Impacts of the invasive reed *Arundo donax* on biodiversity at the community-ecosystem level

Gené Guthrie

A thesis submitted in fulfilment of the requirements for the degree of Magista Scientiae in the Biodiversity and Conservation Biology Department, Faculty of Natural Sciences, University of the Western Cape.

February 2007

Impacts of the invasive reed *Arundo donax* on biodiversity at the community-ecosystem level

Gené Guthrie

Keywords

- *Arundo donax*
- Invasive alien species
- Biodiversity
- Community-ecosystem
- Herbicide
- Fuel properties
- Fire behaviour
- Plant species diversity
- Nutrient cycling
- Decomposition

ABSTRACT

Impacts of the invasive reed *Arundo donax* on biodiversity at the community-ecosystem level

G. Guthrie
MSc Thesis, Biodiversity and Conservation Biology Department,
University of the Western Cape

Arundo donax is an invasive species that mostly impacts on sensitive riparian ecosystems. In California, USA, *Arundo* worsens flood effects, outcompetes and displaces indigenous plant and animal species, creates fire hazards, and has the potential to alter soil nutrient status. *Arundo* is also invasive in South Africa, though less is known about its ecology, biology, and impacts. Since California and the Western Cape of South Africa have similar Mediterranean-type climates, we could assume that the impacts of *Arundo* on ecosystems in California are likely to be similar in the Western Cape, and that control methods used could be extrapolated for use in South Africa.

In this thesis, I attempted to determine what impact *Arundo* has on biodiversity at the community-ecosystem level. Chapters 2 to 5 are written as scientific papers in the format required by the Journal of Applied Ecology, and each chapter includes its own reference list. References for Chapters 1 (Introduction) and 6 (Synthesis) are included in Chapter 7 (References).

Chapter 1 provides an introduction to biodiversity and its attributes, impacts and control of invasive alien species, and the problem of invasive alien species in South Africa. Following that is a review of existing information about the ecology, uses, impacts and control of *Arundo*, and a short introduction to *Arundo* in South Africa.

Chapter 2 investigates current methods of *Arundo* control (annual brush-cutting). Results indicate that cutting *Arundo* stems does not provide a long-term solution for control; it worsens the situation by stimulating growth and increasing stem density. A single targeted application of herbicide only reduced dominance for six months. Integrated control is necessary for managing *Arundo*, and herbicide must be used to some extent.

Chapter 3 investigates whether invasion by *Arundo* alters biomass, and consequently fuel loads, of plant communities relative to uninvaded or seemingly indigenous communities, consequently affecting fire behaviour. *Arundo* increased biomass by 400 %, but since little dry material accumulated within stands of *Arundo*, the fuel load (the component of biomass that will burn) was effectively lower than *Phragmites*'. Fire intensity and rates of spread were predicted to be greater in stands of *Phragmites.* Fire behaviour of *Arundo* is site-specific, with rainfall and temperature largely determining the fuel loads (dry material) of *Arundo*-infested areas.

Chapter 4 determines whether *Arundo* alters plant species composition within communities it dominates. *Arundo*-dominated communities had a greater number and proportion of alien species than indigenous communities. *Arundo* may be facilitating the establishment and growth of alien species ('invasional meltdown'). *Phragmites australis* communities had the lowest species richness, possibly attributable to large proportions of dry material, preventing photosynthesis, and binding nutrients within in its dry material. Mature dense stands dominated by indigenous *Typha capensis* seemed more resistant to invasion by alien species than younger, less dense stands.

Chapter 5 investigates whether *Arundo* alters or has the potential to alter nutrient cycling. I compared decomposition rates, soil nutrient status, and vegetation nutrient status, of *Arundo* and *Phragmites*. *Arundo* had a high decomposition rate, but little dry and decomposing material, so that it binds nutrients within live material. *Arundo* did not appear to alter soil nutrient concentrations under these climatic conditions, but given increased dry material, soil nutrients could be significantly elevated because of the high rate of decomposition.

Arundo appears to have more significant impacts in areas that are drier and colder, where more dry material accumulates within stands.

February 2007

Declaration

I declare that “Impacts of the invasive reed *Arundo donax* on biodiversity at the community-ecosystem level” is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Gené Guthrie

Signed ………………………………………

February 2007

Acknowledgements

Firstly, I thank Jesus, my Lord and Saviour, and co-author.

> Romans 8:28 ‘And we know that in all things God works for the good of those who love Him, who have been called according to His purpose.’

I am grateful to the DST-NRF Centre of Excellence for Invasion Biology (CIB) at Stellenbosch University for funding this research, and for providing my bursary. Thank you also to the CSIR, Stellenbosch, for coordinating project expenses.

Thank you to my supervisors, Dr. Richard Knight and Dr. Brian van Wilgen.

Thank you to Spier Holdings Pty (Ltd) and CapeNature for permission to access study sites at Spier and Silvermine respectively.

A big THANK YOU to my helpers in the field: Isaac Crowster, Russell Main, Bruce d’Hotman, and Jonathan Stewart.

Thanks to Jenny and Henry Nelson, and Isaac Crowster, for caring about their natural environment, and for their encouragement to study *Arundo donax* along the Disa River.

Thank you for advice along the way: Gretchen Coffman, Jeffrey Manual, Dr. Lincoln Raitt, Maryke Meerkotter, Igshaan Samuels, Chantel Petersen and Earl Herdien (CapeNature), and Candice Haskins and Robert Siebritz (Scientific Services, City of Cape Town). Prof. Madsen and Dr. Kotze helped with data analysis.

Thanks to Elsenburg, Department of Agriculture in the Western Cape, for efficient analysis of my samples, and consistently friendly service.

Lastly, I want to thank friends and family for support and encouragement. Thank you Russell, for always being ready to help me, and for being my rock. Thanks to Wendy, Scott, Belinda, Siegi, Michelle, Charné and Bruce, your support is so appreciated. Thanks Mom and Dad, for being supportive, as always.

Table of Contents

Page

Chapter 1: **Introduction** **1**

1. Biodiversity and invasive alien species 2
  1.1 Biodiversity 2
    1.1.1 Composition: richness and diversity 2
    1.1.2 Structure: ecosystem and community patterns and organisation 3
    1.1.3 Function: ecological and evolutionary processes 3
  1.2 Invasive alien species 3
    1.2.1 Impacts 4
    1.2.2 Economic implications 5

2. Invasive alien plant control and management 6

3. Invasive alien species in South Africa 7
  3.1 Current status 7
  3.2 Management 8
    3.2.1 Working for Water 9
    3.2.2 Integrated control 9

4. *Arundo donax* 10
  4.1 Uses 12
  4.2 Impacts 12
    4.2.1 Ecological impacts 12
      4.2.1.1 Composition 12
      4.2.1.2 Structure 13
      4.2.1.3 Function 13
    4.2.2 Impacts on economy and human health 14
  4.3 Control and management 14
    4.3.1 Chemical control 15
    4.3.2 Mechanical control 15
    4.3.3 Biological control 16

5. *Arundo donax* in South Africa 16

6. Aims of the research 18

Chapter 2: **Herbicide treatment affects structure and recovery of invasive *Arundo donax*** **19**

1. Summary 20

2. Introduction 21
  2.1 Ecology 21
  2.2 Uses 21
  2.3 Impacts 21

2.4 Control 22

3. Methods 22
   3.1 Study area 22
   3.2 Data collection 23

4. Results 25
   4.1 Stem density 25
   4.2 Stem height 27
   4.3 Stem growth rates 30

5. Discussion 32
   5.1 Density 32
   5.2 Height 32
   5.3 Growth rate 32
   5.4 Management implications 32

6. Limitations 33

7. Acknowledgements 33

8. References 34

Chapter 3: **Fuel properties and potential fire behaviour of an indigenous and an invasive alien reed species** **36**

1. Summary 37

2. Introduction 38
   2.1 Biological invasions 38
   2.2 Fire 38
   2.3 *Arundo donax* 39
   2.4 *Phragmites australis* 40
   2.5 Fuel models 40

3. Methods 41
   3.1 Study areas 41
   3.2 Data collection 42
   3.3 Laboratory analysis 43
   3.4 Fuel model 45
   3.5 Statistical analysis 45

4. Results 46
   4.1 Percentage moisture content 46
   4.2 Biomass 47
   4.3 Predicted fire behaviour 48
      4.3.1 Surface rate of spread 48

4.3.2 Fireline intensity 50

5. Discussion 53
  5.1 Percentage moisture content 53
  5.2 Biomass 54
  5.3 Predicted fire behaviour 54
  5.4 Management implications 56

6. Limitations 56

7. Acknowledgements 57

8. References 57

Chapter 4: **Plant species diversity in stands of invasive *Arundo donax* and co-occurring indigenous species in South Africa** **64**

1. Summary 65

2. Introduction 66
  2.1 Biodiversity 66
  2.2 Plant species composition 66
  2.3 Disturbance 67
  2.4 Invasive alien species 67
  2.5 *Arundo donax* 67
  2.6 *Phragmites australis* and *Typha capensis* 68

3. Methods 69
  3.1 Study areas 69
  3.2 Field methods 70
  3.3 Statistical analysis 72

4. Results 73
  4.1 Similarity 73
  4.2 Plant species richness 77
  4.3 Percentage cover 78
  4.4 Plant functional types 80
  4.5 Plant species height 81
  4.6 Frequency 83

5. Discussion 83
  5.1 Similarity 83
  5.2 Cover 83
  5.3 Species richness 83
  5.4 ‘Invasional meltdown’ 85
  5.5 Competitive performance of alien versus indigenous species 85

6. Limitations 86

7. Acknowledgements 86

8. References 87

Chapter 5: **Impacts of the invasive alien species *Arundo donax* on the nutrient dynamics of riparian areas**.. **96**

1. Summary.. 97

2. Introduction 98
  2.1 Biodiversity 98
  2.2 Nutrient cycling and decomposition.. 98
  2.3 Disturbance.. 98
    2.3.1 Fire.. 99
    2.3.2 Invasive alien species 99
  2.4 *Arundo donax* 99
  2.5 *Phragmites australis*.. 100

3. Methods 101
  3.1 Study areas.. 101
  3.2 Decomposition experiment... 102
  3.3 Plant material nutrient analysis... 103
  3.4 Soil nutrient analysis 105
  3.5 Statistical analysis 105

4. Results 106
  4.1 Percentage mass lost during decomposition....................................... 106
  4.2 Rate of mass loss during decomposition 106
  4.3 Plant material nutrient concentration.. 106
  4.4 Nutrient pools in vegetation 106
  4.5 Soil nutrients.. 112

5. Discussion.. 113
  5.1 Invasive plant species and nutrient cycling 113
  5.2 Nutrient pools in vegetation 114
  5.3 Rates of decomposition and consequent nutrient cycling 114
  5.4 Plant species composition... 115
  5.5 Soil nutrients and soil development 116
  5.6 Fire and nutrients... 116
  5.7 Global warming 117

6. Limitations.. 117

7. Acknowledgements 118

8. References 118

*Chapter 6***: Synthesis** **128**

1. Brief summary: invasive alien species 129

2. Research findings 130
  2.1 Control 130
  2.2 Composition 130
  2.3 Structure 130
    2.3.1 Height 131
    2.3.2 Biomass 131
    2.3.3 Vegetation nutrient pools 131
    2.3.4 Soil nutrient concentrations 131
  2.4 Function 131
    2.4.1 Fire behaviour 131
    2.4.2 Nutrient cycling 132

3. Limitations 132
  3.1 Availability of suitable sites for study 132
  3.2 Unanticipated practical problems 133
  3.3. Fire behaviour prediction model 133

4. Management implications 133
  4.1 Control 133
  4.2 Species diversity 134
  4.3 Fire behaviour 134

5. Research needs 134

Chapter 7: **References** **137**

Lists of Figures and Tables

Page

Chapter 1

Figure 1. Distribution of *Arundo donax* within South Africa. Each white quarter-degree square indicates *Arundo* presence (Henderson 2001) 17

Table 1. Area of land invaded and estimated water use by *Arundo*, per province per year in South Africa (Versfeld *et al*. 1998) 18

Chapter 2

Figure 1. Map of South Africa showing provincial boundaries. The study occurred in the Western Cape province; Hout Bay is marked with a star; nearby towns are marked with dots 24

Figure 2. *Arundo donax* stem density (stems m^{-2}) in plots treated and untreated with herbicide after cutting, along the Disa River in Hout Bay. Total number of stems consists of both new growth and resprouting growth, and varies at each data collection............. 25

Figures 3a & b. Density of resprouting (a) and new (b) *Arundo* stems in plots treated and untreated with herbicide after cutting, along the Disa River in Hout Bay. Number of stems varies with each data collection.. 26

Figures 4a & b. Average height of resprouting *Arundo* stems in plots untreated (a) and treated (b) with herbicide after cutting, along the Disa River in Hout Bay. Boxes represent the first and third quartiles; the central box represents the mean; and whiskers represent minimum and maximum values. Number of stems varies with each data collection. . 28

Figures 5a & b. Average height of new *Arundo* stems in plots untreated (a) and treated (b) with herbicide after cutting, along the Disa River in Hout Bay. Boxes represent the first and third quartiles; the central box represents the mean; and whiskers represent minimum and maximum values. Number of stems varies with each data collection......................... 29

Figure 6. Average height (m) of new *Arundo* stems in plots treated and untreated with herbicide after cutting, along the Disa River in Hout Bay. Number of stems varies with each data collection. 30

Figures 7a & b. Average growth rate of resprouting (a) and new (b) *Arundo* stems, in plots treated and untreated with herbicide after cutting, along the Disa River in Hout Bay. Number of stems varies with each data collection 31

Chapter 3

Table 1. Location of plots of *Arundo* and *Phragmites* at Hout Bay and Spier........... 43

Figure 1. Map of South Africa showing provincial boundaries. The study occurred in the Western Cape province; study sites are marked with stars; nearby towns are marked with dots. 44

Table 2. Fuel models of *Arundo* and *Phragmites* collected from and measured at the Disa River in Hout Bay and the Eerste River at Spier. Data is derived from five plots (plots size 4 m^2) of *Arundo* at Hout Bay and Spier (10 plots in total), and five plots of *Phragmites* at Hout Bay.. 46

