) was launched in September 1995. Its prerogative consisted of involving local communities in the eradication of vast areas of invasive alien species across the country and by doing so to improve the water supply for rural and urban areas; a social positive impact being job creation (***Appendix I***). Thus WfW was to be driven by multi-disciplinary ecological, hydrological, social and economic goals (**Richardson & van Wilgen, 2004**). The programme was managed under the supervision of the Department of Water Affairs (DWA) and was given strong legal support because of the relevance and challenges encountered in the implementation of its mission. It involved the modification and updating of a number of existing Acts of Parliament and when necessary, introduction of new legislation (**Binns *et al*., 2001**).

1.2.3. Brief description and history of *Acacia mearnsii*

Acacia mearnsii commonly known as Black wattle is a fast growing, light demanding forest species native to Australia. Black wattle is a small to large, evergreen tree. It can reach six to twenty five meters height; the stem is a single straight trunk growing to 50 cm in diameter. Unliker the African *Acacia* species thorns at twigs are absent; the bark is of brownish black colour, hard and fissured; twigs angled, grey, densely hairy, and tinged with yellow when young. The crown of Black wattle is long and round but straight and slender when crowded in plantations. Leaves are compound from eight to twenty one pairs of *pinnae*, fourty to one hundred mm long dark olive, (**van Wyk *et al.*, 2000; Orwa *et al.*, 2009**). Flowers are globoselya and of pale, yellow or cream colour. Seeds have 1-14 mm long, bean-like, elliptical, smoothed, shape and black colour.

Regarding the distribution, Black wattle has been widely introduced in many countries around the world. In South Africa, *A. mearnsii* was introduced in 1858 for tannin bark production. Besides delivering cellulose, the tree is also used as traditional medicine, for shelter, shade and firewood (**van Wyk *et al.*, 2000**). Large Plantations of Black wattle were established in Natal from the late ninetheenth century. It has become an aggressive invasive in places. By 1998, the species had invaded an estimated of 2.5 million ha of South Africa land (**Binnins *et al*., 2001**). Biological controls through the use of pollination vectors are indicated for its management but the cost attached to its control is considerable and might threaten conmmercial plantations. **FAO (2005)** estimated the actual net cost to US$ 1 400 million. Alternative stragies such as the use of sterile triploids **Beck-Pay *et al*. (2013)** is part of the strategies to control the species. However, the invasiveness of current genetic stock remains a problem. In the meanwhile remediation methods have to be developed for the current Black wattle infested aereas.

1.2.4 Ecology and management of invasive alien tree stands

1.2.4.1 Legislation

The large number of publications on invasive alien tree species in South Africa shows that the problem is known and management is concerned. Many people from all sectors of forestry have contributed to the debate during the National Forest Conference, the basis of the White Paper on a National Water Policy for South Africa (**DWAF, 1997**).

The Government through the Department of Water Affairs and Forestry (DWAF) plays an important role as legislator and regulator (**Henderson, 2001**). The Department has the responsibility to ensure the wellbeing of the forestry industry. The essential dispositions and legislations are found in the White Paper and in the National Environment Management Act. In brief, the legislation for the management of invasive alien organisms in South Africa categorised invasive alien plants, and stated how plants in each category should be managed, Black wattle falling in Category 2 (**Henderson, 2001**):

- Category 1: Plants should be removed and destroyed immediately; presence of such plants on a property is liable for a fine.
- Category 2: Plants may only be grown with a permit for commercial reasons; if not, they must be removed.
- Category 3: Plants are permitted to grow where they already exist, but no propagation or new plantings are allowed.

1.2.4.2 Systematic removal approach

The traditional practice used by WfW is to totally clear the alien plant stands, and where necessary, to poison the cut stumps of the invader plants (**Geldenhuys & Bezuidenhout, 2006**). This technique has been applied in the same manner to all biomes and for all categories of invasive alien plants, irrespective of the ecology of the natural vegetation. Successful results have been reported within the Fynbos and grassland biomes (**Richardson & van Wilgen, 2004**). Actually, most of these invader species have a similar ecology than the Fynbos or grassland species. They are adapted to disturbance and intolerant to shade. The two systems (natural vegetation versus invader plant stands) have the same general ecological requirements, and therefore they are in direct competition for the same site (**Geldenhuys & Bezuidenhout, 2006**). The invader plant stands have to be removed to give the natural vegetation a chance to recover. The technique applied by the WfW initiative is adequate in the Fynbos and grassland biomes. The success of the practice has been highly acclaimed (**Huntley, 1996**; **Preston & Williams, 2003; Richardson & Van Wilgen, 2004**) but at the same time such control of the plant invasions involves high costs of regular follow-up actions (**Pieterse & Boucher, 1997; Geldenhuys, 2011**). However, in the forest environment, cutting of such species often leads them to come back in denser regrowth stands. This technique is inadequate and not effective in the forest biome because the disturbance caused by total clearing of the invader plant stands just stimulates rapid recruitment of the light-demanding invader plant species, as has happened with the clearing of Black wattle along the Buffeljagsrivier (**Geldenhuys & Bezuidenhout, 2008**). The approach requires improved understanding of the ecology of each biome and associated species in relation to the ecology of the invasive alien plant species and appropriate techniques need to be adopted (**Geldenhuys, 2011**).

1.2.4.3 Manipulation approach

A new concept was developed called the Manipulation of Invader Plant Stands (MIPS) approach (**Geldenhuys *et al.,* 1986**). The approach applies the basic principles of ecological succession in which the pioneer stands of light-demanding species (invader trees) are gradually invaded by more shade-tolerant species; the process is facilitated by selective removal of the overhead nurse stand (providing the shade and micro-climate) of invader plant species. The concept and approach has been developed and described in several papers to demonstrate the benefits of integrating the concept in the control of the invasive aliens in the forest environment (**Geldenhuys *et al*., 1986**; **Geldenhuys, 1986**, **1992, 1996, 1997, 2004, 2008, 2011, 2013; Geldenhuys & Bezuidenhout, 2006, 2008**; **Geldenhuys & Delveaux 2007).**

Geldenhuys *et al*. (1986) reviewed the status of invasive alien plants in the forest biome under natural conditions and under current land use practices. They found that the natural forest habitat were quite resistant to alien invasion. Most alien plant species were abundant only in disturbed forest margins or in large gaps. With a few exceptions, they related these patterns to the fact that most alien invader plant species were light demanding. In many places the indigenous tree species have expanded their distribution to the understorey of planted stands of introduced species, notably under *Pinus*, *Eucalyptus* and *Acacia* stands. A wide range of natural forest species were reported to establish under many *Acacia* and *Pinus* stands (**Geldenhuys, 1996, 1997**). Even though establishing indigenous species beneath the invasive stands seem to differ according to invasive stand species and stand development stage, the latter were found to improve the conditions of such regeneration. Most of them behaved like pioneer (nurse) stands. A general interpretation was then that most of the indigenous species in the country were shade tolerant to a certain degree.

Most invasive alien species are fast growing tree species responding to disturbance, establish and grow fast into dense stands but cannot readily establish in their own understorey because they are shade intolerant; that explains why they cannot penetrate and invade a closed forest canopy. This pioneer growth behaviour of most invasive trees in South Africa is understandable because they have been selected and introduced for a rapid growth in commercial plantations (eucalypts, pines, *A. mearnsii*) or for dune stabilisation (e.g. *A. cyclops, A. pycnantha, A. saligna*). Their presence in an established stand in a forest implied prior natural or human disturbance (**Geldenhuys *et al.,* 1986**). Once established as an invasive stand or a plantation, they are said to favour the establishment of indigenous forest species, initiating the forest recovery through succession.

Forest succession can be summarised in a few stages with regard to the age and the density of the stand (**Geldenhuys, 1997; Parrotta *et al.,* 1997; Lugo, 1997)**. It starts with the immediate response to disturbance of the light-demanding invader plant species, or indigenous pioneer tree species, to form dense, even-aged, mono-specific stands. Over time, the stand grows taller, and becomes less dense as some stems die due to competition. The opportunity is then given to more shade-tolerant indigenous forest species dispersed into the area to germinate and gradually establish underneath the pioneer stand in clusters, contributing to a progressive increase of species richness and biodiversity going along with a continual decrease in density of the invader or pioneer species.

A cluster is a group of species sharing a specific space with clear boundaries and a different composition than the immediate surrounding area. During forest succession, clusters constitute a microsite. In this unit, edaphic, climatic and structural conditions are modified resulting in attraction of different dispersal agents, and in arrival of more and new species

(**Parrotta *et al.*, 1997; Mascaro, 2011**). The cycle is complete once the canopy is overtaken by indigenous species which form the climax state of the forest (**Geldenhuys & Bezuidenhout, 2012).**

In this study, the term 'forest cluster' was given to one or a group of indigenous trees growing in a stand of an invasive species, in this case the invasive species Black wattle. Within the forest cluster, the presence of at least one reproductively mature tree is a prerequisite, because potentially it could attract dispersal agents.

The establishment of clusters in a stand would greatly depend on the seed availability. For this reason distance of seed sources, seed characteristics and related dispersal mechanisms require investigation for good understanding of the process (**Geldenhuys *et al.*, 1986**). Relating the above information to management of IAPs in the forest environment, such observations need to be considered for adequate management. That is why the new MIPS approach deserves attention.

The phenomenon of IAPs is a real concern globally. Solutions such as intensive forestry and agroforestry systems through ecosystem restoration approaches can yield good results in terms of biodiversity recovery; however, their high costs make them economically unattractive (**Parrotta *et al.*, 1997**). Where regrowing forests are the goal, forest rehabilitation based on natural ecological processes such as forest succession, provides alternative, potentially more cost-effective solutions.

Several studies have shown the catalytic effect of planted tree stands on natural forest biodiversity recovery, initiated by **Parrotta *et al*. (1997).** In Congo, species from the natural vegetation were dominant in the understorey of six to 20 year old stands of *Eucalyptus, Pinus caribaea* and *A. auriculiformis*, and the type and patterns of natural vegetation differed with age and density of the stand (**Loumeto & Huttel, 1997**). Regeneration varied from herbaceous species to saplings and poles to young and more mature trees as the stands increased in age and decreased in stem density. They highlighted the role of wildlife in the process and stated the necessity of adjacent forests as potential seed sources. On Hawaii Island, after 80 years of succession in a non-commercial plantation, native species constituted 4.5% of the basal area and 12.1% of stem density in the plantation, with two promising indigenous species (**Mascaro, 2011**). In Puerto Rico, based on experiments in small plots and observations at landscape scale, **Lugo (1997)** demonstrated that species richness developed on degraded land with tree monocultures, which functioned as pioneer stands. He suggested that monoculture plantations established on degraded sites with arrested succession, could be a solution for re-establishment of species richness on such sites.

In South Africa, the plant invasions are a serious and relevant concern because of the impact of invasive alien plants on the biodiversity of extensive areas of grassland and Fynbos, on the water supply from the catchments, and the control costs. The new MIPS concept and approach introduced earlier, was implemented along the Buffeljagsrivier near Swellendam (**Geldenhuys & Bezuidenhout, 2006**). Black wattle is one of the most widely distributed aggressively invasive plant species in South Africa (**Pieterse & Boucher, 1997**). At Buffeljagsrivier, parts of the current Black wattle stand had been cleared in the conventional approach followed by WfW during the last 10 years, but has regrown back to become a more dense and extensive stand. Discussions between concerned landowners and the WfW team responsible for the area on the potential to implement the MISP approach led to the development of appropriate guidelines for the gradual conversion of the Black wattle stand to natural forest (**Geldenhuys & Bezuidenhout, 2006**). The guidelines included different phases in the planning process, for example a description of stand development stages, and selective thinning of the wattle stand (with another invasive alien species *Solanum mauritianum*) to facilitate the regeneration of more plants of natural forest species. The first phases of the project demonstrated the validity of the new approach as compared to the conventional method of WfW. Unfortunately grazing by cattle from pastures across the river damaged or destroyed many of the developing forest seedlings. Eventually it was decided to implement a research study within the Buffeljagsrivier area with the title 'Rehabilitation of alien invaded riparian zones and catchments using indigenous trees: An assessment of indigenous tree water use at Buffeljagsrivier', funded by the Water Research Commission (project K5/2081). The key question was 'What do we change when we convert a stand of invasive alien plant species to regrowing natural forest in terms of plant species composition and diversity, stand biomass, carbon sequestration rate and water used. This MSc study was embedded in that bigger project and focussed on the first component, i.e. the composition and dynamics of natural forest species establishing within the Black wattle stand. The outcomes of this part would contribute to a more sustainable and cost-effective approach to the rehabilitation of invader plant stands in the forest environment.

1.3 Aims of the study

Strong evidence has been found that plantations from introduced trees can facilitate the establishment of natural forest species in their understorey through modifications of the physical and biological site conditions **(Parrotta *et al.*, 1997**). **Geldenhuys (1997**) reported that stands of invasive light demanding species in the forest play a similar function. However, the ecology of the spread and establishment of such regeneration and the implications on the management of such stands are not well understood.

The overall objective of this study was to develop an understanding of the dynamics of the spread and establishment of natural forest species in a large stand of the invasive alien plant species Black wattle along the Buffeljagsrivier. The overall objective was pursued through four specific objectives:

(i) To map and assess the patterns in the distribution, size and species composition of the clusters within the Black wattle stand;

(ii) To determine the relationship between natural forest clusters establishing within the Black wattle stand and the neighbouring natural moist, dry and riparian forest patches as potential seed sources for the developing forest clusters;

(iii) To determine the subsequent spread of natural forest species from the developing forest clusters into the rest of the Black wattle stand;

(iv) To synthesize the information on the dynamics of the spread and establishment of natural forest species into the Black wattle stand as a basis for developing general guidelines for the conversion of stands of invasive alien tree species in the forest environment towards regrowing natural forest.

Observations within the study area led to four main general hypotheses: **1-** Can natural forest species establish under a stand of wattle**? 2-** Are species from all types of neighbouring forest patches potential seed sources for the developing forest clusters**? 3-** Are the establishing forest clusters secondary sources of seed for the expansion of the clusters into the surrounding *Acacia mearnsii* stand**? 4-** What fruit/seed characteristics and dispersal mechanism determine the potential of natural forest species to spread into and establish within the *Acacia mearnsii* stand**? 5-** How useful is the obtained information and knowledge to improve forest rehabilitation through manipulation of the stands of invasive alien tree species**?**

1.4 Study conceptual framework

The study within each specific objective was designed around specific research questions to address the relevant general hypotheses (***Figure 1.1***). The research questions were expanded with each specific component of the study.

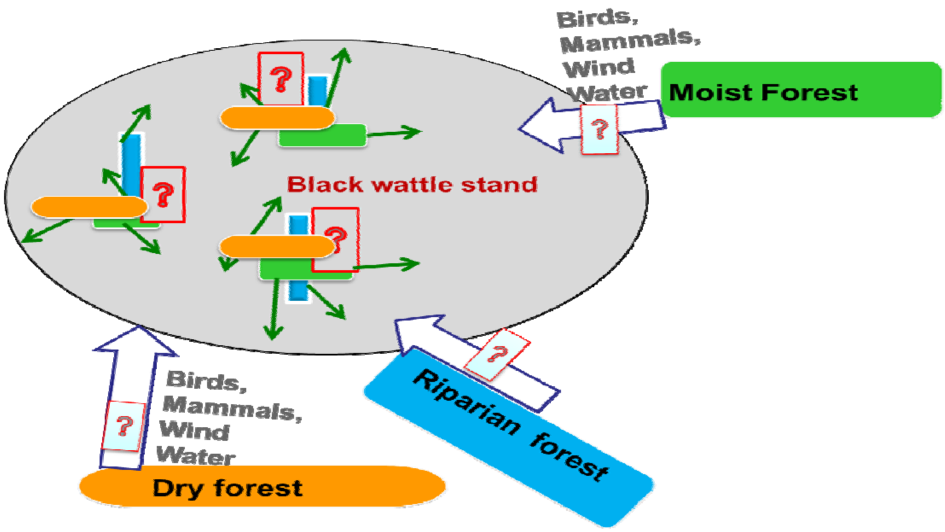


Figure 1.1: The conceptual framework of the study to address five main research questions (Adapted from Atsame-Edda & Geldenhuys, Poster 2011).

1.5 Study area

Buffeljagsrivier study area (34°00'15"S, 20°33'58"E; 95-110 m above mean sea level) is situated east of Swellendam at the southern foot of the Langeberg Mountains. The Langeberg Mountains, to the north of the Buffeljagsrivier, is composed of Table Mountain Sandstone quartzites. A much smaller ridge of shale occurs to the south of the river (***Figure 1.2***).

The climate is typical of the South Western Cape with hot dry summers and cold wet winters, i.e. a Mediterranean climate. The rainfall is fairly evenly spread throughout the year. Swellendam normally receives about 462 mm of rain per year ranging between 23 mm in December and 48 mm in August. The mean monthly daily maximum temperatures range from 17.1°C in July to 27.5°C in January and the mean monthly daily minimum temperatures are 15°C in February and 5°C in July (***Figure 1.3***).

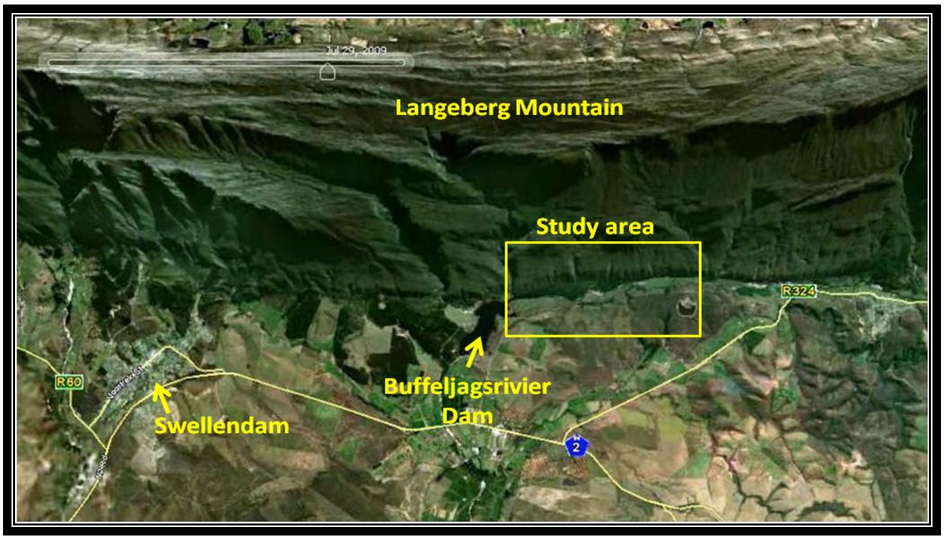


Figure 1.2: Location of Buffeljagsrivier study area east of Buffeljagsrivier dam and between Langeberg Mountains (north of river) and a lower ridge (south of river)

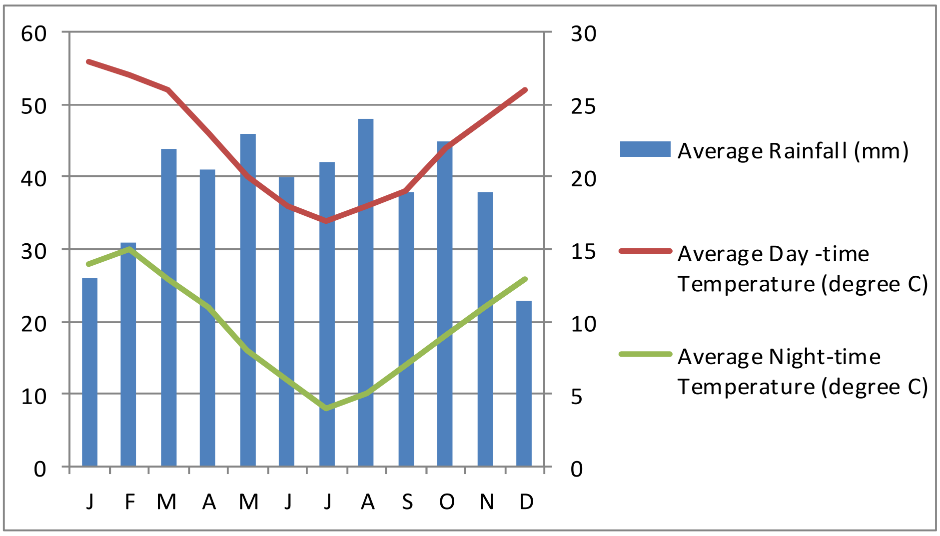


Figure 1.3: Distribution of monthly rainfall throughout the year, with lines showing the average day and night time monthly temperatures at Buffeljags. (Source: www.saexplorer.co.za/south-africa/climate/swellendam_climate.asp).

Several Western Cape Afrotemperate forest patches, such as moist forest, dry forest and riparian forest, grow along the river at the foot of the mountain. The dominant surrounding vegetation is a fire-adapted sclerophyll shrubland (Fynbos) with very high plant species diversity. An extensive Black wattle stand of about 90 ha grows along the northern bank of the river at the foot of the Langeberg Mountain **(*Figure 1.4*).**

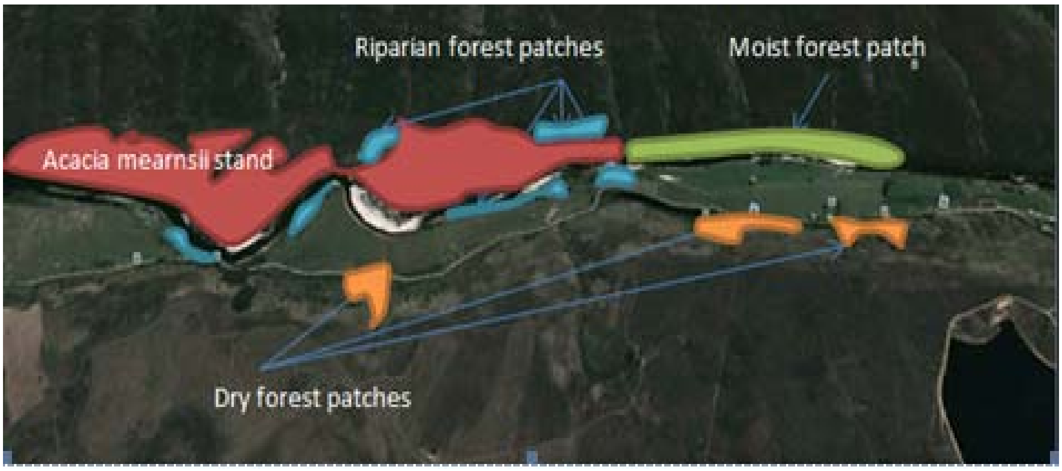


Figure 1.4: Location of small natural forest patches (Moist, Dry & Riparian) in relation to the extensive stand of wattle (*Acacia mearnsii*) along Buffeljagsrivier.

Observations of the site suggest that years ago the natural forest may have been much more extensive along the alluvial sites along the river. It is likely that this forest was cleared for agricultural purposes and created an opportunity for Black wattle invasion.

The area is under the management of the WfW programme. The many dead stems of Black wattle suggests that about 10 years ago these invader trees were cleared according to the traditional technique but due to the inadequacy of the management explained earlier, the Black wattle re-established in a much denser stand. A more detailed study is needed to assess the historical changes of this area, prior to the establishment of the Black wattle stand.

1.6 General methodology

The general methodology that was followed in this study is shown diagramatically in ***Figure 1.5.*** In short, data collection was as follows:

- Specific objective 1: GPS mapping of the forest clusters throughout the black wattle stand along broad transects running from the river to the foot of the mountain, and recording of the zone (Proximal, Intermediate and Distant), size and species of each cluster.

- Specific objective 2: Sampling of plots along transects running along the main environmental gradients through the moist, dry and riparian forest patches and selected large forest clusters to record the species composition; and to classify the sampled plots according to species composition.

- Specific objective 3: (1) Sampling of forest species regeneration on plots in an 18 m radius around seven selected forest clusters, to explain the expansion of forest clusters, and to describe the patterns in terms of distance from the seed sources; (2) Generating a list of species from natural forest patches and to compare this with a list of species from the establishing forest clusters, to assess the influence of fruit and/or seed characteristics of tree species and the dispersal system in this forest recovery process.

- Specific objective 4: Synthesising the findings to answer the overall question and to develop guidelines for the improved rehabilitation of invasive stands to natural forest.

Data analysis varied between the studies designed for each specific objective, and were discussed in more detail with each relevant chapter. Descriptive analyses were done through calculation of means, frequencies, densities, species importance values, analysis of variance and construction of histograms to assess, characterise and describe the vegetation patterns and diversity. Calculation of distance matrices followed by clustering analyses and a constraint ordination Canonical Correspondence Analysis (CCA) were used for site classification, interrelationships between forest patches and forest clusters, species dispersion patterns and the influence of general environmental variables.

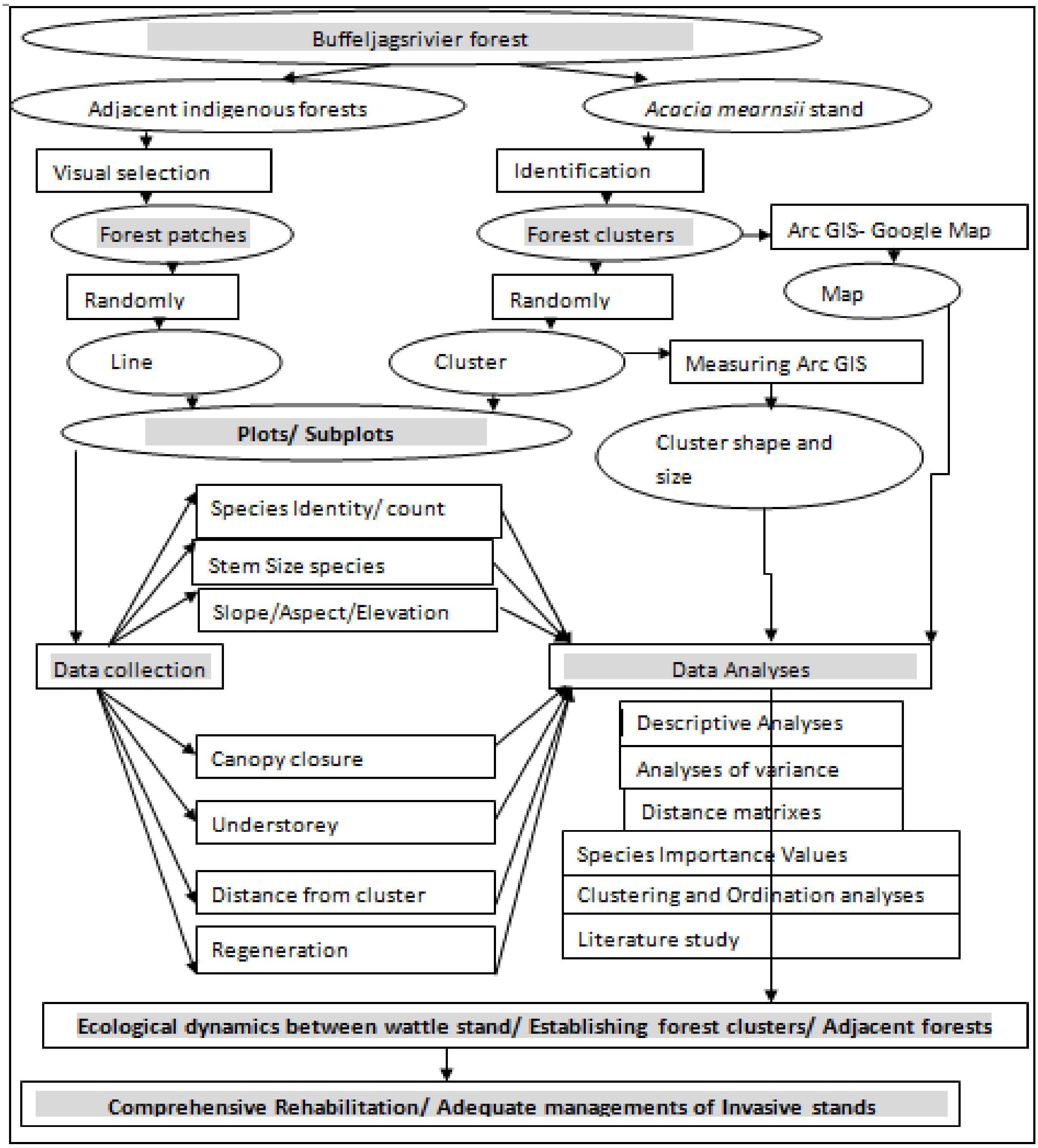


Figure1.5: step by step general methodology of the study.

1.7 Thesis Structure

The thesis is divided into five chapters. Chapter one gives an introduction to the context and the literature review of the study. Chapters two to four deals with the individual studies related to specific objectives one to three and are written in paper format. Chapter five is a synthesis of the study and recommends guidelines towards improved rehabilitation of natural forest from invader plant stands (***Figure 1.6***).

Specific Objectives	General research questions	Relevant chapter in thesis
		Chapter 1: General Introduction
Specific Objective 1	**Question 1**	**Chapter 2**
Map and assess the patterns in the distribution, size and species composition of forest clusters within the Black wattle stand.	Can natural forest species establish under stands of the invasive alien Black wattle	**Patterns in the distribution, size and species composition of forest clusters within a stand of the invasive introduced tree *Acacia mearnsii* at Buffeljagsrivier, Swellendam.**
Specific objective 2	**Question 2**	**Chapter 3**
Determine relationships in species composition between natural forest clusters and neighbouring forest patches at potential seed sources for developing forest clusters.	Are species from all types of neighbouring forest patches potential seed sources for the developing forest clusters?	**Adjacent natural forest patches as potential seed sources for establishing forest clusters within a stand of the invasive introduced tree *Acacia mearnsii.***
Specific objective 3	**Question 3 & 4**	**Chapter 4**
Determine the subsequent spread of forest species from the developing forest clusters into the rest of the Black wattle stand.	**3:** Are the establishing forest clusters secondary sources of seed for the expansion of the clusters into the surrounding Black wattle stand? **4:** What fruit/seed characteristics and dispersal mechanism determine the potential of natural forest species to spread into and establish within the Black wattle.	**Natural forest clusters within a stand of the invasive introduced tree *Acacia mearnsii* become sources for the wider expansion of natural forest.**
Specific objective 4	**Question 5**	**Chapter 5**
Synthesize information on the dynamics of spread and establishment of natural forest species into the Black wattle stand as basis for improving rehabilitation of natural forest from stands of invasive alien tree species in the forest environment.	How useful is the obtained information and knowledge to improve forest rehabilitation through manipulation of the stands of invasive alien tree species?	**Dynamics of the spread and establishment of natural forest species into an *Acacia mearnsii* stand: Synthesis and forest rehabilitation guideline.**

Figure 1.6: The conceptual framework for the study to pursue the overall objective of understanding the dynamics of the spread and establishment of natural forest species within an invasive plant stand through the different chapters of this thesis.

In this circumstance, repetitions on parts such as study area, and methodology across the chapters could not be avoided. The field forms and complementary documents are presented in the appendixes.

1.8 References

Adair, R. 2002. Black Wattle: South Africa manages conflict of interest. *Bio control News & Inform* 23(1): 5-7.

Armstrong, G. 1992. A necessary evil? *Veld and Flora* 78: 10-13.

Beck-Pay, S.L., Ascough, G., Galbraith, M. 2013. Protocol for flow cytometry analysis of *Acacia mearnsii* leaf samples for ploidy determination. ICFR Technical Note 04/2013, Pietermaritzburg, South Africa.

Binns, J.A.; Illgner, P.M. & Nel, E.L. 2001. Water shortage, deforestation and development. South Africa's Working for Water Programme. *Land degradation and development* 12: 341-355.

Brink, A.J. & van der Zel, D.W., 2004.Trends and opportunities in South African forestry. *South Africa Forestry Journal* 115: 17-27.

Campbell, P.L. 1987. The control of Black wattle. Weeds Farming in South Africa.

Clements, F.E. 1916. Plant Succession: An Analysis of the Development of Vegetation. Publication 242, Carnegie Institute of Washington, Washington, DC.

Connell, J.H.& Slatyer, R.O. 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. *The American Naturalist*, 111(982): 1119-1144.

DWAF, 1997. White Paper on a National Water Policy for South Africa. Pretoria, South Africa, Republic of South Africa, Department of Water Affairs and Forestry.