Figure 2. Percentage moisture content taken from leaf samples of *Arundo donax* and *Phragmites australis* between May 2005 and January 2006 (n = 2). Samples were take from along the Disa River in Hout Bay. Bars indicate minimum and maximum values 47

Table 3. Average live (biomass), dead (necromass) and total phytomass (tons ha^{-1}) of *Arundo* and *Phragmites* at Hout Bay and Spier. Average values are derived from five plots each for *Arundo* from Hout Bay and Spier, and five plots for *Phragmites* at Hout Bay 48

Figures 3a & b. Maximum estimated surface rate of spread of fire relative to live herbaceous moisture content in stands of invasive *Arundo* (a) and *Phragmites* (b), at various midflame wind speeds. The thick line indicates the surface rate of spread of fires at maximum influential wind speeds of 10.0 and 30.0 km h^{-1}, respectively. The narrow and dotted lines are marked and represent surface rate of spread of fire at different wind speeds. Herbaceous moisture content is based on monthly sampling of *Arundo* and *Phragmites* along the Disa River in Hout Bay. BehavePlus fuel model input data in Table 2. 49

Figure 4. Average estimated surface rate of spread of fire through *Arundo* and *Phragmites* during different months of the year. Monthly values are associated with monthly moisture contents collected from *Arundo* and *Phragmites* along the Disa River in Hout Bay. Values are averages of surface rate of spread at wind speeds of 0.0 to 50.0 km h^{-1}. BehavePlus fuel model input data in Table 2. 50

Figures 5a & b. Fireline intensity of fire relative to live herbaceous moisture content in stands of invasive *Arundo* (a) and *Phragmites* (b), at various midflame wind speeds. The thick line represents the fireline intensity at maximum influential wind speeds of 10.0 and 30.0 km h^{-1}, respectively. The narrow and dotted lines are marked and represent fireline intensity at different wind speeds. Herbaceous moisture content is based on monthly sampling of *Arundo* and *Phragmites* along the Disa River in Hout Bay. BehavePlus fuel model input data in Table 2. 52

Figure 6. Average intensity of fire (FI) through *Arundo* and *Phragmites* during different months of the year. Monthly values are associated with monthly moisture contents collected from *Arundo* and *Phragmites* along the Disa River in Hout Bay. Values are averages of fireline intensity at wind speeds of 0.0 to 50.0 km h^{-1}. BehavePlus fuel model input data in Table 2. 53

Table 4. Average live, dead and total biomass (tons ha^{-1}) of mature indigenous fynbos communities in the Western Cape (adapted from van Wilgen 1984). *Arundo*-dominated communities are compared with indigenous fynbos and *Phragmites*-dominated communities. *Arundo* values are derived from 10 plots (five from Hout Bay, five from Spier), and Phragmites values are derived from five plots (Hout Bay)........................ 55

Chapter 4

Figure 1. Map of South Africa showing provincial boundaries. The study occurred in the Western Cape province; study sites are marked with stars; nearby towns are marked with dots. 71

Table 1. Plot location for *Arundo*, *Phragmites* and *Typha*. Six plots were selected per species from the sites Hout Bay, Spier and Silvermine... 72

Table 2. An ordered two-way table derived from percentage cover data in plots at Hout Bay, Spier and Silvermine, dominated by *Arundo*, *Phragmites* and *Typha*, and ordered by TWINSPAN. Invasive alien species are indicated in bold type. Vertical lines separate similar groups of plots in terms of species. Horizontal lines delimit groups of species associated with particular groups of plots. Numbers within tables indicate a ranking of the percentage cover, with 5 being the highest (highest percentage cover of a particular species in a particular plot), and 1 the lowest. A = plots dominated by *Arundo*; P = plots dominated by *Phragmites*; T = plots dominated by *Typha*. 74

Figures 2a & b. Ordination plots (non-metric multi-dimensional scaling) of species similarity between plots at Hout Bay, Spier and Silvermine, in terms of presence / absence data (a), and percentage cover data (b)... 75

Figures 3a & b. Similarity cluster of plots based on presence / absence data (a), and percentage cover data (b), of species from plots at Hout Bay, Spier and Silvermine... 76

Figure 4. Plant species richness (species m^{-2}) for *Arundo*, *Phragmites* and *Typha*, from six plots each at Hout Bay, Spier and Silvermine... 77

Figures 5a, b & c. Relationship between the number of species, total (a), indigenous (b), and alien (c), and the percentage cover of dominant species (*Arundo*, *Phragmites* or *Typha*) per plot (15 m^{2}) (n = 6). Linear trendlines indicate positive correlations; each trendline is marked with the relevant dominant species.. 79

Figure 6. Number of species per functional type associated with *Arundo*, *Phragmites*, and *Typha*, from six plots per dominant species at Hout Bay, Spier and Silvermine. 81

Figures 7a, b & c. Plant species (illustrated as functional type) within communities dominated by *Arundo*, *Phragmites* and *Typha*, using data from plots at Hout Bay, Spier and Silvermine, with key alongside illustrating species and functional types referred to. All species are represented in terms of their average height and their functional type. For the purpose of these diagrams (to show differences in species height), the 'herb' category was subdivided into 'herb' and 'creeper'. 82

Chapter 5

Figure 1. Map of South Africa showing provincial boundaries. The study occurred in the Western Cape province; study sites are marked with stars; nearby towns are marked with dots. 104

Table 1. The design of an experiment to assess the rate of decomposition of *Arundo* and *Phragmites* stem and leaf material. Data show the number of replicates........ 105

Figures 2a & b. Percentage mass loss of *Arundo* and *Phragmites* stem (a) and leaf (b) material collected from and buried at Hout Bay for the decomposition experiment. The months indicate the duration for which the litterbags (n = 1) were buried. Note different scales for Fig. 2a and b. 107

Figures 3a & b. Rate of mass loss per month of *Arundo* and *Phragmites* stem (a) and leaf (b) material collected from and buried at Hout Bay. Rate of mass loss is determined by percentage mass loss divided by duration of burial in months. The months indicate the duration for which the litterbags (n = 1) were buried. Note the different scales for Figs. 3a and b. 108

Table 2. Nutrient concentration of stem and leaf material of *Arundo* and *Phragmites*, from samples (n = 5) collected in August 2006. Underlined values are significantly different between species; **bold type** indicates the higher value ($p < 0.05$). Optimum range of values is in the same units as the column they are in. D, U, and W abbreviate nutrient status of deficiency, unknown, and within range (Marschner 2002). 109

Figures 4a, b, c & d. Leaf, stem and total biomass nutrient pools (kg ha^{-1}) of NH_4, K, Ca (a), P, Mg, Na (b), Fe, Mn, Al (c), Zn, Cu, Bo (d), of *Arundo* and *Phragmites*. Nutrient pools determined using estimated biomass values (n = 5) from Hout Bay (Chapter 3 of thesis), and nutrient concentrations from plants sampled at Hout Bay and Bellville in August 2006. 110

Table 3. Average soil nutrient content of soil taken from within *Arundo* stands at Hout Bay, Spier and Silvermine. The overall averages are per plot from all the sites (and not an average of those preceding them in the table). n represents the number of replicates. Underlined values are significantly different between species; **bold type** indicates the higher value ($p < 0.05$). 112

Figure 5. Ordination plot (non-metric multi-dimensional scaling) of similarity in soil nutrient concentrations (Table 2) from plots dominated by *Arundo* and *Phragmites* at Hout Bay, Spier and Silvermine. 113

Table 4. Average plant material nutrient pools (kg ha^{-1}) for living material (biomass) of fynbos systems in the Western Cape, South Africa (van Wyk *et al*. 1992). 114

CHAPTER 1

INTRODUCTION

1. BIODIVERSITY AND INVASIVE ALIEN SPECIES

1.1 Biodiversity

The biodiversity of an area or ecosystem encompasses the biotic and abiotic elements of that system. Biotic elements include species, populations and communities, and the abiotic elements refer to non-living properties in habitats, such as water, soil, and climate or weather. Franklin *et al*. (1981) and Wilson *et al*. (1996) identified the three main attributes of biodiversity as composition, structure, and function. The term biodiversity therefore needs to take into account the processes and ecosystem functions as well (Turpie 2004). Ecosystem functioning refers to the capacity of an ecosystem to carry out the primary processes of capturing, storing and transferring energy, carbon dioxide, nutrients and water (Solbrig 1991; Woodward 1993). Different functions of ecosystems are driven by different mechanisms and processes, and by different components of biodiversity. Biodiversity is important as a regulator of these processes (Loreau *et al*. 2002).

Biodiveristy is also scale-dependent. Noss (1990) expanded on the attributes of biodiversity to provide different levels at which they can be assessed. These four levels are landscape, community-ecosystem, population-species, and genetic (Noss 1990; Poiani *et al*. 2000). Impacts on biodiversity at higher levels trickle down to affect lower levels (Noss 1990).

1.1.1 Composition: richness and diversity

The link between species diversity and ecosystem function is not an obvious one. Vitousek and Hooper (1993) argue that there is no clear link between diversity and function, while most ecologists would assume that the two are intimately linked (Hobbs *et al*. 1995). Ehrlich & Ehrlich (1992) propose that more diverse systems are more capable of supporting ecosystem functions; which also implies that functions could be lost with the loss of species. Ecosystem functions may also be carried out by a relatively small number of keystone species (Solbrig 1992), which implies that beyond a few key members, species are redundant, and biodiversity is not important in ecosystem functioning.

Species composition and species diversity are functions of each other. Species composition will determine the diversity of an ecosystem, and vice versa. As an attribute of biodiversity, species composition (and species diversity) will affect other attributes, such as ecosystem functioning (e.g. nutrient cycling, water purification, resource use) (Tilman *et al.* 1997; Wardle *et al.* 2002) and ecosystem structure (vegetation and soil nutrient pools, leaf litter) (Schmid *et al.* 2002). Plant species diversity can be used as an indicator of environmental change, such as disturbance to soil conditions (Lee 1999). High plant species diversity may lead to high litter diversity, which in turn supports a greater diversity of decomposers and detritivores (Hansen 2000), and in turn this may lead to an increased variety of food resources and greater habitat complexity (Bardgett 2002).

1.1.2 Structure: ecosystem and community patterns and organisation

Ecosystem structure largely depends on scale. Patterns and patches may appear more obviously at wider landscape scales. Smaller scales are also important, and changes in vegetation height and density, or in soil structure and nutrient content, are all important aspects in biodiversity at the ecosystem scale. Altered vegetation structure (amount of leaf litter for decomposition, nutrient content in soil and vegetation, increased plant size) will impact on ecosystem functioning (nutrient cycling, resource allocation), and consequently on species composition.

1.1.3 Function: ecological and evolutionary processes

These include the natural functions of and within ecosystems, such as decomposition and nutrient cycling in the soil, species germination, growth and spread. In some cases natural functioning of ecosystems depends on disturbances to which the system is adapted, such as fire regimes, floods and drought (Brooks *et al.* 2004). Ecosystem functioning depends to a large degree on plant species diversity (or composition) and vegetation structure (Hobbs *et al.* 1995).

1.2 Invasive alien species

Richardson (2001) and Pyšek *et al.* (2004) provide pertinent definitions relevant to invasion biology. *Indigenous species* are those that originated, evolved or arrived (from an area in which they are indigenous) in a given area without human intervention (Pyšek *et al.* 2004). *Alien species* are species in a given area whose presence there is due to intentional or accidental introduction as a result of human activities (synonyms: exotic, introduced, non-indigenous) (Richardson 2001; Pyšek *et al.* 2004). *Naturalised species* are alien species that reproduce consistently and sustain populations over many life cycles, without the input of resources or direct intervention by humans; they do not necessarily invade natural ecosystems. *Invasive alien species* are naturalised species that produce reproductive offspring, and have the potential to spread over a considerable area (Richardson 2001). *Transformer species* are usually *invasive* species (not necessarily *alien*) that change the character, condition, form or nature of ecosystems over a substantial area (Pyšek *et al*. 2004), and are the most damaging.

1.2.1 Impacts

Biological invasions constitute the second largest threat to biodiversity globally, after direct habitat destruction (Walker & Steffen 1999). They threaten indigenous plant and animal species, and alter ecosystem function and natural disturbance regimes. Invasive alien plants affect the capacity of ecosystems to deliver goods and services (Richardson & van Wilgen 2004), such as water purification, soil generation, decomposition, and nutrient cycling (Vitousek 1986; Olson 1999). Invaded ecosystems often have altered species composition and community structure (Vitousek *et al*. 1997).

Transformer species are the most damaging. They may use excessive amounts of resources (water, light and oxygen), add resources (nitrogen, litter, salt), promote or suppress fire, or stabilise and / or promote erosion (Richardson *et al.* 2000). Invasive alien plants often form complete monocultures, by dominating an ecosystem or habitat, and displacing indigenous species (Vitousek 1986). Invasive alien plants usually reduce indigenous plant species diversity and richness (Keeley *et al.* 2003; Perkins & Wilson 2005), and may even lead to the collapse of indigenous plant and animal populations, as is the predicted impact of catclaw mimosa *Mimosa pigra* invasion into Australia (Braithwaite *et al.* 1989). Invasion by alien plant species into South African fynbos threatens many indigenous and endemic plant species (Musil 1993). Invasive alien plants cause changes in animal species richness and population sizes due to the loss of forage and cover for protection, breeding, nesting and juvenile habitat (Braithwaite *et al.* 1989; Bell 1996). They decrease populations of indigenous, ground-living invertebrates (Samways *et al.* 1996) and reduce bird species richness (Breytenbach 1986). Invasive alien plants cause stream banks to become unstable (Wiesenborn 1996), affect erosional processes (Mack and D’Antonio 1998) and alter stream flows (Dudley 2000). Invasive alien plants have altered fuel loads of communities, and hence, altered fire behaviour and fire regimes (Mack & D’Antonio 1998). Invasion by cheatgrass (*Bromus tectorum*) in the USA increased fire frequency and intensity, and eventually transformed shrublands to grasslands (Whisenant 1990). The invasion of alien grasses into Californian chaparral also increased fire frequency and intensity, and altered indigenous plant species composition (Zedler *et al.* 1983).

Disturbed and unstable habitats can readily and rapidly be colonised by most invasive alien species (Bell 1997), to the extent that disturbance is often associated with invasion (Ewel 1986; Crawley 1987; Hobbs 1989). Changes to disturbance intensity or frequency often have the largest influence on species diversity (Hobbs & Huenneke 1992). Invasive alien species can alter disturbance regimes (by introducing, enhancing or suppressing disturbance events such as fire and erosion) and facilitate new invasions (Mack & D'Antonio 1998; Simberloff & Von Holle 1999). Invasion can result in a positive feedback between disturbance and alien plant species (D'Antonio *et al*. 1999), such as those between fire, nutrients and plant invasions (Wedin 1999; Vilà *et al*. 2001).

1.2.2 Economic implications

Alien tree species (such as *Pinus*, *Eucalyptus* and *Acacia*) are important sources of pulp, timber and fuelwood, but in South Africa they are estimated to consume seven percent of available water (Le Maitre *et al*. 2000). The Nile perch *Lates niloticus* has great economic value in many African countries, but it has also caused the loss of endemic species and altered ecosystems (IUCN / SSG / ISSG 2004). Black wattle *Acacia mearnsii* has been used in Africa in commercial plantations for many years, and is also used in the production of soft leather (tannin compounds extracted from the bark); resins, thinners and adhesives (bark extract); building materials (timber); charcoal; and paper production (pulp and woodchips) (IUCN / SSG / ISSG 2004). It is highly invasive, producing large quantities of long-lived seeds and out-competing indigenous vegetation (IUCN / SSG / ISSG 2004). Giant reed *Arundo donax* provides material for thatching, basketry and building construction. People rely on these products to support their families and households, and it becomes difficult to justify control or eradication of these alien species. Another example is *Echium plantagineum* in Australia, known as Paterson's Curse or Salvation Jane. It is a major pasture weed throughout southern Australia (Piggin & Sheppard 1995). It has been considered desirable by certain beekeepers, for its pollen, and farmers, because it is sometimes the only source of grazing in drier regions, despite being poisonous (Nordblom *et al*. 2002). However, most people consider *E. plantagineum* a problem because it is poisonous to people and grazing animals (Culvenor 1956), it replaces nutritious and palatable pasture and indigenous vegetation, and it reduces soil fertility. Shortly before the release of biological control (*Dialectica scalariella*) in 1980, two beekeepers and two graziers obtained an interim injunction preventing further releases. A legal battle followed, and eventually the injunction was lifted in 1988. Economic studies showed that costs far outweighed benefits, so permission to release the biological control agent was given. It is now considered as one of Australia's worst weed species (Parsons & Cuthbertson 1992).

Worldwide, invasive alien species cause more than US $ 314 billion per year in damage (Pimentel *et al*. 2001). In agricultural and forest systems, there is the cost of clearing rivers and canals clogged by invasive alien plants. There is potentially the cost of water provision via irrigation, if alien plant species deplete water resources (Enright 2000; Eiswerth & Johnson 2002). In US agriculture, weeds cause a reduction of 12 % in potential crop yields (Perrings *et al*. 2002). In South Africa, alien weeds cause total crop losses of about US $ 1.5 billion per year (Perrings *et al.* 2002). Water hyacinth reduces water resources in South Africa (Richardson *et al*. 1997), and more than US $ 25 million is spent per year on the control of water hyacinth. More than US $ 5 million per year is spent on preventing future alien plant invasions in South Africa (van Wilgen *et al*. 1998).

2. INVASIVE ALIEN PLANT CONTROL AND MANAGEMENT

An integrated approach involving the combined use of different control methods is necessary to manage invasive alien plants effectively (van Wilgen *et al*. 2000). Integrated weed control usually involves a combination of at least two of the primary elements of control: chemical, mechanical and biological. Chemical control implies the use of environmentally safe herbicide. There is growing concern about impacts of herbicides on non-target species and ecosystems.

Mechanical control is the physical control of alien plants by removal or suppression, such as felling or burning (van Wilgen *et al*. 2000). Mechanical control is labour-intensive, and expensive to use in extensive and dense infestations, or in remote areas and rugged terrain. Biological control is the use of organisms to feed upon, parasitise or interfere with an alien species' ecology; usually invertebrates and diseases from the alien plant's region of origin are utilised (Cory & Myers 2000).

The selection of methods for control and management is complex and depends on the biological attributes of the species (population growth, reproduction), environmental factors (climate, drought, fire), and human activities (budget, skills, knowledge, commitment) (van Wilgen *et al*.

2000). It also depends on the stage of establishment or spread of the alien species (Hobbs & Humphries 1995). Species arriving in new environments must be prevented from establishing, and be quarantined if necessary. Those in the process of adapting and establishing must be detected early on and eradicated. Eradication in most cases is impossible (B. van Wilgen pers. comm.), unless the infestation is caught early or the reproducing population is small (Myers *et al*. 2000). Where species are in a stage of exponential growth, integrated control methods are required, with monitoring of the affected ecosystem, the invader species, and the methods. Once invasive alien species have become dominant in an environment, biological control is sometimes the only effective method of control (van Wilgen *et al*. 2000). In many cases, managers have to make decisions without a comprehensive understanding of the potential consequences (van Wilgen *et al*. 2000). They therefore need to learn from previous experiences, successes and failures, and where necessary, adapt their management practices (Holling 1978).

3. INVASIVE ALIEN SPECIES IN SOUTH AFRICA

3.1 Current status

South Africa has one of the largest problems with invasive alien plants in the world (Richardson *et al.* 2005). The most important invasive species in South Africa originated from Australia and the areas of Mediterranean-type climate in Europe and North America (Stirton 1978). Many invasive alien species are well-established and cause substantial damage, and many others are at early stages of invasion (Nel *et al*. 2004). More than 160 of the approximately 8 750 plants that have been introduced to South Africa are known to be 'seriously invasive' (according to the Conservation of Agricultural Resources Act (CARA) 43 of 1983) (van Wilgen *et al.* 2001). Several estimates have been made of the geographic range of alien plant invasions in South Africa. Le Maitre *et al*. (2000) claim that 10 million hectares have been invaded to some extent. The most comprehensive set of records for South Africa is the South African Plant Invaders Atlas (SAPIA) (Henderson 1998). The SAPIA database records the abundance of species in different categories. Abundant species occur in more than 15 % of the quarter-degree squares where they were mapped. Many of these species develop into near-monocultures in many ecosystems, for example, *Pinus* species and *Hakea sericea* in fynbos, and *Acacia* species, *Eucalyptus* species and *Arundo donax* along rivers (Richardson & van Wilgen 2004). Another classification is that of Nel *et al*. (2004), who classify invasive alien plants into two main categories: major invaders and emerging invaders. Major invaders are those species likely to be of highest concern to landowners and managers, at which most funding should be directed for control. These species have already had a substantial impact on natural and semi-natural ecosystems of South Africa (Nel *et al*. 2004), and again include *Pinus* species, *Hakea sericea, Acacia* species, *Eucalyptus* species and *Arundo donax*.

In South Africa, dense stands of alien trees and shrubs have rapidly reduced abundance and diversity of indigenous plants (Richardson *et al.* 1989; van den Berckt 2000). They have also increased total biomass (ith its subsequent effect on fuel properties) (Milton 1981a; Versfeld & van Wilgen 1986), altered change litterfall dynamics (Milton 1981b), and altered nutrient cycling (Musil 1993; Stock *et al*. 1995; Yelenik *et al*. 2004). These changes have had varied effects on fire regimes (Richardson & van Wilgen 2004). The impacts of alien stands intensify with time as they replace indigenous vegetation (Holmes & Cowling 1997).

Grasses are often overlooked because of the major problems currently being experienced with woody invaders (Richardson & van Wilgen 2004). Invasive alien grasses are nonetheless important transformer species in South African ecosystems. Seven grass species are declared weeds in South Africa (Henderson 2001), and all of these species have shown invasive behaviour in fire-driven or littoral ecosystems (D'Antonio 2000; Richardson *et al.* 2000). Problems caused by alien grasses are likely to increase as a result of climate change (Milton 2004). Global change is likely to increase nitrogen availability in the soil (i.e. nutrient additions with fertilization), giving most C_3 grasses an advantage over C_4 plants (Milton 2004).

3.2 Management

Peter MacOwan (1888) and Rudolf Marloth (1908) initially raised concerns regarding the potential for introduced plants to replace natural vegetation, with detrimental consequences (van Wilgen *et al*. 1997). These warnings were ignored until the 1900s when invasion was realised as a serious problem in South Africa. Invasive alien plant control started primarily to conserve natural vegetation. Initial attempts were uncoordinated and erratic, and largely unsuccessful, because of a poor understanding of invasive plant ecology as well as a lack of follow-up funds. In the 1970s and 1980s more research encouraged coordinated, nationwide control programmes, which were successful but short-lived. In the 1980's, government funding was reduced and invasive plant control efforts were financially strained (van Wilgen *et al*. 2002).

3.2.1 Working for Water

The Working for Water Programme was started in October 1995, with the aim of protecting water resources and creating employment opportunities (Marais *et al*. 2004). It has grown successfully, largely due to political support, local and international funding, and the programme's many benefits (van Wilgen *et al*. 2002; Richardson & van Wilgen 2004). The annual expenditure on Working for Water operations increased from R25 million in 1995 / 1996 to over R400 million in 2003 / 2004 (Anon. 2002). The costs of clearing increase dramatically with the density of invasive alien plants. Twelve species (or genera) accounted for 89 % of the costs of clearing in 2002 / 2003, mostly *Acacia* spp. (Marais *et al*. 2004). Most of the costs of clearing, and the largest areas cleared, were related to the large tree species with significant impacts on water resources (Marais *et al*. 2004), such as *Acacia*, *Pinus*, *Eucalyptus*, *Populus*, and *Prosopis* species. Large amounts were also spent on *Lantana camara*, *Chromalaena odorata*, *Solanum mauritianum* and *Cereus jamacarus*, which have impacts on biodiversity, catchment stability and the agricultural potential of land. The Working for Water Programme does not target *Arundo donax* and *Salix babylonica*, probably because they are less-researched and appear to have less serious impacts, even though that are both listed as very widespread and common by Nel *et al*. (2004). There is more focus on riparian areas (Marais *et al*. 2004).

3.2.2 Integrated control

Some examples of integrated control used on invasive alien species in South Africa include the control of *Hakea* species and *Opuntia stricta*. *Hakea sericea* has invaded thousands of hectares of fynbos in South Africa. Plants are killed by fire, after which the winged seeds are released and dispersed by wind (Richardson & van Wilgen 1986). Control programmes incorporate mechanical methods (felling and fire) and biological control. The plants are felled using chainsaws, and left for 12 to 18 months, then burnt. This practice has been successful in clearing large areas of invasions, but problems occur with burning because the stands produce such high fuel loads. Fires in stands of alien plants have high intensity and damage the soil, seedbanks and soil microbial populations (Cilliers *et al*. 2005). Biological control in the form of seed-feeding insects is also used (Gordon 1999), but these insects don't disperse readily or over long distances. Similar control strategies are applied to *Hakea sericea*, *H. drupacea*, *H. gibbosa* and *Pinus* species (van Wilgen *et al*. 2000).

Prickly pear *Opuntia stricta* is a significant weed (cactus) in South African savannas. Early attempts at mechanical control were ineffective because the fruit was spread over long distances by baboons and elephants. The introductions of biological control agents in the form of Cactoblastis (*Cacroblastis cactorum*) and Cochineal (*Dactylopius* species) (Hoffmann *et al.* 1999) have been successful in the control of *O. stricta*. Herbicide is used on scattered populations, and biological control agents are released on larger infestations (Lotter & Hoffmann 1998).

4. *ARUNDO DONAX*

Arundo donax L. (hereafter referred to as *Arundo*) is also known as Giant Reed, Bamboo Reed, Spanish Reed, Spanish Cane, Wild Cane and Arundo. *Arundo* belongs to the Arundineae tribe, along with *Phragmites* species (Renvoize 1980). *Arundo* is reported as indigenous to Egypt, India, Spain, Nepal, Eurasia, eastern Asia and the Mediterranean (Polunin & Huxley 1987; Fornell 1990; Hickman 1993). Most recent evidence reports *Arundo* as being indigenous to the Indian sub-continent (Bell 1997). *Arundo* has been intentionally distributed around the world because of its many uses (Dudley 2000). It does particularly well in areas with a Mediterranean-type climate. It is naturalized and invasive in many regions, including southern Africa, the Caribbean and Pacific Islands, South America, Australia, Southeast Asia, and United States through to Mexico (Hafliger & Scholz 1981). *Arundo* was first detected in the USA in the 1850s (Herrera & Dudley 2003), and today is invasive in sub-tropical, temperate, arid and semi-arid regions of North America (Langeland & Burks 1998).

Arundo is a hydrophyte, growing along lakes, streams, drains, and other wet sites (Bell 1997). Although it usually grows in wetter areas, it does not need a constant supply of water, and can grow on drier banks and roadsides. *Arundo* has pale green to blue-green leaves, and may be confused with bamboo and corn. Younger plants resemble the common reed *Phragmites australis*. *Arundo* is a perennial C_3 grass species (Rossa *et al.* 1998), and stems may reach 10 metres in height (Dudley 2000). It usually grows in large stands many metres wide, and contains hundreds of stems per stand (Spencer *et al.* 2005). It does not produce viable seed in most areas where it has been introduced (Perdue 1958), and reproduction occurs almost entirely from rhizomes and stem fragments (Boose & Holt 1999). Fragments are usually carried by floodwaters into new habitats where they sprout new culms (Else 1996). Rhizomes are tough and fibrous, forming thick mats that penetrate deep into the soil (Mackenzie 2004). Each plant can have a root span of up to 12 metres in diameter (Jackson 1993).

Arundo forms one of the most biologically productive populations (Bell 1997). Ideal growth conditions would be low gradient riparian areas with well-drained soils (Perdue 1958), high water nutrient levels (such as at agricultural, industrial and residential wastewater discharge sites), low salinity (Grossinger *et al.* 1998), full sun, and high temperatures. Under these conditions *Arundo* produces more than 20 tons per hectare above-ground biomass (Perdue 1958), but even when conditions are not ideal, *Arundo* produces approximately three tons per hectare above-ground biomass (Christou 2001). Rieger & Kreager (1989) record *Arundo* growing as much as seven centimetres in one day, and up to eight metres in a few months. *Arundo* outcompetes indigenous woody species in terms of growth rate and height (Else 1996). Once *Arundo* is established, it spreads at a rapid rate, excluding most other species. Plant species most capable of competing with *Arundo* are those reproducing via rhizomes and seeds (Else 1996).