FOA, 2005. *Acacia mearnsii* in South Africa the Biosecurity in forestry: A case study on the status of an invasive forest tree. *Forestry Department* Chapter 6: 216-218.

Geldenhuys, C.J. 1986. Costs and benefits of the Australian blackwood *Acacia melanoxylon* in South African forestry. In Macdonald, I.A.W.; Kruger, F.J. & Ferrar, A.A., (eds). The ecology and management of biological invasions in southern Africa: 275–284. Cape Town, South Africa, Oxford University Press.

Geldenhuys, C.J. 1992. Plantation forestry can contribute to the conversion of open areas to rainforest. Annals of FOREST'92.

Geldenhuys, C.J. 1996. The Blackwood Group System: its relevance for sustainable forest management in the southern Cape. *South African Forestry Journal* 177: 7-21.

Geldenhuys, C.J. 1997. Native forest regeneration in pine and *Eucalyptus* plantations in Northern Province, South Africa. *Forest Ecology and Management* 99: 101-115.

Geldenhuys, C.J. 2004. Concepts and process to control invader plants in and around natural evergreen forest in South Africa. *Weed Technology* 18: 1386-1391.

Geldenhuys, C.J. 2008. Can I manipulate alien plant stands to rehabilitate natural forest? *Dendron* 40: 38-44.

Geldenhuys, C.J. 2011. Most invasive alien plants facilitate natural forest recovery – how is that possible? *SAPIA News* 18: 2-5.

Geldenhuys, C.J. 2013. Converting invasive alien plant stands to natural forest nature's way: Overview, theory and practice. In: Jose, S., Singh, H.P., Batish, D.R. & Kohli, R.K. (eds). Invasive plant ecology, CRC Press, Taylor & Francis Group, Boca Raton: 217-237.

Geldenhuys, C.J. & Bezuidenhout, L. 2006. Guideline for conversion of invader plant stands to regrowth natural forest along the Buffeljagsrivier, Swellendam Invader conversion Buffeljagsrivier progress. Report Number FW-01/06, Forestwood cc, Pretoria.

Geldenhuys, C.J. & Bezuidenhout, L. 2008. Practical guidelines for the rehabilitation of forest-related streambank vegetation with removal of invader plant stands along the Berg River, Western Cape. Report FW-02/08, FORESTWOOD cc, Pretoria. 39 pp.

Geldenhuys, C.J. & Bezuidenhout, L. 2012. Rehabilitation of natural forests using stands of alien trees of plantations or invasions as allies. In: Bredenkamp, B.V & Upfold, S.J. (eds). South African forestry handbook, 5th edition. Southern African Institute of Forestry, Pretoria: 585-604.

Geldenhuys, C.J. & Delvaux, C. 2007. The *Pinus patula* plantation … A nursery for natural forest seedlings. In: Bester, J.J.; Seydack, A.H.W.; Vorster, T.; van der Merwe, I.J. & Dzivhani, S. (eds). Multiple use management of natural forests and woodlands:

Policy refinement and scientific progress. Natural Forests and Savanna Woodland Symposium IV, Port Elizabeth, South Africa, 15-18 May 2006: 94-107.

Geldenhuys, C. J., P. J. Le Roux, and K. H. Cooper. 1986. Alien invasions in indigenous evergreen forest. *In* Macdonald, I.A.W.; Kruger, F.J. & Ferrar, A.A. (eds.). The Ecology and Management of Biological Invasions in Southern Africa. Cape Town, South Africa: Oxford University Press: 119–131.

Henderson, L. (ed.). 2001. Alien weeds and invasive plants: A complete guide to declared weeds and invaders in South Africa. Plant Protection Research Institute Handbook No12, Plant Protection Research Institute, Agricultural Research Council, Pretoria.

Huntley, B.J. (eds.). 1996. South Africa's experience regarding alien species: impacts and controls. Proceedings of the Norway/UN Conference on Alien Species. The Trondheim Conferences on Biodiversity, 1-5 July 1996. Sandlund, O.T., Schei, P.J. & Viken, Å.: 182-188.

IUCN. 2000. Guidelines for the prevention of Biodiversity loss caused by alien invasive species. 51 st meeting of the council. Gland, Switzerland.

Loumeto, J.J. & Huttel, C. 1997. Understorey vegetation in fast growing tree plantation on savanna soils in Congo. *Forest Ecology and Management* 99: 65-81.

Lugo, A.E. 1997. The apparent paradox of re-establishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management* 99: 9-19.

Macdonald, I.A.W.; Kruger, F.J. & Ferrar, A.A. 1986. The ecology and management of biological invasions in southern Africa. Proceedings of the National Synthesis Symposium on the ecology of biological invasions. Oxford University Press, Cape Town.

Mascaro, J. 2011. Eighty years of succession in a non-commercial plantation on Hawaii Island: are native species returning? *Pacific science* 65(1): 1-15.

Orwa, C.; Mutua, A.; Kindt, R.; Jamnadass, R. & Anthony, S. 2009. *Acacia mearnsii* Fabaceae- Mimosoideae De World- world. Agroforestry Database: a tree reference and selection guide version 4.0. World Agroforestry Centre, Kenya.

Parrotta, J.A.; Turmbull, J.W. & Norman, J. 1997. Catalysing native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99: 1-7.

Phillips, J. 1931. Forest-succession and ecology in the Knysna region. . Shaughnessey, G.L. Historical ecology of alien. Memoir Botanical Survey of South Africa 14: 1-327 Government Printer, Pretoria

Phillips, J. 1963. The forest of George, Knysna and the Zitzikama. A Brief history of their management pp1778-1939. Government Printer, Pretoria.

Pidwirny, M. 2006. "Plant Succession". Fundamentals of Physical Geography.

Pieterse, P.J. & Boucher, C. 1997. A.C.A.C.I.A. (A Case Against Controlling Introduced Acacia) 19 years later. *South African Forestry Journal* 180: 37-44.

Preston, G. & Williams, H. 2003. Case Study: The Working for Water programme: Threats and Successes. Service Delivery Review 2(2): 66-69.

Rejmanek, K.M.; Richardson, D.M. 1996. What attributes make some plant species more invasive? *Ecology* 77(6): 1655-1661.

Richardson, D.M. 2008. Forestry as Invasive aliens. *Conservation Biology* 12(1): 18-26.

Richardson, D.M. & van Wilgen, B.W. 2004. Invasive alien plants in South Africa: How well do we understand the ecological impacts? *South African Journal of Science* 100: 45-52.

van Wyk, B.; Wyk, P.B. & van Wyk, E. 2000. Photo guide to tree of Southern Africa Pretoria.

Chapter 2:
Patterns in the distribution, size and species composition of forest clusters within a stand of the invasive alien tree *Acacia mearnsii* at Buffeljagsrivier, South Africa

Abstract

Natural forest tree species can establish in the understorey of a stand of an invasive light demanding species as part of natural forest succession. They are expected to establish in denser and more diverse groups closer to the seed sources. The main question is: What are the implications of such information on the common perception of invasive stands in the forest environment? Investigations were carried out in a stand of the invasive introduced Black wattle along the Buffeljagsrivier in the Western Cape, South Africa, to assess the reality of this expectation. A total of 329 clusters of natural forest species were mapped, showing their existence and distribution throughout this dense Black wattle stand. Patterns in the distribution of natural forest clusters suggested a progressive colonization of the introduced Black wattle stand from the proximal to the distant zone in relation to the adjacent natural forest patches. Shapes of seven clusters randomly selected from the sample suggested existence of several dispersal mechanisms. The actual species composition of the clusters and their distribution through the stand did not show any distinct pattern related to the sequence of their establishment as proposed in the literature. Canopy tree and shrub species occurred scattered in all the cluster sizes. The results confirmed both of the stated hypotheses. The results provide evidence to change the common perception that such invasive stands in the forest environment threaten forest diversity. Policy makers need to review the method applied to control invasive species in natural forests and to extend this concept to all natural forests in South Africa. In addition, the results provide a basis for further studies to improve the understanding of the relationship between the establishing forest clusters, the adjacent patches of natural forest and the ecology of seed sources and related dispersal systems.

Key words: Forest cluster, Natural forest species, *Acacia mearnsii*, Forest succession process, Forest recovery, Rehabilitation, Invasive species, Buffeljagsrivier, Black wattle

2.1 Introduction

It is surprising to observe several stems of indigenous forest species beneath an invasive stand or a plantation of introduced tree species when common thinking is that invasive stands are dead in terms of natural forest species. People try to secure all the benefits provided by natural forests through different management interventions, but they often lack understanding of the natural ecological processes and this can lead to management approaches that are inefficient and costly (**Geldenhuys, 1997; Lugo, 1997**; **Parrotta *et al.*, 1997**), with sometimes outcomes that are opposite to what had been expected. For example, people think to clear invasive alien plant stands to recover natural forest but they end up with more dense stands of the invasive species (**Geldenhuys & Bezuidenhout, 2006**). Ecological understanding of natural forest recovery could have guided the intervention cited in this example for better results.

The establishing of indigenous forest species in an invasive stand or in a monoculture of an introduced species constitute evidence of a natural process called natural forest succession. Forest succession is one of the oldest concepts in ecology **(Clements, 1916)**. The concept has been used to study forest dynamics in time and space. One of the most common definitions of succession in forest stands is directional and sequential changes in community attributes over time (**Clements, 1936; Finegan, 1984; Otsamo, 2000, Parmesan, 2006**). These changes involve species patterns, species composition or diversity. In ecology, two types of succession are distinguished, i.e. primary and secondary succession. Both evoke the changes in patterns and composition of a given area but they start from different ecological bases. Primary succession always begins from a new land formation of inorganic material, such as rock or volcanic rock. Secondary succession begins from a disturbed, but not destroyed, organic source or soil, such as roots, seeds, lichen and mosses (**Clements, 1916**). For the scope of this paper, forest recovery as response to a clearing, causing canopy disturbance, is studied in the light of a secondary succession process in the forest environment.

Generally, pioneer species, usually light demanding species, are the first tree species to germinate and become established, often in the form of dense monoculture stands

(Geldenhuys, 1997; Hardwick *et al.*, 1997; Lugo, 1997; Parrotta *et al.*, 1997). Within disturbances such as superficial fire or clearings that result in completely opened canopies, forest would develop through secondary succession. As pioneers, their role is to initiate the recovery process and to improve the conditions that would attract dispersers and favour the change in the understorey microsite. These changes include introducing shade or modifying the nutrients or acidity of the soil with development in litter and humus layers, all resulting in new conditions which are suitable for certain species and inappropriate to others. Several types of wildlife may visit the site and affect increasing seed input from adjacent forests, resulting in vegetation diversity and changes in the microsite.

Many studies focused on the species composition of the understorey vegetation diversity, during forest succession. Numerous shrub and forest tree species are often recorded with some other vegetation growth forms (grasses, herbs, climbers, ferns, etc.) depending on the successional stage **(Geldenhuys, 1997; Loumeto & Huttel, 1997**). After establishment of a monoculture of even-aged pioneer species, secondary succession develops, as described by **Clements (1916**), and observed by **Geldenhuys *et al.* (1986), Geldenhuys (1997)** and **Loumetto and Huttel (1997**). The understorey is first colonised by grasses and herbs followed by sparse shrubs under which forest canopy and sub-canopy tree species later establish.

The establishment of forest species in the understorey of planted stands (nurse stands) is explained by the fact that most of the nurse (pioneer) species are light demanding and most of the indigenous forest species are shade tolerant **(Geldenhuys, 1997**). Pioneer species are generally light-demanding and fast-growing, are not able to establish under closed canopy conditions without disturbance, and are therefore unable to replace themselves in the understorey. The opportunity is then given to other more suitable species to establish **(Geldenhuys, 1997; Lugo, 1997; Parrotta *et al.*, 1997)**. These forest species are described to establish most of the time in small and scattered clusters which progressively expand to larger clusters of trees (**Mascaro, 2011; Geldenhuys & Bezuidenhout, 2012**). At the same time the stands grow taller and decrease in density through self-thinning due to competition with more vigorous stems (**Geldenhuys & Delvaux, 2007**).

Within forest succession, plantation stands of introduced tree species or naturalising stands of shade-intolerant invasive species are to be considered as pioneer species (**Parrotta *et al.*, 1997**). In our case the introduced invasive species is the Australian Black wattle. The two types of stands described here have similar attributes such as fast-growing, and light-demanding species. They respond to fire or opened canopy disturbance and yield similar results during the forest recovery process. Their stands should be managed the same way where natural forest recovery is the goal.

Four development stages have been identified in the succession process (***Figure 2.1;*** **Geldenhuys, 2004, 2008; Geldenhuys & Bezuidenhout, 2006**). The cycle is completed once the stand canopy has been replaced by a mixed regrowth forest (stage 4).

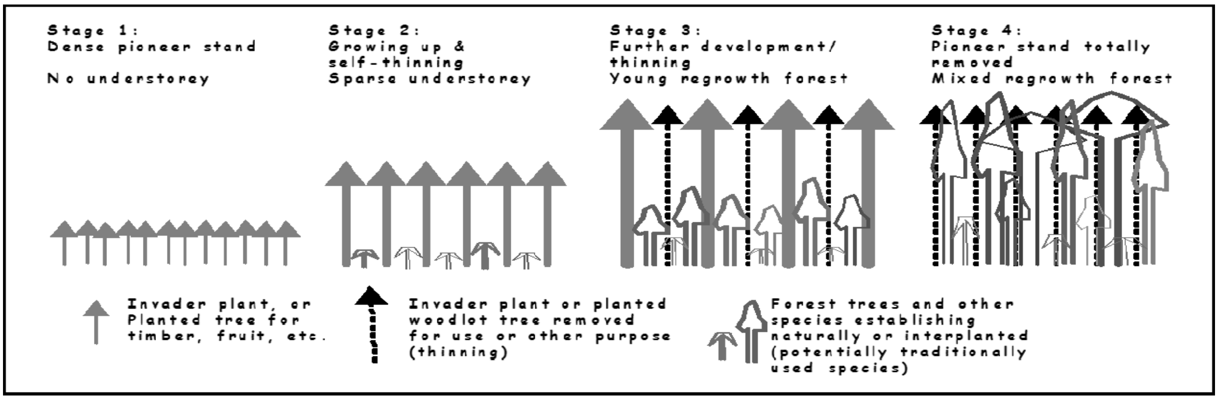


Figure 2.1: The four development stages in the forest succession process over time (Adapted from Geldenhuys 2004).

The idea of trees establishing naturally in the form of clusters form part of this study. The term ‘forest cluster’ has been adopted as one or a group of several indigenous trees establishing in a stand of an invasive species. Within the cluster group, the presence of at least one reproductively mature tree that is able to attract dispersal agents is a prerequisite. The term has been used as separate from forest patches that refer to stands of natural forest adjacent to the Black wattle stand. The process is considered to be directional because most of the seeds are expected to come from the adjacent natural forest. The pattern of establishing forest clusters are expected to show a higher density and older clusters of more advanced development closer to the potential seed sources (**Geldenhuys, 1997; Lugo, 1997; Parrotta *et al.*, 1997**).

The purpose of this paper was to map and assess the patterns in the distribution, size and species composition of the forest clusters within the Black wattle stand to show the forest recovery process within the Black wattle stands at Buffeljagsrivier. The hypothesis was that natural forest species can establish under the invasive Black wattle stand and establish more readily close to the potential seed sources.

2.2 Study Area

The Buffeljagsrivier study area (34^{o}00’15”S, 20^{o}33’58”E; altitude between 95-110 m above mean sea level) is situated east of Swellendam at the southern foot of the Langeberg Mountains. The Langeberg Mountain is a Table Mountain Sandstone quartzite (north of the Buffeljagsrivier) and a low ridge of shale occurs to the south of the river**.** The climate is typical of the South Western Cape with hot summers and cold winters, i.e. a Mediterranean climate. The rainfall is fairly evenly spread throughout the year. Swellendam normally receives about 462 mm of rain per year ranging between 23 mm in December and 48 mm in August, but it is expected that the rainfall along the river in the study area will be higher. The mean monthly daily maximum temperature ranges from 17.1°C in July to 27.5°C in January and the mean monthly daily minimum temperature is 15°C in February and 5°C in July.

Along the river at the foot of the mountain, the forest vegetation occurs as several small patches of Western Cape Afrotemperate forest, such as moist forest, dry forest and riparian forest. They cover a total area of about 3 ha, within a matrix of the very diverse fire-adapted sclerophyll shrubland (Fynbos). A Black wattle (*Acacia mearnsii*) stand with an area of about 90 ha grows for a distance of 3.12 km along the northern bank of the river at the foot of the Langeberg Mountain (***Figure 2.2*****).**

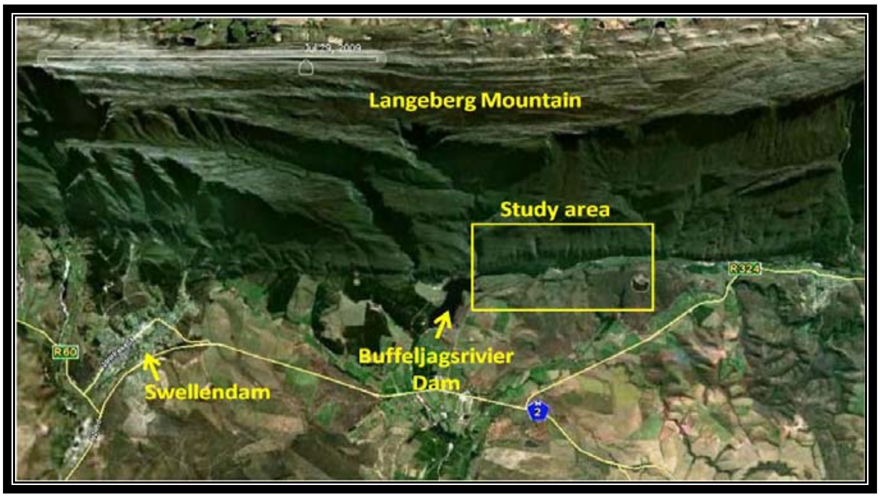


Figure 2.2: The location of the study Area

The area is rich in birdlife and several mammals such as baboons, bushbuck and porcupines, have been observed. The human presence in the area is marked by farming activities (mainly cattle grazing with pastures) and ecotourism business (holiday cottages around the dam, camping, water sport activities, fishing, paging, walking, cycling through the wattle and natural forest and hiking). The Buffeljagsrivier area is well visited, and the dam and the river offer good reserves in terms of stream flow.

Presence of the extensive Black wattle stand along the river is viewed as a permanent threat, not only to the biodiversity of the area but also to the above-cited activities and services. Black wattle is a fast-growing forest tree species native to Australia. It has become an invasive tree in South Africa after it has been introduced in the middle 19th century for tanning bark production. The species is described as the most widespread invasive plant species in South Africa (**Binns *et al*., 2001**; **Richardson & van Wilgen, 2004**).

Observations of the site suggest that years ago the natural forest may have been much more extensive on the alluvial sites along the river. It is likely that this forest was cleared for agricultural purposes and that gave the opportunity to Black wattle to invade the zone. The WfW, a governmental programme in charge of the eradication of invasive alien plants in the country, had probably cleared the wattle about 10 years ago, according to the conventional technique of clear-felling. However, the Black wattle regrew into an even denser stand than before. Presently the stand is the focus of a forest rehabilitation study under the Water Research Commission programme (project K5/2081)

2.3 Study methodology

2.3.1 Zonation of the area

The Black wattle stand was divided into three zones in relation to the proximity to the indigenous forest patches: Proximal zone, Intermediate zone and Distant zone (***Figure 2.3***), using natural bounderies.

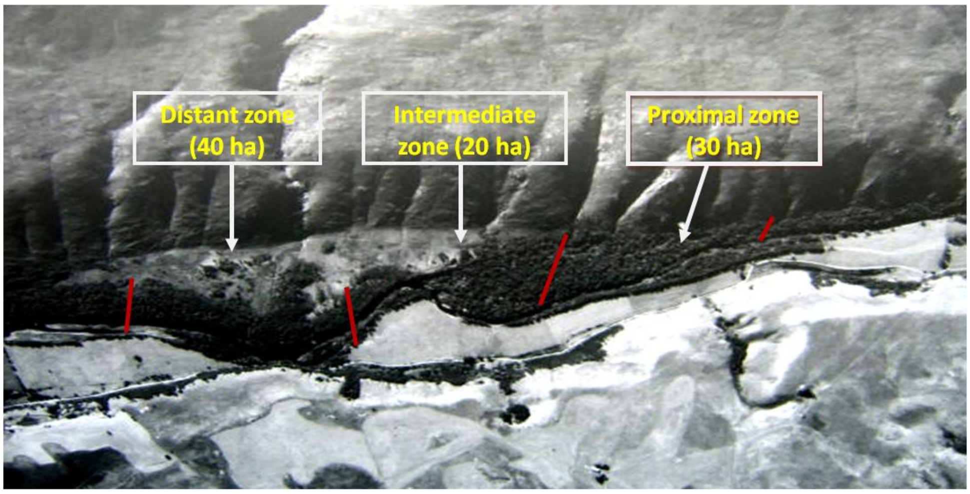


Figure 2.3: The three zones with approximate area of the Black wattle stand in relation to the proximity to the natural forest patches (Google image January 2011).

2.3.1.1 Proximal zone

The zone starts at the western limit of the largest moist forest patch, with no physical boundary between the two areas. It also has patches of riparian forest, some to the north and some to the south of the Black wattle stand. It is the most accessible one and regularly visited by both humans and domestic animals such as cattle. The cattle caused considerable browsing of the establishing seedlings of the natural forest species.

2.3.1.2 Intermediate zone

The Intermediate zone (***Figure 2.4***), middle of Black wattle stand, is also subject to regular human and cattle movements. This zone has two parts; the eastern part is most easily accessed by cattle with associated heavy browsing, and it was cleared of the wattle before 2004 (***Figure 2.4a***). A strip was also cleared during 2006 (***Figure 2.4b***) in the conventional WfW practice to compare with the new approach of selected removal of wattle around establishing forest clusters (**Geldenhuys & Bezuidenhout, 2006**). The western part of this zone has more difficult access for cattle with possible less heavy browsing.

Figure 2.4: A comparison of the images of the middle zone of the Black wattle stand at Buffeljagsrivier during November 2004 (a; Top) and April 2013 (b; Bottom). (Google Earth historical images, 15 December 2013).

2.3.1.3 Distant zone

This zone forms the largest part of the wattle stand with a generally low accessibility to cattle, but is relatively far from the potential seed sources. The general view of this part of the stand is relatively small and dense stocking of Black wattle with many dead big old trees (probably natural forest species and Black wattle or other introduced species). This area has many signs of past human activities such as vestiges of houses, empty containers, and shallow drainage channels.

2.3.2 Mapping of forest clusters

A forest cluster for this study was defined as one to several natural forest trees growing on a limited area within the Black wattle stand. A requirement was that within the group there should be at least one reproductively mature tree present that would be able to attract dispersal agents. Three cluster size classes were defined: Small cluster, with one to three trees; Medium cluster with four to nine trees; and Large cluster with 10 and more trees.

The total Black wattle stand of 90 ha was traversed along parallel 20 m wide transects belts between the river and the foot of the mountain. The location coordinates of each existing cluster were recorded with a GPS. In the case of larger clusters, the GPS coordinates of the largest tree in the cluster were marked and recorded, with the species name (***Appendix II***).

A sample of clusters was selected by stratified sampling as described by **Kindt and Coe (2005)** to assess the shapes and the species composition of the forest clusters. The hypothesis that species composition would differ with the distance to seed sources and with the succession development stage of the stand guided the selection. The accessibility of the cluster was set as an additional condition for selection. When a random number presented an inaccessible cluster, it was replaced by the nearest accessible one. Initially 63 clusters were randomly selected, using tables of thousand digit random numbers, and proportional to the total number of small, medium and large clusters within the three identified zones (Proximal zone, Intermediate zone, and Distant zone). After sampling, the large clusters surrounded by Riparian Forest North appeared to be more like forest patches and were then excluded from this selection. This reduced the selected clusters to 59 (***Table 2.1***). Clusters within the sample were then measured in order to draw their shape and calculate their area.

The shape of each of the selected clusters was determined according to the following procedure (***Figure 2.5***): A line (principal axis) was marked and measured between the outer crown boundaries of the two most distant indigenous trees within a selected cluster. A perpendicular line was measured from the principal axis to each tree within the cluster boundary. The position of each tree within this cluster was recorded through X and Y coordinates. The X-axis was the distance from the origin of the principal axis to the point on this line of the perpendicular line to each tree. The Y-axis was the length of the perpendicular line from the principal axis to the middle of the stem of the tree for tree position and to the crown boundary for the cluster boundary. In the case of a single-tree cluster, the shape and size of the cluster was basically the crown projection onto the ground. The total measurements obtained were then captured in an Excel spread sheet.

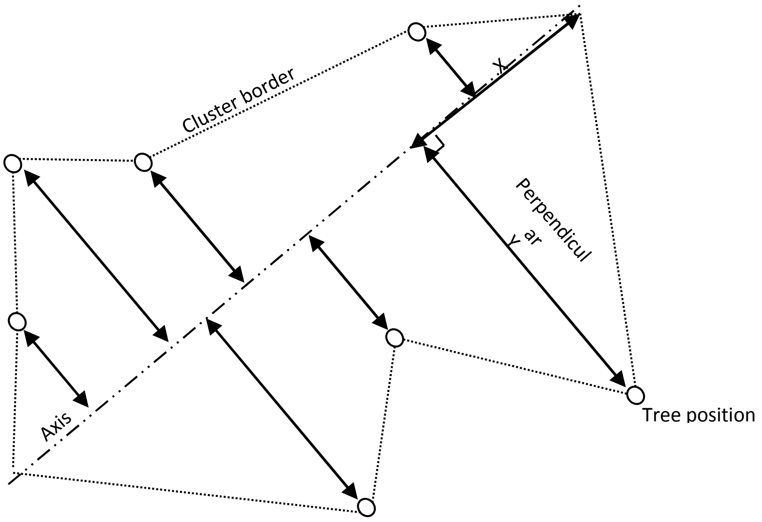


Figure 2.5: The principal axis and perpendicular lines to each tree within the cluster, as used to measure the shape and size of the selected clusters.

After measuring, the following general information was recorded for each of the 59 selected forest clusters: forest cluster number; GPS coordinates; site slope (level, gentle, steep or very steep); canopy closure (1 = ≤ 25%; 2 = 51-75%, 4 = ≤ 75+ %) Main growth forms of the ground cover (grass, herbs, climbers, ferns, and/or tree regeneration). In addition, information on the species composition of the trees within the forest cluster was recorded: All stems ≥5 cm DBH (stem diameter at 1.3 m breast height above ground level) by species and DBH; Count of stems <5 cm DBH per species as regeneration, by three categories (seedlings = stems <50 cm height; saplings = stems ≥50 cm height and <1 cm DBH; poles = stems one to 4.9 cm DBH). For multi-stem trees, each stem was measured and recorded separately but the tree number was the same for each stem of the tree (to indicate that they belong to the same tree). Unknown species were recorded as such but material was collected for later identification. The field forms can be seen in ***Appendix III.***

2.3.3 Data analysis

A geo-referenced aerial photograph of the study site was obtained from the National Geo-spatial information institute (NGI) to map the recorded forest clusters. The aerial photograph was opened in Arc-map and the GPS points collected in the field were superimposed on the image. Then the map was created and patterns were highlighted. The Excel file containing measurements of different forest clusters was loaded in Arc map to draw the forest cluster shapes by interpolation of the points. Stems of natural forest species were differentiated from stems of invasive species, and the biggest stems were highlighted, using different colors and generating a legend. The surface areas of forest clusters were calculated using area menu in Arc-map.

The mean number of clusters per ha per zone (the zones varied in total surface area) were calculated and described in relation to the location of natural forest patches in order to investigate the patterns of forest cluster size distribution within the Black wattle stand stand. Analyses of Variance (ANOVA) were performed on the mean cluster size per zone, to test the hypothesis that more stems will be found close to the potential seed sources and that number of Black wattle stems will decrease with the cluster size. A Bonferroni comparison test was applied to the cluster size distribution to reinforce the ANOVA results. Mean species abundance per zone were calculated and histograms were generated to explain the species composition and distribution per cluster size and per stand zone to check if the expected sequences of species establishment in relation to the succession stage as described in the literature is verified in this study.

2.4 Results

2.4.1 Distribution of natural forest clusters within the Black wattle stand

A total of 329 forest clusters were recorded and they were distributed across the total Black wattle stand (***Figure 2.6***). The majority of large clusters (59.2 %; 0.53 ha) occurred in the Proximal zone and the majority of small clusters (53.0 %; 3.52 ha) in the Distant zone (***Table 2.1***). Medium-sized clusters were present in similar proportions in the Proximal (44.4 %; 0.53 ha) and Intermediate zones (33.3 %; 0.6 ha). The number of clusters differed significantly across the size classes and zones (***Table 2.1***). A P-value = 0.009 was calculated in the one-way ANOVA.

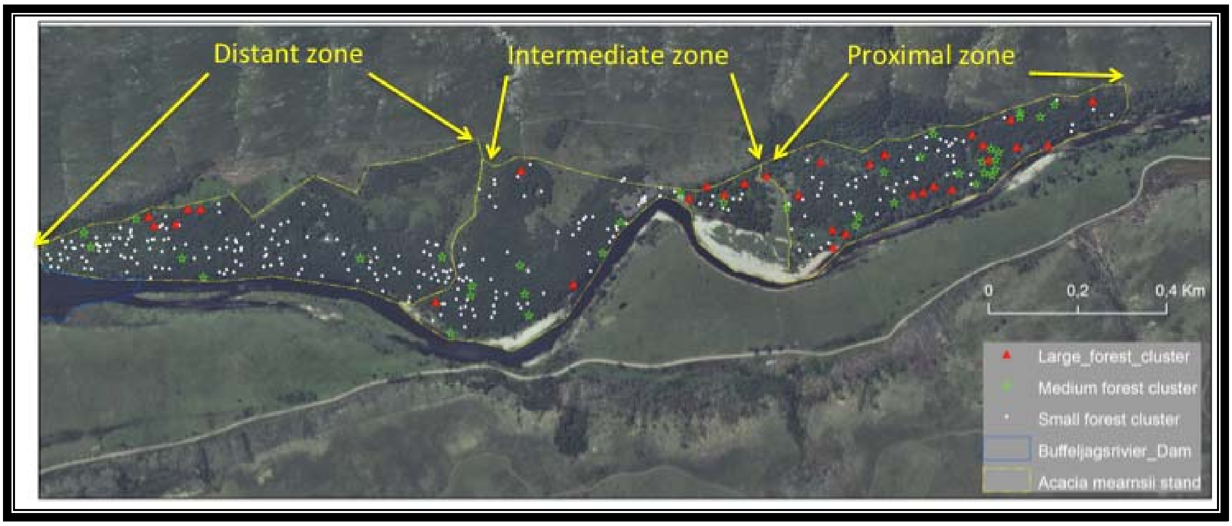


Figure 2.6: Map of the distribution of small, medium and large forest clusters in the Proximal. Intermediate and Distant zones within the Black wattle stand at Buffeljagsrivier.

Table 2.1: Summary table of the total number of clusters by size category sampled in the different zones, and the selected clusters for more detailed study.

Black wattle stand zone	**Zone Area (ha)**	**All clusters**	**All mapped clusters**						**Clusters selected for study**		
			Cluster size								
			Small		**Medium**		**Large**		**Small**	**Medium**	**Large**
			n	n/ha	n	n/ha	n	n/ha	n	n	n
Proximal zone	30	94	62	2.07	16	0.53	16	0.53	11	5	5
Intermediate zone	20	81	63	3.15	12	0.60	6	0.30	11	4	2
Distant zone	40	154	141	3.52	8	0.05	5	0.13	17	2	2
Total	90	329	266		36		27		39	11	9

The Bonferroni test showed that forest cluster distribution differs significantly between Small and Large clusters between the Proximal and Distant zones, and between the Proximal and Intermediate zone, whereas distributions of Medium and Large clusters were quite similar (***Table 2.2)***.

Table 2.2: Bonferroni test results; the stand zones differ in cluster size distribution at Buffeljagsrivier.