Arundo can tolerate a wide variety of ecological conditions (Perdue 1958), mostly due to its rhizomes and deeply penetrating roots. Individual plants can survive periods of drought or of excessive moisture. *Arundo* is primarily a freshwater species but can tolerate excessive salinity (Perdue 1958; Grossinger *et al.* 1998). It survives and flourishes in all types of soils, from heavy clays to loose sands and gravel (Perdue 1958). It is usually associated with higher soil nutrient levels than indigenous plants (Coffman *et al.* 2004). *Arundo* can survive low temperatures when dormant (during winter), but is vulnerable to damage by frosts after the start of spring growth (Decruyenaere and Holt 2001). *Arundo* does not appear to tolerate high elevation or inland environments where sustained freezing occurs (Team Arundo del Norte 1999a). *Arundo* is usually associated with rivers that have been physically disturbed or dammed, but it can invade indigenous stands of plant species, even in full shade (Bell 1997). *Arundo* is one of the few alien species that invades undisturbed or naturally disturbed systems (Rejmánek 1989), and does not need some form of human intervention to become established. However, disturbance has played a major role in the successful invasion and establishment of *Arundo* (Bell 1997), since certain human alteration of ecosystems (such as fertilizer addition, or cleared land and removed competition) provides more suitable conditions for its growth. Floods and anthropogenic modification to riparian environments have helped spread *Arundo* along river courses (Coffman *et al.* 2004). Recent nutrient loading of rivers is hypothesized to be a major factor contributing to *Arundo* invasion in California (di Castri 1991).

4.1 Uses

Arundo plants are often used as erosion control (Bell 1997), because the root masses stabilize stream banks and terraces (Zohary & Willis 1992). *Arundo* has been suggested as a source of biomass for fuel energy production (Duke 1983). It does not make a good livestock forage because the leaves mature and become unpalatable quickly. Leaves may be woven into mats and baskets. Stems can be used for building material, plant supports, fences, screens, roofing, walking sticks, measuring rods, fishing poles and brooms (Duke 1983; Usher 1974). The stems are used make musical instruments like clarinets and bag-pipes (Usher 1974). Young stems or branches can be used in roof thatching. The stem fibre can be used to make paper (Duke 1983). In Italy, the plant is used in the manufacture of rayon (Duke 1983). Yellow dye may be made from the pollen (Moerman 1998). Rhizomes are edible, raw or cooked. They can be dried out and ground into a powder to make bread, usually in conjunction with cereal flours (Chiej 1984). They can be roasted or boiled (Coyle & Roberts 1975). *Arundo* is also used to treat dropsy (Duke & Wain 1981).

4.2 Impacts

Arundo is rapidly invading riparian ecosystems of rivers in Mediterranean-type climates (Coffman *et al.* 2004), impacting on both ecological and economic sectors.

4.2.1 Ecological impacts

4.2.1.1 Composition

The presence and spread of *Arundo* changes community composition. *Arundo* has the potential to reduce the diversity of riparian fauna and flora, partly due to its large biomass and height, and rapid growth rate (Milton 2004). *Arundo* quickly colonises disturbed areas, like those left bare after flooding or fires, and dominates riverbanks and estuaries (Dudley & Collins 1995). *Arundo* outcompetes and replaces indigenous riparian plants, reducing the value of riparian habitats and resources for indigenous fauna (Bell 1997). Gaffney & Gledhill (2003) found reduced indigenous plant species diversity as well as increased abundance of other alien plants associated with *Arundo*.

Areas dominated by *Arundo* tend to have lower diversity of aquatic animals (Chadwick & Associates 1992). Herrera & Dudley (2003) found lower diversity of invertebrates within stands of *Arundo* when compared to indigenous vegetation. In the Simi Valley area (USA), *Arundo* has reduced the available habitat of the three-spined stickleback (*Gasterosteus aculeatus*), an endangered fish species (Frandsen & Jackson 1993). Large and medium sized mammals cannot penetrate densely infested areas (Coffman *et al.* 2004). Smaller or less dense patches are occasionally used by birds, snakes, and rodents, for nesting and cover (Coffman *et al.* 2004). *Arundo* stems and leaves contain a wide variety of noxious chemicals (Mackenzie 2004), making it unsuitable and unpalatable to most insect and animal species (Miles *et al*. 1993).

4.2.1.2 Structure

Arundo invasion alters the vegetation structure of riparian zones (Herrera & Dudley 2003). It is competitive, forming extensive stands or monocultures, and physically inhibits indigenous plant species from establishing (Bell 1997). Gaffney & Gledhill (2003) report a reduction in vegetative structure in communities dominated by *Arundo*. *Arundo* can occupy entire river channels from bank to bank (Frandsen & Jackson 1993). Biomass creates obstacles during storm events, and can lead to flooding of adjacent land, erosion of stream banks, and change to natural flow patterns (Coffman *et al.* 2004). Large clumps of *Arundo* sometimes break off from river banks and are deposited in the middle of the channel, forming islands. *Arundo* is often much taller than co-occuring plant species, and has greater above- and below-ground biomass. *Arundo* provides no significant shade over water (Iverson 1993), and areas dominated by *Arundo* tend to have warmer water temperatures, with lower oxygen concentrations and lower diversity of aquatic animals (Chadwick & Associates 1992). The lack of stream shading may increase algal growth and pH, causing further degradation of water by the production of ammonia (Chadwick & Associates 1992). As well as affecting water quality, *Arundo* affects water quantity. Iverson (1993) and Zimmerman (1999) report that *Arundo* uses and transpires three times more water than indigenous plants in the USA. Every year, *Arundo* along the Santa Ana river basin in California evaporates approximately 7.6 million kilolitres of water (Jackson 1993).

4.2.1.3 Function

Arundo alters ecological processes, functions and ecosystem services in riparian systems (Milton 2004), much of it due to the changes to ecosystem structure. *Arundo* alters stream hydrology and sedimentology (Milton 2004), increasing the risk of flooding (Coffman *et al*. 2004).

Arundo appears to use more soil nutrients (especially nitrogen) than indigenous species (Coffman *et al.* 2004). *Arundo* decomposes at rates similar to indigenous litter in riparian environments, but changes the structure of the soil, making it unsuitable for decomposer organisms (B. Lichtman, unpublished data, in Herrera & Dudley 2003).

Arundo is highly adapted to fires and is flammable throughout most of the year (Bell 1997). It produces large quantities of biomass that increase the available fuel for unseasonal and higher intensity fires (Coffman *et al*. 2004). *Arundo* increases fire frequency, rates of spread and intensity in Californian riparian areas (Coffman *et al*. 2004). The spread of *Arundo* in riparian ecosystems is also accelerated by fire: fire clears away indigenous and other vegetation. The remaining *Arundo* rhizomes are well-adapted to fire can easily resprout without any competition for resources. New *Arundo* shoots appear within days after a fire (personal observation). *Arundo* has changed some ecosystem processes from being flood-regulated to fire-regulated (Rieger & Kreager 1989).

4.2.2 Impacts on economy and human health

Arundo grows densely enough to reduce the carrying capacity of small waterways by constricting and narrowing the channel from both banks (Robbins *et al*. 1951). Vast amounts of *Arundo* biomass pile up against flood control and transportation structures such as bridges and culverts (Frandsen & Jackson 1993). Costly removal strategies are needed after large storms to clear *Arundo* blockages from channels (Douce 1993).

Studies indicate that air quality of the West Coast of the USA may have been adversely affected by the introduction of *Arundo*, which emits high levels of isoprene (Evans *et al*. 1982; Hewitt *et al*. 1990). *Arundo*’s flammability poses safety risks and causes economic problems, such as the need for evacuation programs, firefighting equipment and labour, potential damage to housing and infrastructure by fire (Team Arundo del Norte 1999b).

4.3 Control and management

Arundo is adaptive and thrives in most habitats. Once established, *Arundo* maintains itself and spreads via its extensive rhizome system. *Arundo* is a difficult and expensive species to control, and notorious for its resistance to chemical spraying. *Arundo* will not die unless the rhizomes are killed (Boose & Holt 1999). Management of *Arundo* must include post-treatment monitoring and re-application of herbicides to regrowth (US EPA 1997). Revegetation may be needed for bank stabilisation after clearing (Boose & Holt 1999).

4.3.1 Chemical control

Chemical control is the most widely used method for controlling *Arundo*. Glyphosate-based herbicides such as Rodeo (Dow Agrosciences) and Roundup (Monsanto) are popular and cost effective. They provide effective control of vegetation, degrade rapidly in soil and have low mammalian toxicity (Giesy *et al.* 2000; Williams *et al.* 2000). Glyphosate applications are most successful when made at, or just after, *Arundo* flowering (Bell 1997). Follow-up treatments are usually necessary for up to five years after eradication (Team Arundo del Norte 1999b). The three main methods of herbicide application are foliar spray (spraying herbicide onto leaves and stems without cutting), cut-and-spray (spraying or painting herbicide directly onto cut stem surface), and cut-resprout-spray (cutting stems, allowing resprouting, and spraying resprouts with herbicide). The ecological risks of glyphosate use are small, especially when compared to the damage by noxious and invasive weeds (Monheit 2003).

4.3.2 Mechanical control

Mechanical control is effective only if the entire rhizome mass is removed, which is almost impossible (Boose & Holt 1999; Bromilow 2001). Rhizome fragments left in the ground will resprout. Three major types of mechanical control are physical removal (using hand-held tools or heavy equipment), soil solarisation (covering cut stems with plastic sheeting), and prescribed burning or grazing. Soil solarization (Katan *et al*. 1987), also referred to as tarping, involves placing a cover or tarpaulin (tarp) (usually transparent or black plastic sheeting) over the soil surface. In theory, the plastic is supposed to trap solar radiation and cause an increase in soil temperatures, killing plants, seeds, pathogens and insects below the tarp (Tu *et al*. 2001). Darkness beneath black plastic further prevents photosynthesis (Elmore 1990). It is expensive when used on large expanses of *Arundo*, and may lead to soil erosion following removal of the tarp.

Prescribed burning is mostly not successful, since rhizomes sprout soon after burning (personal observation), and may even promote *Arundo* regrowth (USDA 1993). Prescribed grazing involves training goats or cattle to graze on *Arundo* only. *Arund*o is not palatable to cattle (Wynd *et al*. 1948) but Angora and Spanish goats are potential controls (Daar 1983). Mechanical control usually results in some soil disturbance, as well as piles of unwanted biomass. Biomass is expensive to remove and dispose of, and leaving it on site may pose flood or fire hazards, and will impede revegetation by indigenous species. Biomass may be chipped or mowed. High-powered drum chippers work well (Team Arundo del Norte 1999a), even on green stems. Material is finely chipped, and only a small amount of resprouting occurs from larger pieces. Chipped material dries out quickly, providing good mulching material. Mowing is carried out using a mowing attachment on a tractor. It is generally best suited to dense stands, but old stands may be difficult to manoeuvre through. Mowing is limited by access to the site, terrain and noise issues.

4.3.3 Biological control

No biological control for *Arundo* has yet been approved in the USA, or in South Africa (Milton 2004). A USDA evaluation of the potential benefits of biological control against *Arundo* ranked it as a promising candidate (Tracy & DeLoach 1999). Cummins (1971) and Tracy & DeLoach (1999) list 48 species as potential biological controls for *Arundo*. Specifically, there is the green bug *Schizaphiz graminum* (Zuňiga *et al*. 1983) in Africa and / or Eurasia, the caterpillars *Phothedes dulcis* in France and *Zyginidia guyumi* in Pakistan (Ahmed *et al*. 1977), and a moth borer *Diatraea saccharalis* in Barbados (Tracy & DeLoach 1999). The Agricultural Research Service laboratory in Australia is surveying the closely related grass *Monochater paradoxus* for natural enemies (Kirk *et al*. 2003). A stem-boring wasp *Tetramesa romana* is currently (2006) being monitored in California (T. Dudley & A. Lambert pers. comm.).

5. *ARUNDO DONAX* IN SOUTH AFRICA

Arundo was introduced into South Africa in the late 1700s (Henderson 2001). In South Africa, *Arundo* is listed as a Category 1 species (the most serious type of invasive species), and landowners are obligated to remove or control the plant where possible. It is mentioned in many research papers as a species of concern (Wells *et al*. 1980; Henderson 1998; Robertson *et al*. 2003; Nel *et al*. 2004; Rouget *et al*. 2004). Sensitive vegetation types such as the fynbos are particularly susceptible and vulnerable to invasion of *Arundo* because of its ecosystem-changing capabilities, especially the impact it has on fire behaviour and fire regimes, since fynbos is a fire-driven ecosystem. *Arundo* is one of eleven invasive alien plant species in the fynbos biome in

South Africa that occur in more than 50 quarter degree squares (Henderson 1998), and it has the potential to invade more than a million hectares of the fynbos biome (Rouget *et al*. 2004). It is listed as one of six of the most important invasive plant species, current and future, that will have economic impacts of significance in the fynbos biome (Henderson 1998). *Arundo* is within the top 21 % of invasive species in South Africa (Nel *et al.* 2004) in terms of impact (type of habitat invaded, abundance and range) (Parker 1999).

Arundo was listed among the five worst invaders in the provinces of Gauteng and Limpopo in 1976, and was later recognised as a national problem because of its threat to water security (Wells *et al*. 1980). *Arundo* is present in all provinces of South Africa (Henderson 1998), and uses considerable amounts of water (Table 1). The south-western Cape and the semi-arid Highveld regions of South Africa may suffer further water losses due to the rapid growth rate of *Arundo (*Samuels *et al.* unpublished data).

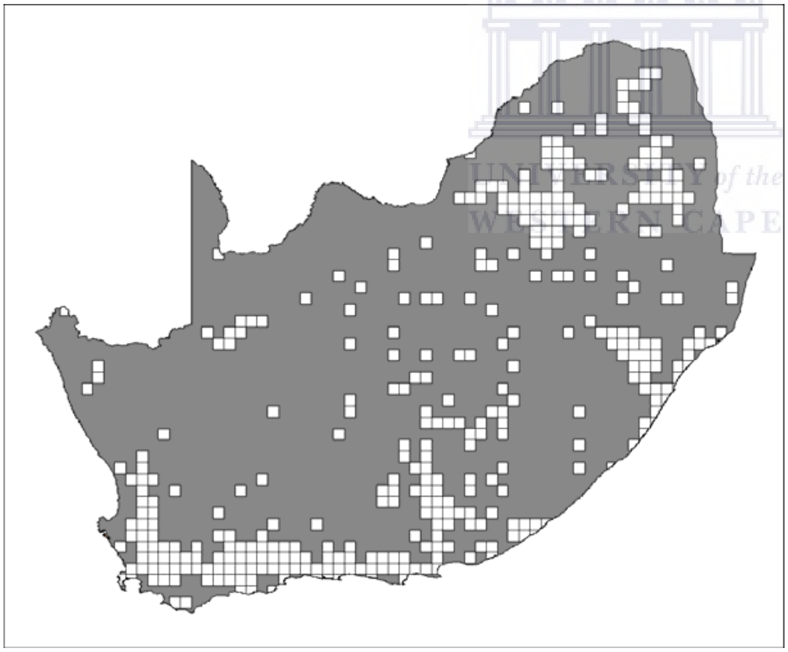


Fig. 1. Distribution of *Arundo* within South Africa. Each white quarter-degree square indicates *Arundo* presence (Henderson 2001).

Table 1. Area of land invaded and estimated water use by *Arundo*, per province per year in South Africa (Versfeld *et al*. 1998).

	Area invaded (hectares)	Water use (m^3)
Eastern Cape	15 078	214 000
Free State	695	28 000
Gauteng	unknown	unknown
Kwazulu-Natal	112 307	2 168 000
Northern Cape	456	2 000
Northern Province	392	9 000
North-West	47 948	1 758 000
Western Cape	11 072	170 000
South Africa	187 948	4 348 000

6. AIMS OF THE RESEARCH

This study sought to investigate aspects of the impact of invasion of indigenous plant communities by *Arundo donax* in the Western Cape Province, South Africa. The aspects investigated included ecosystem features related to composition, structure and function (Noss 1990). In terms of composition, it examined and compared the plant species diversity present in sites invaded by *Arundo*, with the plant species diversity in sites dominated by indigenous *Phragmites australis* and *Typha capensis*, dominant indigenous species that occur in the same or similar habitats. In terms of structure, it examined the density, biomass, height, and growth rates of *Arundo* as compared to *Phragmites*. In terms of function, it examined predicted fire behaviour and decomposition of *Arundo* as compared to those of *Phragmites*.

CHAPTER 2

HERBICIDE TREATMENT AFFECTS STRUCTURE AND RECOVERY OF INVASIVE *ARUNDO DONAX*

1. SUMMARY

1. *Arundo donax* is an important invasive reed species in South Africa. It is highly productive and highly resilient. Current methods of control are limited and consist of annual brush-cutting in some areas. This study sought to compare the effects of herbicide applications on the regrowth of *Arundo* with that of untreated sites.
2. Plots of *Arundo* were cut, and stems painted with concentrated herbicide. Growth and recovery of treated and untreated plots were compared to determine whether cutting and / or herbicide could serve as an effective control method.
3. Height and growth rates of treated *Arundo* were consistently lower than untreated *Arundo* for the full period of study. In some months, untreated stems were three to four times taller than untreated stems.
4. The density of treated *Arundo* stems was lower than untreated for a period of seven months, after which the treated stems increased in density to levels surpassing that on the treated plot.
5. Herbicide reduced the density, height and growth rates of *Arundo*, but without follow-up treatment within six months, stem density increased exponentially. Cutting alone is therefore ineffective for controlling *Arundo* in the long term, and it actually increases *Arundo* density, height and growth rates.
6. Stem cutting is ineffective as a control method, and increases the density of *Arundo* stems. A single application of herbicide is effective in controlling height and growth rates of stems. Follow-up treatment is necessary to target new growth.
7. Herbicide is effective for short-term control, more so than cutting alone, but further research is necessary to determine the best control for *Arundo* in South Africa. Methods could be extrapolated and tested from the USA.

2. INTRODUCTION

Arundo donax L. (hereafter referred to as *Arundo*) is an important invasive reed species in South Africa (Henderson 2001). It is indigenous to the Indian sub-continent (Bell 1997), and is likely to have been intentionally introduced because of its many uses (Dudley 2000) during the 1700s (Henderson 2001).

2.1 Ecology

Arundo is adaptive and thrives in most habitats, doing particularly well in areas with Mediterranean-type climates, such as the Western Cape of South Africa. It has high growth rates, growing up to seven centimetres per day, and stems may reach eight metres in height after a few months (Rieger & Kreager 1989). *Arundo* can produce high volumes of biomass, more than 20 tons per hectare under ideal conditions (Perdue 1958). *Arundo* does not produce viable seed (Perdue 1958) but spreads rapidly via its extensive root and rhizome system (Boose & Holt 1999). *Arundo* usually establishes in riparian habitats because it is spread by floodwaters or ordinary flow (Else 1996), but is not restricted by water availability.

2.2 Uses

In South Africa, *Arundo* plants are widely used for bank stabilisation. Stems are used for building and thatching materials, screens and fences, and leaves are woven into baskets and mats, providing livelihoods for communities with high rates of unemployment.

2.3 Impacts

Arundo spreads rapidly, outcompeting and displacing indigenous plant species (Bell 1997). Monospecific stands of *Arundo* are often too dense for animals to move through (Spencer *et al*. 2005). *Arundo* reduces available terrestrial and aquatic habitat (it grows within and alongside streams) for indigenous animal species, thus reducing the overall indigenous species diversity. Its fast growth rates require it to use more soil nutrients than indigenous species (Coffman *et al*. 2004). *Arundo* uses and transpires up to three times more water than indigenous species (Iverson 1993; Zimmerman 1999). It poses flood risks because it forms debris piles and decreases channel sizes (Frandsen & Jackson 1993). *Arundo* is highly adapted to fires and flammable throughout most of the year (Bell 1997), increasing fire frequency and intensity (Milton 2004). It is tolerant of a wide range of climatic and environmental factors (Perdue 1958), and has the potential to invade and establish in most conditions, being limited only by extreme cold (Samuels *et al.* unpublished data; Team Arundo del Norte 1999).

2.4 Control

Arundo has been overlooked, ignored or allowed to establish and spread because it has many uses, is difficult to eradicate, and is similar in appearance to the indigenous common reed *Phragmites australis*. *Arundo* is a difficult and expensive species to control, and notorious for its resistance to chemical spraying. *Arundo* will not die unless the rhizomes are killed. *Arundo* is not well known in South Africa, therefore management of *Arundo* stands usually consist of annual cutting at best. Combining mechanical and chemical control is usually most effective. Chemical control involves applying herbicide, via spraying or painting, and in conjunction with cutting stems. Sometimes stems are cut and allowed to resprout before spraying with herbicide. Mechanical control involves physical removal, either using heavy equipment or handheld tools, or covering with plastic sheeting (tarping), or prescribed burning. Clearing must proceed from the top of a watershed, downstream, to avoid re-invasion. Successful control includes follow-up treatments and monitoring (US EPA 1997). Banks may need revegetation for stabilisation after clearing (Boose & Holt 1999). No biological control has been approved in South Africa.

In this experiment I determined the effectiveness of a single application of concentrated herbicide to cut stems of *Arundo*, as a simple addition to current control methods of cutting. I compared this to the current management strategy in Hout Bay, Western Cape, which involves annual cutting alone. Cut biomass is usually piled on site, though some may be removed. I measured growth rates, heights and density of the two treatments.

3. METHODS

3.1 Study area

The Western Cape of South Africa has a Mediterranean-type climate: warm, dry summers and wet, temperate winters. Rainfall varies from 200 to 2 000 mm per year, and falls mainly during the winter months. Strong south-easterly winds blow primarily during summer, from November to February. The study was undertaken in the lower reaches of the Disa River in Hout Bay. The Disa River runs through Hout Bay, a coastal town about 11 km from Cape Town. The lower reach is characterised by a broad floodplain and most of it falls within residential or commercial zoning. The Disa River is heavily disturbed and impacted on by agriculture, residential and light industrial wastewater, and formal and informal developments. *Arundo* stands on the site are dense and extensive, and span the entire distance between the Victoria and Princess Road bridges, with fewer and less dense clumps upstream. *Arundo* stems are cut annually (brush-cutter) by the town council along this stretch of land, along one riverbank for safety, aesthetic and flood prevention purposes (I. Crowster pers. comm.). However, the untreated cut biomass is mostly left on the banks or piled slightly away from the original site (personal observation).

3.2 Data collection

Two plots of 1 x 5 m were selected and marked, within monospecific stands of *Arundo*. On one plot, all *Arundo* stems were cut to a height of 200 mm above ground level and counted. This plot served as the control plot (S 34° 01' 56.2", E 18° 21' 13.1"). In the second plot (S 34° 01' 56.6", E 18° 21' 13.0"), all *Arundo* stems were cut to a height of 200 mm above ground level, and treated with 100 % concentration herbicide (RoundUp, Monsanto, 360 g L^{-1} active ingredient glyphosate). Herbicide was applied to the cut stems using a paintbrush within one to two minutes after cutting. Cut biomass was chipped using a drum chipper, spread out and dried on site. All stems were counted and measured at monthly intervals for a period of nine months. New stems (from rhizomes) and resprouting stems (from an existing stem or group of stems) were recorded. I compared height, growth rates and densities of treated and untreated stands of *Arundo*.

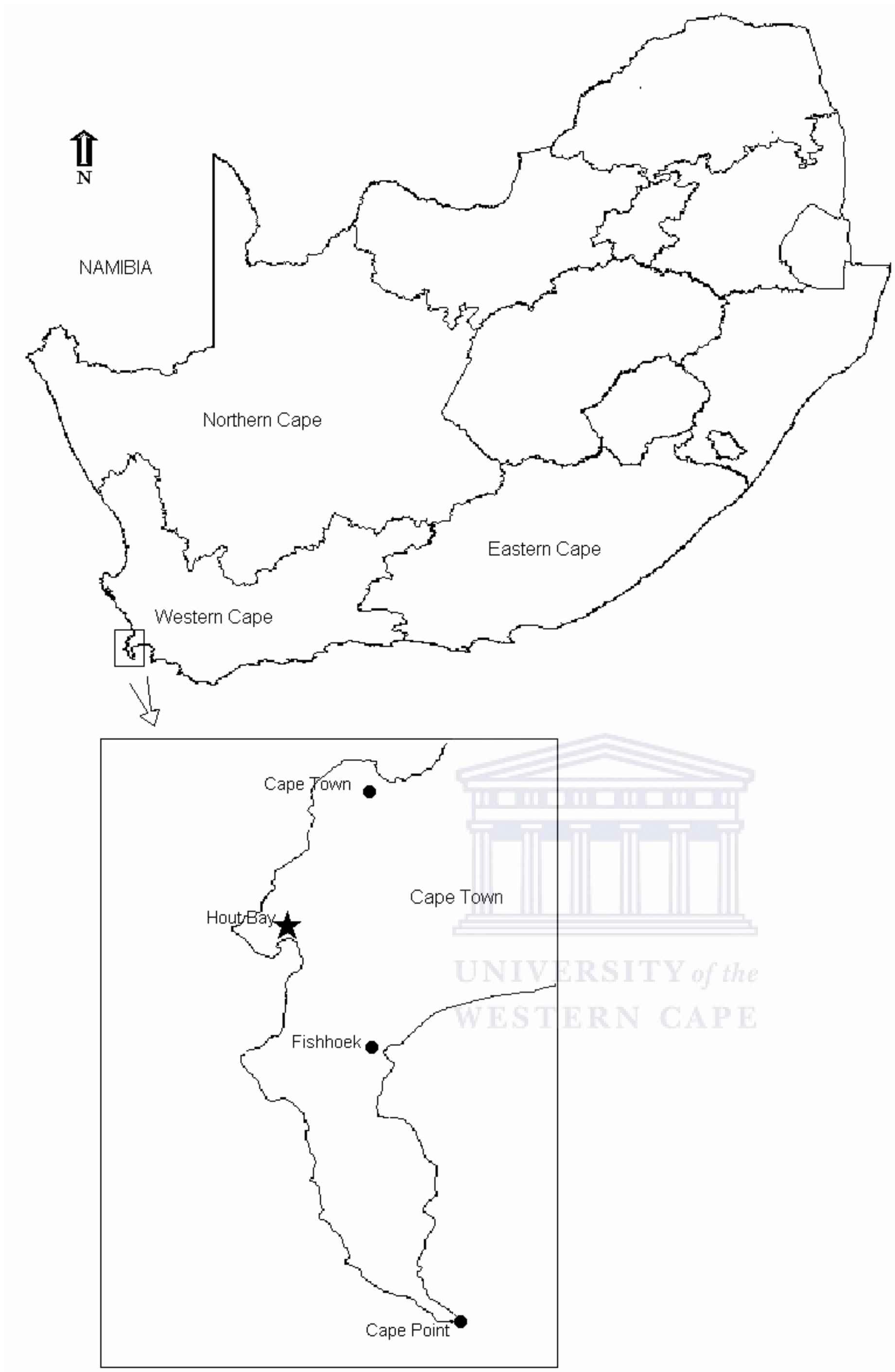


Fig. 1. Map of South Africa showing provincial boundaries. The study occurred in the Western Cape province; Hout Bay is marked with a star; nearby towns are marked with dots.

4. RESULTS

4.1 Stem density

Herbicide application resulted in lower overall stem density than the control (no treatment), for the first seven months after the initial treatment. Thereafter, the stem density on the plot treated with herbicide increased to levels exceeding those on the untreated plot (Fig. 2). The untreated plot had consistently higher density (three to five times higher) of resprouting stems than the treated plot (Fig. 3a). However, the overall density remained relatively stable for resprouting stems; there were no major increases or decreases. The density of new stems on the untreated plot was higher until seven months after initial cutting (Fig. 3b), implying that the increase in overall stem density after seven months is due to the increased density of new stems. New stem density increased with time, for both treated and untreated plots. Note the different scales in Figs. 3a and b. The maximum density of resprouting stems overall was 10.2 stems m^{-2}, while the maximum density of new stems was 32.2 stems m^{-2}.