Means with the same letter are not significantly different			
Bonfer Grouping	Mean	N	Size
A	2.9120	3	small
B	0.3933	3	medium
B	0.3183	3	large

2.4.2 Shape of 7 forest clusters

An expanding forest cluster acquires a particular shape, which can explain the history and direction of its expansion. A cluster shape can also just be used for area and density calculations. Only seven shapes are presented here. In general, the shape differed in shape, orientation and density**.** The shapes go from regular (pL070; iL139, dL348) to very uncommon (pL020, pL048, iL101 and dM268) (Respectively ***Figure 2.7*** **and** ***Fiigure 2.8***).

In terms of density, two groups can be distinguished. Forest clusters pL048, pL070 and dM268 have low density, they are constituted mostly by large size trees and few small trees, and few Black wattle stems. Distribution in the forest clusters pL020, iL101, iL139 and dL348 looks much denser, around every big tree there are many trees of small size and the number of stems of Black wattle is also high. With regard to the direction, forest clusters pL048, pL020, iL101, and dM268 would be defined as multiple globular shapes; pL070 would be a parse shape while forest clusters iL139 and dL348 exhibit a linear shape.

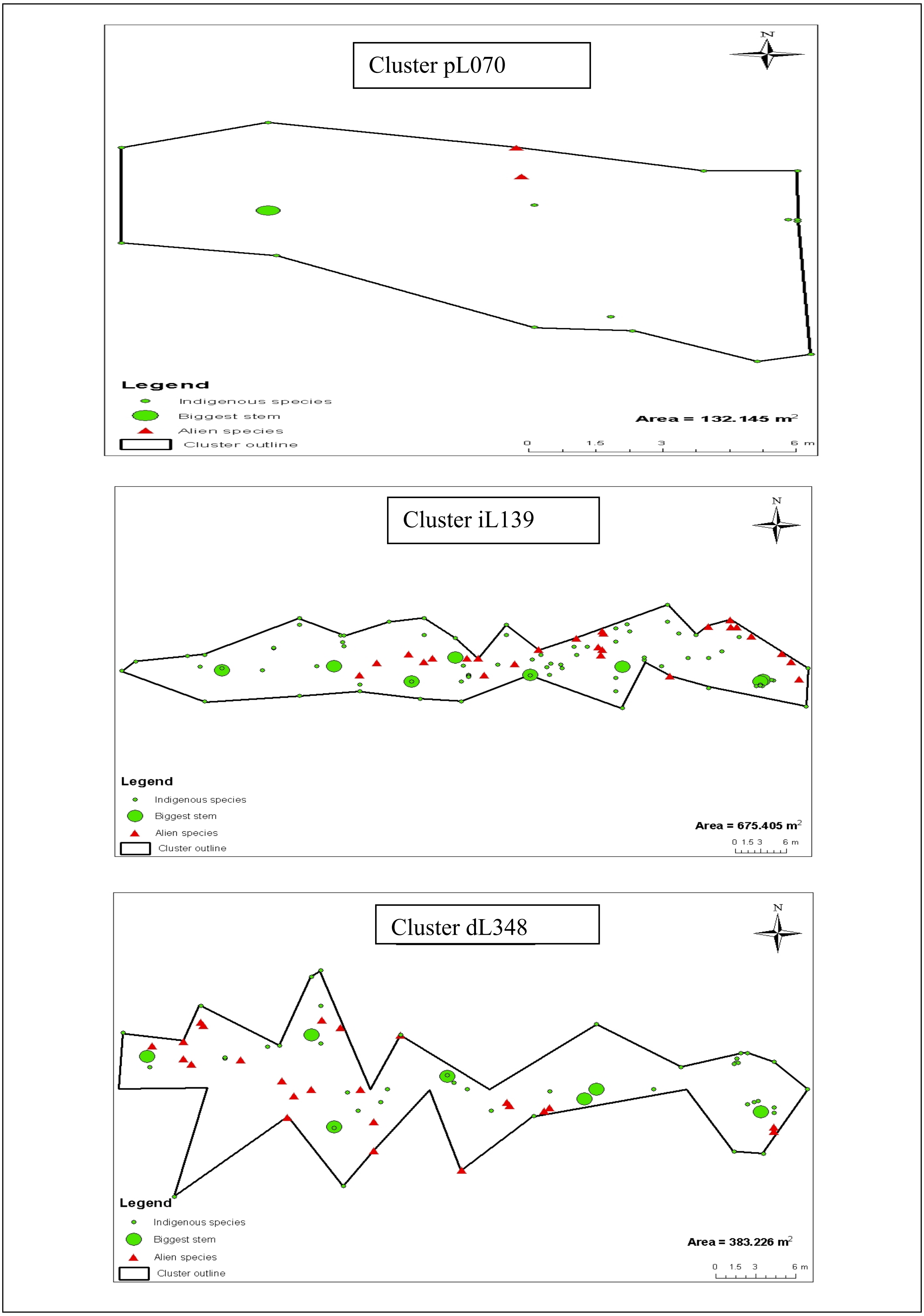


Figure 2.7: Regular shapes of three forests clusters at Buffeljagsrivier, a) pL070; b) iL139; c) dL348

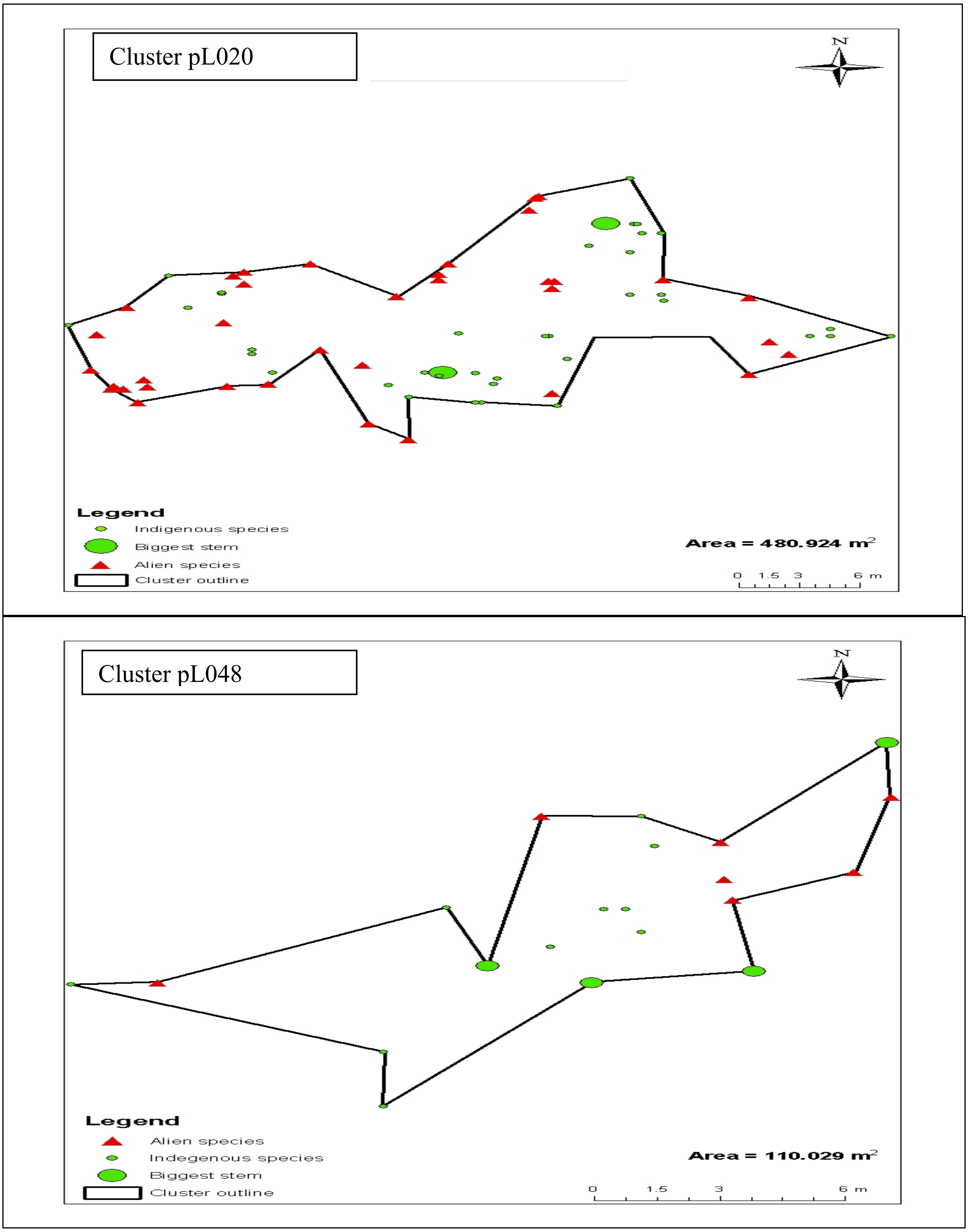


Figure 2.8: Uncomun shapes of four forest clusters at Buffeljagsrivier, a) pL020; b) pL048.

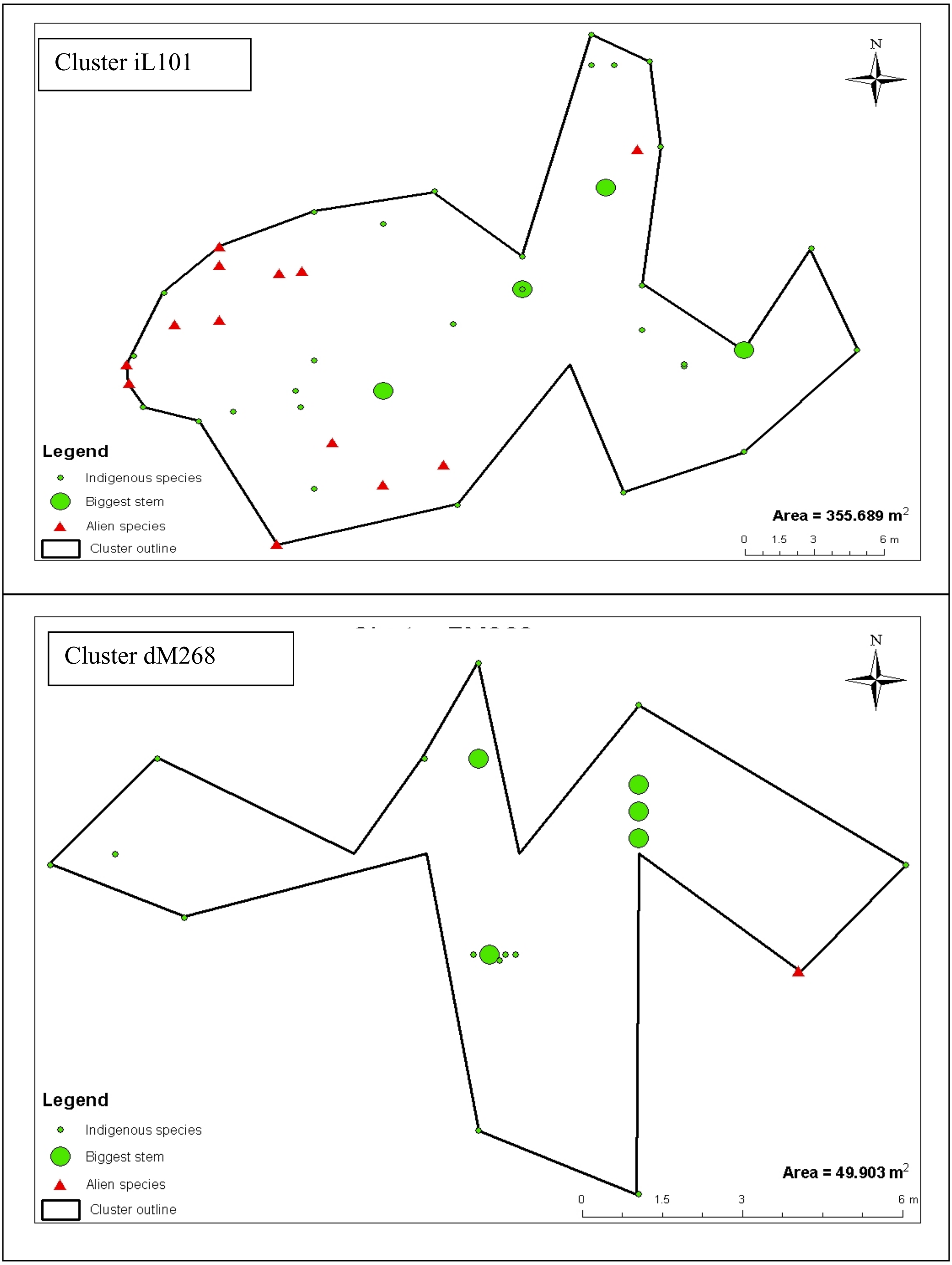


Figure 2.8: Uncomun shapes of four forest clusters at Buffeljagsrivier, a) pL020; b) pL048; c) iL101; d) dL268.

2.4.3 Species composition of forest clusters per zone and per size

The distribution of 28 species recorded in the 59 selected forest clusters (***Table 2.1***) varied per stand zone and cluster size (***Table 2.3***) and included 78.6% trees and 21.4% shrubs.

Table 2.3: Summary of species distribution across the 59 selected forest clusters within the wattle stand at Buffeljagsrivier

Species	Common name	Family	Tree-Shrub	Total tree stems	Mature - Regeneration	Zones of *Acacia mearnsii* stand								
						Proximal			Intermediate			Distant		
						Cluster size								
						Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
Acacia mearnsii	Black wattle	Mimosoideae	T *	265	M	17	25	75	15	1	29	3	52	48
					R	38			10			21		
Gymnosporia buxifolia	Common Spikethorn	Celastraceae	T	263	M	9	92	106	5	18	14	17	2	-
					R	52			2			38		
Rapanea melanophloeos	Cape-beech	Myrsinaceae	T	175	M	3	9	34	10	6	8	9	64	32
					R	27			25			137		
Solanum mauritianum	Bugweed	Solanaceae	T *	135	M	15	47	57	-	-	14	1	-	1
					R	40			2			6		
Canthium inerme	Turkey-berry	Rubiaceae	T	134	M	12	16	22	3	9	60		1	11
					R	50			38			0-		
Celtis africana	White-stinkwood	Celtidaceae	T	117	M	13	13	40		1	48	-	-	2
					R	96			141			2		
Vepris lanceolata	White ironwood	Rutaceae	T	62	M	12	3	17	-	2	26	1	-	1
					R	27			84			2		
Canthium mundianum	Rock-alder	Rubiaceae	T	41	M	6	-	4	-	10	21	-	-	-
					R	12			14			0		
Rhus pyroides	Common Currant	Anacardiaceae	S	18	M	-	-	1	12	1	-	2	2	-
					R	0			28			8		
Halleria lucida	Tree-fuchsia	Scrophulariaceae	T	15	M	1	1	-	-	1	-	9	1	2
					R	6			1			12		
Olea africana europaea	African Olive	Oleacea	T	14	M	2	-	1		4	1	6	-	-
					R	3			1			5		
Diospyros glabra	Fynbos Star-apple	Ebenaceae	S	11	M	2	1	-	1	-	-	-	4	3
					R	2			3			15		
Olinia ventosa	Hard-pear	Oliniaceae	T	11	M	-	-	1	-	-	-	-	-	10
					R	0			0			1		
Metrosideros angustifolia	Cape-gum	Myrtaceae	S	10	M		-	5	5	-	-	-	-	-
					R	2-			26			0		
Melia azedarach	Persian lilac	Meliaceae	T *	9	M	-	-	4		-	5	-	-	-
					R	0			0			0		
Maytenus acuminata	Silky-bark	Celastraceae	T	8	M	-	-	-	2	-	3		1	2
					R	0			0			1		
Apodytes dimidiata	White-pear	Icacinaceae	T	7	M	-	-	-	-	-	3	-	4	-
					R	0			0			0		
Rhus	Willow	Anacardiaceae	S	6	M	-	-	-	5	-	-	-	1	-

Species	Common name	Family	Tree-Shrub	Total tree stems	Mature - Regeneration	Zones of *Acacia mearnsii* stand								
						Proximal			Intermediate			Distant		
						Cluster size								
						Small	Medium	Large	Small	Medium	Large	Small	Medium	Large
					R		0			26			0	
Brabejum stellatifolium	Wild-almond	Proteaceae	T	4	M	-	3	1	-	-	-	-	-	-
					R		12			0			0	
Rhus tomentosa	Bicoloured Currant	Anacardiaceae	S	4	M	1	-	-	-	-	-	3	-	-
					R		1			0			3	
Kiggelaria africana	Wild-peach	Flacourtiaceae	T	3	M	-	1	2	-	-	-	-	-	-
					R		13			0			0	
Lantana camara	Lantana	Verbenaceae	S*	3	M	-	-	-	-	-	-	-	-	3
					R		0			0			1	
Ocotea bullata	Stinkwood	Lauraceae	T	3	M	-	-	-	-	-	-	-	-	3
					R		0			0			1	
Rothmannia capensis	Forest gardenia	Rubiaceae	T	3	M	-	-	3	-	-	-	-	-	-
					R		2			0			0	
Scolopia mundii	Red-pear	Flacourtiaceae	T	3	M	-	-	-	-	1	-	2	-	-
					R		1			1			0	
Diospyros whyteana	Bladder-nut	Ebenaceae	T	2	M	-	-	-	-	1	1	-	-	-
					R		0			2			0	
Ilex mitis	African Holly	Aquifoliaceae	T	2	M	-	1	-	-	-	-	-	-	1
					R		1			0			1	
Virgilia oroboides	Keurboon	Papilionoideae	T	1	M	-	-	-	-	-	-	-	-	1
					R		0			0			0	

The 28 species belong to 20 families. The majority of species were represented in the larger size classes, as well as regeneration, with few exceptions. The two main alien invasive species were black wattle and *Solanum mauritianum* (Bugweed*),* and both are light-demanding. A third alien invasive species was present (*Melia azedarach*) but only as mature trees. The six most commonly found species in the forest clusters were *Canthium inerme, Celtis africana, Diospyros glabra, Gymnosporia buxifolia, Rapanea melanophloeos* and *Vepris lanceolata*.

Although species composition differ across the stand zones and between the three forest cluster size classes, there was no distinct pattern in terms of trees or shrubs distribution Species seem occurring scattered through the three zones for all the size classes. However some species were dominant in one zone and completely absent in other zones. For example, *C africana*, dominant in the Proximal zone was almost absent in the Distant zone, and *V. lanceolata*, with good representation in the Proximal and Intermediate zone, became rare in the Distant zone. *Rapanea melanophloeos*occurs in all three zones, but was dominant in the Distant zone (***Table 2.3***). Most of the species recorded within the three zones were found in the small clusters and large clusters. However, many species were not found in the medium sized clusters, notably in the Intermediate and Distant zones (***Figure 2.9***).

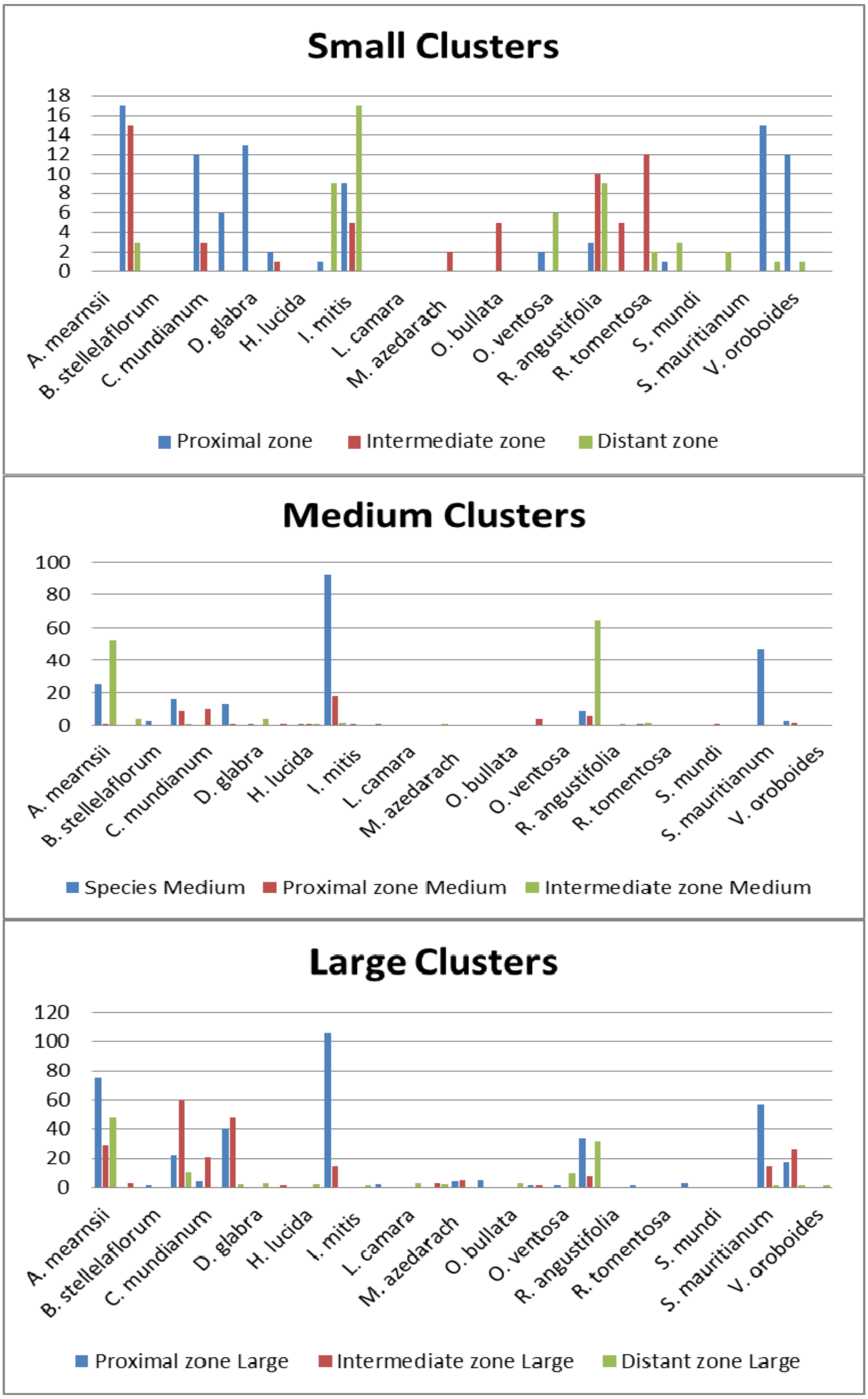


Figure 2.9: Species distribution of the three stand zones for a) Small, b) Medium and c) Large clusters.

2.5 Discussion

2.5.1 Evidence of establishment of natural forest species under the Black wattle stand

The general perception around invasive tree species is that wherever they occur there is no chance of establishment of indigenous tree species. However, within the 90 ha stand of the invasive, a total of 329 natural forest clusters were recorded. From these forest clusters 81% consisted of one to three trees, 11% of four to nine trees and 8% of more than ten trees. The forest clusters contained 22 tree (78.6 %) and six shrub (21.4 %) species. This is evidence for the successful establishment of natural forest species within this Black wattle stand, contrary to the general perception. The shade caused by canopy closure of the Black wattle stand prevents the regeneration and replacement of this light demanding invasive alien species under its own canopy. The Black wattle stand therefore facilitates germination and establishment of more shade-tolerant natural forest species and contributes to forest succession (**Geldenhuys, 1997; Lugo, 1997; Parrotta *et al*., 1997**).

2.5.2 More large forest clusters closer to natural forest patches.

The unequal distribution of forest clusters across the Black wattle stand suggests a directional process in the establishment of natural forest clusters within the Black wattle stand (***Table 2.1*****).** The nearest (proximal) zone to the natural forest patches has the highest number of large natural forest clusters (16), followed by the Intermediate zone (six) and Distant zone (five). However, the Distant zone had the highest number (141) of small, newly establishing forest clusters. In terms of the forest succession process, the understanding is that most of the trees first established near to potential seed sources, formed clusters and as they expand, they facilitate the progressive establishment of new small forest clusters to the distant zone, via the intermediate zone. The existence of adjacent natural forest patches seems a necessity to expect such succession to take place. The majority of such case studies highlighted this requirement (**Geldenhuys, 1986; 1997; 2004; Loumeto & Huttel, 1997; Lugo, 1997; Parrotta *et al*., 1997**). However, the arrival of forest species at points far away from the seed source areas may relate to the characteristics of the dispersal agents. For example, some species such as *Ocotea bullata*, *Apodytes dimidiata* and *Olinia ventosa,* arrived in the distant zone but were absent from the proximal and/or intermediate zones because the baboons may have taken them there.

Traditional forest rehabilitation practices tend to rely on nurseries for seedlings to be established on the site to be rehabilitated. However, the associated costs are always a limiting factor to the success of such management actions (**Geldenhuys, 2013**). The role of adjacent remnant forests as potential seed sources in forest succession and recovery has been confirmed in this study and should be considered as perhaps a better approach to forest rehabilitation.

2.5.3 Variability in the shape of seven large forest clusters

Structural analysis of cluster shape provides information relative to the dynamics of its establishment (**Richard & Forman, 1997**). For example, in this study, a double-globular shape cluster was viewed as two initial clusters that over time have fused to form one bigger cluster (***Figure 2.7 & 2.8***), i.e. two clusters in close proximity would eventually merge and form a larger cluster. Two highly uncommon shapes (***Figure 2.8,*** pL048 and dM268) could relate to the unpredictable side of nature (**Richard & Forman, 1997**). Shapes pL020 and iL101 showed multi lobes, which could indicate that several individual forest clusters (small to large) merged over time to form these actual large clusters. The shape of a cluster can also be viewed as a consequence of different dispersal modes. Forest clusters iL139 and dL348 present linear shapes and both happened to occur along the river, suggesting running water as main dispersal mode which would explain the linear and directional shape (**Richard & Forman, 1997; Van Andel & Aronson, 2006**). Mixed or more regular shapes would be attributed to forest clusters that occur in the flat zone of the stand, where the dispersal influence seems to exist with fewer irregularities (pL070). At this level of the study, the interpretation of these shapes could just be speculative; a much longer term study of the development of individual clusters in close proximity is required to develop a better understanding of this process. There were no specific pattern regarding the number of invasive stems and the stem density within the forest clusters. Number of black wattle stems varied from 1 to 75 stems per cluster size and per zone (***Table 2.3 & Figure 2.9)***.

2.5.4 Species distribution in relation to forest succession

The sample of 59 clusters represented 18% of the identified forest clusters within the stand. In total, 1329 indigenous stems were recorded, with 678 stems in the Proximal zone alone (51.01%). The recorded stems belonged to 20 species of 18 families (***Table 2.3***). This is an indication of diversity reconstruction. There was no clear pattern relating to the sequence of establishment of the species in the forest succession process. According to **Lugo (1997)** the expected pattern is that woody shrub species would be associated with Small clusters in the Distant zone or the early successional stage and that more mature forest canopy species would be associated with the large clusters in the Proximal zone or advanced successional stage. However, most of the common species of the stand were well represented in the Proximal zone which would suggest that this zone is in an advanced successional stage (***Table 2.3***)

Some species are dominant in one particular zone but completely absent from another zone (***Table 2.3***). For example, *C. africana* is abundant in the Proximal zone but almost absent from the Distant zone. *R. melanophloeos* is the best presented canopy tree species in the three zones. This indicates that certain conditions would favour some species and limit others. This is a fundamental principle that allows succession of plant species diversity in forests (**Geldenhuys, 1986; 1997; 2004; Loumeto & Huttel, 1997; Lugo, 1997; Parrotta *et al.*, 1997**). It is important to understand such useful information in forest rehabilitation interventions, such as what species need to be used in what kind of conditions when planting is necessary (**van Daalen, 1981**). The rare species are useful indicators when trying to understand the interactions between type of forest and the dynamics at a regional scale. *O. bullata* and *O. ventosa* were recorded once in the Distant zone and not at all in the Proximal zone. Such information may not relate to the site conditions but to the mode of seed dispersal (in this case most likely by baboons), and shows the importance to understand the type of interactions that may prevail between the rehabilitation area (the Black wattle stand) and the adjacent natural forest patches.

2.6 Conclusion and Recommendations

The objective pursued in this study has been met and the stated hypotheses confirmed: Natural forest species have been found and mapped within the extensive stand of Black wattle and they were more abundant and first established in the zone close to the potential seed sources (the nearby forest patches). Natural forest species are able to regenerate and establish within an extensive stand of a vigorous introduced invader species such as Black wattle .The function attributed to the invader stand here is one of nursing the establishment of natural forest species. The 329 natural forest clusters identified, mapped and described at Buffeljagsrivier forest are evidence for this statement.

The findings are expected to change the common perception of invasive species stands in the forest environment and to persuade policy makers of the need to review the current approach of total clearing of invasive species stands to control invasive species. The approach of total clearing of invasive stands would stop and restart the on-going succession process. Careful interventions with selective thinning while preserving the closed canopy would give the chance to most of these 329 clusters to grow into natural forest canopy species and gradually replace the Black wattle stand. Eventually this approach of selective manipulation of the invader plant stand to facilitatte the succession process, rather than clearing the invader plant stand, should be extended to other natural forests in South Africa.

The existence of neighbouring forest patches seems to have an accelerating impact on the process. Results of the presented study suggested that natural forest species would start to colonise the stand from zones close to the remnant adjacent forests, and their density would also be high in the same zones. Results from this study provide a baseline for potential further studies on the relationship between the establishing clusters and the adjacent patches of natural forest in order to better understand the ecology of seed sources and the related dispersal systems.

2.7 References

Binns, J.A.; Illgner, P.M. & Nel, E.L. 2001. Water shortage, deforestation and development. South Africa's Working for Water Programme. *Land degradation and development* 12:341-355.

Clements, F.E. 1916. Plant Succession: An analysis of the development of vegetation. Publication 242, Carnegie Institute of Washington, Washington, DC.

Clement, F.E. 1936. Nature and structure of the climax. *Journal of Ecology* 24: 252-284.

Finegan, B. 1984. Forest succession. *Nature* 312: 109–114.

Geldenhuys, C.J. 1997. Native Forest regeneration in pine and Eucalyptus plantation in Northern Province, South Africa. *Forest Ecology and Management* 99: 101-115.

Geldenhuys, C.J. 1997. Composition and biogeography of forest patches on the inland mountains of the Southern cape. *Bothalia* 27(1): 57-74.

Geldenhuys, C.J. 2004. Concepts and process to control invader plants in and around natural evergreen forest in South Africa. *Weed Technology* 18: 1386-1391.

Geldenhuys, C.J. 2008. Can I manipulate alien plant stands to rehabilitate natural forest? *Dendron* 40: 38-44.

Geldenhuys, C.J. 2013. Converting invasive alien plant stands to natural forest nature's way: Overview, theory and practice. In: Jose, S.; Singh, H.P.; Batish, D.R. & Kohli, R.K. (eds). Invasive plant ecology, CRC Press, Taylor & Francis Group, Boca Raton: 217-237.

Geldenhuys, C.J. & Bezuidenhout, L. 2006. Guidelines for conversion of invader plant stands to regrowth natural forest along the Buffeljagsrivier, Swellendam. Report Number FW-01/06.

Geldenhuys, C.J. & Bezuidenhout, L. 2012. Rehabilitation of natural forests using stands of alien trees of plantations or invasions as allies. In: Bredenkamp, B.V & Upfold, S.J.

(eds). South African forestry handbook, 5th edition. Southern African Institute of Forestry, Pretoria: 585-604.

Geldenhuys, C.J. & Delvaux, C. 2007. The *Pinus patula* plantation … A nursery for natural forest seedlings. In: Bester, J.J.; Seydack, A.H.W.; Vorster, T.; van der Merwe, I.J. & Dzivhani, S. (eds). Multiple use management of natural forests and woodlands: Policy refinement and scientific progress. Natural Forests and Savanna Woodland Symposium IV, Port Elizabeth, South Africa, 15-18 May 2006: 94-107.

Geldenhuys, C. J., P. J. Le Roux, and K. H. Cooper. 1986. Alien invasions in indigenous evergreen forest. *In* Macdonald, I.A.W.; Kruger, F.J. & Ferrar, A.A. (eds.). The Ecology and Management of Biological Invasions in Southern Africa. Cape Town, South Africa: Oxford University Press: 119–131.