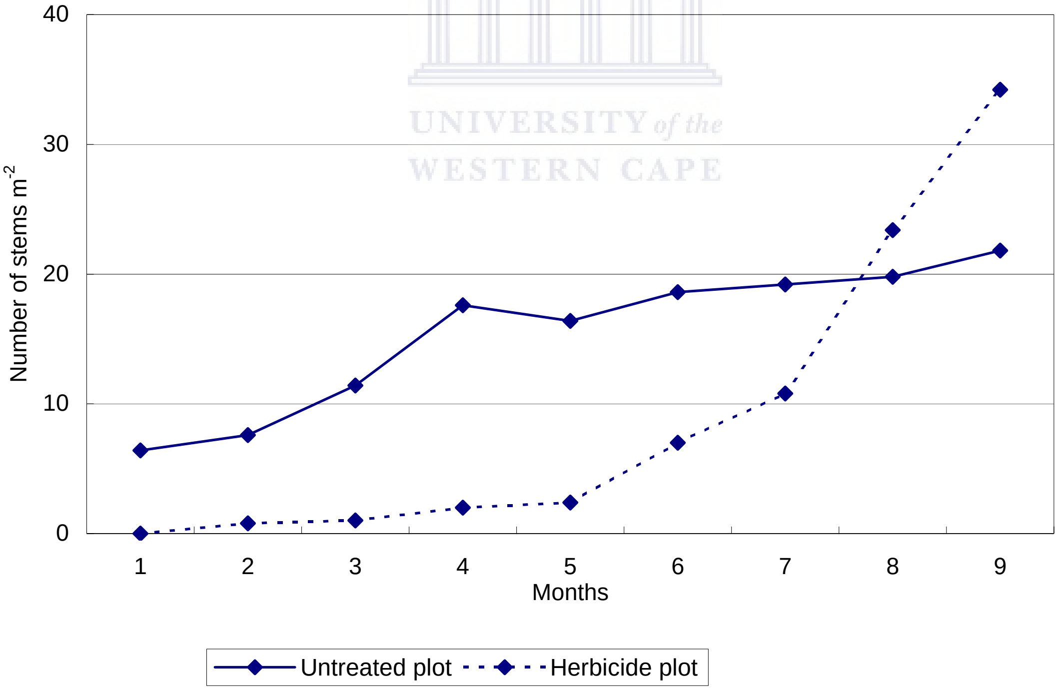
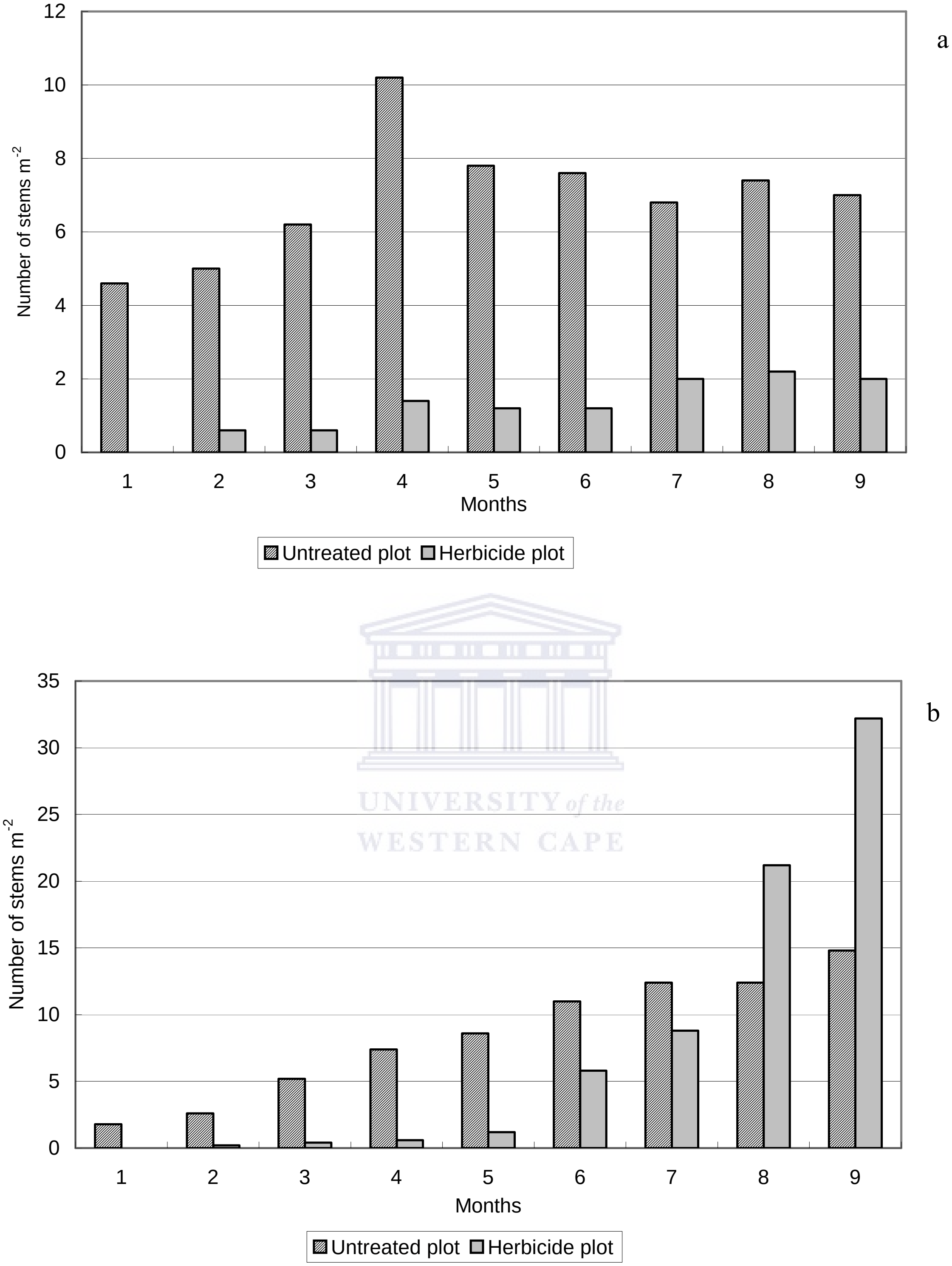


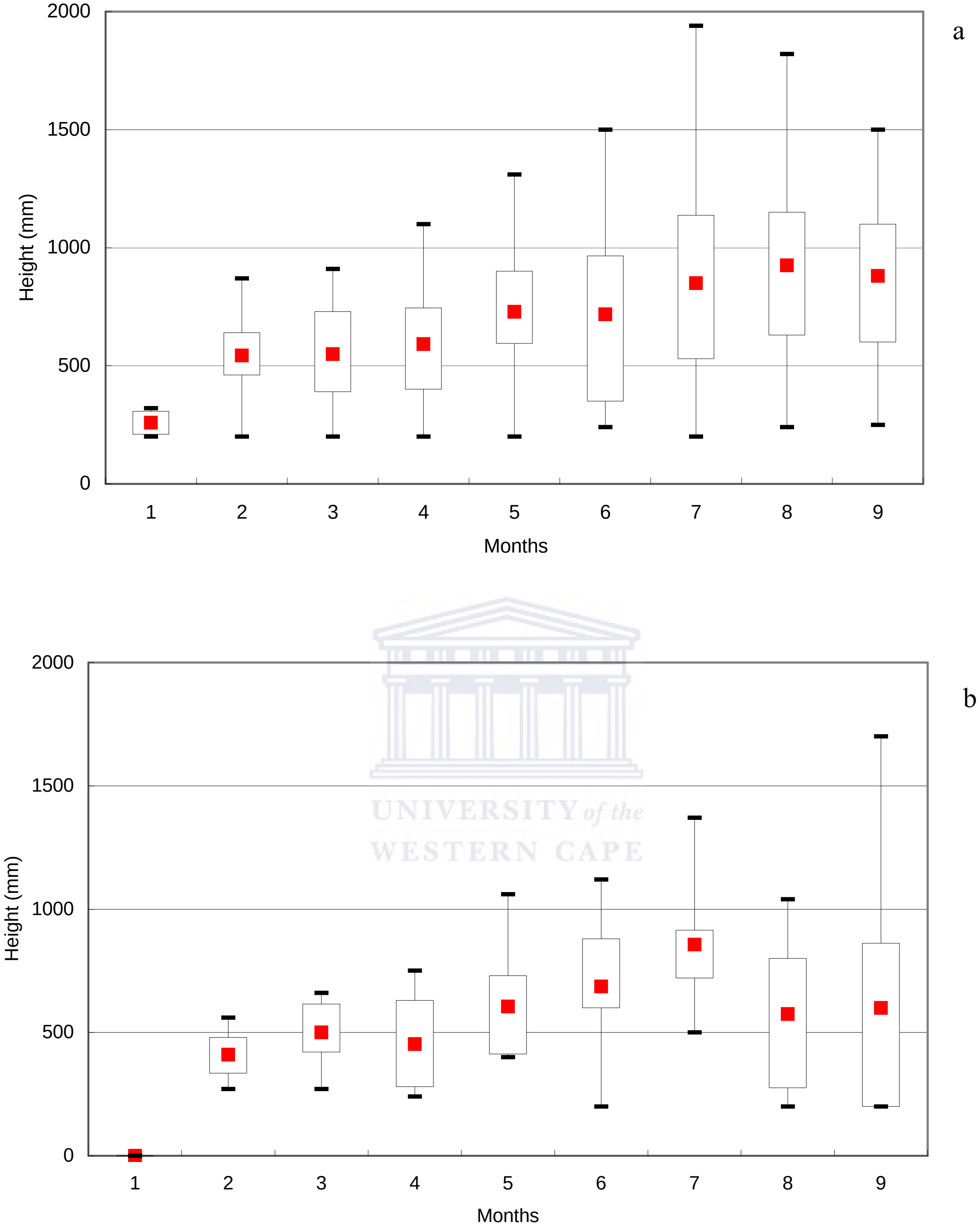
Fig. 2. *Arundo donax* stem density (stems m^{-2}) in plots treated and untreated with herbicide after cutting, along the Disa River in Hout Bay. Total number of stems consists of both new growth and resprouting growth, and varies at each data collection.



Figs. 3a and b. Density of resprouting (a) and new (b) *Arundo* stems in plots treated and untreated with herbicide after cutting, along the Disa River in Hout Bay. Number of stems varies with each data collection.

4.2 Stem height

Resprouting stems had similar average heights for both treated and untreated plots, with the untreated plot (Fig. 4a) having slightly higher average heights, as well as the few outlying taller stems. Herbicide may therefore have a slight negative effect on height of resprouting stems (Fig. 4b). New stems on the untreated plot were significantly taller ($p < 0.05$) (almost three times taller) than new stems in the herbicide-treated plot, from five months onwards (Figs. 5a and 5b). Prior to five months' growth, new stem height on the untreated plot was still taller than on the treated plot (Fig. 6).



Figs. 4a and b. Average height of resprouting *Arundo* stems in plots untreated (a) and treated (b) with herbicide after cutting, along the Disa River in Hout Bay. Boxes represent the first and third quartiles; the central box represents the mean; and whiskers represent minimum and maximum values. Number of stems varies with each data collection.

Figs. 5a and b. Average height of new *Arundo* stems in plots untreated (a) and treated (b) with herbicide after cutting, along the Disa River in Hout Bay. Boxes represent the first and third quartiles; the central box represents the mean; and whiskers represent minimum and maximum values. Number of stems varies with each data collection.