Hardwick, K.; Healey, J.; Elliott, S.; Garwood, N. & Anusarnsunthorn, V. 1997. Understanding and assisting natural regeneration processes in degraded seasonal evergreen forests in northern Thailand. *Forest Ecology and Management* 99: 203–214.

Kindt, R. & Coe, R. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological studies. Nairobi: World Agroforestry Centre (ICRAF).

Otsamo, R. 2000. Secondary forest regeneration under fast-growing forest plantations on degraded *Imperata cylindrica* grasslands. *New Forests* 19: 69-93.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637-669.

Parrotta, J.A.; Turmbull, J.W. & Norman, J. 1997. Catalysing native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99: 1-7.

Loumeto, J.J. & Huttel, C. 1997. Understorey vegetation in fast growing tree plantation on Savanna soils in Congo. *Forestry Ecology and Management* 99: 65-81.

Lugo, A.E. 1997. The apparent paradox of re-establishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management* 99: 9-19.

Mascoro, J. 2011. Eighty years of succession in a non-commercial plantation on Hawaii Island: are native species returning? *Pacific science* 65(1): 1-15.

Richardson, D.M., van Wilgen, B.W. 2004. Invasive alien plants in South Africa: How well do we understand the ecological impacts? *South Africa Journal of science*.100: 45-52.

Richard, T.T. & Forman. 1997.handbook. Land mosaics: the ecology of landscape and regions. Cambridge University press: 286-287; 395-402; 415.

Van Andel, J. & Aronson, J. 2006. textbook, Restoration Ecology, the new frontier. Blackwell science ltd p38.

Van Daalen, J.C., 1981, 'The dynamics of the indigenous forest-fynbos ecotone in the southern Cape', *South African Forestry Journal* 119, 14–23.

Chapter 3:
Adjacent natural forest patches as potential seed sources for establishing forest clusters within a stand of the invasive alien *Acacia mearnsii* at Buffeljagsrivier, South Africa

Abstract

Where do the natural forest species come from that spontaneously regenerate and establish in clusters underneath stands of invasive trees during the forest succession process? The relationship between seven natural forest clusters establishing within a 90-ha stand of the invasive introduced Black wattle and four types of adjacent natural forest patches were investigated along the Buffeljagsrivier. Natural forest patches consisted of Riparian forest north, Riparian forest south, Moist forest, and Dry forest. The purpose was to determine the potential seed sources of the forest clusters and to see if site factors (aspect, slope and canopy closure) explain the patterns in species distribution across the study area. The sampled data on species composition of stands in the forest clusters and forest patches were analysed by hierarchical cluster analysis, followed by Canonical Correspondence Analyses (CCA) and descriptive analysis.

Results indicate that riparian patches were more similar in species composition to the forest clusters. Common species with large trees of the moist forest canopy and sub-canopy were mostly absent from the forest clusters; dry forest sub-canopy tree species with good regeneration were also absent from the forest clusters. Projection of the three factors, aspect slope and canopy closure, correlated with patterns in species distribution among communities.

The understanding is that riparian patches of natural forest are the major seed sources for the establishing forest clusters at this stage of the process. However, some large-sized stems of indigenous tree species were present in some of the forest clusters within the black wattlestand. This suggests that they may be part of remnant forest patches, and the role of

those trees as seed sources could be considerable. Also, because of the presence of some canopy and sub-canopy species, from both Moist forest and Dry forest patches in the forest clusters, they are not to be excluded as influencing the actual colonisation of the Black wattle stand. The study proposed further investigations that would include small and young clusters in the analysis and would look closely at the dispersal systems, particularly in terms of seed characteristics as main factors of species composition of natural forest spcies in the wattle stand.

Key words: Forest cluster; Forest patches; Black wattle; Seed sources, Riparian forest; Succession, *Acacia mearnsii*, Rehabilitation.

3.1 Introduction

Stands of fast-growing tree species such as of invasive introduced species, commercial timber species, and pioneer and/or secondary forest species are now known to have a catalytic effect on the germination and establishment of natural forest species in their understorey through the forest succession processes (**Geldenhuys, 1997, 2004, 2008; Loumeto & Huttle, 1997; Parrotta *et al.*, 1997; Geldenhuys & Delvaux, 2007**). Generally, adjacent forests are expected to be the seed sources because forest ecosystems are dynamic entities, with habitats for several populations of organisms, including mammals, birds, insects and even plants (**Howe & Smallwood, 1982; Howe & Westley, 1997**). The interactions between neighbouring forests and species population dynamics have certain consequences ranging from simple presence to a complete modification of the targeted environment (**Geldenhuys, 1989b; Johnson & Miyanishi, 2008; Mascaro, 2011**). **Loumeto and Huttle (1997)** pointed out the importance of neighbouring forests in forest succession or forest rehabilitation. During disturbance events, adjacent forests could serve as refuge zone for most remnant fauna. For forest recovery after disturbance, these adjacent forests could be viewed as flora and fauna reserves necessary for development of a new ecosystem. Local communities recover from disturbance through immigration from neighbouring regions (**Altermatt *et al.*, 2011**). The dynamics, diversity and speed of recovery of a specific forest community depend on the spatial arrangement of adjacent forest communities within the landscape (**Tilman, 1994; Le Coeur *et al.*, 2002; Johnson and Miyanishi, 2008; Mascaro, 2011).**

Adjacent forests and remnant trees in case of moderate disturbance are expected to play a major role as seed sources for natural forest succession but often the species composition of the establishing understorey differ from these potential seed sources (**Geldenhuys, 1997, 2004, 2008; Loumeto & Huttle, 1997; Parrotta *et al.*, 1997; Geldenhuys & Delvaux, 2007**). Explaining such differences is a complex task because of many variables that affect the interactions between neighbouring stands at small and large scale (**Lugo, 1997**). The variables include species, their fruit/seed characteristics and presence of dispersal agents, as part of external drivers (**Polis *et al.*, 1997**), as well as stand conditions such as local landscape topography (slope, aspect, altitude, etc.), geology affecting local microclimate (temperature, humidity, solar radiation, etc.), edaphic conditions (soil moisture, soil nutrient status, ground cover, etc.), and stand structure (stem density, canopy cover, species of specific type of foliage, flowers and fruits, etc.) as internal influences. Time itself is also a determining factor in the succession process (**Lugo, 1997**). It is necessary to identify at least the main seed sources and the main drivers for a specific area of interest to develop a rehabilitation strategy or management framework based on this natural process.

Manipulation of the Invasive Plant Stand (MIPS), as promoted by **Geldenhuys (1997, 2004, 2008, 2011)**, is a forest rehabilitation approach based on the natural forest succession process. It is being implemented at Buffeljagsrivier. Preliminary studies have shown that a diverse range of indigenous forest species established within the wattle stand as part of the natural forest succession process (***Chapter 2***). The establishment of the natural forest species was denser close to the neighbouring forests. The objective of this study was to determine the relationships in species composition between establishing natural forest clusters within the invasive stand and neighbouring forest patches to determine the potential seed sources of the developing forest clusters.

3.2 Study area

Buffeljagsrivier study area (34°00'15"S, 20°33'58"E; 95-110 m above mean sea level) is situated east of Swellendam at the southern foot of the Langeberg Mountains. The Langeberg Mountains are composed of Table Mountain Sandstone quartzites (north of the Buffeljagsrivier) and the ridge to the south of the river is composed of shale**.** The climate is typical of the South Western Cape with hot summers and cold winters, i.e. a Mediterranean climate. The rainfall is fairly evenly spread throughout the year. Swellendam normally receives about 462 mm of rain per year ranging between 23 mm in December and 48 mm in August. The mean monthly daily maximum temperatures range from 17.1°C in July to 27.5°C in January and the mean monthly daily minimum temperature is 15°C in February and 5°C in July.

Along the river at the foot of the mountain, vegetation occurs in several Western Cape Afrotemperate forest patches such as moist forest, dry forest and riparian forest. The dominant vegetation in the broader landscape is a fire-adapted sclerophyll shrubland (Fynbos) with very high plant species diversity. An extensive wattle stand of about 90 ha grows along the northern bank of the river at the foot of the Langeberg Mountain (***Figure 3.1***), and was the focus of this study**.** In the understorey of the wattle stand, 329 clusters of indigenous tree species of small, medium and large size have become established (***Chapter 2***). The area is rich in birdlife and several mammals such as baboons, vervet monkeys and porcupines, have been observed. The human presence in the area is marked by farming (grazing for cattle) and ecotourism activities (holiday cottages and camping, forest walks, hiking, cycling, water sports, fishing, etc.).

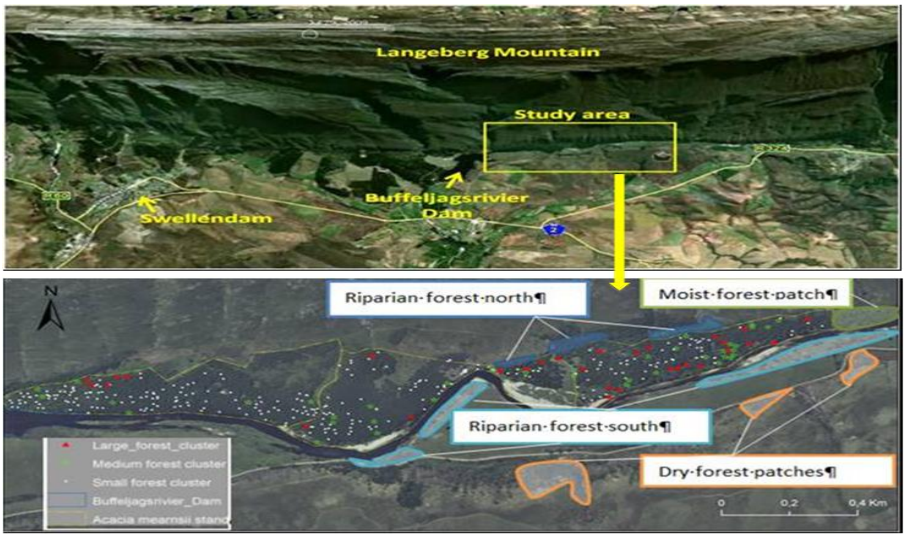


Figure 3.1: Location of the study area and components involved in the study (adapted from Chapter 2)

3.3 Study methodology

3.3.1 Selection of study sample

Natural forest patches of different size, canopy characteristics and site conditions in close proximity to the Black wattle stand were selected: Moist forest (three patches); Dry forest (three patches); Riparian forest south of the wattle stand (Riparian forest south) (four patches); and Riparian forest north of the Black wattle stand (Riparian forest north) (five patches). The species composition and structure of these patches were compared with the seven selected large forest clusters (***Table 3.1***).

Randomly located line transects were sampled to cover a topographical gradient and general composition and structure of a patch or cluster. Rectangular plots (10 m x 20 m) were systematically sampled along the line transect, with the long axis of the plot perpendicular to the direction of the transect line (***Table 3.1*****).**

Table 3.1: Sample size within forest patches and forest clusters

Site	**Code**	**Number Line transects**	**Number plots**
Dry forest, line transect x plot x	DLxPx	5	9
Moist forest line transect x plot x	MLxPx	5	17
Riparian forest south line transect x plot x	RSLxPx	6	8
Riparian forest north line transect x plot x	RNLxPx	11	12
Proximal zone large forest cluster 020 plot a &b	pL020a/b	1	2
Proximal zone large forest cluster 048	pL048	1	1
Proximal zone large forest cluster 070	pL070	1	1
Intermediate zone large forest cluster 101	iL101	1	1
Intermediate zone large forest cluster 139a&b	iL139a/b	2	2
Distance zone medium forest cluster 268	dM268	1	1
Distance zone large forest cluster 348	dL348	1	1

3.3.2 Data collection

The following data were recorded on each main (10 m x 20 m) plot: All stems ≥ 5 cm DBH, by transect and plot number, tree number, species and DBH. In the case of multiple stems of a tree, each stem was recorded with the same number to indicate that they belonged to the same tree. In a 5 m x 10 m sub-plot centred within the main plot, all stems <5 cm DBH were recorded by stem counts per species. The following was recorded at the centre of each plot: canopy closure (1 = <30% closed, 2 = 31-50%, 3 = 51-75%, 4 = >75% closed); altitude; aspect (N, NE, E, SE, S, SW, W, NW); slope (1 = gentle, 2 = steep and 3 = very steep). Ground cover was described by dominant growth forms, such as grass, trees, regeneration, ferns or others.

3.3.3 Data analysis

A hierarchical cluster analysis (**Legendre & Legendre, 1998; Kindt & Coe, 2005**) was performed in Biodiversity R to differentiate forest clusters according to their resemblance in species composition. It consists of grouping together plots with high similarities based on their **Bray and Curtis (1957)** distance matrix. In that way two matrices were constructed; the first, a species matrix with species abundance (number of stems) as response variable and species identity and plots as factors (***Appendix IV***). The second matrix was an environmental matrix (two-way table) which has in the first column the plot codes for the sampled forest clusters and forest patches, followed by columns for the three selected environmental factors: slope, aspect and canopy closure. Cell values were the values for each as recorded on site (see previous section). Results were given in a hierarchical dendogram placing plots gradually into distinctive community groups according to their average similarities in species composition. A Mantel test (**Mantel, 1967**) was performed to establish the correlation between the two matrices, i.e. to check the accuracy of the selected ecological distance measures. If the calculated Cophenetic-distance was high, it meant that the representation in the diagram is more accurate. In order to explain any possible pattern through the clustering results, a follow-up ordination analysis was conducted using the environmental factors slope, aspect, and canopy closure. Canonical Correspondence Analysis (CCA) of **Ter Braak (1986)** was used to relate the species and environmental variables with the identified communities. Communities were then described through the Importance Value (IV) of different species to explain the relationship between the forest patches and forest clusters. The IV of each species with stems ≥ 5 cm DBH in each species group was calculated as follows:

IV = (RF + RD + RBA)/3, where

- RF = Relative frequency, calculated from the number of plots in a species group in which the species was present, and expressed as a percentage of all plots sampled in the species group;
- RD = Relative density, calculated from the number of stems of a species in a species group and expressed as a percentage of all stems of all species in the species group;
- RBA = Relative basal area, calculated from the total basal area (horizontal surface area of a stem at 1.3 m above ground level) of a species in a species group and expressed as a percentage of total basal area of all stems of all species in the species group (***Appendix V***).

Histograms of stem diameter distributions of selected important species were analysed to evaluate the population dynamics of those species in the different stand conditions.

3.4 Results

3.4.1 General characteristics of forest clusters and forest patches

A broad comparison of the forest patch types and the sampled clusters show the following (***Table 3.2***): Clusters relate more to the Riparian forest south and north in terms of similar very gentle south-westerly slope and mean stem diameter.

Forest tree regeneration was lacking within the Riparian forest patches, but was the dominant ground cover within the Moist and Dry forest patches and Forest clusters. Dry forest has steep north-westerly slopes (warm), a high crown cover (> 75 % closed), the highest stem diameter per ha but with small trees. Moist forest has relatively steep south-easterly slopes (cool), with the mean stem diameter (13.6 cm DBH) between that of Dry forest and the Riparian forest north and south and the forest clusters. Crown cover was similarly relatively closed in Moist forest, Riparian forest north and forest clusters (51 – 75 % closed). Riparian forest south has relatively sparse crown cover (31 – 50 % closed).

Table 3.2: Characteristics of the forest patches in relation to the forest clusters

Forest patches/ forest Clusters	**Dry forest**	**Riparian forest S**	**Riparian forest N**	**Moist forest**	**Clusters**
Transect lines	5	6	11	5	8
Number of plots	9	8	12	17	9
Sampled area, ha	0,18	0,16	0,24	0,34	0,18
General slope	3	1	1	2	1
General aspect	NW	SW	SW	SE	SW
Crown cover	4	2	3	3	3
Ground growth form	Other	Grass	Grass	Regeneration	Regeneration
Mean DBH, cm	9,5	15,6	14,6	13,4	14,8
Stems (≥5 cm DBH)/ha	2244	825	1771	1559	1328

3.4.2 Relationship between forest clusters and forest patches

3.4.2.1 Classification

A hierarchical clustering method of **Legendre and Legendre (1998)** and **Kindt and Coe (2005)**, helped to group plots according to their similarities in number of stems per species recorded within each plot independently of the forest type (***Figure 3.2***). A matrix of the calculated Bray-Curtis ecological distances (minimum value of 0.17, mean value of 0.79 and one as maximum value with absolute dissimilarity in species composition) showed connectivity and sufficient dissimilarities between plots to generate classification categories. This is supported by the Mantel cophenetic distance statistic (calculated with 100 permutations) of r = 68.3% with a p-value of 0.0099, indicating that classification is a good representation of ecological differences between plots (reliability increase with a higher Mantel statistic).

Three main groups were formed at a Mantel value of 0.8, named G1, G2 and G3, representingthe three main types of forest (Moist forest, Riparian forest and Dry forest). The main groups were subdivided into 10 subgroups at Mantel value of 0.7, described as community groups G1a, G1b and G1c within Moist forest, G2a, G2b, G2c, G2d and G2e within Riparian forest, and G3a and G3b within Dry forest (***Figure 3.2***). However, Riparian forest north (G2a, G2d and G2e) and Riparian forest south (G2b and G2c) were classified in separate subgroups.

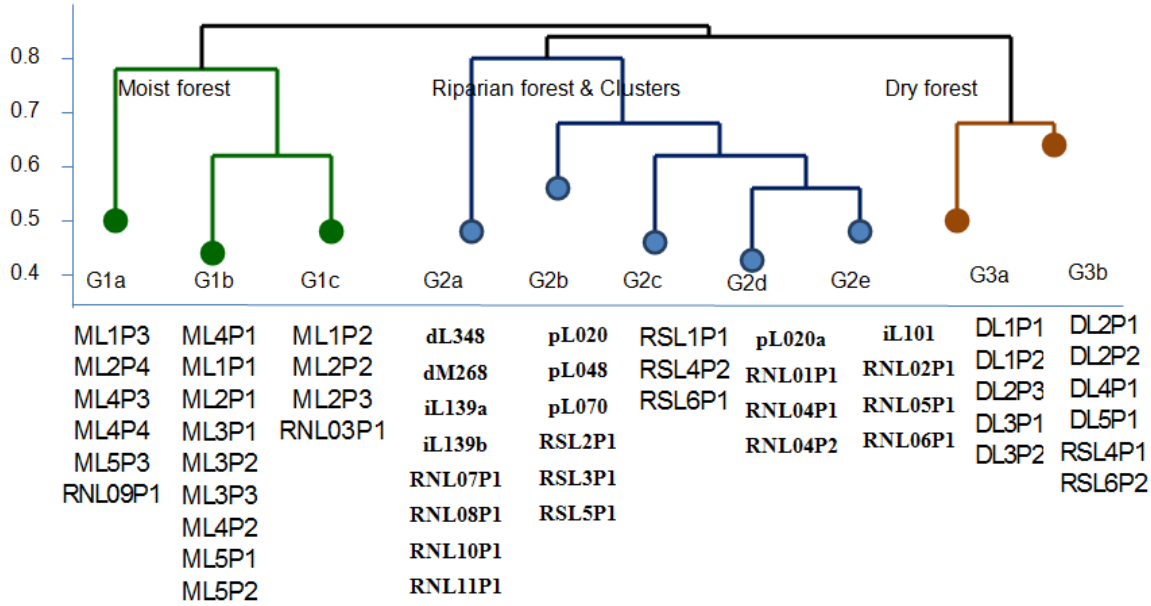


Figure 3.2: Classification of plots of different sites into groups and subgroups (plant communities) according to the similarities in species composition. Note: All the forest clusters were grouped within the G2.

Plots from the forest clusters were distributed in four community subgroups within the Riparian forest (G2): four in G2a, three in G2b, and one each in G2d and G2e. Moist forest (G1) and Dry forest (G3) did not share any group with the forest clusters. Two plots of Riparian forest north shared subgroups within Moist forest (G1a and G1c) and two plots of Riparian forest south were found in the Dry forest subgroup (G3b) (***Figure 3.2***).

The Canonical Correspondence Analysis (CCA), applied to the same sampled matrix and related to the three factors aspect, slope and canopy closure, reinforced the grouping obtained by the classification analysis. The ordination plot highlights specific patterns (***Figure 3.3***): Riparian and Cluster forest community (G2) is associated with SW Aspect and flat areas, Dry forest community (G3) is associated with NW Aspect and steeper slope (***Table 3.2***). The Moist forest community (G1) was associated with SE aspect and canopy closure.

Similarly, ***Figure 3.4*** shows the association between the main communities and certain species in ordination space.

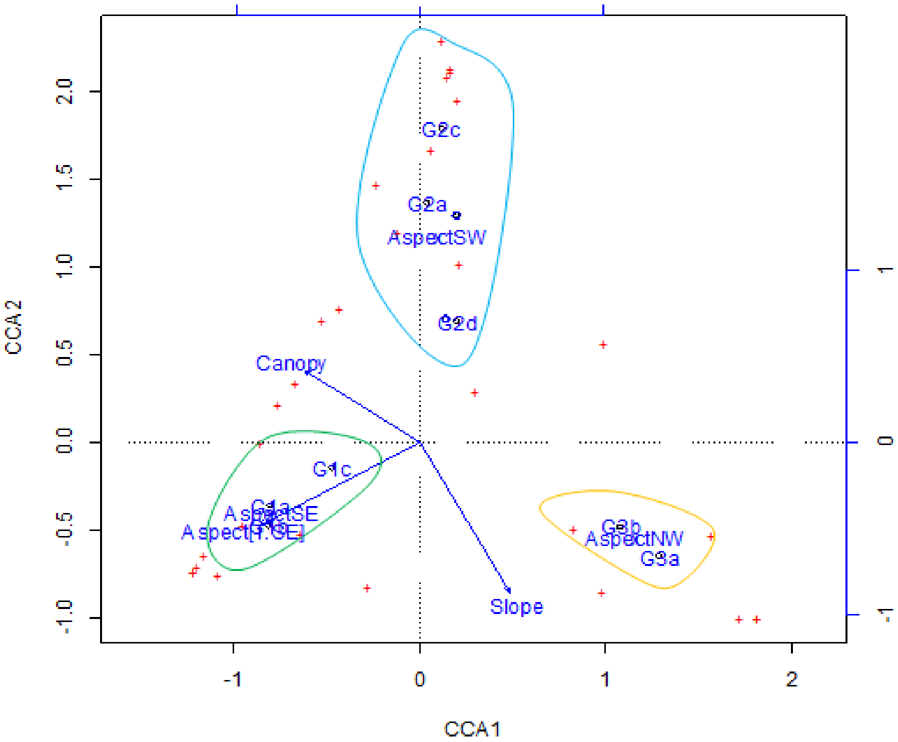


Figure 3.3: Ordination diagram showing how forest types (G1, G2 and G3) and communities (G1a to G3b) are associated with the environmental vectors (aspect, slope, canopy).

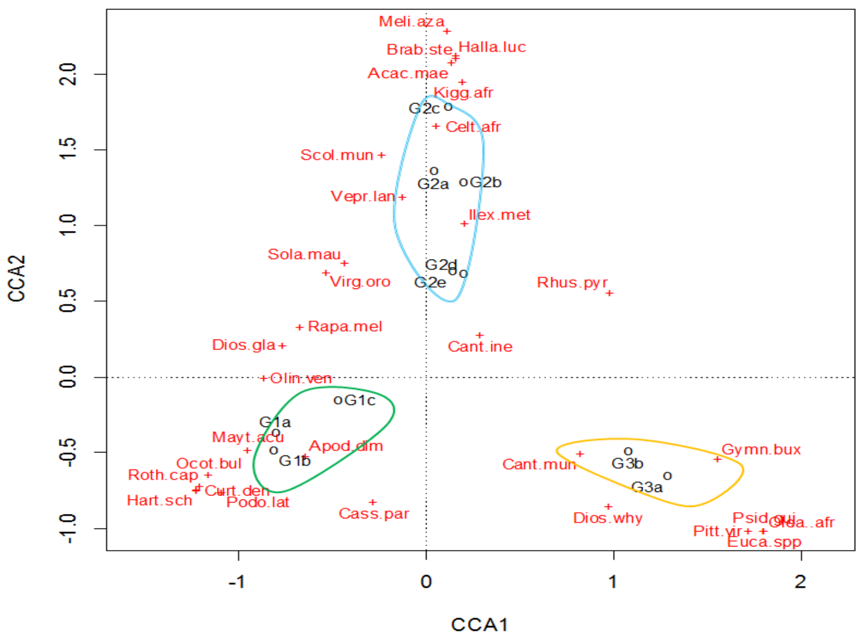


Figure 3.4: Ordination diagram showing how species and communities are related.

Apodytes dimidiata was important within G1 in the moist forest patches, *Gymnosporia buxifolia* was more important within G3 in the dry forest patches, *Celtis africana*, within G2 in the forest clusters, and *Vepris lanceolata* within G2 in the riparian patches, together with scattered *Ilex mitis*, and that group (normally it is associated with moist forest). *Canthium inerme* and *Rapanea melanophloeos* were recorded in all the forest patches and in the ordination diagram, the two species are not really site specific; they are displayed close to the origin of the axes (***Figure 3.4***).

3.4.2.2 Community species composition in relation to the forest clusters

3.4.2.2.1 Species importance value (IVs)

Communities highly differ from one another when looking at the species importance values (***Table 3.3***).

- Moist forest (G1) was dominated by *Hartogiella schinoides* (IV 24.3) and *Olinia ventosa* (IV 17.4) in subgroup G1a, *Rothmannia capensis* (IV 20.5) and *O. ventosa* (IV 11.4) in subgroup G1b, and *Vepris lanceolata* (20.9), *R. capensis* (17.4) and *Celtis africana* (11.8) in subgroup G1c.

- Riparian forest and forest clusters (G2) were dominated by Black wattle (IV 31.8) and *Rapanea melanophloeos* (IV 11.7) in subgroup G2a (this subgroup is in several comparisons of species relatively similar to Moist forest), *V. lanceolata* (IV 32.1), *Gymnosporia buxifolia* (IV 17.0), black wattle (IV 15.6), *C. africana* (IV 13.1) and *R. melanophloeos* (IV 10.5) in subgroup G2b, *C. africana* (IV 51.0), *V. lanceolata* (IV 32.1), *Kiggelaria africana* (IV 12.8) and *Canthium inerme* (IV 12.1) in subgroup G2c, *C. africana* (IV 25.2), *C. inerme* (IV 20.7) and *Solanum mauritianum* (IV 19.2) in subgroup G2d, and *V. lanceolata* (IV 28.0), *C. inerme* (IV 27.4) and *C. africana* (IV 16.1) in subgroup G2e. In this Group 2 the main species in most subgroups are *C. africana*, *V. lanceolata* and *C. inerme*.

Table 3.3: Species importance values (IVs) over different sub-groups (forest communities) at Buffeljagsrivier.

Species	Moist forest			Riparian forest & Forest cluster					Dry forest	
	G1a	G1b	G1c	G2a	G2b	G2c	G2d	G2e	G3a	G3b
Hartogiella schinoides	24.3	4.8	6.5	3.1	-	-	-	-	-	-
Olinia ventosa	17.4	11.4	1.6	7.2	-	-	-	-	1.9	-
Rothmannia capensis	1.7	20.5	17.4	5.1	-	-	1.9	6.9	-	-
Vepris lanceolata	8.8	4.1	20.9	2.3	32.1	15.5	8.5	28.0	4.0	2.3
Celtis africana	0.9	0.6	11.8	4.2	13.1	51.0	25.2	16.1	3.5	4.2
Acacia mearnsii	1.3	-	3.0	31.8	15.6	-	5.6	3.8	-	1.1
Rapanea melanophloeos	9.2	7.5	3.8	11.7	10.5	4.4	5.5	2.4	1.9	1.0
Gymnosporia buxifolia	-	-	1.8	1.3	17.0	4.2	4.9	2.1	10.9	31.2
Kiggelaria africana	-	-	2.5	-	-	12.8	2.1	1.7	-	-
Canthium inerme	7.9	9.1	6.2	8.9	9.4	12.1	20.7	27.4	5.4	17.7
Solanum mauritianum	-	-	3.7	-	2.4	-	19.2	4.6	-	-
Olea europaea africana	-	-	-	0.6	-	-	-	-	24.7	6.2
Pittosporum viridiflorum	-	0.8	2.5	-	-	-	-	-	17.8	2.9
Diospyros whyteana	1.6	2.7	5.0	0.6	-	-	1.8	-	13.6	5.1
Canthium mundianum	3.8	5.9	2.5	6.0	-	-	2.7	2.6	7.3	14.6
Podocarpus latifolius	2.8	9.9	1.7	-	-	-	-	-	-	1.1
Ocotea bullata	8.9	3.2	2.6	0.8	-	-	-	-	-	-
Maytenus acuminata	8.8	5.2	-	0.5	-	-	-	-	4.0	-
+ Apodytes dimidiata, Brabejum stellatifolium, Ilex mitis, Melia azedarach, Curtisia dentata, Virgilia oroboides Rhus pyroides, Halleria lucida.										

- Dry forest (G3) was dominated by *Olea europaea africana* (IV 24.7), *Pittosporum viridiflorum* (IV 17.8), *Diospyros whyteana* (IV 13.6) and *G. buxifolia* (IV 10.9) in subgroup G3a and by *G. buxifolia* (IV 31.2), *C. inerme* (IV 17.1) and *Canthium mundianum* (IV 14.6) in subgroup G3b.

- The two invasive species, Black wattle and Bugweed, were more prominent within Riparian forest and forest clusters, but were dominant in only one subgroup each, respectively G2a (IV 31.8) and G2d (IV 19.2) (***Table 3.3***). Both have a low to zero presence in Moist and Dry forest. The considerable number of empty cells within ***Table 3.3*** indicates a number of species which only occur in some subgroups. For example, *Podocarpus latifolius, Ocotea bullata, H. schinoides and R. capensis* are mostly absent from the Riparian forest and forest clusters, and also from Dry forest. *P.*

viridiflorum and *O. africana* are mostly absent from the Riparian forest and forest clusters, and from Moist forest.

3.4.2.2.2 Stem diameter distribution

In general, small trees (5 - 20 cm DBH) dominated the stem diameter distributions for all the important species over all communities, but the actual peaks varied between species and communities (***Figures 3.5 to 3.8***). Many species show the inverse-J shaped stem diameter distribution with many small stems and gradually fewer larger stems such as *P. latifolius* in Moist forest (***Figure 3.6b***), *O. africana* in Dry forest (***Figure 3.5d***) with no clear examples in Riparian forest except *R. capensis* (***Figure 3.7b***) and *C. mundianum* (***Figure 3.8b***) in Riparian forest G2a. Some species show the opposite distribution pattern such as *O. ventosa* in Moist forest and Riparian forest G2a (***Figure 3.6c***) and *A. dimidiata* in Riparian forest G2a (it has an inverse J-shape curve in Moist forest) (***Figure 3.6d***). Some species show a typical bell-shaped curve with high numbers in the intermediate sizes and fewer stems in the smaller and larger sizes such as *C. africana* in Riparian forest G2 (***Figure 3.5a***) and *R. melanophloeos* in Riparian forest G2a (***Figure 3.5b***), but also Black wattle in ***Figure 3.9a***.