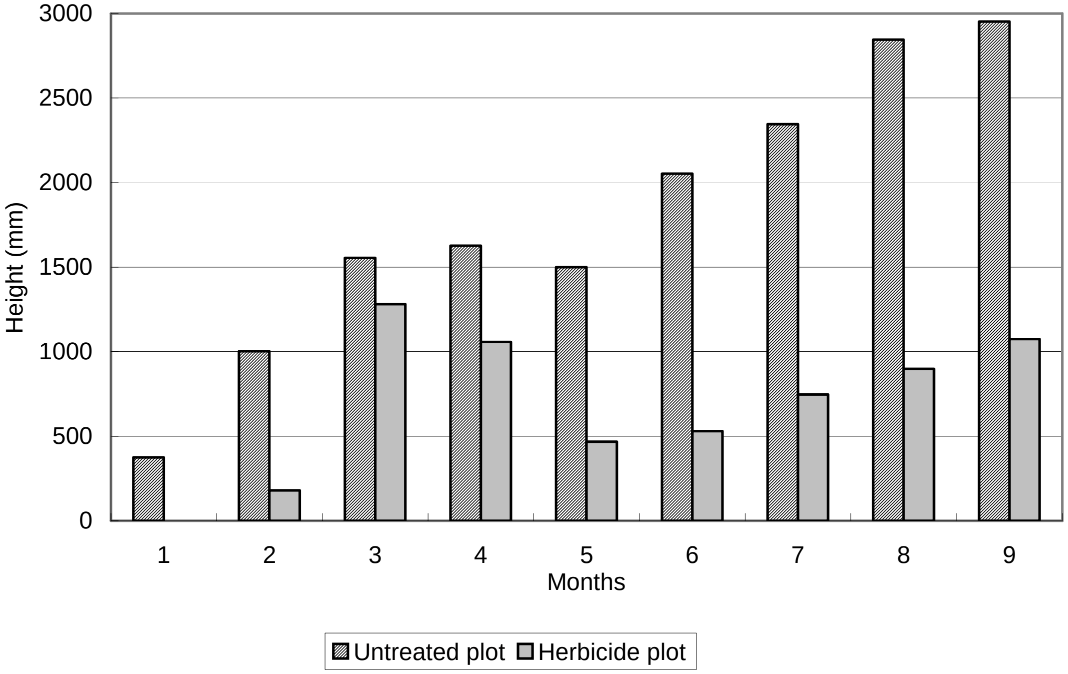
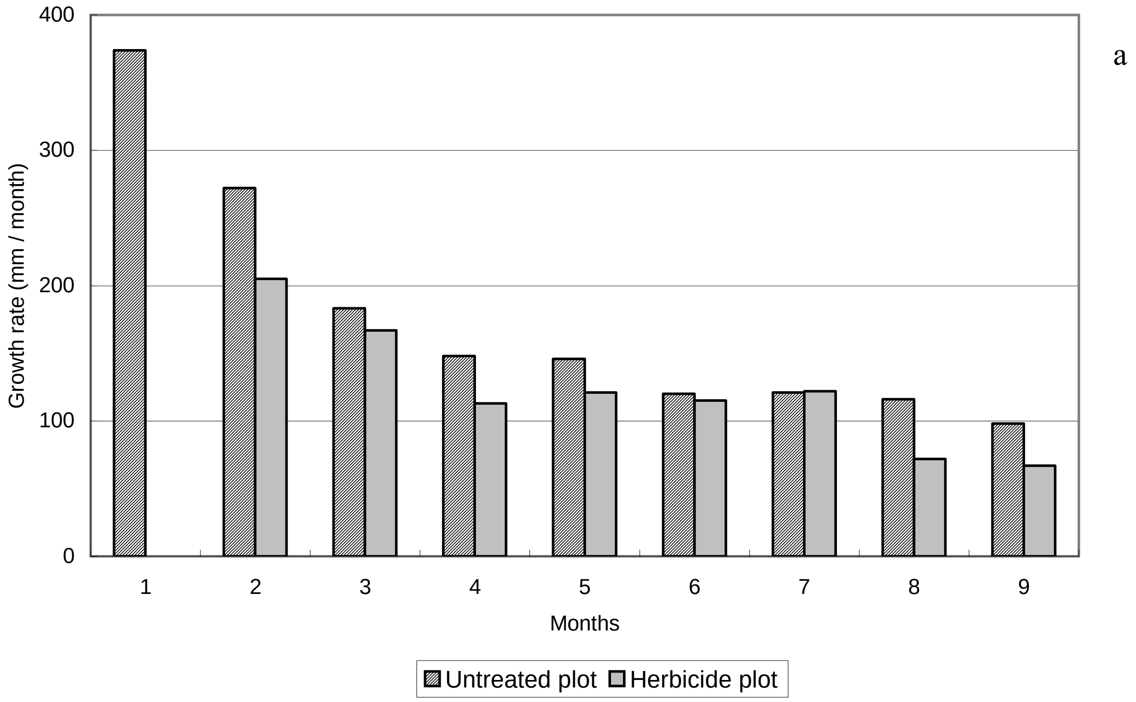
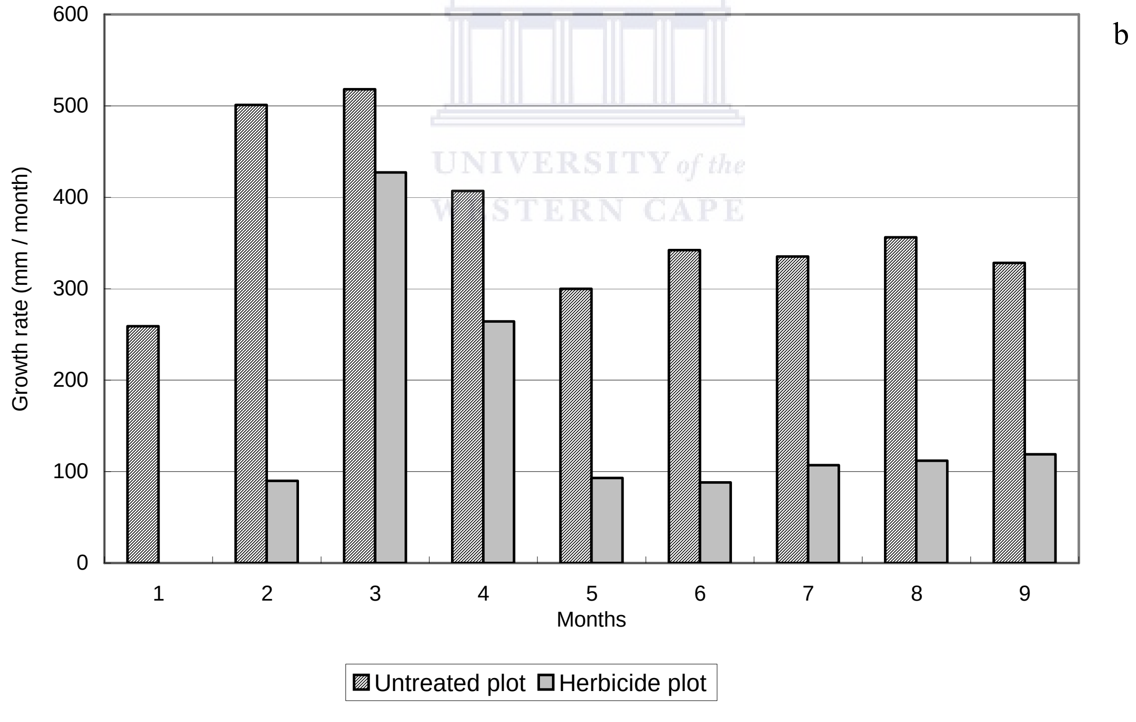


Fig. 6. Average height (m) of new *Arundo* stems in plots treated and untreated with herbicide after cutting, along the Disa River in Hout Bay. Number of stems varies with each data collection.

4.3 Stem growth rates

Growth rate appeared similar for resprouting stems in plots treated and not treated with herbicide (Fig. 7a). There were no resprouting stems on the treated plot one month after initial cutting. There was an obvious decrease in growth rate (in terms of height) over time for resprouting stems on both treated and untreated plots. Growth rates of new stems were consistently higher on the untreated plot than on the treated plot (Fig. 7b). From months five to nine, the growth rates were almost three times higher on the untreated plot.





Figs. 7a and b. Average growth rate of resprouting (a) and new (b) *Arundo* stems, in plots treated and untreated with herbicide after cutting, along the Disa River in Hout Bay. Number of stems varies with each data collection.

5. DISCUSSION

5.1 Density

Herbicide initially reduced density, height and growth rates of *Arundo*, but over time it stimulated density. Increases in density will lead to increased fuel load (fire risk), reduced habitat quality for indigenous animal species, and increased competition with indigenous plant species for resources. If no herbicide is used in conjunction with cutting, then cutting must be avoided, since it stimulates the growth of new stems. If herbicide for follow-up is limited, application of herbicide can be concentrated on new growth (and not to previously cut and treated stems). Herbicide provides a short-term management option, but without follow-up within six months, stem density will increase. Without killing the rhizomes, they may continuously send up new shoots regardless of the treatment.

5.2 Height

Herbicide effectively reduced the height of *Arundo* plants. Stands of treated *Arundo* were shorter therefore follow-up treatment may be easier.

5.3 Growth rate

Fastest growth occurred in the months immediately following cutting. As height increased, growth rate decreased. Herbicide reduced the growth rate of new stems.

5.4 Management implications

Mechanical control may be limited to smaller, younger patches of *Arundo*, where it may be possible to remove the entire plant, rhizomes included. Tarping involves placing a cover or tarpaulin (tarp) (usually transparent or black plastic sheeting) over the soil surface. Tarping can be effective (Gaffney & Gledhill 2003) but is not practical in most conditions. Since *Arundo* can grow through debris and shading (Else 1996), and through warm soil after fire (personal observation), the intended effects of darkness and heat beneath the tarpaulin are not likely to be significantly effective. Tarping is expensive and difficult to do on steep banks (Gaffney & Gledhill 2003). Preliminary investigations into tarping as a potential control for *Arundo* as part of this study were unsuccessful. Within weeks the plastic sheeting was torn and subsequently missing, and time did not allow for this part of the experiment to be restarted.

Integrated control is the best option for managing large stands of *Arundo*. To adequately and effectively control *Arundo* populations, herbicide must be used to some extent. There is growing opposition to the use of herbicides in invasive species management because of the potential effects on non-target species, soil and water. The effects of herbicide are small when compared to the long-term environmental damage (and subsequent economic costs) of *Arundo* (Bell 1997; Monheit 2003). Careful application using a paintbrush ensures application only to target species and no spillage, but is not viable for large expanses of *Arundo* since it is labour-intensive and time-consuming. Chemical foliar spray is largely ineffective, wasteful and has effects on non-target species and ecosystems. Cut-resprout-spray is the most effective method used in the USA (US EPA 1997), and can be used in areas where *Arundo* stands are extensive, and further from indigenous vegetation, streams and human settlements.

6. LIMITATIONS

Individual stems should possibly have been marked and monitored. Because of the changing number of new stems, the averages were skewed and not really and indication of the changing structure and growth of the stand or site. A lack of suitable study sites (secure and safe) hampered the experimental design and analysis of results. Results mentioned in this research should be used with caution, and the experiment repeated in more habitats with more replicates. It may be useful to perform the experiment in other provinces with a different climate. The measured growth of *Arundo* may be due to seasonal changes as well as the impact of herbicide and cutting.

7. ACKNOWLEDGEMENTS

I gratefully acknowledge the DST-NRF Centre of Excellence for Invasion Biology (CIB) at Stellenbosch University for funding, and the CSIR for coordinating project expenses; Drs. Richard Knight and Brian van Wilgen as supervisors; Jenny and Henry Nelson for initial introduction to the *Arundo donax* problem in Hout Bay; Isaac Crowster and Russell Main for assistance with fieldwork; Gretchen Coffman for advice; and Prof. Madsen and Dr. Kotze for assistance with data analysis.

8. REFERENCES

Bell, G.P. (1997) Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in southern California. *Plant invasions: studies from North America and Europe*. (eds J.H. Brock, M. Wade, P. Pyšek & D. Green), pp. 103-113. Backhuys Publishers, Leiden, The Netherlands.

Boose, A.B. & Holt, J.S. (1999) Environmental effects on asexual reproduction in *Arundo donax*. *Weed Research*, **39**, 117-127.

Coffman, G.C., Ambrose, R.F. & Rundel, P.W. (2004) Invasion of *Arundo donax* in river ecosystems of Mediterranean climates: causes, impacts and management strategies. *Proceedings of the 10th MEDECOS Conference*, 25 April – 1 May 2004, Rhodes Island, Greece. (eds M. Arianoutsou & W. Papanastasis), pp. 1-8. Millpress Science Publishers, Rotterdam.

Dudley, T.L. (2000) *Arundo donax*. *Invasive plants of California's wildlands*. (eds C.C. Bossard, J.M. Randall & M.C. Hoshovsky), pp. 53-58. University of California Press, Berkeley.

Else, J.A. (1996) Post-flood establishment of native woody species and an exotic, *Arundo donax*, in a southern Californian riparian system. MSc thesis, San Diego State University.

Frandsen, P. & Jackson, N. (1993) Impact of *Arundo* donax on flood control and endangered species. *Proceedings of the* Arundo donax *workshop*, 19 November 1993, Ontario, Canada. (eds N.E. Jackson, P. Frandsen & S. Duthoit). California Exotic Pest Plant Council, Riverside.

Gaffney, K.A. & Gledhill, K. (2003) Influence of giant reed on floodplain riparian plant communities: implications for invasive plant control and habitat restoration at the watershed level. *Proceedings of the Riparian Habitat and Floodplains Conference*, 12-25 March 2001, Sacramento, USA. (ed P.M. Faber). University of California Press, Sacramento.

Henderson, L. (2001) *Alien Weeds and Invasive Plants. A complete guide to declared weeds and invaders in South Africa*. Plant Protection Research Institute Handbook No. 12. Agricultural Research Council, Pretoria.

Iverson, M. (1993) The impact of *Arundo* donax on water resources. *Proceedings of the* Arundo donax *workshop*, 19 November 1993, Ontario, Canada. (eds N.E. Jackson, P. Frandsen & S. Duthoit). California Exotic Pest Plant Council, Riverside.

Milton, S.J. (2004) Grasses as invasive alien plants in South Africa. *South African Journal of Science*, **100**, 69-75.

Monheit, S. (2003) Glyphosate-based aquatic herbicides – an overview of risk. California Department of Food & Agriculture, Integrated Pest Control. *Noxious Times*, **Summer 2002**, 5-9.

Perdue, R.E. (1958) *Arundo donax* – source of musical reeds and industrial cellulose. *Economic Botany*, **12**, 368-404.

Rieger, J.P. & Kreager, A. (1989) Giant reed (*Arundo donax*): a climax community of the riparian zone. *Proceedings of the California Riparian Systems Conference*, 22-24 September 1988, Davis, California, USA. (technical coordinator D.L. Abell), pp. 222-225. USDA Gen. Tech. Report PSW-110.

Spencer, D.F., Ksander, G.G. & Whitehand, L.C. (2005) Spatial and temporal variation in RGR and leaf quality of a clonal riparian plant: *Arundo donax*. *Aquatic Botany*, **81**, 27-36.

Team Arundo del Norte (1999) *Controlling Arundo in your watershed: a guide for organizations*. US Environmental Protection Agency and California Department of Fish and Game. Available http://teamarundo/org/education/org_guide.pdf. Accessed 22/08/2006.

United States Environmental Protection Agency (1997) Control of Giant Cane in Riparian and Wetland Areas of Northern and Central California. US EPA Grant, Gray Lodge Wildlife Area, Butte County.

Zimmerman, P. (1999) Rates of transpiration by a native willow, *Salix exigua*, and by a non-native invasive, *Arundo donax*, in a riparian corridor of northern California. *Proceedings of the California Exotic Pest Plant Council*, October 1999, Sacramento, California.