The common more widespread natural forest canopy species such as *C. africana* (Riparian forest and foest clusters), *R. melanophloeos* (very prominent in Riparian forest G2a) and *V. lanceolata* (Riparian forest G2b-e), and also the sub-canopy species *C. inerme* (Riparian forest G2) (***Figure 3.5***) occurred more prominently within Riparian forest and forest clusters than in the Moist and Dry forest patches, and in all the sizes (for canopy species). The smaller sizes were relatively few to absent in the forest

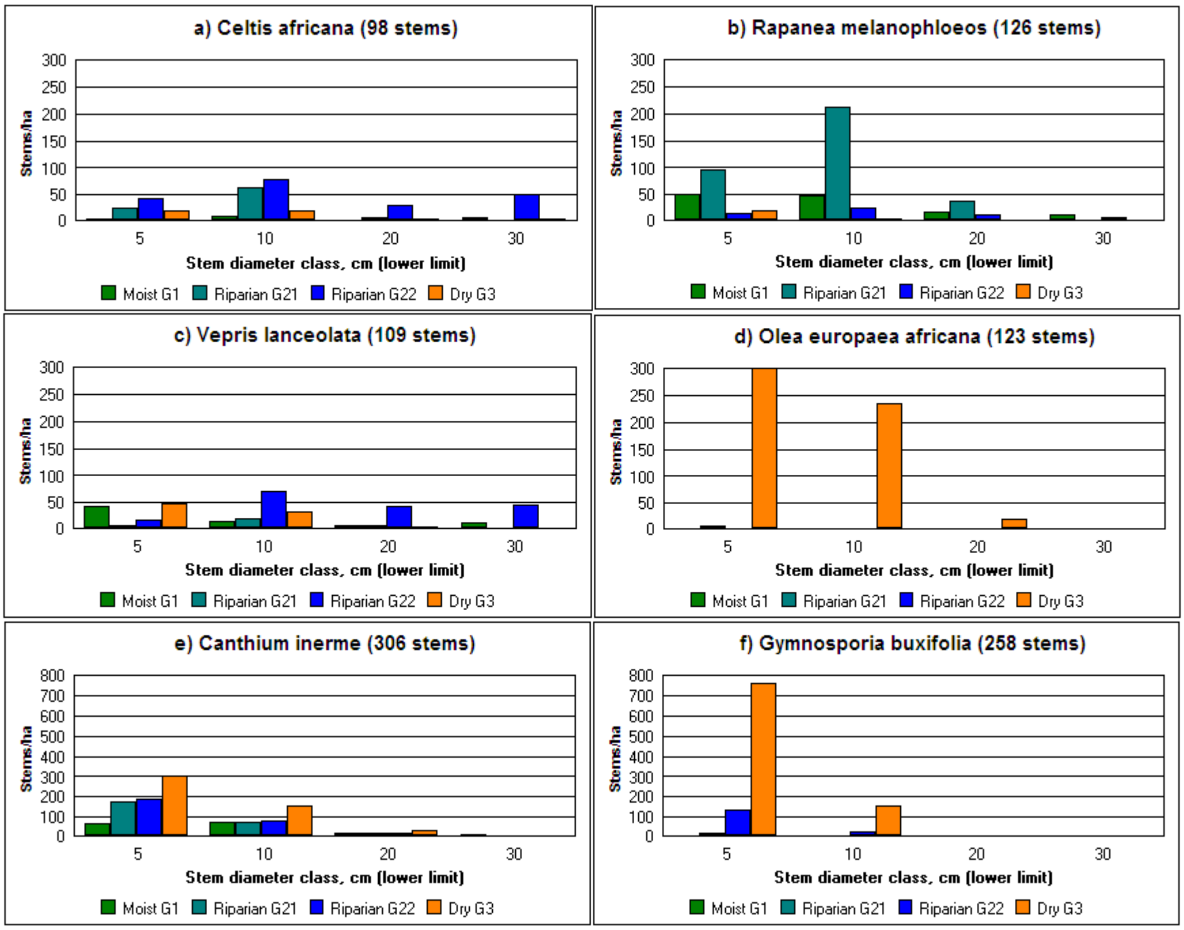


Figure 3.5: Stem diameter distribution of common spreading natural forest canopy species (a) *Celtis africana*, (b) *Rapanea melanophloeos*, (c) *Vepris lanceolata* and (d) *Olea europaea africana*, and sub-canopy species (e) *Canthium inerme* and (f) *Gymnosporia buxifolia*.

patches. However, the two Dry forest species that are also present in some clusters, *O. africana* and *G. buxifolia*, have very strong regenerating populations in the Dry forest, less in the Riparian forest and forest clusters (***Figure 3.5d,f***).

The four species presented in ***Figure 3.6*** are known as canopy species were more related to the moist forest. Their stem diameter distribution showed that they were more prominent in the Moist forest community (G1) compared to the other forest communities (G3, G22) and notably to the Riparian and forest Cluster (G21) with which they share a few species. That was the case with *A. dimidiata*, *O. ventosa*, and to some extent *O. bullata*. *P. latifolius* was absent from Riparian and forest cluster community (G21) even though the species exhibited very good regeneration in Moist forest. *O. ventosa* has little to no stems < 10 cm DBH, but in both Moist forest and Riparian forest G2a the species has a relatively large number of stems ≥

30 cm DBH. *A. dimidiata* shows an inverse J-shaped curve in Moist forest but the opposite trend in Riparian forest G2a (with relatively many stems ≥ 30 cm DBH). Both species are present in Dry forest, but are absent from Riparian forest G2b-e.

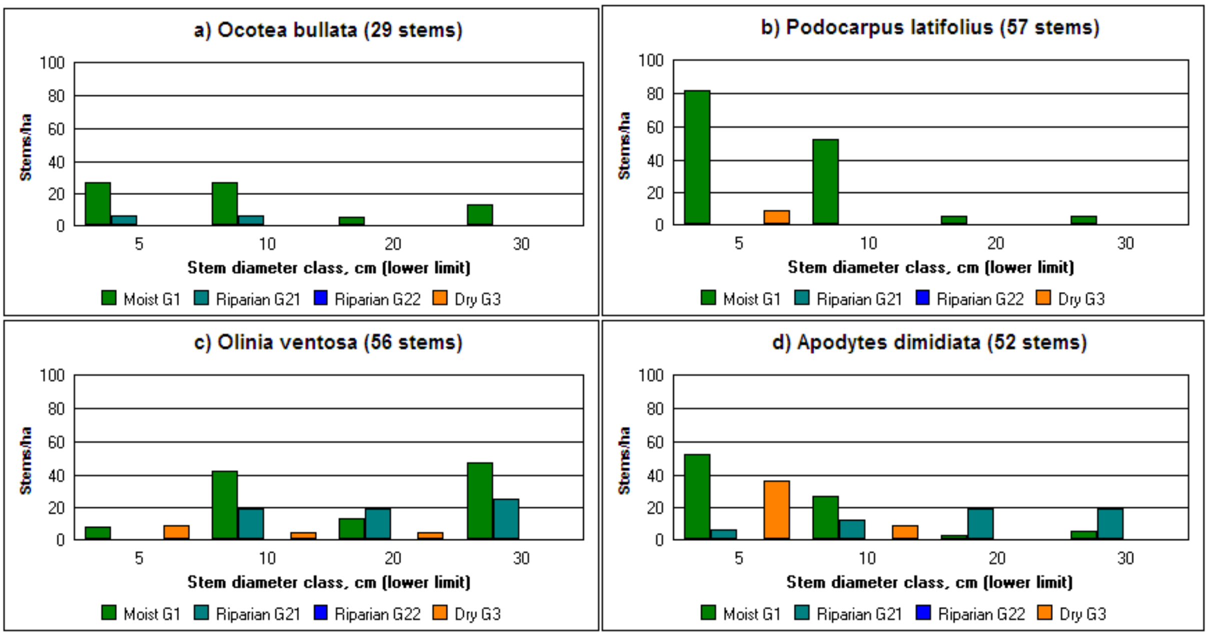


Figure 3.6: Stem diameter distribution of moist forest canopy species with large trees: (a) *Ocotea bullata,* (b) *Podocarpus latifolius,* (c) *Olinia ventosa* and (d) *Apodytes dimidiata.*

The three common moist forest sub-canopy tree species, *H. schinoides*, *R. capensis* and *Maytenus acuminata*, exibited a similar inverse J-shaped distribution (good regeneration) (***Figure 3.7***) as in the Moist forest canopy species (***Figure 3.6)***. They are also present in Riparian forest G2a (G21), and particularly *R. capensis* has a relatively large number of stems < 20 cm DBH.

P. viridiflorum, *C. mundianum* and *D. whyteana* were prominent in the Dry forest community G3 with an abundance of small stems (inverse J-shaped) (***Figure 3.8***). *C. mundianum* was also present in Moist forest and with good numbers in Riparian forest G2a (G21).

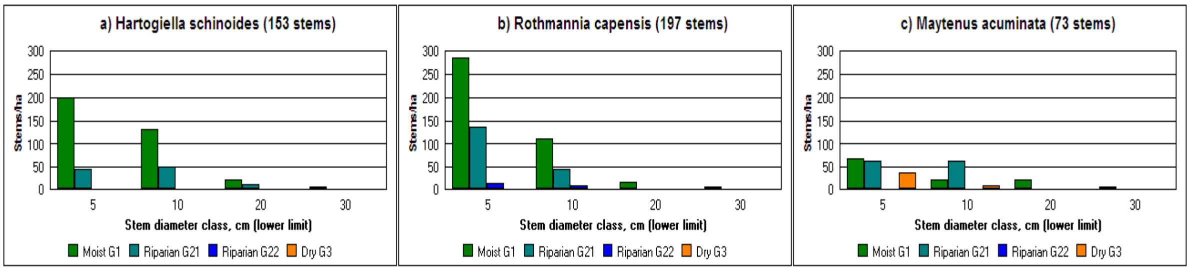


Figure 3. 7: Common moist forest sub-canopy tree species with some stems within the wattle stands: (a) *Hartogiella schinoides*, (b) *Rothmannia capensis* and (c) *Maytenus acuminata*. *Spp names italics in graph headings.* As the legend is the same for all the graphs, just place it ones.

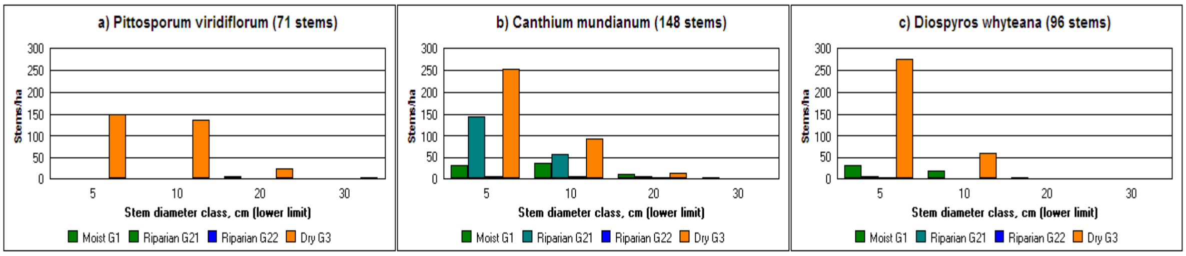


Figure 3.8: Stem diameter distribution of dry forest species with abundant regeneration but mostly absent from the wattle stand: (a) canopy species *Pittosporum viridiflorum*, and sub-canopy species (b) *Canthium mundianum* and (c) *Diopsyros whyteana*.

The two common invasive alien species, *Black wattle* and Bugweed, showed different diameter class distributions in different parts of the Riparian forests and forest clusters (***Figure** 3.9*). Black wattle was prominent in Riparian forest and some clusters related to Group2a, but had a low presence in the other parts of Riparian forest and related forest clusters. It showed a more advanced development of the population with a decline in stems < 10 cm DBH (a typical bell-shaped curve of a light-demanding species). Bugweed was absent from the G2a community and more prominent in the other Riparian forests and associated forest clusters (G2b-e), but it is a smaller-sized tree. The two invasives were almost absent from Moist and Dry forest patches (G1 and G3).

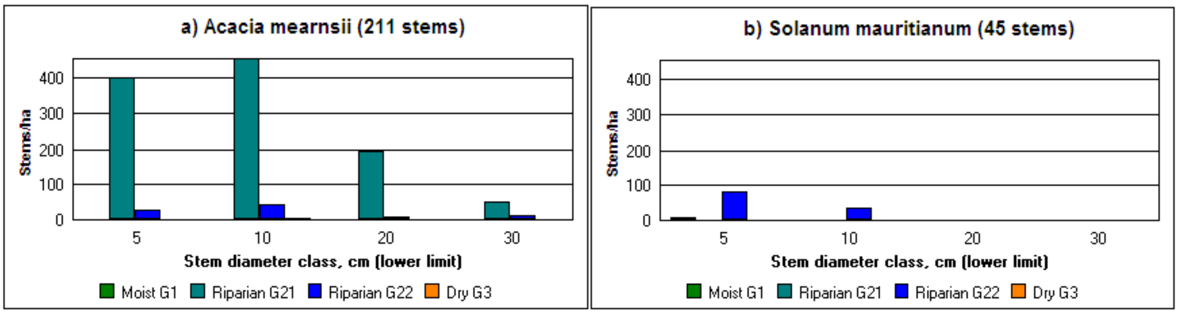


Figure 3.9: Stem diameter distribution of the two main invasive species: (a) *Acacia mearnsii* and (b) *Solanum mauritianum*.

3.5 Discussion

3.5.1 Forest clusters and forest patches

Natural forest patches adjacent to the Black wattle stand were expected to influence the forest succession process through the natural forest clusters establishing within the Black wattle stand (***Figure 3.1***). The assumption was that seeds from these adjacent forest patches would influence the establishing clusters within the Black wattle stand. A number of forest species such as *C. inerme, C. africana, G. buxifolia, R. melanophloeos* and *V. lanceolata* were found to be common across the forest patches and forest clusters. The species are well known to generally occur widely through different forest types (**Geldenhuys, 1989; Mucina *et al.,* 2002**). Their presence in all the five sampled forest zones would not really help to determine the type of relationship that exist between each of the forest patches and these establishing forest clusters; but the common widespread species differ in stem number, in importance values and in stem diameter distribution for each type of forest patch sampled. That variability allowed some comparisons between the three generated distinct forest communities: G1, G2 and G3 (***Figure 3.2***).

3.5.2 Moist forest patches and forest clusters species

Geographically moist forest patches occur directly next to the black wattle stand in which natural forest clusters are establishing (***Figure 3.1***). The expectation was to see similar species to be common between the two compartments. But, results from investigations revealed numerous differences between the two compartments. From general characteristics (***Table 3.2***), Moist forest patches generally grow on steep South-Easterly slopes, whereas the forest clusters grow on sites with a gentle South-Westerly slope. Even the species composition between the Moist forest (G1) and forest clusters (G2, as part of Riparian forest) was significantly different. Analyses of species importance values and stem diameter distributions showed that canopy and sub-canopy tree species of the moist forest patches that had large stem diameters also had good regeneration within those patches, but some were almost absent from the sampled forest clusters in the black wattle stand but present within the Riparian/forest cluster community (G2a)(***Figure 3.2*** **&** ***Figure 3.6***). The three sub-canopy species, *H. schinoides*, *R. capensis* and *M. acuminata*, showed some presence in the Riparian forest G2a with associated forest clusters (***Figure 3.7***).

These results may suggest that it is unlikely that the moist forest patches are the principal seed sources of the establishing forest clusters. Because of the presence of three Moist forest canopy species and some sub-canopy species in the forest clusters, Moist forest cannot be excluded as influencing the colonisation of the wattle stand. However, the close proximity of the two components is not enough to ensure seed movement of more species from the moist forest into the establishing forest clusters. It is necessary to have a closer look at other factors such as seed characteristics and dispersal systems.

3.5.3 Dry Forest patches and forest clusters

Dry forest (G3) was clearly different from the establishing forest Clusters (G2, as part of Riparian forest) in terms of classification based on species similarities, IVs and ordination analyses. The two sites shared very few species, and most of the species related to the dry forest were almost absent from the forest clusters (***Figure 3.5d,f*** and ***Figure 3.8***). However, *G. buxifolia* was present in many parts of the Black wattle stand but as small plants < 5 cm DBH, *C. mundianum* was present in the Riparian forest G2a (***Figure 3.8b***), and to a lesser degree also *O. africana* (***Figure 3.5a***), a typical dry forest species (**Aerts *et al.*, 2007**). Species of Dry forest were related to steep North-Westerly slopes, whereas forest clusters occurred on gentle slope or flat areas (***Table 3.2***). The distance and the river as physical obstacle between the two sites may limit seed movement and may explain the species dissimilarities. However, possible interactions between these two sites cannot be excluded, even though statistically such interactions were negligible. The examples mentioned above of some of the Dry forest species suggest that the seeds of some Dry forest species do arrive and establish in the black wattle stand, but still at an early stage of colonization.

3.5.4 Riparian forest patches potential principal seed source of establishing forest clusters

Forest clusters were more similar to Riparian forest patches in terms of species composition. They were displayed in the same community, G2 (***Figure 3.2***). The interpretation is that the established species found in those forest clusters would have their seed sources from the two Riparian forests. From their spatial position, Riparian forest south occurs along the southern side of the Black wattle stand and Riparian forest north at the foot of the mountain slope (***Figure 3.1***). These sites share the longest borders with the Black wattle stand, which gives them the advantage of interconnection compared to Moist forest patches and notably Dry forest patches. Distance from the source has always been an important factor influencing the seedling establishment. However, species from both the Moist forest and the Dry forest patches also contributed to forest cluster development. Seed characteristics of species may therefore also be a determinant factor in forest cluster development (**Hooper *et al.*, 2004; Geldenhuys & Bezuidenhout, 2012**)

One could expect that most large-size stems of species recorded within the forest Clusters would be found in the parent site, i.e. Riparian forest north and south patches. A comparison of the average stem DBH of common species between Riparian forest patches and forest clusters showed no significant differences between these three zones (***Figure 3.10***). This indicates that common species in the three sites have similar sizes. This suggests that most of large trees in the clusters in the Black wattle stand have existed before the recent disturbance of the site, and may have contributed to the rapid expansion of the larger clusters. Remnant trees are known to accelerate forest succession (**Keeton & Francklin, 2005**).

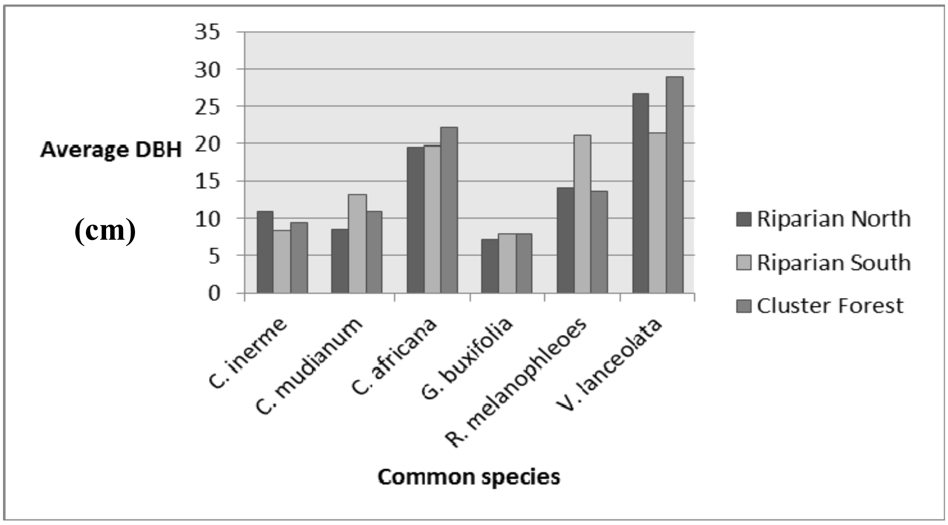


Figure 3.10: Comparison of average stem diameter between Riparian forest patches and Forest clusters in the Black wattle stand.

3.5.5 Introduced Black wattle not susceptible to establish in closed canopy forests

The two main invasive species present in the study area, Black wattle and Bugweed, were almost absent from the moist and dry forest patches (***Table 3.3***). This is in agreement with results from many previous studies in South Africa (**Geldenhuys *et al.*, 1986; Macdonald *et al.*, 1986; Geldenhuys & Bezuidenhout, 2006; Geldenhuys & Delvaux, 2007; Geldenhuys, 2008; 2013)**. These two species, like all the light demanding invasive species, are unable to establish under closed canopies such as the moist or dry forest patches. Their germination and establishment requires light. That is why the well-developed Black wattle stand of 90 ha at Buffeljagsrivier was most likely caused by clearing of possible forest patches in this area some time ago. The smaller stems shown in **Figure 3.9a** are more likely suppressed stems of the same age as the larger trees. The results confirm the notion that in the absence of disturbances, Black wattle is not a threat in the forest environment.

3.5.6 Environmental factors

The plots of the Riparian forest patches and of the forest clusters had similar relatively flat to gentle aspect (***Figure 3.1*** and ***Table 3.2***) and may moderate the temperature conditions between more southern or more northern aspects. The plots possibly also have similar light and radiation conditions (opposite end of slope arrow in ***Figure 3.3***). Adequate light is known to stimulate the seeds of certain species to germinate (**Bazzaz, 1979**). The similar site conditions may explain the similarities in species composition of the three sites. Aspect however, only explains 49 % of the variance of species composition of the sample. Some other factors that were not subjected to measurement may contribute better to the observed patterns.

3.6 Conclusion and further studies

Every type of forest patch contributes to a greater or lesser degree to the development of forest clusters within the black wattle stand. Riparian forest were pointed to be the primary seed source of the establishing forest clusters.The developing forest clusters related more to the Riparian forest in terms of similar very gentle south-westerly slope and mean stem diameter. Remnant forest species in many large forest clusters contributed as local seed sources. Because of presence of Moist and Dry forest species in some forest clusters, both forest type Moist and Dry were also viewed as contributing as seed sources for the developing forest clusters within the black wattle stand.

The study has used a comparative approach to underline the relationship between forest patches and forest clusters. For this reason similar plots had to be used in both forest patches and forest clusters. Only large clusters were able to accommodate a 10m x 20m rectangular plot, which automatically excluded the medium and small clusters from the sample. However, observation of species composition of these excluded clusters shows an important number of forest species that are more characteristic of the Moist and Dry forest patches. The interpretation of this observation is that by including small and medium clusters in the analysis the contribution of Moist and Dry forest patches might be more perceptible than the actual results. Additional investigations which could integrate the small and medium clusters, focusing on individual behaviour of species of the sample, are needed. The expectation is that seed characteristics and dispersal systems would constitute the main explanatory factors for the actual natural forest species distribution in the wattle stand.

3.7 References

Aerts, R.; Negussie, A.; Maes, W.; November, E.; Hermy, M. & Muys, B. 2007. Restoration of dry Afromontane forest using pioneer shrubs as nurse-plants for *Olea europea* ssp. cuspidata. *Restor. Ecology* 15: 129–138.

Altermatt, F.; Schreiber, S. & Holyoak, M. 2011. Interactive effects of disturbance and dispersal directionality on five species richness and composition in metacommunities. *Ecology* 92(4): 859-870.

Bazzaz, F.A. 1979. The physiological ecology of plant succession. *Ecology and Systematics* 10: 351-371.

Bray, J.R. & Curtis, J.T. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* 27: 325-349.

Geldenhuys, C.J. 1989. Biogeography of the mixed evergreen forests of southern Africa. Ecosystems Programmes Occasional Report no. 45. FRD, Pretoria.

Geldenhuys, C.J. 1997. Native forest regeneration in pine and *Eucalyptus* plantation in Northern Province, South Africa. *Forest Ecology and Management* 99: 101-115.

Geldenhuys, C.J. 2004. Concepts and process to control invader plants in and around natural evergreen forest in South Africa. *Weed Technology* 18: 1386-1391.

Geldenhuys, C.J. & Bezuidenhout, L. 2006. Guidelines for conversion of invader plant stands to regrowth natural forest along the Buffeljagsrivier, Swellendam. Report Number FW-01/06.

Geldenhuys, C.J. 2008. Can I manipulate alien plant stands to rehabilitate natural forest? *Dendron* 40: 38- 44.

Geldenhuys, C.J. 2011. Most invasive alien plants facilitate natural forest recovery – how is that possible? *SAPIA News 18: 2-5.*

Geldenhuys, C.J. 2013. Converting invasive alien plant stands to natural forest nature's way: Overview, theory and practice. In: Jose, S., Singh, H.P., Batish, D.R. & Kohli, R.K. (eds). Invasive plant ecology, CRC Press, Taylor & Francis Group, Boca Raton: 217-237.

Geldenhuys, C.J. & Bezuidenhout, L. 2006. Guideline for conversion of invader plant stands to regrowth natural forest along the Buffeljagsrivier, Swellendam Invader conversion Buffeljags progress. Report Number FW-01/06.

Geldenhuys, C.J. & Bezuidenhout, L. 2012. Rehabilitation of natural forests using stands of alien trees of plantations or invasions as allies. In: Bredenkamp, B.V. & Upfold, S.J. (eds). South African forestry handbook, 5th edition. Southern African Institute of Forestry, Pretoria: 585-604.

Geldenhuys, C.J. & Delvaux, C. 2007. The *Pinus patula* plantation … A nursery for natural forest seedlings. In: Bester, J.J., Seydack, A.H.W., Vorster, T., Van der Merwe, I.J. & Dzivhani, S. (eds). Multiple use management of natural forests and woodlands: Policy refinement and scientific progress. Natural Forests and Savanna Woodland Symposium IV, Port Elizabeth, South Africa, 15-18 May 2006: 94-107.

Geldenhuys, C. J., P. J. Le Roux, and K. H. Cooper. 1986. Alien invasions in indigenous evergreen forest. *In* Macdonald, I.A.W.; Kruger, F.J. & Ferrar, A.A. (eds.). The Ecology and Management of Biological Invasions in Southern Africa. Cape Town, South Africa: Oxford University Press: 119–131.

Hooper, E.R.; Legendre, P. & Condit, R. 2004. Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. *Ecology* 85(12): 3313-3326.

Howe, H.F. & Smallwood, J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst*. 13: 201–228.

Howe, H. & Westley, L. 1997. Ecology of pollination and seed dispersal. In: Crawley, M. (ed.). *Plant Ecology. Oxford*: 185–216.

Johnson, E.A. & Miyanishi, K. 2008. Testing the assumption of chronosequences in succession. *Ecology letters* 11: 419-431.

Keeton, W.S. and J.F. Franklin. 2005. Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecological Monographs* 75:103-118.

Kindt, R. & Coe, R. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological studies. Nairobi: World Agroforestry Centre (ICRAF).

Le Coeur, D.; Baudry, J.; Burel, F. & Thenail, C. 2002. Why and how we should study field boundary biodiversity in an agrarian landscape context. *Agriculture, Ecosystems and Environment* 89: 23-40.

Legendre, P. & Legendre, L. 1998. *Numerical ecology.* Amsterdam. Elsevier Science BV. 853 pp.

Loumeto, J.J. & Huttel, C. 1997. Understorey vegetation in fast-growing tree plantations on savanna sols in Congo. *Forest Ecology and Management* 99: 65-81.

Lugo, A.E. 1997. The apparent paradox of re-establishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management* 99: 9-19.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27(2): 209–220.

Mascaro, J. 2011. Eighty years of succession in a non-commercial plantation on Hawaii Island: are native species returning? *Pacific science* 65(1): 1-15.

Mucina, L.; Geldenhuys, C.J.; Lawes, M.; Eeley, H.; Adie, H.; Graham von Maltitz, P.; Vink, D.; Fleming, G. & Bailey, C. 2002. Classification System for South African Indigenous Forests. Final draft: 1-9.

Polis, G.A.; Anderson, W.B. & Holt, R.D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. In: Fautin, D.G. (Ed.), *Annual Review of Ecology and Systematics*: 289–316.

Ter Braak, C.J.F. 1986. Canonical correspondence analysis: anew eigenvector technique for multivariate gradient analysis. *Ecology* 67: 1167–1179.

Tilman, D. 1994. The resource-ratio hypothesis of succession. *American Naturalist* 125: 827-852.

Chapter 4:
Expansion of natural forest clusters within an *Acacia mearnsii* stand at Buffeljagsrivier, South Africa: seed source and influence of dispersal mechanisms

Abstract

It has been shown that natural forest succession processes in alien invasive stands can include a gradual colonisation of the stand by indigenous forest tree species. The indigenous tree species often establish beneath the alien nursing stand in clusters. The cluster becomes a microsite, which is expected to expand progressively by (1) allowing regeneration of more species through seed production and (2) by increasing the seed input from adjacent forests through attraction of several dispersal agents. Forest cluster development through these two functions was tested at Buffeljagsrivier where a 90 ha stand of the invasive alien Black wattle is nursing 329 clusters of natural forest species as part of the forest recovery process.

Regeneration of the forest species was assessed within an 18 m radius beyond the boundary of seven selected forest clusters each composed of more than 10 indigenous trees. Two species lists were generated. The first list represented the species of the establishing forest clusters within the Black wattle stand and the second list represented the species of the adjacent natural forest patches. Evidence of dispersal agents was collected on site and information was extracted from existing literature on seed characteristics and species dispersal mechanisms. A list of potential dispersal agents was generated. The results indicated two main interpretations: (1) Natural forest clusters, once established, become the main seed source for their gradual expansion within the Black wattle stand; (2) Within young clusters, seed characteristics and dispersal mechanisms explain the distribution of scattered small clusters. The absence of some species in the forest clusters that are present in the nearby forest patches was explained by their fruit characteristics, with a predominance of large sized fruit, making them inadequate for effective dispersal by most birds and mammals. The seed

sources of most of the woody shrubs, viewed as first establishing species in the forest clusters, were not well understood.

These findings provide useful information for revision of the rehabilitation framework of alien invasive stands within the forest environment in South Africa.

Key words: *Acacia mearnsii*; Dispersal mechanism, Forest cluster, Regeneration, Rehabilitation, Seed source distance. Black wattle

4.1 Introduction

The facilitation concept of forest succession suggests that the first established trees are grouped into clusters and from then, more and different species would be added making the cluster progressively larger (**Clements, 1936; Loumeto & Huttel, 1997**; **Lugo, 1997; Geldenhuys, 2004, 2010; Mascaro, 2011**). In the context of this study a forest cluster is a group of indigenous tree species establishing within a stand of an invasive species, in this case Black wattle. A cluster of natural forest species within invasive plant stands is expected to expand within the nursing stand, whereas regeneration of the invasive pioneer trees is often unable to establish under its own canopy because of intolerance to shade. A prerequisite for the forest cluster is the presence of at least one reproducing mature tree, which could potentially bear fruit as source for future seed regeneration and to attract further dispersal agents. The ability of a species to reach the targeted site depends on several factors such as seed availability, distance from seed source, seed characteristics, and dispersal mechanisms (**Geldenhuys, 1989a, 1996a; Cain *et al.*, 2000; Nathan & Muller-Landau, 2000; Bullock & Moy, 2004; Navarro *et al.*, 2009**).

Seed availability is linked to the presence of seed producing species and the abundance of reproducible mature trees. At Buffeljagsrivier, several natural forest patches occur within the study area. However, the ability of a species to reach suitable regeneration sites depends both on how many seeds it produces and how these seeds are dispersed (**Grubb, 1997**). Consequently, species with large production of seed could be rare or absent in the adjacent sites because of the lack of suitable dispersers. The available fruit and seed attract birds, mammals, bats and insects. The presence of a diversity of forest species within an area would support a diversity of dispersers that could select the preferred food at different times of the year. In Brazil, the absence of animals that disperse large seed in a 10 year old plantation delayed the entry on site of certain tree species (**Parrotta *et al*., 1997**). The absence of such species could slow down the progress of succession (**Lugo, 1997**). The capacity of a given stand or a cluster to expand depends on the ability of the available species from the surrounding areas to regenerate within the site and on the interactions with adjacent sites (**Schupp, 1993; Schupp & Fuentes, 1995; Polis *et al.,* 2000; Willson & Traveset, 2000**). In this study several patches of Western Cape Afrotemperate forest were present at the one end of Black wattle stand. Thus there was an expectation that many of the forest species would be present within the study site, including the fauna that are related to this type of forest (**Geldenhuys, 1989b; Mucina *et al.,* 2002; Palgrave, 2002**).

Seed mobility greatly depends on the presence of both seeds and dispersal agents on the site (**Geldenhuys, 1997; Parrotta *et al*., 1997; Wilson & Downs, 2012**). Regeneration from a specific seed source is expected to decrease with increasing distance from the seed source, i.e. at longer distances, not all the seeds of the potential tree species would reach the targeted site (**Grubb, 1997; Parrotta *et al*., 1997; Wilson & Downs, 2012**). However, Wilson and **Downs (2012)** have reported that seed and seedlings tend to show increased survival with increasing distance from the parent plants. Seed size influences the process of succession. Small seeds are easily carried by birds and are often dispersed over considerable distances **(Geldenhuys, 1997; Zhishu *et al*., 2005**). However, not all the dispersers can reach long distance sites due to the existence of natural obstacles (mountain ridges, ravines, rivers) or due to the limitation of their ecological niche (**Geldenhuys, 1989b**).

Species have developed different fruit/seed characteristics to ensure their successful dispersal (**Tiffney, 1984**). Seeds present many different adaptations for dispersal, including mass, shape and appendages (**Snow, 1981; Howe, 1986; Wilson & Downs, 2012**). Fruit shapes can be oval, globose, ovoid, pear-shaped, winged, ellipsoid, round, oblong etc (**van Wyk & van Wyk, 1993**) and determines the ability of being held and carried by for example animals. Fruit structure can be described as fleshy with berries or drupe, and dry within pod, capsules and nuts. Combinations of these characteristics lead to several adaptations for dispersal (**Snow, 1981; Tiffney, 1984**).

Numerous means of seed dispersal are known. Seeds can be dispersed by birds, mammals, bats, wind, water and even by gravity (**Tilman, 1994**.). The existence of a particular trend in the distribution of the regeneration is indicative of the predominant dispersal mechanisms of species in the area (**Willson & Traveset, 2000**): Wind dispersal will tend to exhibit a directional regeneration pattern; bird dispersal will show a disparate distribution as birds move from one fruit tree to the next; mammal dispersal would follow a line (**Willson & Traveset, 2000**). Birds and bats often cause dispersed plant species to cluster underneath perch trees (**Geldenhuys, 1993a**). Patterns of establishing regeneration of species correlated with their dispersal system (**Hooper *et al.*, 2004**): Wind dispersed species were found at small distances, bat dispersed species at intermediate distances, and bird or mammal dispersed species at considerable distances in the succession process. Tree species in the Southern Cape Afrotemperate Forests have predominantly bird and animal dispersed fruits/seeds, whereas shrubby and herbaceous species have predominantly dry, wind dispersed fruits/seeds (**Geldenhuys, 1989b, 1993b**).

Regeneration patterns around seed sources can indicate the intensity of dispersal activities around the site (**Wilson & Downs, 2012**): Regeneration limited to the proximal zone from the source would suggest minimum movement around the source area, i.e. low dispersal activity; Regeneration present at considerable distances from the source would imply a high dispersal activity.

In an initial study in a 90 ha stand of the invasive alien Black wattle at Buffeljagsrivier, 329 clusters of indigenous forest species were mapped and recorded. The objective of this study is to determine the subsequent spread of indigenous forest species from these developing forest clusters into the rest of the Black wattle stand. Three main questions were posed for the study: (1) Are the reproductively mature plants in the establishing clusters of natural forest species becoming secondary seed sources for exapnsion of the clusters? (2) Are seeds dispersed from adjacent forest patches still contributing to the expansion of the clusters into the surrounding Black wattle stand? (3) What is the influence of the distance from seed sources, seed characteristics and the dispersal mechanisms on the expansion of forest clusters?

4.2 Study area

Buffeljagsrivier study area (***Figure 4.1***; 34°00'15"S, 20°33'58"E; 95-110 m above mean sea level) is situated east of Swellendam at the southern foot of the Langeberg Mountains in the Western Cape, South Africa. The Langeberg Mountains north of the Buffeljagsrivier is composed of Table Mountain quartzite sandstone and the ridge south of the river is composed of shales (**Geldenhuys, 2011**). The area experiences the typical Mediterranean climate of the Southwestern Cape, i.e. with hot and dry summers and cold and wet winters. The mean annual rainfall in Swellendam is 462 mm/year and is fairly evenly spread throughout the year (www.saexplorer.co.za/south-africa/climate/swellendam_climate.asp), ranging between 23 mm in December and 48 mm in August. The mean daily maximum temperature ranges from 17.1°C in July to 27.5°C in January and the mean daily minimum temperature is 15°C in February and 5°C in July.

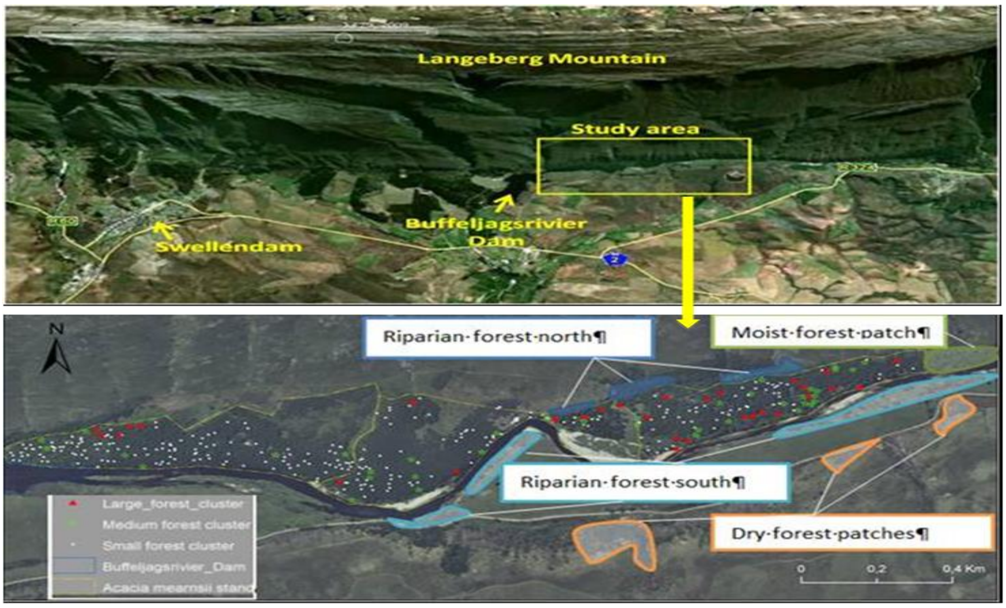


Figure 4. 1: Location of the study area along the Buffeljagsriver near Swellendam in the South-western Cape, indicating the extensive *Acacia mearnsii* (wattle) stand (dark area north of the river), the 329 small, medium and large forest clusters within the wattle stand (Chapter 2), and the moist, dry and riparian forest patches.

The main vegetation in the area is Mountain Fynbos (a very diverse shrubland) on the slopes of the Langeberg Mountain, grassy Fynbos on the ridge south of the river, and scattered patches of Western Cape Afrotemperate forests (moist, dry and riparian forest) with a total area of about 3.5 ha. The extensive stand (90 ha) of the invasive alien black wattle (*Acacia mearnsii*) along the northern bank of the river invaded an area that may have carried more riparian forest before it was cleared for crop cultivation long ago (the original riparian forest does not show on available aerial photographs since 1942).The forest patches have a high socio-economic value. They provide for ecotourism and recreational activities such as hiking, and preserve the stream banks. They may have provided timber for construction and furniture in the past and may provide in sources for traditional medicine. The wattle stand was cleared before but grew back with higher density and over a larger area. In 2006, it was decided to convert the wattle stand to natural forest (**Geldenhuys & Bezuidenhout, 2006**) according to the concept of the wattle being a pioneer stand facilitating the recovery of the shade-tolerant forest species (**Geldenhuys *et al*., 1986; Geldenhuys, 2004**).

4.3 Study Methodology

4.3.1 Sampling forest expansion around clusters

The wattle stand was divided into three zones, namely Proximal zone, Intermediate zone and Distant zone respectively, according to their proximity to the forest patches. A total of 329 forest clusters were mapped and recorded within the Black wattle stand (***Chapter 2***), and classified into size categories according to the number of reproductively mature stems: Small clusters have one to three mature stems; Medium clusters have four to nine mature stems, and Large forest clusters have ten or more mature stems.

Seven forest clusters (six large, one medium) were systematically selected from the three black wattle stand zones to assess the possible expansion of the forest clusters and the influence of distance from seed sources. Large and medium clusters were preferred since they contain several mature indigenous trees of different species, which would assure visit of different dispersal agents. Finally, criteria for selection of specific large and medium clusters were accessibility and the ability to accommodate the plot design.

The pattern of regeneration found in the immediate surroundings (expansion) of a selected forest cluster was investigated only within 18 m distance away from the boundary of the forest cluster. Fruit/seed characteristics and dispersal system were the considered factors for the expansion.

The borders and centre of each selected forest cluster were marked. Forest cluster borders were determined by simple projection of crown limits of indigenous trees on the boundary of the cluster, onto the ground. The cluster centre was the centre of the main axis of the forest cluster. From that cluster centre, eight line directions were considered (N, NE, E, SE, S, SW, W, NW). Four lines were then randomly selected. Three directions were tolerated when the position did not allow four, because of natural obstacles such as river, ravine, etc. Along each selected line, two to three 10 m x 5 m rectangular plots (expansion plots) were sampled every 6 m from the cluster border (***Figure 4.2***). Two plots were used in the case of an obstacle or to avoid interference when another existing but non-selected cluster was in close proximity. Information on the number and directions of the lines, and the number of sampled plots for each selected forest cluster is provided in ***Appendix VI.***

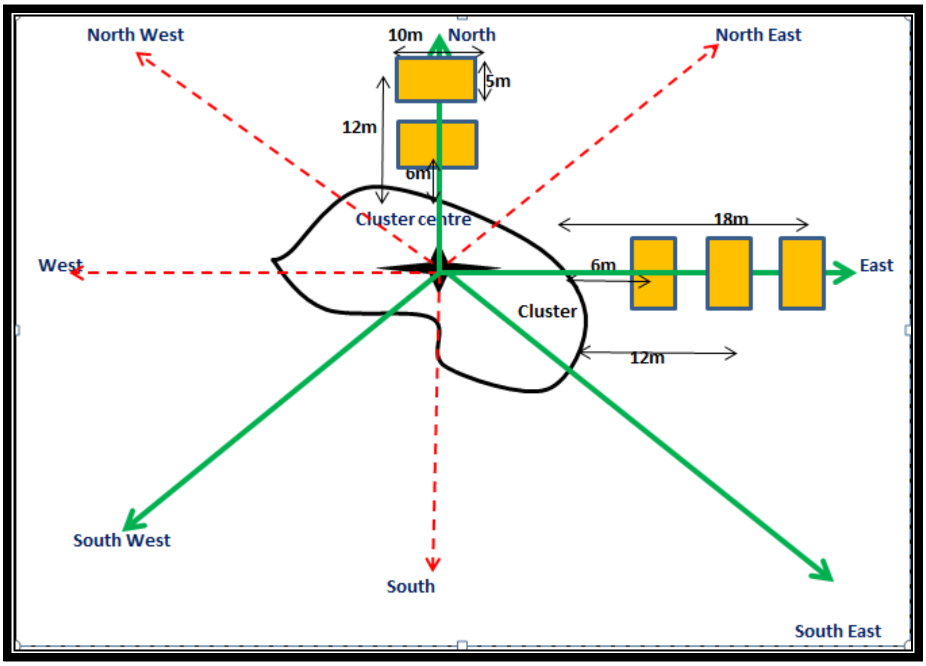


Figure 4.2: Sampling design within and around each selected cluster to assess patterns of cluster expansion. Four lines (green) were selected from the potential eight lines (green plus red).

All stems ≥ 5 cm DBH (stem Diameter at Breast Height, i.e. 1.3 m) within the cluster area were recorded by species and DBH. Stems <5 cm DBH were recorded as part of regeneration within the cluster, by species and stem counts. On the 50 m^2 expansion plots, regeneration was recorded by species and stem counts and number of mature Black wattle stems was recorded. Unknown plants were collected for later identification.

4.3.2. Sampling of seed and dispersal characteristics of tree species

Two species lists were generated to assess the contribution of seed characteristics and the influence of dispersal mechanisms (***Appendix VII***). The first list contained species from sampled plots (***Chapter 3***): nine plots in three patches of dry forest, 17 plots in two patches of moist forest, eight plots in four patches of riparian forest south of the wattle stand (South), and 12 plots in six patches of riparian forest north of the Black wattle stand (North). The second list contained species from 59 forest clusters proportionally selected through the wattle stand, and covering small, medium and large clusters. Information on fruit/seed characteristics and dispersal mechanism of each species was obtained from the literature (**Geldenhuys, 1993a, 1996b**) and supported by field observations. The size of the fruit and seed was defined as small or large in relation to potential easy and effective dispersal by smaller birds: small = < 5 mm diameter; large = ≥ 5 mm diameter (**Geldenhuys, 1996b)**. The generated species lists allowed the comparison between species composition of the clusters and species composition in the neighbouring forest patches, and avoided the constraint of plot uniformity.

4.4 Data analysis

Species composition of clusters were compared with species composition of their surrounding regeneration by calculating their ecological distance, following **Kindt and Coe (2005)**, to test the hypothesis that established clusters within the wattle stand are the main seed sources of their expansion. Similarities would confirm the hypothesis while dissimilarities would suggest external influences. A Mantel test (**Mantel, 1967**), which tests the correlation between two matrices, was applied on the collected data to indicate the statistical significance of the link. Patterns of number of species regenerating per distance class were analysed through histograms using descriptive analyses, to establish the influence of the distance from clusters as potential seed source. A list of recorded species from establishing clusters and adjacent forest patches were used to evaluate the contribution of dispersal mechanism in the species distribution for this forest recovery. In that way presence, dominance or absence of a given species could be explained.

4.5 Results

4.5.1 Cluster expansion and seed sources

Similarities in composition of natural forest species between clusters and surrounding regeneration, based on Bray-Curtis ecological distance, differed between clusters. Cluster pL048 presented the highest similarity with its surrounding regeneration (0.07 Bray-Curtis distance matrix value) followed by pL070, and iL101 both with 0.38 Bray-Curtis distance matrix (***Table 4.1***). Forest clusters pL020 and dL348 were intermediate with 0.45 and 0.5 as distance matrix value. Forest clusters dM268 and iL139 showed the lowest similarities with distance matrices of respectively 0.60 and 0.64.

Table 4.1: Matrix of ecological distance between species composition of the clusters and their surrounding regeneration (R). A value close to 1 means a high dissimilarity and close to zero means high similarity. p=Proximal zone, L=large cluster, i=Intermediate zone, d= Distant zone, M=medium cluster.

Species regeneration around forest cluster	Species composition within forest cluster						
	pL020	pL048	pL070	iL101	iL139	dM268	dL348
(R)pL020	0.45						
(R)pL048		0.07					
(R)pL070			0.38				
(R)iL101				0.38			
(R)iL139					0.64		
(R)dM268						0.60	
(R)dL348							0.50

The Mantel test gave non-significant p-value (0.26) demonstrating the similarities between clusters and their respective surrounding regeneration. Most dominant species in the surrounding regeneration had an adult tree within the clusters (*Celtis africana* for forest clusters pL020, pL048 and pL070, *Rapanea melanophloeos* for dM268 and dM348, *Vepris* *lanceolata* for iL101 and *Maytenus acuminata* for iL139). Dominant species in some forest clusters were not found dominant in the regeneration, such as in pL020 dominated by *Gymnosporia buxifolia* with surrounding regeneration dominated by *Celtis africana*; iL139 cluster dominated by *Canthium inerme* with its surrounding regeneration dominated by *Maytenus acuminata*. Some of the dominant species in the clusters were even absent while the existence of several different species were recorded in the regeneration outside the forest cluster (*Olinia ventosa,* dominant species in dL348 but completely absent in the regeneration zone). Species such as *Halleria lucida, Brabejum stellatifolium*, *Olea europaea africana*, were recorded only in the regeneration zone (***Appendix 4.2***).

4.5.2 Influence of distance from seed sources

Looking at distance class levels (6 m – 12 m – 18 m), analysis of patterns showed three visible scenarios (***Figure 4.3***). The first scenario exhibited decreasing regeneration with increasing distance (pL020, pL048, pL070). The second scenario showed greater regeneration occurring with increasing distance, with relative decrease in the intermediate distance (iL139, dM268). The third scenario showed no pattern; all distance classes had the same amount of regeneration (dL348).

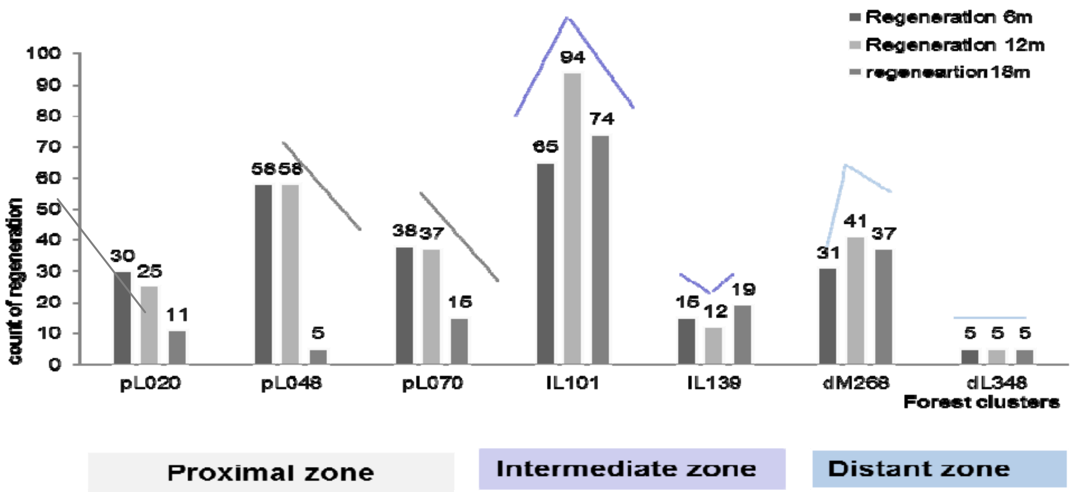


Figure 4.3: Species regeneration count per distance class around the seven selected clusters sampled within the wattle stand at Buffeljagsrivier.

Species composition at the same distance class showed that *C. africana* presented its best regeneration at the intermediate distance (12 m). This was verified in all the forest clusters where the species was present apart from forest cluster pL020 where regeneration increased with increasing distance. The same results were found with *G. buxifolia*, in the forest cluster pL048 where the regeneration was higher in the first distance classes (6 m). There was no noticeable pattern with other species.

4.5.3 Contribution of fruit-seed characteristics and dispersal mechanism on the cluster expansion into the Black wattle stand.

The two lists combined included 40 species, including the two main invasive species (Black wattle and begweed) The species presented a wide range of fruit and seed characteristics that are important for understanding the movement of tree and shrub species between the forest patches and the Black wattle stand, and within the Black wattle stand away from the establishing forest clusters (***Table 4.2***). In summary (***Table 4.3***), species with fleshy and large fruit dominated the list of 40 species (34 or 85%), followed by dry and large fruit (three or 7.5%), with two species with fleshy and small fruit (two or 5%) and one dry and small fruit (one or 2.5%). Species with soft and small seeds dominated the sample with 22 species (55%), followed by 12 species with soft and large seeds (32.5%); four species with hard and large seeds (10%), and one of hard-Small seed (2.5%)

Table 4.2: Characteristics of the fruit and seed and potential dispersal mode of species recorded within the forest patches and forest clusters in the Buffeljagsrivier.

Recorded species[1] ***=Introduced species**	**Presence in clusters & patches[2]**	**Fruit type[3]**	**Seed type[4]**	**Dispersal agents[5]**	**General notes**
***Acacia mearnsii**	C-M-D-Rs-Rn	Pod, d,L	H,L		
Apodytes dimidiata	C-M-D	Nut, f,L	S,L	B/M	
Brabejum stellatifolium	C-M-Rn	Nut, f,L	S,L	Wa+/M	Stream water
Buddleja saligna	Rs-C-	Capsule, d,S	S,S	Wi+	windy

Recorded species[1] ***=Introduced species**	**Presence in clusters & patches**[2]	**Fruit type**[3]	**Seed type**[4]	**Dispersal agents**[5]	**General notes**
Canthium inerme	C-M-D-Rs-Rn	Drupe, f,L	S,L	B+/M+	Rameron pigeon
Canthium mundianum	C-M-Rn-D	Drupe, f,L	S,S	B+/	Rameron pigeon
Cassine peraqua	C-D-	Drupe f,L	S,L	B	
Carissa bispinosa	D-	Berry, f,L	S,S	B	
Celtis africana	C-M-D-Rs-Rn	Drupe, f,L	S,L	B+	Rameron pigeon
Cussonia spicata	D-	Berry, f,S	S,L	B	
Curtisia dentata	Rn-	Drupe, f,L	H,S	B/M	
Diospyros glabra	C-Rn-	Berry, f,L	H, L	B/M	Chacme baboon
Diospyros whyteana	C-M-D-	Berry, f,L	H,L	B+/M+	Chacme baboon
****Eucalyptus sp***	D-	Capsule, d,L	S,S		
Grewia occidentalis	D-	Drupe, f,L	S,S	B+	Birds
Gymnosporia buxifolia	C-M-D-Rs-Rn	Capsule, f,L	S,f,L	B+	Birds
Halleria lucida	C-	Berry, f,L	S,S	B+	Birds
Hartogiella schinoides	M-Rn	Berry, f,L	S,S	B+	Rameron pigeon
Ilex mitis	Rn-C-	Berry, f,L	S,S	B+	Birds
Kiggelaria africana	Rn-C-	Capsule, f,L	S,f,S	B+	Birds
****Lantana camara***	C-	Drupe, FL	SS	B	
Maytenus acuminata	C-D-M	Capsule, f,L	S,f,S	B+	Birds
****Melia azedarach***	C-Rn	Drupe, f,L	S,L		
Metrosideros angustifolia	C-	Capsule, f,S	SS		
Ocotea bullata	C-M	Berry, f,L	S,L	B+	Bushbuck Rameron pigeon
Olea europaea africana	C-D	Drupe, f,L	S,S	B+	Birds
Olinia ventosa	C-M-Rn	Drupe, f,L	H,L	B+/M+	Chacme baboon
Pittosporum viridiflorum	C-D-M	Capsule, f,L	S,f,S	B+/M+	Birds/ Baboon

Recorded species[1] ***=Introduced species**	**Presence in clusters & patches[2]**	**Fruit type[3]**	**Seed type[4]**	**Dispersal agents[5]**	**General notes**
Podocarpus latifolius	M-	Nut, f,L	S,L	B+/M+	Chacme baboon
Pterocelastrus tricuspidatus	Rn	Capsule, f,L	S,f,L	B+/M?	Birds
Rapanea melanophloeos	C-M-Rs-Rn	Berry, f,L	S,L	B+/M+	Rameron pigeon
Rhoicisus tomentosa	C-M-D-Rs-Rn	Berry, f,L	S,L	M+	Chacme baboon
Rothmannia capensis	M-Rn-C-	Berry, f,L	S,S	B+/M+	Chacme baboon
Searsia (Rhus) pyroides	C-	Drupe, f,L	S,S?	B+/M+	Chacme baboon
Searsia (Rhus) tomentosa	C-	Drupe, f,L	S,S?	B+	Birds
Scolopia mundii	M-C-	Berry, f,L	S,S	B+	Birds
Scutia myrtina	C-	Berry, f,L	S,S	B+	Birds
****Solanum mauritianum***	C-Rs-Rn	Berry, f,L	S,S	B+	Birds
Vepris lanceolata	C-M-Rs-Rn	Berry/cap, f,L	S,S	B+/M+	Rameron pigeon
Virgilia oroboides	M-C-	Pod, d,L	H,L	M/Wa+	stream water

1 = * introduced species; 2 = C for Cluster, D for Dry forest, M for Moist forest, Rs for Riparian forest South, Rn for Riparian forest North; 3 = f for fleshy, d for dry; L for large (> 5 mm diameter), S for small (< 5 mm diameter); 4 = H for hard, S for soft; f for fleshy attachment; L for large(> 5 mm), S for small (< 5 mm); 5 = B for birds, M for mammal, Wa for water, Wi for Wind; + for observed on site (Adapted from Geldenhuys, 1996a).

Table 4.3: Summary of the fruit and seed characteristics of species within the sample

	Fruit Characteristics				
Seeds Characteristics	Fleshy-Large	Fleshy-Small	Dry-Large	Dry-Small	Total
Soft-Small	19	1	1	1	22
Soft-Large	12	1	0	0	13
Hard-Small	1	0	0	0	1
Hard-Large	2	0	2	0	4
Total	34	2	3	1	40

Four distinct species groups can be extracted from the species listed in ***Table 4.2*** in relation to their presence/absence in the forests patches and forest clusters (***Table 4.4)*** and their fruit and seed characteristics.

Most of the recorded species are bird and/or mammal dispersed (**Geldenhuys, 1989b, 1996a**; **Palgrave, 2002; Mucina *et al*., 2002**); Exceptions are *Buddleja saligna* with very small seeds mostly dispersed by wind; *Virgilia oroboides* could use a balistic mechanism and wind-dispersal could be from the shake of the branches that would release the seed from the open pods. Both mentioned species are also known to be dispersed by water.

A non-exhaustive list of birds and mammal that could potentially play a role in seed dispersal within the area, obtained from the literature and field observation (underlined names), include: Rameron pigeon (*Columba arquatrix*), Sombre bulbul (*Andropadus importunes*), Cape thrush (*Monticola rupestris*) and Cape White-eye (*Zosterops pallidus*), and mammals such as Chacma baboon (*Papio ursinus*), Vervet monkey (*Cercopithecus pygerythrus*), Cape porcupine (*Hystricomorph hystricidae*), Bush pig (*Potamochoerus larvatus*) and Bushbuck (*Tragelaphus scriptus*). The list is merely indicative and should be verified with more detailed observation.

Table 4.4: Summary of species distribution groups in terms of their fruit-seed characteristics

Group 1: combined for the three forest types / Present in the clusters. 8 species: *Canthium inerme, Canthium mundianum, Celtis africana, Gymnosporia buxifolia, Maytenus accuminata, Rapanea melanophloeos Rhoicisus tomentosa* and *Vepris lanceolata*
Fruit type: Drupe 37.5%, Capsule 25%, Berry 37.5%; **Fruit texture**: Fleshy 100%; Fruit size: Large 100 %
Seed texture/size: Soft -Large 62.5%, Soft-Small 37.5%
Group 2: Confined to forest patches / present in forest clusters. **16 species**: **Acacia mearnsii; Apodytes dimidiata, Brabejum stellatifolium, Buddleja saligna, Diospyros glabra, Diospyros whyteana, Ilex mitis, Kiggelaria africana, Melia azedarach*, Ocotea bullata, Olea eur. africana, Olinia ventosa, Rothmannia capensis, Solanum mauritianum*, Scolopia mundii, Virgilia oroboides*

Fruit type: Drupe 18.8%, Capsule 12.5%, Berry 43.7%, Pod 12.5%, Nut 12.5%; **Fruit texture/size**: Fleshy Large 81.3%, Dry-Large 12.5%; Dry-Small 6.2%
Seed texture/size: Soft- Small 43.8%, Soft-Large 31.2%, Hard-Large 25%
Group 3: Present in forest patches / absent in clusters. 10 species: *Cassine peragua, Cussonia spicata, Curtisia dentata, Eucalyptus sp*, Grewia occidentalis, Hartogiella schinoides, Pittosporum viridiflorum, Podocarpus latifolius, Pterocelastrus tricuspidatus, Scutia myrtina*
Fruit type: Drupe 30%, Capsule 30%, Berry 40%; **Fruit texture/size**: Fleshy-Large 80%, Fleshy-Small 10%; Dry-Large 10%
Seed texture/size: Soft-Small 50%, Hard-Small 10%; Soft-Large 40%,
Group 4: Absent in forest patches / present in forest clusters. 6 species: *Halleria lucida, Lantana camara*, Metrosideros angustifolia, Searsia angustifolia, Searsia pyroides, Searsia tomentosa.*
Fruit type: Drupe 16.7%, Capsule 16.7%; Berry 66.6%; **Fruit texture/size**: **Fleshy-** Large 100% **Seed texture/size**: Soft-Small 83.3%; Soft-Large 16.7%

4.6 Discussion

4.6.1 Clusters: main seed sources of cluster expansion at relative short distance from seed sources.

In general, regeneration around the clusters showed similarities with species composition of the forest clusters. These results confirm what was expected, i.e. that (1) forest clusters would expand toward the rest of the Black wattle stand, and (2) they would constitute the main seed sources for their expansion. They are in line with reports in the literature about forest recovery through succession in which shade tolerant indigenous forest tree and shrub species establish in clusters under the closed canopy of early successional pioneer stands of light-demanding species, which will then favour regeneration of more late successional species (**Clements, 1936; Geldenhuys, 1996b, 2008, 2010; Hooper *et al.*, 2004**).

Different patterns were observed in terms of the distance of expansion of regeneration from the clusters, and they could be explained in terms of mature species present within the forest clusters. The first scenario showed a decrease in regeneration with increasing distance from the cluster. This scenario related mainly to clusters dominated by species such as *Celtis africana, Gymnosporia buxifolia*, *Rapanea melanophloeos* and *Vepris lanceolata.* It was more visible in the Proximal zone of the stand where most of the large and well established clusters have been identified to contain many remnant indigenous trees. Following the nucleation succession model of **Yarranton and Morrison (1974)**, remnant trees are said to play an accelerative role in the succession process (**Guevara *et al*., 1986; Finegan, 1984; Keeton & Francklin, 2005**). This scenario suggests a relatively low dispersal activity since not many seeds were moved far from the clusters. The second scenario showed increasing regeneration with increasing distance from the cluster. This scenario related to clusters in the Intermediate and Distant zone. The observed pattern seemed to be influenced by species such as *Canthium inerme* and *Maytenus acuminata*. The third scenario showed no distinct pattern and was observed around cluster dl348 in the Distant zone. It is characterised by a lack of regeneration of the dominant species of the clusters (*Ocotea bullata* and *Olinia ventosa)* which could be explained by the early stage of the succession in the Distant zone with a high density of the black wattle stand and very low light infiltration. The tendency of increasing of dissimilarities in regeneration as clusters approach the Distant zone, suggests that their expansion in the faraway zone depended on external contributions. The expansion seems to vary strongly with species. , and that would be important to develop a better understanding of the behaviour of individual species in terms of their fruit or seed characteristics and the related dispersal modes.

4.6.2 Fruit-Seed characteristics as determinant factors for establishing forest clusters within the stand.

Even though the sites were composed of different forest types, from riparian to dry to moist forest patches, the majority of species were described as widespread species and could be recorded in all three forest types. The assessment of fruit-seed characteristics of those species, summarized in ***Table 4.4*** showed that most species that were common to the forest patches and to the forest clusters had large fleshy fruit but 37.5% had soft small seeds that in general, confer them the ability to easily colonize new areas (**Geldenhuys, 1996a**)

Only few species with hard seeds were counted within the second group of ***Table 4.4***. The two species with dry pods with dry hard seeds are *A mearnsii* and *V. oroboides*. Both are known as light-demanding pioneer species. *Virgilia oroboides* was recorded just once in moist forest and once in the Distant zone of the Black wattle stand. The two other species with hard seeds were *Olinia vintosa* and *Diospyros glabra* but both have fleshy fruit and have a low presence within the Black wattle stand. Their presence in the clusters relate to they being eaten by baboons and spread in that way and dropped in baboon faeces (***Table 4.2***).

The reason why the third group of species are absent from the forest clusters is not clear. Most of those species (*Cassine peragua, Cussonia spicata, Curtisia dentata, Grewia occidentalis, Hartogiella schinoides, Podocarpus latifolius and Scutia myrtina*) have large fleshy fruits and 50 % had soft small seeds. The large fruits may be too large to be dispersed by the smaller birds, but they can be eaten by the Rameron pigeon, some other intermediate-sized bird's area and by baboons. *Cussonia spicata* has relatively small fleshy drupes and could be dispersed by a variety of birds (**Geldenhuys, 1993b**). *Pittosporum viridiflorum* capsules open to expose the small orange seeds and are often dispersed by a variety of birds, but in the study area they may be a too distant source for dispersal into the Black wattle stand. For more distant dispersal the frugivorous birds need to swallow the whole fruit or at least the seeds from very large fleshy fruit (**Geldenhuys, 1993b**). Sometimes when mammals such as the baboon and bush pig eat the fruit they may destroy the seed (such as of *Podocarpus latifolius* as shown by Geldenhuys, 1993a), but often some seeds escape destruction (**Geldenhuys, 1996a**). Several of the species in this group are associated with the dry patches (***Table 4.2***), with most likely very limited exchanges of seeds taking place between dry forest patches and the forest clusters. Dry forest patches occur south of the river at some distance from the river, with much human activity in the transition zone between the Dry forest patches and the Black wattle stand across the river. Physical obstructions and human activities have been listed among obstacles or limitations of seed dispersal (**Hardwick *et al*., 1997; Neuschulz *et al*., 2011**)

The fourth group of species (only recorded in the forest clusters) generally has large fleshy fruits with mainly small soft seeds. *Halleria lucida* is present in low numbers in the moist forest but was not recorded within the sampled plots. *Searsia angustifolia, S. pyroides* and *S. tomentosa* are more related to the drier forest margins and are dispersed by a variety of small birds and baboons. *Metrosideros angustifolia* grows along stream banks, often within the Fynbos biome, the species is light-demanding and with many-seeded small dry capsules (maybe wind and water-dispersed). *Lantana camara* is an invasive introduced species and has escaped from gardens through dispersal by a variety of birds. Most of the species within the group are known to be woody shrubs and early pioneer species during forest succession (**Geldenhuys 1993b; Lugo, 1997**).

4.6.3 Dispersal agents: Contributing factors for cluster establishing forest clusters within the stand

Frugivorous animals disperse up to 90 % of tropical tree species and between 30 % and 50 % of tree species in temperate zones (**Howe** and **Smallwood, 1982**). Large frugivorous mammals are also expected to disperse a wider range of fruit and seed sizes than smaller frugivors (**Wilson & Downs, 2012**).

The results of this study show a near dominance of large fleshy fruit with small soft seeds suggesting that there are sufficient species that potentially can colonise the Black wattle stand. It is then comprehensible that birds and mammals constitute the major dispersal agents for this site. The fleshy part of the fruit or seed of most fruits is large enough to attract birds and mammals. It is generally said that in Africa, frugivorous birds play a more important role in forest seed dispersal than mammals and other mechanisms (**Medellin & Gaona, 1999**; **Otsamo, 2000**; **Wilson & Downs, 2012**) and in the Buffeljagsriver area there are several bird species that can contribute to the dispersal of forest species. The role of the Rameron pigeon and baboons was just more obvious and more detailed observation would be needed to understand this dispersal process in the establishment and development of forest clusters within the wattle stand. The irregular flowering and fruiting phenology of many species may also play a role in their less active colonisation within the Black wattle stand (**Geldenhuys 1996a**)

4.7 Conclusion

Forest clusters in the stand play a major role as a seed source of the surrounding regeneration. They have been found main seed sources for the expansion of well-established forest clusters in the study. In general, quantity of regeneration decreased with distance from forest clusters.

Most of the species recorded in the forest clusters were found with seedlings in the surrounding area, with the exception of species such as *Ocotea bullata* and *Olinia ventosa*. Both species generally produce small numbers of fruit, with infrequent and irregular production of large numbers of fruit, and their relatively large fruit limit their dispersal over longer distances, except by agents such as the Rameron pigeon (**Geldenhuys, 1996b**).

Compiling the list of woody plant species from the area, with their associated fruit and seed characteristics based on literature, field observations together with information on the faunal diversity of the area as potential seed dispersal agents (**Palgrave, 1983; 2002**; **Smithers, 1983; Mucina *et al.,* 2002**) proved to be useful for the interpretation of the observed patterns in forest cluster development within the black wattle stand. Species with large, fleshy fruits with small soft seeds dispersed by birds and mammals dominated the species distribution through the Black wattle stand. However, some species with similar fruit-seed characteristics with good regeneration in the forest patches where they are present, such as *Hartogiella schinoides*, *Podocarpus latifolius* and *Pittosporum viridiflorum,* were absent in the forest clusters. The reasons of this absence are speculative, and may be outside the possible limitations of dispersal. Very few exchanges were observed between dry forest patches and forest clusters. The distances and existence of natural obstacles could explain this low interaction. Some isolated species were found within the newly establishing clusters in the zones distant from large clusters and neighbouring forest patches. Their seed sources are not clear. Further studies with a focus on first establishing and isolate species are needed to provide more conclusive interpretation.

4.8 References

Bullock, J.M.; Moy, I.L. 2004. Plants as seed traps: inter-specific interference with dispersal *Acta Oecologica* 25: 35–41.

Cain, M.L.; Milligan, B.G.; Strand, A.E. 2000. Long-distance seed dispersal in plant populations. *Am J Bot* 87:1217–1227.

Clements, F.E. 1936. Nature and structure of the climax. *Journal of Ecology* 24: 252-284.

Finnegan, B. 1984. Forest succession. *Nature* 312: 109–114.

Geldenhuys, C.J. 1989a. Environmental and biogeographic influences on the distribution and composition of the Southern Cape forests. Thesis presented for the degree of Doctor of Philosophy. Department of Botany, University of Cape Town Rondebosch.

Geldenhuys, C.J. 1989b. Biogeography of the mixed evergreen forests of southern Africa. Ecosystems Programmes Occasional Report no. 45. FRD, Pretoria.

Geldenhuys, C.J. 1993a. Reproductive biology and population structures of *Podocarpus falcatus* and *P. latifolius* in southern Cape forests. *Botanical Journal of Linnean Society* 112: 59-74.

Geldenhuys, C.J. 1993b. Floristic composition of the southern Cape forest flora with an annotated checklist. *South African Journal of Botany* 59: 26-44.

Geldenhuys, C. J. 1996a. Fruit/seed characteristics and germination requirements of tree and shrub species of the southern Cape forests. Report FOR-DEA 954. Pretoria, South Africa: CSIR, Division of Forest Science and Technology: 85 p.

Geldenhuys, C.J. 1996b. The Blackwood Group System: its relevance for sustainable forest management in the southern Cape. *South African Forestry Journal* 177: 7-21.

Geldenhuys, C.J. 1997. Composition and biogeography of forest patches on the inland mountains of the Southern cape. *Bothalia* 27(1): 57-74.

Geldenhuys, C.J. 2004. Concepts and process to control invader plants in and around natural evergreen forest in South Africa. Weed Technology 18: 1386-1391. Proceedings

IPINAMS Invasive Weed Symposium, November 3-7, 2003. Wyndham Bonaventure Ressort, F.T. Lauderdale, F.L.

Geldenhuys, C.J. 2008. Can I manipulate alien plant stands to rehabilitate natural forest? *Dendron* 40: 38-44.

Geldenhuys, C.J. 2010. Recovery of forest biodiversity by natural ecological processes through native or alien tree stands Paper presented at XIXth AETFAT Congress, Antananarivo, Madagascar.

Geldenhuys, C.J. 2011. Most invasive alien plants facilitate natural forest recovery – how is that possible? *SAPIA News* 18: 2-5.

Geldenhuys, C. J., P. J. Le Roux, and K. H. Cooper. 1986. Alien invasions in indigenous evergreen forest. *In* Macdonald, I.A.W.; Kruger, F.J. & Ferrar, A.A. (eds.). The Ecology and Management of Biological Invasions in Southern Africa. Cape Town, South Africa: Oxford University Press: 119–131.

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev*. 52: 107-145.

Guevara, S.; Purata, S.E. & Van Der Maarel, E. 1986. The role of remnant forest trees in tropical secondary succession. *Vegetatio* 66:77–84.

Hardwick, K.; Healey, J.; Elliott, S.; Garwood, N. & Anusarnsunthorn, V. 1997. Understanding and assisting natural regeneration processes in degraded seasonal evergreen forests in northern Thailand. *Forest Ecology and Management* 99: 203–214.

Hooper, E.R.; Legendre, P. & Condit, R. 2004. Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. *Ecology* 85(12): 3313-3326.

Howe, H.F. 1986. Seed dispersal by fruit-eating birds and mammals. In: Murray, D. (ed.). Seed dispersal. Academic Press, New York: 123–189.

Howe, H.F. & Smallwood, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.

Keeton, W.S. & Franklin, J.F. 2005. Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecological Society of America Ecological Monographs*, 75(1): 103–118.

Kindt, R. & Coe, R. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological studies. Nairobi: World Agroforestry Centre (ICRAF).

Loumeto, J.J. & Huttel, C. 1997. Understorey vegetation in fast-growing tree plantations on savanna soils in Congo. *Forest Ecology and Management* 99: 65-81.

Lugo, A.E. 1997. The apparent paradox of re-establishing species richness on degraded lands with tree monocultures. *Forest Ecology and Management* 99:9-19.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research* 27(2): 209–220.

Mascaro, J. 2011. Eighty years of succession in a non-commercial plantation on Hawai'i Island: Are native species returning? *Pacific Science* 65(1): 1–15.

Medellin, R.A. & Gaona, O. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica* 31: 478–485.

Mucina, L.; Geldenhuys, C.J.; Lawes, M.; Eeley, H.; Adie, H.; Graham von Maltitz, P.; Vink, D.; Fleming, G. & Bailey, C. 2002. Classification System for South African Indigenous Forests. Final draft: 1-9.

Nathan, R. & Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Ecology and Evolution* 15: 278–285.

Navarro, T.; Oualidi, J.; SghirTaleb, M.; Pascual, V. & Cabezudo, B., 2009 Dispersal traits and dispersal patterns in an oro-Mediterranean thorn cushion plant formation of the eastern High Atlas. *Morocco Flora* 204: 658–672.

Neuschulz, E.L.; Botzat, A. & Farwig, N. 2011. Effects of forest modification on bird community composition and seed removal in a heterogeneous landscape in South Africa. *Oikos* 120: 1371-1379.

Otsamo, R., 2000. Secondary forest regeneration under fast-growing forest plantations on degraded Imperata cylindrica grasslands. *New Forests* 19: 69–93.

Palgrave, K.C. 1983. Trees of Southern Africa. Struik Publishers, South Africa.

Palgrave, K.C. 2002. Trees of southern Africa. 3rd Edition. Struik Publishers, Cape Town, South Africa. 1212 pp.

Parrotta, J.A.; Turmbull, J. W. & Norman, J. 1997. Catalysing native forest regeneration on degraded tropical lands. Forest Ecology and Management 99: 1-7.

Polis, G.A.; Sears Anna, L.W.; Huxel, G.R.; Strong, D.R. & Maron, J. 2000. When is a trophic cascade a trophic cascade? *TREE* 15(11).

Schupp, E.W. 1993. Quantity, quality and the effectiveness of seed dispersal by animales. *Vegetatio* 107/108: 13-29.

Schupp, E.W. & Fuentes, Y.M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Écoscience* 2: 267-275.

Smithers, R.H.N. 1983. The mammals of the Southern African sub-region. University of Pretoria.

Snow, D.W. 1981. Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13: 1-14.

Tiffney, B.H. 1984. Seed size, dispersal syndromes, and the rise of the angiosperms: Evidence and hypothesis. *Annals of the Missouri Botanical Garden* 71: 551–576.

Tilman, D. 1994. The resource-ratio hypothesis of succession. *American Naturalist* 125: 827-852.

van Wyk, B. & van Wyk, P. 1993. Field Guide to trees of Southern Africa. In: Struik Chapman, C. A.; Chapman, L.J. 1999. Forest restoration in abandoned agricultural land: a case study from East Africa. *Conservation Biology* 13: 1301–1311.

Will+son, M.F. & Traveset, A. 2000. The ecology of seed dispersal. In: Fenner M (ed.). Seeds: the ecology of regeneration in plant communities. CAB Int, Wallingford: 85–110.

Wilson, A.L. & Downs, C.T. 2012. Fruit nutritional composition and non-nutritive traits of indigenous South African tree species. *South African Journal of Botany* 78: 30–36.

Yarranton, G.A. & Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation. *Journal of Ecology* 62: 417–428.

Zhishu, X.; Zhibin, Z. & Yushan, W. 2005. Effect of seed size on dispersal distance in five rodent dispersed fagaceous species. *Acta Oecologia* 28: 221-229.

Chapter 5:
Dynamics of the spread and establishment of natural forest species into a stand of *Acacia mearnsii*: Synthesis and forest rehabilitation guidelines

5.1 Introduction

It was noted that stands of invasive alien plants in the natural forest environment can facilitate the rehabilitation and recovery of such forests and challenged the general and global perception that such invasive species threaten the biodiversity and functioning of natural vegetation systems. The question was asked what the underlying processes are that drive natural forest species to invade or colonize stands of invasive alien stands, and whether those processes can be managed towards natural forest recovery. The study was developed to address some of those perceptions through a sound scientific concept towards sustainable and cost-effective management of invasive alien plant stands in the natural forest environment in South Africa.

The study was carried out at Buffeljagsrivier in South Africa with the aim of developing an understanding of the dynamics of colonization and establishment of natural forest species into a 90-ha stand of the invasive alien plant species *Acacia mearnsii* (Black wattle) along the river. Fieldwork has been conducted between 2011 and 2012, and data were analysed to address four specific objectives. This chapter provides a synthesis of the findings and gives some guidelines on rehabilitation of such invasive stands towards natural forest recovery. It presents a summary of the main findings in relation to the concept and specific objectives of the study, followed by a discussion and general management guidelines. It concludes with challenges and potential further studies.

5.2 Study concept

The overall concept was that invasive alien plant species are intolerant of shade, cannot establish under the canopy of such stands but facilitate and nurse the establishment and recovery of shade-tolerant natural forest species towards regrowing forest. The main objective was to develop an understanding of the dynamics of the spread and establishment of natural forest species in a large stand of the invasive introduced Black wattle along the Buffeljagsrivier. The research focused to answer five questions relative to four specific objectives (Figure 5.1): **(1)** Can natural forest species establish under a stand of Black wattle**?** **(2)** Are species from all types of neighbouring forest patches potential seed sources for the developing forest clusters**?** **(3)** Are the establishing forest clusters secondary sources of seed for the expansion of the clusters into the surrounding Black wattle stand**?** **(4)** What fruit/seed characteristics and dispersal mechanisms determine the potential of natural forest species to spread into and establish within the Black wattle stand**?** **(5)** How useful is the obtained information and knowledge to improve forest rehabilitation through manipulation of the stands of invasive alien tree species**?**

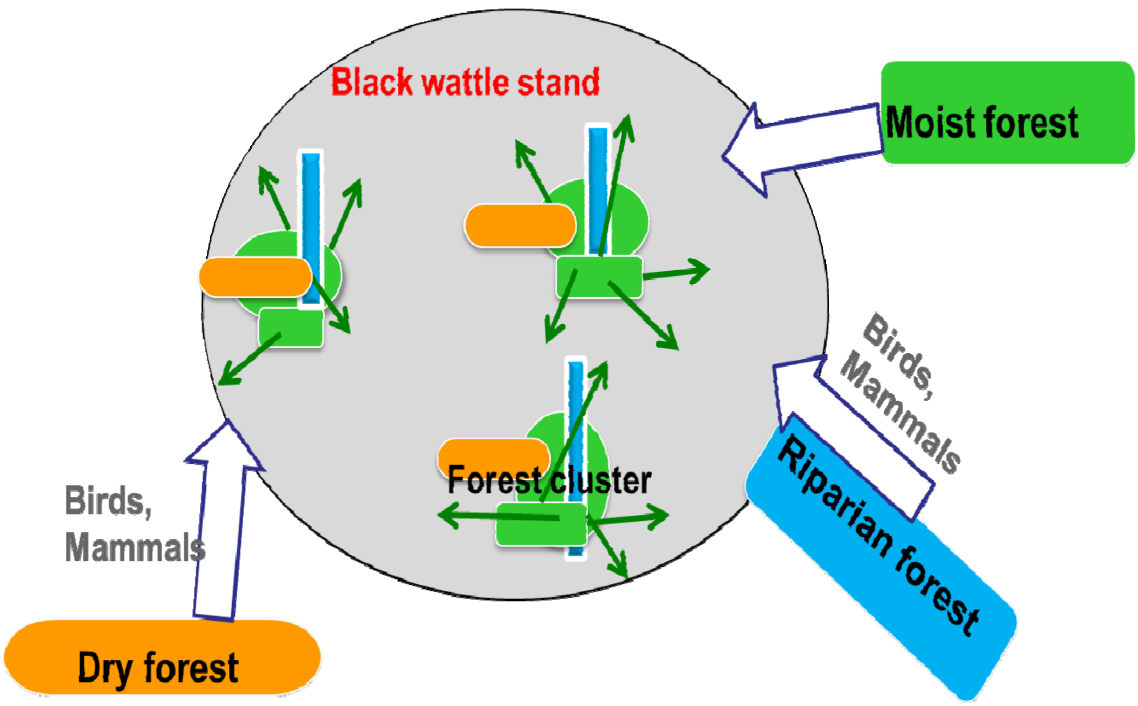


Figure 5.1: The conceptual framework of the study to address five mainresearch questions (Adapted from Atsame-Edda & Geldenhuys, Poster 2011).

5.3 Summary and main findings

5.3.1 Chapter 2

The first objective was achieved, and the answer to question (1) is yes. A total of 329 clusters of natural forest species were identified and mapped as evidence of the establishment of indigenous forest species within a Black wattle stand at Buffeljagsrivier. Large forest clusters (with ten or more reproductively mature natural forest species) were more abundant in the zone closer to the adjacent forest patches. The number of small forest clusters (one to three mature trees) increased with increasing distance from adjacent forest patches. The results showed that the mono-specific stand of the invasive alien Black wattle does not prevent the natural forest species to colonize and reclaim the area over time. The size and distribution of the forest clusters through the Black wattle stand suggest that forest succession processes are shifting the vegetation gradually from the light-demanding Black wattle stand to a mixed stand with diverse indigenous species. Species diversity increased towards 28 species of trees and shrubs belonging to 20 families.

5.3.2 Chapter 3

The second specific objective has been met. The answer to question (2) was not clear. The final conclusion was that every forest patch type contributes to a greater or lesser degree to the development of forest clusters within the Black wattle stand. Three main forest types (Dry, Moist and Riparian) differ in their general characteristics and site conditions, and this was supported by the ordination analyses: aspect, slope and canopy closure correlated with patterns in species distribution among communities. The developing forest clusters within the Black wattle stand relate more to Riparian forest South and North in slope and mean stem diameter. Forest tree regeneration dominated the ground cover of the forest clusters, as well as for Dry, Moist and Riparian North forests. The crown cover was found relatively closed in the Black wattle stand.

In terms of species composition, the tree main forest types were separated into 10 sub-groups (communities):

- Moist forest presented three communities G1a, G1b and G1c dominated respectively by *Hartogiella schinoides, Olinia ventosa* and *Rothmannia capensis*.
- Dry forest had two communities: G3a dominated by *Olea europaea africana* and G3b dominated by *Gymnosporia buxifolia*.
- Both Riparian forest North and South were grouped into group G2 with five communities: G2a dominated by Black wattle and *Rapanea melanophloeos*; G2b dominated by *Vepris lanceolata*; G2c dominated by *Celtis africana* and *V. lanceolata*; G2d dominated by *C. africana* and *Canthium inerme*; and G2e dominated by *V. lanceolata* and *C. inerme*.
- Plots from the forest clusters were all grouped within Riparian forest (G2): four in G2a, three in G2b, and one each in G2d and G2e. They were absent from the Moist forest (G1) and Dry forest (G3) groups.

The two main invasive species present on the site (Black wattle and Bugweed (*Solanum mauritianum*) were almost absent from the closed-canopy Moist and Dry forest patches.

However, many of the natural forest species occurred across the different identified groups/sub-groups. In general, small trees (5-20 cm DBH) dominated the stem diameter distributions for all the important species over all communities. Many species, both canopy and sub-canopy species, had an inverse-J shaped stem diameter distribution, with many small stems and gradually fewer larger stems, indicating a good regeneration across the communities. Two moist forest canopy tree species, *Olinia ventosa* and *Apodytes dimidiata*, showed the opposite trend within community G2a with Riparian forest North and forest clusters. This could relate to a delay in regeneration from the local parent trees because the parent tree first has to mature before regeneration can occur.

Both riparian forest patches were more similar to forest clusters in their species composition than to Moist forest and Dry forest patches. Therefore, the first reaction would be to consider Riparian forest patches to be the main seed sources for the developing forest clusters in the Black wattle stand. However, the large-sized stems of common species were not significantly different between Riparian forest patches and forest clusters. This may suggest that those large-sized stems in the forest clusters could be part of remnant forest patches. The role of such trees as seed sources could, however, be considerable. In the same logic, some common moist forest canopy and sub-canopy species with large trees, were mostly absent from the forest clusters. Similarly, some dry forest sub-canopy tree species with good regeneration were also absent from the forest clusters to exclude Moist and Dry forest patches as major seed sources. However, detailed evaluation of species importance values and stem diameter distributions show that some important Moist and Dry forest species are present in the forest clusters. The Moist forest species are *A. dimidiata, O. bullata* and *O. ventosa*, and the Dry forest species are *O.africana* and *G. buxifolia*. That means that every type of forest patch contributes to a greater or lesser degree to the development of forest clusters within the black wattle stand.

5.3.3 Chapter 4

The third objective was met satisfactorily through answering the stated questions. The answer to question (3) is yes, but there is regeneration present that comes from other sources, and the pattern of expansion depends on the contributing tree species.

Mature trees of well-established forest clusters were the main seed sources for the cluster expansion in all directions. Two points supported this conclusion:

(1) Analyses of the shape of the individual total forest cluster suggest expansion of several individual small clusters resulted in fusion after a certain period;

(2) Significant similarities between species composition of the forest clusters and species composition of the seed shadow regeneration.

Three different patterns were observed in terms of the distance of expansion of regeneration from the clusters. Scenario one showed a decrease in regeneration with increasing distance from the forest cluster margin, in forest clusters dominated by *C. africana, G. buxifolia, R. melanophloeos* and *V. lanceolata*. It was more visible in the Proximal zone of the stand where most of the large and well established clusters have been identified to contain many remnant indigenous trees. This scenario would suggest a relatively low dispersal activity since not many seeds were moved far from the forest clusters. Scenario two showed increasing regeneration with increasing distance from the forest cluster, in clusters dominated by *C. inerme* and *M. acuminata*. Scenario three showed no distinct pattern and was observed around one cluster in the Distant zone, with a lack of regeneration of the dominant species of that cluster (*O. bullata* and *O. ventosa).* It could be explained by the early stage of the succession in the Distant zone with a high density of the Black wattle stand with low light conditions. Contributions of species from elsewhere, most likely from adjacent forest patches, were recorded within the young developing forest clusters.

The answer to question (4) is that the main contribution is from fleshy fruit with soft small seeds dispersed by birds and mammals. The limited to no movement of many Moist and Dry forest canopy and sub-canopy species could be attributed to the predominance of species with large-sized fruit, as such fruit can only be moved by mammals and some larger birds into the Black wattle stand. In general, the presence of a species in the forest clusters was more depending on the species characteristics than the proximity to the stand.

The 40 species recorded within the Buffeljagsrivier site, including the two main invasive species (Black wattle and Bugweed) present a wide range of fruit and seed characteristics. Four main groups of woody species were identified, based on their presence/absence in forest patches and forest clusters (***Table 4.4***). Group one included eight species that were common in the forest patches and present in the forest clusters. Their fruit types were dominated by large fleshy drupes and berries. Their seed types were dominated by soft, large seeds (62.5 %). Group two included 16 species that were confined to particular forest patches and present in the forest clusters. Their fruit types were dominated by fleshy, large berries and soft, small seeds. Group three included ten species that were present in the forest patches but absent from the forest clusters. Their fruit types were dominated by fleshy, large berries with relatively important amont of soft-large seeds. Group four included six species that were absent from the forest patches but present in the forest clusters. Their fruit types were dominated by fleshy, large berries and soft, small seeds.

The majority of recorded woody species were most likely dispersed by birds and mammals. A non-exhaustive list of birds and mammals that could potentially play a role in seed dispersal within the area was developed from the literature. However, field observations verified the role of one bird, Rameron pigeon (*Columba arquatrix*), and the mammal Chacma baboon (*Papio ursinus*) (***Figure 5.2***).

Figure 5.2: Chacma baboon and their droppings containing tree seeds viewed in the Black wattle stand at Buffeljagsrivier during field work

5.4 Discussion and rehabilitation guidelines

The high rate of invasiveness of Australian *Acacia* species in South Africa, the high costs involved with their control and the search for cost-effective and sustainable methods for their eradication (**Kaplan *et al.*, 2011**), require alternative strategies to deal with the problem in different situations (**Wilson *et al*., 2011; Geldenhuys, 2013**).

The general results from this study are an encouraging contribution towards cost-effective and sustainable strategies within the forest environment. The Buffeljagsrivier forests are currently not in a process of being invaded, but in the process of recovery. The existing natural forest stands are free of invasive species. The establishing forest clusters and regeneration of natural forest species within the Black wattle stand clearly indicate that the indigenous species are colonizing the Black wattle stand. However, it is not clear how long it would take for the Black wattle stand to become regrowth forest. The recovery of natural forest may eventually be completed, but this could take several years (as in some large clusters) to a few decades (**Geldenhuys, 1996**) or centuries as with the indigenous legume, *Virgilia divaricata* (**Geldenhuys, 1994**), or by successive disturbances a mixture of indigenous and introduced species might establish in the long run, where Black wattle takes over the role of a pioneer species in a typical succession scenario. It is possible that through specific stand manipulation actions one could do a considerable conversion the regrowing natural forest within a 10-year period.

However, results of this study should lead to a reconsideration of the mind-sets on invasive alien species in the forest environment. Many forests considered as invaded throughout the country could be in a stage of recovery as at Buffeljagsrivier.

It is recommended that before embarking into those costly and not often effective systematic eradications of the invasive plant stands that management plans should consider in the first place the type of investigation done at the Buffeljagsrivier Black wattle stand **(Chapter 2)** that may lead to a different assessment of what to do.

Within stands of invasive species, where regrowth natural forest is the rehabilitation objective, from this study, the guidelines are given in tree steps: (1) Investigation phase, (2) Planning phase and (3) Action phase.

- In the Investigation phase, the objective is to get the knowledge and understanding of the ecology of natural forest species involved in the rehabilitation site: Knowing their existence, determining their light status and identifying their main seed sources and associated dispersal mechanisms. It is recommended that, once the succession phase of the invasive stand is identified, the information on the light requirements and the dispersal mechanisms of both the invasive and the understorey species be determined to enable a better choice of the appropriate rehabilitation approaches (**Geldenhuys, 2011**).
- The Planning phase ought to determine the development stages of natural forest species throughout the stand of the invasive species; map them so that different interventions can be planned accordingly. Natural forests have intrinsic adaptations to recover from diverse disturbance regimes, including plant invasions (**Geldenhuys, 2010**). During natural forest succession towards recovery, the indigenous species establish in clusters. The improved ecological conditions in the clusters favour the establishment of new species and gradually the clusters expand. Their expansion is accompanied by progressive regression of the invasive stem density (**Geldenhuys, 2013**). This progressive evolution of single species grouped into forest clusters and forest clusters to expand for larger stand till regrowth natural forest is described as stage development in the process which are managed differently. A good framework would include a map showing clearly the different development stages.
- The Action phase gives orientation on the execution of the MIPS approach. Rehabilitation tasks are given with regards to each development stage. Instead of the traditional systematic clearing of invasive stems approach, here rehabilitation actions can be focused on those points of initial recovery (developing forest clusters)

(**Geldenhuys, 2013**). During these actions, the ground cover should not be disturbed, and light conditions above the developing cluster can be slightly improved through selective thinning to also provide for more growing space. For many, the rehabilitation practice implies planting. Even though the practice is generally associated with high costs and often with poor results, the tendency to plan forest rehabilitation with planting as a main approach is still common (**Binns, *et al*., 2001**). The MIPS approach described and promoted by **Geldenhuys (2013)**, suggests planting only in sites with arrested succession. The establishment of nurseries is seldom required. This study has shown that *in situ* seedlings may be present in abundance. They could be transplanted locally into the desired place immediately (during rainy conditions in the rainy season). This excludes the need for all nursery-related costs (construction, material, maintenance and transport). Seed sources of indigenous forest species on site should be investigated to make the MIPS approach successful. Seed and seedling banks and adjacent forests are the recommended potential sources for the recovery process. This is where information on seedling sources, shade-tolerance of species, initially establishing species, and main dispersal systems will be useful.

At Buffeljagsrivier the majority of recorded indigenous forest species were shade tolerant, had fleshy fruits with soft small seeds, and were dispersed by birds or mammals. Once established, forest clusters expand. Seeds for regeneration come from the closest cluster. No high dispersal activities were noticed and regeneration decreased with increasing distance from the clusters. Most common species of the site were also common in the regeneration. Where access to the stand for cattle and wildlife was easy, the ground cover was disturbed with very high intensity of browsing. In such cases, it is recommended that the rehabilitation site be fenced. Alternatively, stems and branches of cut stems of the overhead stand can be packed around seedling banks to constrain browsers; moreover, the procedure seems to have an accelerating effect on regeneration of forest species (***Figure 5.3***).

Figure 5. 3: Indigenous seedlings amongst packed branches in the wattle stand at Buffeljagsrivier.

A general conceptual framework to guide the MIPS approach is shown in ***Figure 5.4***. In ***Figure 5.5*** the Buffeljagsrivier study is used as an example. It could easily be adapted to any particular case.

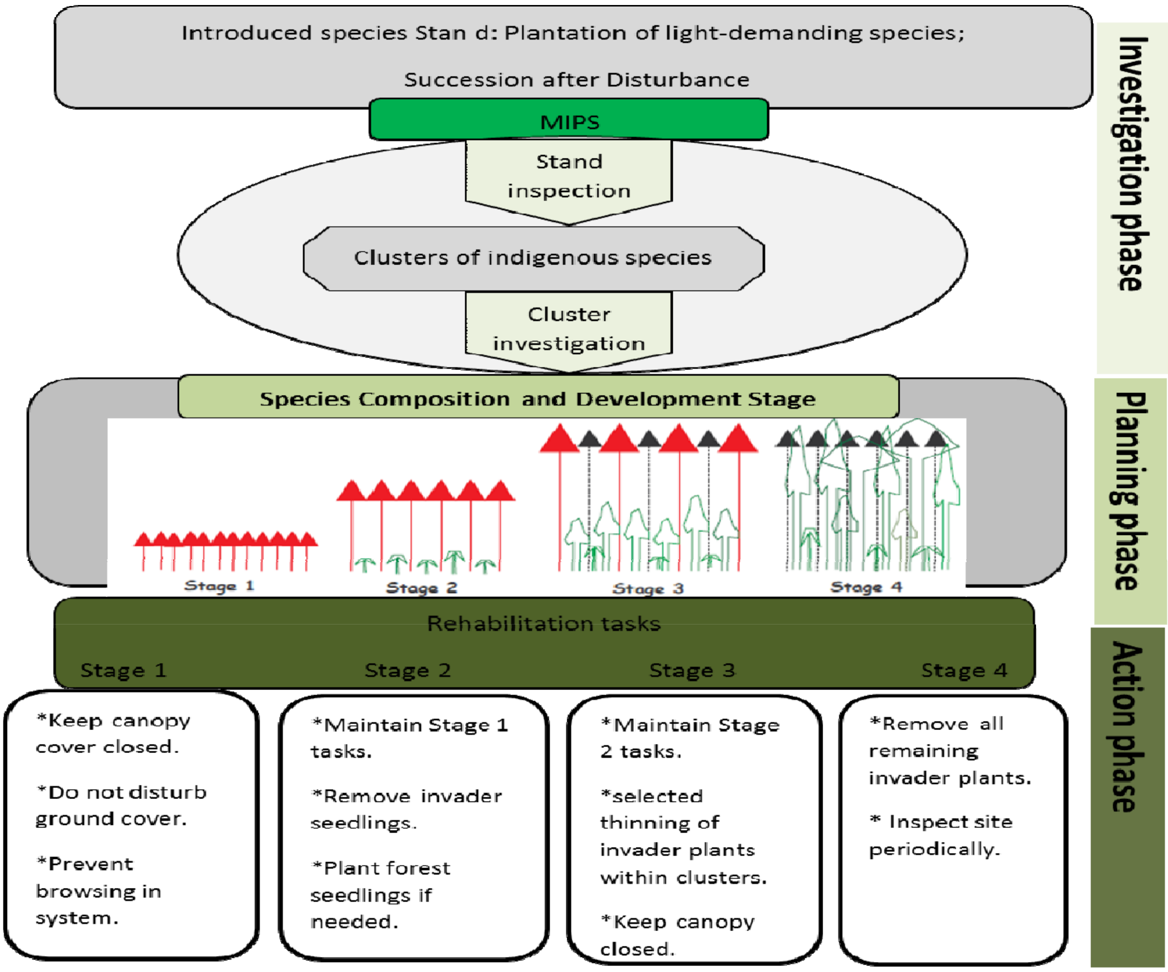


Figure 5.4: General conceptual framework for the MIPS approach to regrowth forest rehabilitation

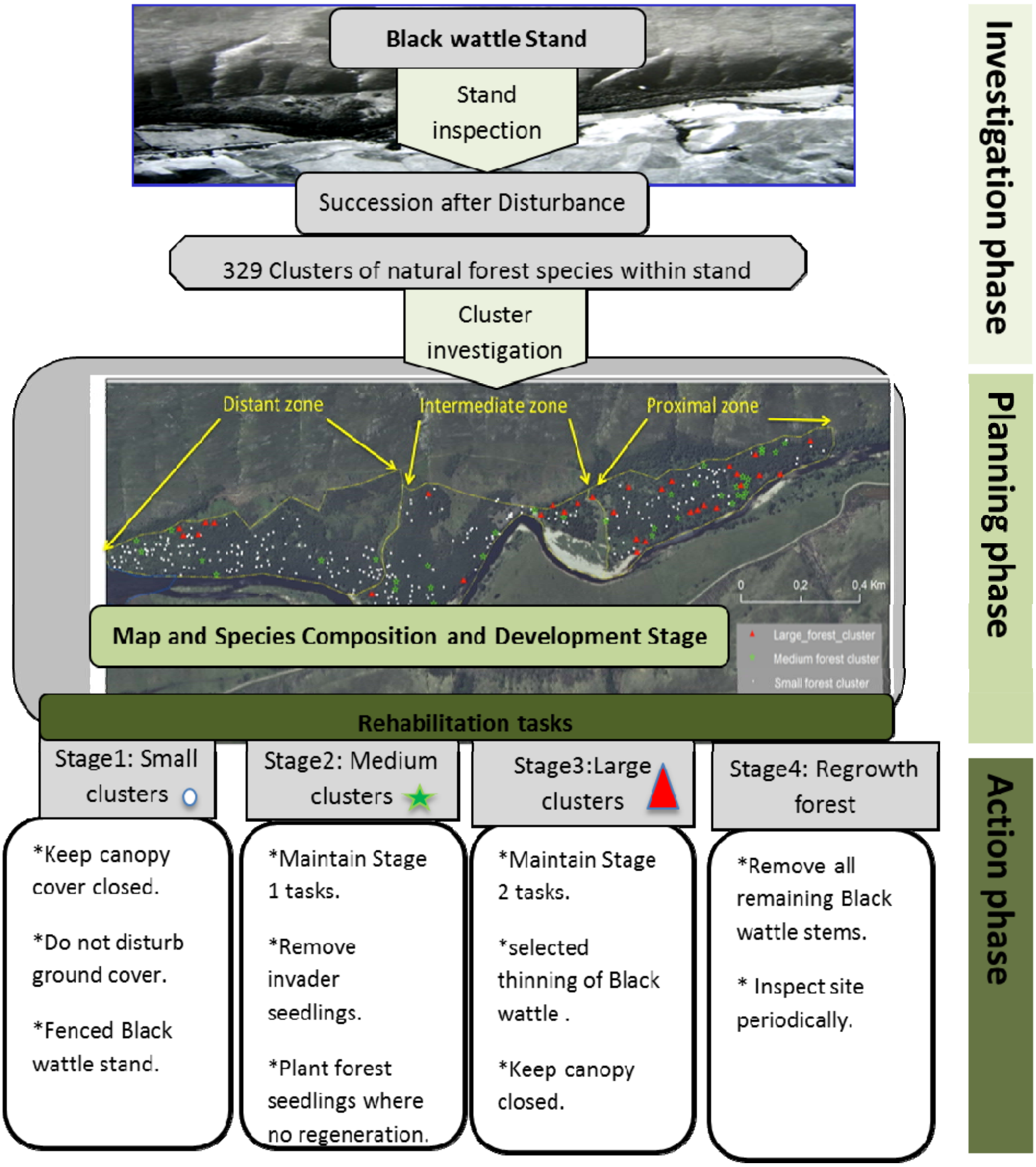


Figure 5.5: The MIPS conceptual framework adapted for application in this study

5.5 Challenges and potential further studies

- The coexistence of different forest types in diverse conditions makes the Buffeljagsrivier an interesting site for multi-research studies.

- The historical change in land used of this area is not well known. Information on this aspect would have helped to better understand the type of historical disturbances and the results of the current rehabilitation.

- The data were collected under conditions where the level of browsing was very high and this could have influenced some of the results, particularly in terms of sampled regeneration. The Black wattle stand was fenced since June 2012. This would provide the opportunity for further studies, as has already been initiated through exclosure plots.

- Natural forest recovery through natural thinning of the Black wattle stand can take long. The MIPS approach can speed up the process. A study of the influence of the MIPS approach on the rate of recovery of regrowth natural forest over time can be a useful contribution.

- The current study listed potential dispersal agents involved in this recovery process. Further longer-term studies are needed to provide more specific and accurate information on the dispersal systems involved for more explicit results.

- The conceptual framework to guide rehabilitation is a proposal. It should be tested in different sites and the results scientifically evaluated during the recovery process. The unpredictable characteristics of nature should always be considered. It is suggested that the basic principles of the MIPS approach should be understood and the application actions be adapted according to observations in different situations.

5.6 Conclusion

Considering the many plant invasion issues in South Africa and the high costs related to their control, the MIPS approach in the forest environment would likely emerge as a cost-effective approach to suppress and control alien plant invasions in the natural forest environment. The general concept is the careful assistance of a natural process; management would need to consider the time factor and the necessity of regular monitoring in order to adjust the actions with regards to the unexpected characteristic of nature. The Buffeljagsrivier MIPS project could serve as pilot site.

5.7 References

Binns, J.A., Illgner, P.M. & Nel, E.L. 2001. Water shortage, deforestation and development. South Africa's Working for Water Programme. *Land degradation and development* 12: 341-355.

Geldenhuys, C.J. 1994. Bergwind fires and the location pattern of forest patches in the southern Cape landscape, South Africa. *Journal of Biogeography* 21: 49-62.

Geldenhuys, C.J. 1996. The Blackwood Group System: its relevance for sustainable forest management in the southern Cape. *South African Forestry Journal* 177: 7-21.

Geldenhuys, C.J. 2010. Recovery of forest biodiversity by natural ecological processes through native or alien tree stands. Paper presented at XIXth AETFAT Congress, Antananarivo, Madagascar.

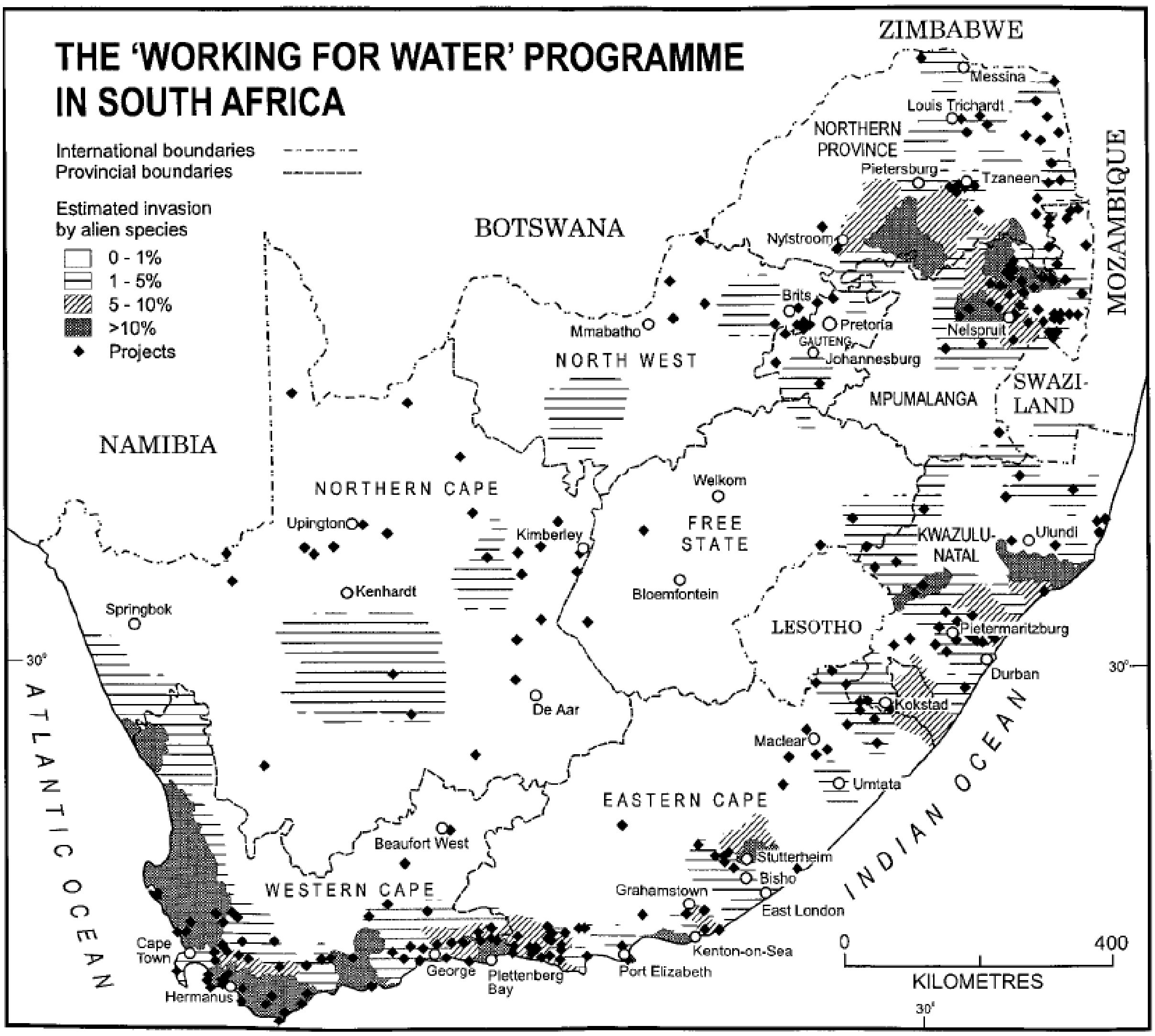
Geldenhuys, C.J. 2011. Most invasive alien plants facilitate natural forest recovery – how is that possible? *SAPIA News* 18: 2-5.

Geldenhuys, C.J. 2013. Converting invasive alien plant stands to natural forest, nature's way: Overview, theory and practice In: Jose, S, Singh, Hp., Batish, D.R. & Kohli, R.K. (eds). Invasive Plant Ecology, CRC Press, Taylor & Francis Group, Boca Raton.: 217-237.

Kaplan, H., Van Zyl, H.W.F., Le Roux J.J., Richardson D.M. & Wilson, J.R.U. 2011. Distribution and management of Acacia implexa (Benth.) in South Africa: A suitable target for eradication? *South African Journal of Botany* 83: 23–35.

Wilson, J.R.U., Gairifo, C., Gibson, M.R., Arianoutsou, M., Bakar, B.B., Baret, S., Celesti Grapow, L., Dufour-Dror, J.M., Kueffer, C., Kull, C.A., Hoffmann, J.H., Impson, F.A.C., Loope, L.L., Marchante, E., Marchante, H., Moore, J.L., Murphy, D., Pauchard, A., Tassin, J., Witt, A., Zenni, R.D., Richardson, D.M., 2011. Risk assessment, eradication, containment, and biological control: global efforts to manage Australian acacias before they become widespread invaders. *Diversity and Distributions* 17: 1030–1046.

APPENDIX I: Map of invasive alien cover and WfW programme in South Africa (Source Binns *et al.*, 2001).



APPENDIX II GPS coordinates of the Black wattle stand sampled

Forest zone	Cluster	Size	Latitude	Longitude	slope	Elevation
E	BC003	1	20.580314	-34.000597	1	98.42
E	BC009	1	20.579529	-34.000433	2	108
E	BC020	3	20.578266	-34.001285	1	94.57
E	BC023	1	20.578131	-34.000995	1	94.33
E	**BC026**	3	20.577553	-34.001574	1	91.21
E	**BC048**	2	20.576301	-34.000722	1	95.53
E	**BC031**	1	20.577392	-34.000544	1	89.52
E	**BC072**	3	20.575199	-34.000942	2	102.02
E	**BC070**	3	20.575744	-34.001171	1	100.58
E	**BC036**	3	20.577376	-34.001887	1	101.06
E	**BC041**	1	20.577241	-34.000935	1	92.65
E	**BC038**	1	20.577256	-34.001605	1	91.93
E	**BC047**	2	20.576613	-34.001240	1	94.09
E	**BC059**	1	20.576031	-34.001788	1	97.45
E	**BC076**	1	20.575039	-34.001841	1	98.66
E	**BC078**	1	20.575285	-34.001638	1	100.82
E	**BC067**	1			1	104.66
E	**BC092**	1	20.574111	-34.002012	1	93.85
E	**BC095**	2	20.573476	-34.002694	1	92.65
E	**BC089**	2	20.573988	-34.001640	1	93.85
E	**BC068**	1			1	104.66
E	**BC080**	2	20.575028	-34.002619	1	100.34
E	**BC100**	2	20.574375	-34.002981	1	91.45
	BC101	3	20.574486	-34.003054		21.99
F	**BC113**	1	20.571414	-34.001803		91.21
F	**BC127**	1	20.568642	-34.002421	2	98.9
F	**BC134**	1	20.569005	-34.003159		102.5
F					1	
F	**BC131**	1				98.9
F	**BC139**	3	20568158	-34003783		97.21
F	**BC141**	1	20566344	-34003976		96.73
F	**BC150**	1	20566250	-34001664		103.46
F	**BC153**	1	20566132	-34002002		101.3
F	**BC159**	1	20566285	-34003932		97.69
F	**BC163**	1	20565516	-34003065		96.01
F	**BC170**	1	20565661	-34004019		102.02
F	**BC175**	2	20565170	-34004764		99.62
F	**BC177**	1	20564936	-34004406		97.93

Forest zone	Cluster	Size	Latitude	Longitude	slope	Elevation
F	**BC181**	2	20565357	-34004082		96.73
F	**BC182**	3	20565034	-34004182		97.69
F	**BC187**	1	20566221	-34004222		99.14
F	**BC0BF**	2				
G	**BC199**	1	20564412	-34003832	1	100.58
G	**BC209**	1	20564681	-34003427		102.02
G	**BC211**	1	20564872	-34003707		100.58
G	**BC217**	1	20565178	-34003489		99.62
G	**BC225**	1	20563197	-34003441		100.34
G	**BC227**	1	20563389	-34003682		102.25
G	**BC255**	1	20561693	-34002811		100.34
G	**BC251**	1	20561206	-34002964		105.14
G	**BC253**	1	20561562	-34003460		103.94
G	**BC236**	1	20562107	-34002168		100.82
G	**BC267**	1	20559153	-34003618		96.97
G	**BC268**	1	20558637	-34003224		94.57
G	**BC276**	1	20559735	-34002844		93.37
G	**BC277**	1	20559968	-34002912		91.93
G	**BC266**	1	20559554	-34003516		98.66
G	**BC270**	1	20558941	-34003229		93.61
G	**BC282**	3	20558779	-34002219		90.96
G	**BC281**	3	20559089	-34002229		93.37
G	**BC326**	2	20556432	-34002992		91.21
G	**BC327**	1	20556616	-34003068		90.48
G	**BC348**	3				

APPENDIX III: Field data collection forms

Field Form for Inventory: Buffeljagsrivier near the Dam Swellendam South Africa.

Date of assessment..............................Assessed by.......................

Compartment: ....

1 General description of location and environment

Forest ....**GPS**............S,............E Aspect......^{0} **elevation**......

Slope: Gentle........Steep.......Very steep........**General height**...........m

Canopy: (1-2-3-4-) **Understorey growth form**: grass.......Shrubs.......Trees regeneration...... Other.................**Wattle canopy cover**: closed.......open.....

2.\ Field form for measuring of clusters

Cluster	Tree N°	Axis position (X)	Distance perpendicular (Y)	Species	DBH	Seedling	Saplings	Pole

General comments

Field Forms for Inventory: Buffeljagsrivier near the Dam Swellendam South Africa.

Date of assessment...............................Assessed by.......................

Compartment: ....

General description of location and environment

Forest....................**GPS**......................S,.................E Aspect..............^{0} **distance**............

Slope: Gentle........Steep.......Very steep........**General height**............m **Canopy**: closed......open.....**Understorey**: open........medium dense.......dense.....**Form**: grass.......Shrubs.......Trees regeneration...... Other...................................**Wattle canopy cover**: closed.......open...........

Species composition- structure and regeneration

DBH of stems ≥5 cm DBH by species on 200 m^2 plot

Counts of stems <5 cm DBH by species on 50 m^2 sub-plot

Plot	Tree N°	Species	DBH	Specie	Seedling	Sapling	Pole<5cmdbh	browsin

General comments

APPENDIX IV: Species matrix used for relationship between forest patches cluster

Site	Acac mae	Apod dim	Brab ste	Cant ine	Cant mun	Cass par	Celt afr	Curt den	Dios gla	Dios why	Euca sp	Gymn bux	Hala luc	Hart sch
NL020	0	0	0	7	2	0	2	0	0	0	0	2	0	0
NL020b	7	0	0	3	0	0	1	0	0	0	0	1	0	0
NL048	9	0	0	0	0	0	1	0	0	0	0	3	0	0
NL070	10	0	0	0	0	0	4	0	0	0	0	6	0	0
IL101	0	0	0	5	0	0	1	0	0	0	0	0	0	0
IL139	14	0	0	7	4	0	0	0	0	0	0	0	0	0
IL139b	21	2	0	2	3	0	1	0	0	1	0	0	1	0
FM268	22	0	0	1	0	0	0	0	0	0	0	1	0	0
FL348	24	0	0	1	0	0	0	0	0	0	0	0	0	0
ML1P1	0	0	0	6	4	0	1	0	0	1	0	0	0	0
ML1P2	0	1	0	0	2	0	1	0	0	1	0	0	0	4
ML1P3	0	0	0	0	6	0	0	0	0	2	0	0	0	20
ML2P1	0	0	0	2	1	0	0	0	0	3	0	0	0	1
ML2P2	0	0	0	3	0	0	0	0	0	1	0	0	0	0
ML2P3	0	0	0	3	0	0	2	0	0	0	0	0	0	2
ML2P4	0	0	0	2	3	0	1	0	0	1	0	0	0	14
ML3P1	0	1	0	0	3	0	0	0	0	0	0	0	0	1
ML3P2	0	0	0	1	1	0	0	0	0	0	0	0	0	1
ML3P3	0	0	0	1	0	0	0	0	0	1	0	0	0	1
ML4P1	0	1	0	4	4	0	0	0	0	0	0	0	0	0
ML4P2	0	0	0	0	0	0	0	0	0	0	0	0	0	5
ML4P3	0	1	0	1	0	0	0	0	0	0	0	0	0	13
ML4P4	0	4	0	1	0	0	0	0	0	0	0	0	0	14
ML5P1	0	3	0	5	3	0	0	0	0	0	0	0	0	1
ML5P2	0	8	0	4	0	0	0	0	0	0	0	0	0	0
ML5P3	0	7	0	0	1	0	0	0	0	0	0	0	0	8
RNL1P1	0	0	0	1	0	0	4	0	0	0	0	2	0	0
RNL2P1	0	0	0	6	0	0	1	0	0	0	0	0	0	0
RNL3P1	1	0	0	0	0	0	0	0	0	0	0	1	0	0
RNL4P1	0	0	0	4	0	0	8	0	0	1	0	0	0	0
RNL4P2	1	0	0	2	0	0	2	0	0	0	0	0	0	0
RNL5P1	1	0	1	9	2	0	4	0	0	0	0	0	0	0
RNL6P1	1	0	0	14	0	0	6	0	0	0	0	2	0	0
RNL7P1	20	0	16	8	4	0	0	0	0	0	0	0	0	2
RNL8P1	15	0	0	4	0	0	0	0	1	0	0	0	0	15
RNL9P1	2	0	0	11	0	0	0	5	0	0	0	0	0	6
RNL10P1	25	0	0	2	14	0	2	0	0	0	0	2	0	0
RNL11P1	34	0	0	2	2	0	2	0	0	0	0	0	0	0
RSL3P1	1	0	0	1	0	0	1	0	0	0	0	5	0	0
RSL4P1	0	0	0	1	7	0	4	0	0	0	0	5	0	0
RSL4P2	0	0	0	2	0	0	6	0	0	0	0	1	0	0
RSL5P1	1	0	0	2	0	0	2	0	0	0	0	6	0	0
RSL6P1	0	0	0	0	0	0	4	0	0	0	0	0	0	0
RSL6P2	0	0	0	0	0	0	0	0	0	0	0	35	0	0
DL1P1	0	0	0	8	14	0	1	0	0	9	0	9	0	0
DL1P2	0	0	0	0	4	0	0	0	0	6	3	10	0	0
DL2P1	0	0	0	3	1	0	0	0	0	1	0	8	0	0
DL2P2	1	0	0	2	4	0	0	0	0	4	1	2	0	0
DL2P3	0	0	0	0	0	0	0	0	0	12	4	3	0	0
DL3P1	0	0	0	6	1	0	2	0	0	13	0	7	0	0
DL3P2	0	0	0	3	0	3	0	0	0	11	0	11	0	0
DL4P1	0	4	0	7	15	4	0	0	0	1	15	5	0	0
DL5P1	0	0	0	20	9	1	0	0	0	1	7	4	0	0
RSL1P1	0	0	0	2	0	0	5	0	0	0	0	0	0	0
RSL2P1	0	0	0	4	0	0	2	0	0	0	0	2	0	0

Site	Ilex met	Kigg afr	Mayt acu	Meli aza	Ocot bul	Olea afr	Olin ven	Pitt vir	Podo lat	Psid guj	Rapa mel	Roth cap	Rhus pyr	Scol mun	Sola mau	Vepr lan	Virg oro
NL020	0	0	0	0	0	0	0	0	0	0	2	0	0	0	6	0	0
NL020b	0	0	0	0	0	0	0	0	0	0	3	0	0	0	5	0	0
NL048	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	2	0
NL070	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
IL101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0
IL139	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	2	0
IL139b	0	0	1	0	0	0	0	0	0	0	8	0	1	0	0	0	0
FM268	6	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
FL348	0	0	1	0	1	0	8	0	0	0	1	0	0	0	0	0	1
ML1P1	0	0	0	1	0	0	0	0	0	0	3	17	0	0	0	3	0
ML1P2	0	0	0	0	0	0	1	0	0	0	1	4	0	0	0	2	0
ML1P3	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0
ML2P1	1	0	0	0	1	0	1	0	2	0	4	19	0	0	0	4	0
ML2P2	0	0	0	0	0	0	0	1	0	0	0	5	0	1	0	2	0
ML2P3	0	0	0	0	3	0	0	0	1	0	1	6	0	0	0	3	0
ML2P4	0	0	0	0	3	0	1	0	6	0	5	0	0	0	0	1	0
ML3P1	0	0	0	0	0	0	4	0	5	0	0	5	0	0	0	0	0
ML3P2	0	0	0	0	0	0	1	0	1	0	0	11	0	1	0	0	0
ML3P3	1	0	0	0	0	0	0	0	5	0	1	26	0	0	0	1	0
ML4P1	0	0	0	0	0	0	0	1	10	0	4	0	0	1	0	0	0
ML4P2	0	0	2	0	2	0	2	0	6	0	5	13	0	0	0	0	0
ML4P3	0	0	2	0	3	0	2	0	0	0	1	1	0	0	0	0	0
ML4P4	0	0	1	0	1	0	6	0	0	0	3	0	0	0	0	0	1
ML5P1	0	0	3	0	1	0	1	0	6	0	2	16	0	1	0	0	0
ML5P2	0	0	0	0	4	0	0	0	8	0	1	13	0	1	0	2	0
ML5P3	0	0	2	0	6	0	2	0	3	0	1	1	0	1	0	0	0
RNL1P1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	6	0	0
RNL2P1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	0
RNL3P1	0	1	0	0	0	0	0	0	0	0	0	7	0	0	5	5	0
RNL4P1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1	0
RNL4P2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	1	0
RNL5P1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	4	0
RNL6P1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	2	0
RNL7P1	0	0	1	0	0	0	0	0	0	0	2	2	0	0	0	2	0
RNL8P1	1	0	5	0	0	0	1	0	0	0	2	1	0	0	0	0	0
RNL9P1	0	0	7	0	0	0	6	0	0	0	0	0	0	0	0	0	0
RNL10P1	0	0	1	0	0	0	0	0	0	0	15	1	0	0	0	1	0
RNL11P1	0	0	0	0	0	1	0	0	0	0	3	14	0	0	0	0	0
RSL3P1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	6	0
RSL4P1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RSL4P2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
RSL5P1	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	8	0
RSL6P1	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
RSL6P2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
DL1P1	0	0	0	0	0	7	0	9	0	0	0	0	0	0	0	0	0
DL1P2	0	0	1	0	0	18	0	18	0	0	0	0	0	0	0	0	0
DL2P1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
DL2P2	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
DL2P3	0	0	0	0	0	17	0	10	0	0	0	0	0	0	0	0	0
DL3P1	0	0	1	0	0	2	2	1	0	0	4	0	0	0	0	3	0
DL3P2	0	0	0	0	0	13	0	4	0	0	0	0	0	0	0	9	0
DL4P1	0	0	0	0	0	2	0	0	0	5	1	0	0	0	0	0	0
DL5P1	0	0	0	0	0	0	0	6	2	0	0	0	0	0	0	0	0
RSL1P1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
RSL2P1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0

Community group matrix used for ordination analyses.

Site	Acac mae	Apod dim	Brab ste	Cant ine	Cant mun	Cass par	Celt afr	Curt den	Dios gla	Dios why	Euca spp	Gymn bux	Halla luc	Hart sch	Ilex met	Kigg afr	Mayt acu	Meli aza	Ocot bul	Olea afr	Olin ven	Pitt vir	Podo lat	Psid guj	Rapa mel	Roth cap	Rhus pyr	Scol mun	Sola mau	Vepr lan	Virg oro
G1a	2	12	0	16	10	0	1	4	2	1	0	0	0	79	0	0	12	0	13	0	16	0	9	0	22	2	0	1	0	1	1
G1b	0	13	0	17	11	11	1	0	0	5	0	0	0	8	2	0	6	0	7	0	7	0	32	0	16	122	0	2	4	2	0
G1c	0	0	0	6	0	0	2	0	0	2	0	0	0	2		0	0	0	3	0	0	1	1	0	0	11	0	1	0	3	0
G2a	82	3	15	11	8	0	5	0	1	1	0	1	1	0	6	0	2	0	1	0	8	0	0	0	14	0	1	0	0	2	1
G2b	26	0	0	3	0	0	7	0	0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	5	0	5	0
G2c	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G2d	0	0	0	7	2	0	2	0	0	0	0	2	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	6	0	0	0
G2e	2	0	1	34	2	0	12	0	0	0	0	2	0	0	1	1	0	0	0	0	0	0	0	0	1	2	0	0	5	9	0
G3a	0	0	0	11	23	0	1	0	0	16	3	21	0	0	2	0	1	0	0	26	0	27	0	0	0	0	1	0	0	0	0
G3b	1	5	0	32	29	5	0	0	0	6	24	19	0	0	0	0	0	0	0	6	0	7	2	4	1	0	0	0	0	0	0
G3c	0	0	0	0	0	0	0	0	0	0	0	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

APPENDIX V: Data used for species Importance Value calculations

	G1a	G1a	G1a	G1a	G1a	G1a		
#VALUE!	32.1	8.3	9.4	12.3	11.3	11.4	Basal area	RBA
Acac mea	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Apod dim	0.00	0.00	0.00	0.29	0.01	0.05	0.34	6.6
Brab ste	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Cant ine	0.02	0.00	0.15	0.00	0.03	0.00	0.21	4.0
Cant mun	0.02	0.02	0.03	0.01	0.00	0.00	0.08	1.5
Cass per	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Celt afr	0.00	0.00	0.01	0.00	0.00	0.00	0.02	0.3
Curt den	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Dios gla	0.00	0.01	0.00	0.00	0.00	0.00	0.01	0.1
Dios why	0.08	0.00	0.04	0.00	0.00	0.00	0.11	2.1
Euca spp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Gymn bux	0.04	0.00	0.00	0.00	0.00	0.00	0.04	0.7
Hall luc	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Hart sch	0.00	0.27	0.27	0.11	0.15	0.35	1.15	22.0
Ilex mit	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Kigg afr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Mayt acu	0.00	0.00	0.00	0.00	0.01	0.01	0.02	0.4
Meli aze	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Ocot bul	0.00	0.00	0.04	0.47	0.21	0.01	0.74	14.2
Olea afr	0.18	0.00	0.00	0.00	0.00	0.00	0.18	3.5
Olin ven	0.00	0.00	0.04	0.71	0.23	0.58	1.57	30.1
Pitt vir	0.17	0.00	0.00	0.00	0.00	0.00	0.17	3.2
Podo lat	0.00	0.00	0.03	0.03	0.00	0.00	0.07	1.3
Psid guj	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Rapa mel	0.00	0.06	0.22	0.00	0.01	0.02	0.31	6.0
Rhus pyr	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Roth cap	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.1
Scol mun	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.1
Sola mau	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.0
Vepr lan	0.07	0.00	0.00	0.00	0.00	0.00	0.07	1.4
Virg oro	0.00	0.00	0.00	0.00	0.00	0.12	0.12	2.3
	0.58	0.36	0.83	1.64	0.65	1.14	5.21	100

Appendix VI: Information on clusters and expansion plots sampled on the selected lines in each selected.

Cluster code	Line number	Line direction	Number of plots	Distance (m) to furthest plot
pL020 (Proximal Large cluster 020)	1	W	3	18
	2	NW	3	18
	3	N	3	18
	4	NE	3	18
pL048 (Proximal Large cluster 048)	1	S	2	12
	2	SW	2	12
	3	NE	2	12
	4	E	3	18
pL070 (Proximal Large cluster 070)	1	S	3	18
	2	SW	3	18
	3	N	2	12
iL101 (Intermediate Large cluster 101)	1	S	3	18
	2	W	3	18
	3	N	2	12
iL139 (Intermediate Large cluster 139)	1	NW	3	18
	2	N	3	18
	3	NE	3	18
dM268 (Distant Medium cluster 268)	1	W	3	18
	2	NW	3	18
	3	N	3	18
	4	NE	3	18
dL348 (Distant Large cluster 348)	1	W	3	18
	2	NW	3	18
	3	N	3	18
	4	E	3	18

Appendix VII: Two lists of species compiled to extract seed characteristics and dispersal influence on the forest cluster expansion into the Black wattle stand at Buffeljagsrivier (Source: Primary data collected by author

Forest Patches	***Forest clusters***
Acacia mearnsii	*Acacia mearnsii*
Apodytes dimidiata	*Apodytes dimidiata*
Brabejum stellatifolium	*Brabejum stellatifolium*
Canthium inerme	*Canthium inerme*
Canthium mundianum	*Canthium mundianum*
Cassine peragua	*Celtis africana*
Carissa bispinosa	*Diospyros glabra*
Celtis africana	*Diospyros whyteana*
Cunonia spicata	*Halleria lucida*
Diospyros whyteana	*Gymnosporia buxifolia*
Eucalyptus species	*Ilex mitis*
Gymnosporia buxifolia	*Kiggelaria africana*
Hartogiella schinoides	*Lantana camara*
Ilex mitis	*Maytenus acuminata*
Kiggelaria africana	*Melia azedarach*
Maytenus acuminata	*Metrosideros angustifolia*
Melia azedarach	*Ocotea bullata*
Ocotea bullata	*Olea africana europaea*
Olea europaea africana	*Olinia ventosa*
Olinia ventosa	*Rapanea melanophloeos*
Pittosporium viridiflorum	*Rhus angustifolia*
Podocarpus latifolius	*Rhus pyroides*
Psidium gujava	*Rhus tomentosa*
Rapanea melanophloeos	*Rothmannia capensis*

Forest Patches	***Forest clusters***
Rhus pyroides	*Scolopia mundi*
Rothmannia capensis	*Solanum mauritianum*
Scolopia mundii	*Vepris lanceolata*
Solanum mauritianum	*Virgilia oroboides*
Vepris lanceolata	