CHAPTER 3

FUEL PROPERTIES AND POTENTIAL FIRE BEHAVIOUR IN COMMUNITIES DOMINATED BY AN INDIGENOUS AND AN INVASIVE ALIEN REED SPECIES

1. SUMMARY

1. *Arundo donax* is a highly productive invasive alien species that produces large quantities of above-ground biomass (up to 47 tons ha^{-1} in this study). High biomass can increase fuel loads in fire-prone communities. *Arundo* is highly flammable throughout most the year and causes significant fire hazards in the USA by increasing fire frequency and intensity. *Arundo* may increase fire intensity of invaded areas in South Africa.
2. Estimates of the biomass of *Arundo* and indigenous *Phragmites australis* were used to develop fuel models. Those were then used along with environmental scenarios to predict fire behaviour, to estimate whether invasion by *Arundo* alters natural fire behaviour. The BehavePlus fire behaviour modelling system was used.
3. *Arundo* had 4.5 times more biomass than *Phragmites*. *Phragmites* had a higher proportion of dead material (50 %) than did *Arundo* (16.5 %).
4. BehavePlus predicted that stands of *Phragmites* burn at higher intensities (12 700 kW m^{-1}) than stands of *Arundo* (72 kW m^{-1}), and that fires would spread more rapidly through *Phragmites* (86 m min^{-1}) than through *Arundo* (2 m min^{-1}), despite lower fuel loads in *Phragmites*. This indicates that invasion by *Arundo* is likely to decrease fire intensity and rates of spread. This is probably because the arrangement of fuel (packing ratios) and high proportion of live fuels in stands of *Arundo* are not conducive to spreading fire, despite higher fuel loads.
5. The fire behaviour model may have incorrectly predicted fire behaviour since it could not adequately accommodate tall vegetation (limit 3.05 m), did not take into account that some species such as *Arundo* may be flammable when green, and did not simulate fire behaviour under extreme weather conditions well. However, less dry material in *Arundo* stands may have been the main factor in predicting reduced fire intensity and rates of spread.
6. *Arundo* is highly flammable and has the potential to alter natural fire regimes in South African ecosystems. Other fire behaviour predication models must be tested or developed to accurately predict fire behaviour of *Arundo*.

2. INTRODUCTION

2.1 Biological invasions

Biological invasions are the second highest threat to biodiversity, after direct habitat destruction (Wilcove *et al.* 1998; Walker & Steffen 1999). Globally, invasive alien species have out-competed indigenous species for resources and space, changed fire and water regimes, and altered soil nutrient status (Macdonald *et al.* 1989; Cronk & Fuller 1995). Biological invasions have also altered ecosystem processes such as production, decomposition, and nutrient cycling, mostly as a result of structural and compositional changes made to ecosystems (D'Antonio & Vitousek 1992; Binggeli *et al.* 1998).

Invasive alien species alter ecosystem structure by differing from indigenous species in height, biomass and nutrient content, among others. They usually have greater biomass and growth rates than the indigenous species they replace (van Wilgen & Richardson 1985). Above-ground biomass determines fuel properties (Brooks *et al.* 2004), hence, fuel tends to be greater where there is greater biomass and productivity. Invasion of new species may alter fuel properties and fire behaviour of an ecosystem. Greater flame lengths, higher temperatures and greater heat release have all been recorded or predicted for alien shrubs and trees invading various vegetation types (van Wilgen & Richardson 1985; Lippincott 2000). Altered fuel loads, fuel properties and fire behaviour potentially increase fire hazards (Brooks *et al.* 2004). In South Africa, and recently in the Western Cape, fires are the cause of environmental, economic and social losses. van Wilgen & Scott (2001) report that alien invasive plants were responsible for increasing fuel loads over most of the areas that burned on the Cape Peninsula in January 2001.

2.2 Fire

Fire is a natural phenomenon and an important disturbance process necessary for the functioning of many ecosystems (Agee 1993; Bond & Keeley 2005). Fire can also have negative impacts on ecosystems. When fire and invasive alien species occur together in an area, their effect is synergistic, and the threat to ecosystems' integrity and sustainability becomes much more serious (van Wilgen *et al.* 1990; D'Antonio & Vitousek 1992).

In general, fires in stands of invasive species are of higher intensity and/or frequency than those to which indigenous ecosystems are adapted (e.g. cheatgrass *Bromus tectorum*), but sometimes the presence of alien invasive species may decrease fire frequency and intensity (e.g. diffuse knapweed *Centaurea diffusa*) (Harrod & Reichard 2001). Fire may alter the relative abundance of plant species (Vilà *et al*. 2001) by killing existing plants or causing them to resprout, by stimulating germination, or by eliminating competition (Hobbs & Huenneke 1992; Brooks *et al.* 2004). Fire-modified ecosystems most often favour fire-adapted species or create opportunities for other species to colonise or expand their distribution into previously filled niches (Agee 1993). Many invasive alien plant species are well suited to disperse rapidly into disturbed ecosystems and persist under altered disturbance regimes (D'Antonio *et al*. 1999). If the changes to fire regimes consequently support and promote the dominance of the invaders, then an 'invasive plant - fire regime' cycle can be established (Brooks *et al.* 2004). Grass-fire feedbacks have been documented in many parts of the world (Mack & D'Antonio 1998). In the western USA, grass-fire feedbacks are responsible for the conversion of mixed vegetation to stands of introduced annual grasses (Whisenant 1990). In Hawaii Volcanoes National Park, both fire frequency and extent have increased since grass invasion (Smith & Tunison 1992), and in seasonal submontane woodlands, fires have promoted the spread and increased the density of introduced grasses (Hughes *et al.* 1991). Similarly, in South African fynbos, fires are thought to stimulate germination and facilitate the establishment of new stands of invaders (Holmes *et al.* 1987).

2.3 *Arundo donax*

Arundo donax L. (hereafter referred to as *Arundo*) is a grass species that is invasive in many parts of the world. It originated and spread from the Indian sub-continent (Bell 1997), and today invades many sub-tropical and Mediterranean-type regions of the world (Herrera & Dudley 2003). *Arundo* is usually associated with rivers that have been physically disturbed or dammed, but it can colonize within undisturbed indigenous stands of species (Dudley 2000). *Arundo* is an important invasive species in South Africa, from an economic and ecological perspective, and it has the potential to invade more than a million hectares of the fynbos biome (Rouget *et al.* 2004). *Arundo* is a national problem because it poses a threat to water security for South Africa (Wells *et al.* 1980). It invades mainly along rivers, where its impact may include reduced richness and diversity of indigenous species, and possible increases in fire intensity (Milton 2004).

Arundo is highly productive and produces large quantities of above-ground biomass (up to 20 tons dry mass per hectare) (Perdue 1958). *Arundo* is highly flammable for most of the year (Scott

1993); even green stems are flammable (Bell 1993). In California, *Arundo* increases the fuel available for fires (Coffman *et al.* 2004). High productivity rates and flammability throughout the year increase the probability of unseasonal and higher intensity fires (Scott 1993). *Arundo* has changed ecosystem processes in some Californian riparian areas from flood-regulated to fire-regulated (Rieger & Kreager 1989; Bell 1997). The spread of *Arundo* is also accelerated by fire: fire clears away indigenous and other vegetation, and the remaining fire-adapted *Arundo* rhizomes easily resprout without competition for resources. New *Arundo* shoots appear within days after a fire (Coffman *et al.* 2004; personal observation). Increased fire frequency due to *Arundo* creates a positive feedback, contributing to further invasion success of *Arundo* (Coffman *et al.* 2004).

2.4 *Phragmites australis*

Phragmites australis (Cav.) Trin. ex Steud. (hereafter referred to as *Phragmites*) is a reed species indigenous to South Africa, also occurring in the USA. It is a cosmopolitan species, considered to be the most widely distributed reed species in the world (Bird 1962). *Phragmites* is similar in appearance to *Arundo*, usually only when young. Mature *Arundo* is taller, with larger leaves and thicker, stronger stems. It is also a large clonal grass species, and reaches heights of two to six metres. *Phragmites* reproduces mainly by vegetative reproduction, from its rhizomes (Ekstam 1995), which can reach a depth of one to two metres (Burdick *et al*. 2001). It is a C_3 species although its photosynthetic rates resemble that of a C_4 species (Antonielli *et al*. 2002). It is tolerant to climate, altitude (Welsh *et al*. 1987), disturbance and invasion by other species (Duke 1983; Meyerson *et al*. 2000). *Phragmites* usually grows in open wet areas, along streams, marshes, ditches and roadsides (Meyerson *et al*. 2000).

2.5 Fuel models

The fuel properties of vegetation influence the occurrence, nature and effects of fires to a large degree (van Wilgen & van Hensbergen 1992). Different vegetation types can have quite different fuel properties (Rundel 1981; van Wilgen *et al*. 1990). Dominant species are described in terms of fuel types in order to predict possible fire scenarios using fire behaviour models (Vilà *et al.* 2001). Fuels are categorised according to the fuel load and fuel particle size classes (Anderson 1982). Where total above-ground material is referred to as phytomass, specific distinctions are being made between live (biomass) and dead (necromass) material. Where biomass is mentioned without distinctions into phytomass and necromass, it is in fact referring to phytomass, total above-ground material (live + dead). BehavePlus is the successor to the BEHAVE fire behavior prediction and fuel modelling system (Burgan & Rothermel 1984; Andrews & Bevins 2003). BehavePlus uses site-specific input to predict fire behaviour parameters such as fire spread rate, fireline intensity and flame length under stated climatic conditions at a point in time (Andrews & Bevins 2003).

This study determined whether invasion by *Arundo* would alter fuel loads and subsequently fire behaviour of an ecosystem. Fuel models for *Arundo* and *Phragmites*, and subsequent predicted fire behaviour, are compared under different climatic conditions for the Western Cape.

3. METHODS

3.1 Study areas

The Western Cape of South Africa has a Mediterranean-type climate: warm, dry summers and wet, temperate winters. Rainfall varies from 200 to 2 000 mm per year, and falls mainly during the winter months. Strong south-easterly winds blow primarily during summer, from November to February. The study was undertaken in the lower reaches of two rivers in the Western Cape: the Disa River in Hout Bay and the Eerste River on the Spier Wine Estate in Stellenbosch. The Disa River runs through Hout Bay, a coastal town about 11 km from Cape Town. The lower reach is characterised by a broad floodplain and most of it falls within residential or commercial zoning. The area between the Victoria and Princess Road bridges constitutes the first study site. The Disa River is heavily disturbed and impacted on by agriculture, residential and light industrial wastewater, and formal and informal development. *Arundo* stands on the site are dense and extensive, and span the entire distance between the two bridges, with fewer and less dense clumps upstream. *Arundo* is annually cleared by the town council along this stretch of land, along one riverbank for safety, aesthetic and flood prevention purposes (I. Crowster pers. comm.). However, the untreated biomass is then mostly left on the banks or piled slightly away from the original site (personal observation).

The Eerste River is one of three rivers on the Spier Wine Estate. It is heavily impacted and polluted along most of its course. It flows through the town of Stellenbosch and is exposed to urban pollution and waste. This second study site, on the Spier Wine Estate, is surrounded by agricultural, grazing and open land. The public have little or no access to this site since it is a privately owned enterprise. The *Arundo* stand at this site is extensive, but there appears to be only one major stand, spanning a distance of 300 – 400 m. Smaller clumps of *Arundo* exist in other locations along the river. Many other invasive plants are present along the river. There has been little other disturbance, except for some minor mowing or grazing around the site.

3.2 Data collection

Above-ground biomass of *Arundo* and *Phragmites* was collected from the sites. *Phragmites* biomass was collected from Hout Bay, and *Arundo* biomass was collected from Hout Bay and Spier. Five plots of 2 m x 2 m within a stand of the dominant species were selected per river (i.e. five plots of 2 m x 2 m for *Arundo* at the Disa and Eerste Rivers, five plots of 2 m x 2 m for *Phragmites* at the Disa River) (Table 1). At each plot, all the aboveground *Arundo* and *Phragmites* biomass was clipped to ground level and collected. This biomass was divided into dead and live material. Dead material was separated into size classes of smaller (1 hour fuel[*]) or larger (10 hour fuel[*]) than 6 mm in diameter. Branches smaller than 6 mm in diameter were clipped off stems and added to the smaller size class. In each size class (1 h and 10 h) and category (dead or live), the stems were counted and measured, and the biomass weighed. From each of these fifteen plots, leaf and stem samples per size class and category were used to determine moisture content and total dry mass. These samples were collected between 11h00 and 13h00 and stored in cool conditions in sealed ziplock bags until they could be analysed. Monthly leaf samples were collected of *Arundo* and *Phragmites* from the Disa River site, in order to determine monthly leaf moisture content (live herbaceous moisture content). Heat content (KJ kg^{-1}) of *Arundo* and *Phragmites* were determined using bomb calorimetry analysis on leaf samples.

---

[*] Dead fuels are divided into moisture time-lag classes based on rates of moisture loss. Smaller diameter fuels (0 to 6 mm) lose moisture faster during a fire than do the larger diameter fuels (25 to 75 mm). Standard classes used to partition dead fuels based on diameter are: 1 hour (0-6 mm), 10 hour (6-25 mm) and 100 hour (25-75 mm) (Deeming and Brown, 1975). Fuels of diameter less than 6 mm lose moisture within 1 hour, and fuels of diameter greater than 6 mm tend to take upwards of 10 hours to lose moisture.

3.3 Laboratory analysis

Leaf samples to determine moisture content were dried in an oven at 60 - 70º C in paper bags for 24 hours. The samples were weighed before and after drying, and percentage moisture content was determined per leaf sample. Leaf and stem biomass samples were dried in paper bags for 24 hours at 60 – 70 ºC. The samples were weighed before and after drying, and percentage moisture content was determined per size class and category. Percentage moisture content was used to determine total biomass and dry mass.

Table 1. Location of plots of *Arundo* and *Phragmites* at Hout Bay and Spier.

Plot number	*Arundo* (Hout Bay)	Plot number	*Arundo* (Spier)	Plot number	*Phragmites* (Hout Bay)
A1	S 34° 01' 57.6" E 18° 21' 13.0"	A6	S 33° 59' 14.7" E 18° 47' 36.9"	P1	S 34° 01' 49.9" E 18° 21' 15.7"
A2	S 34° 02' 02.8" E 18° 21' 13.3"	A7	S 33° 59' 15.1" E 18° 47' 37.7"	P2	S 34° 01' 49.3" E 18° 21' 15.9"
A3	S 34° 02' 02.4" E 18° 21' 13.4"	A8	S 33° 59' 15.7" E 18° 47' 39.0"	P3	S 34° 01' 50.7" E 18° 21' 15.0"
A4	S 34° 02' 01.0" E 18° 21' 13.4"	A9	S 33° 59' 16.3" E 18° 47' 40.8"	P4	S 34° 01' 51.6" E 18° 21' 14.5"
A5	S 34° 02' 00.8" E 18° 21' 13.3"	A10	S 33° 59' 12.6" E 18° 47' 34.3"	P5	S 34° 01' 51.8" E 18° 21' 14.3"

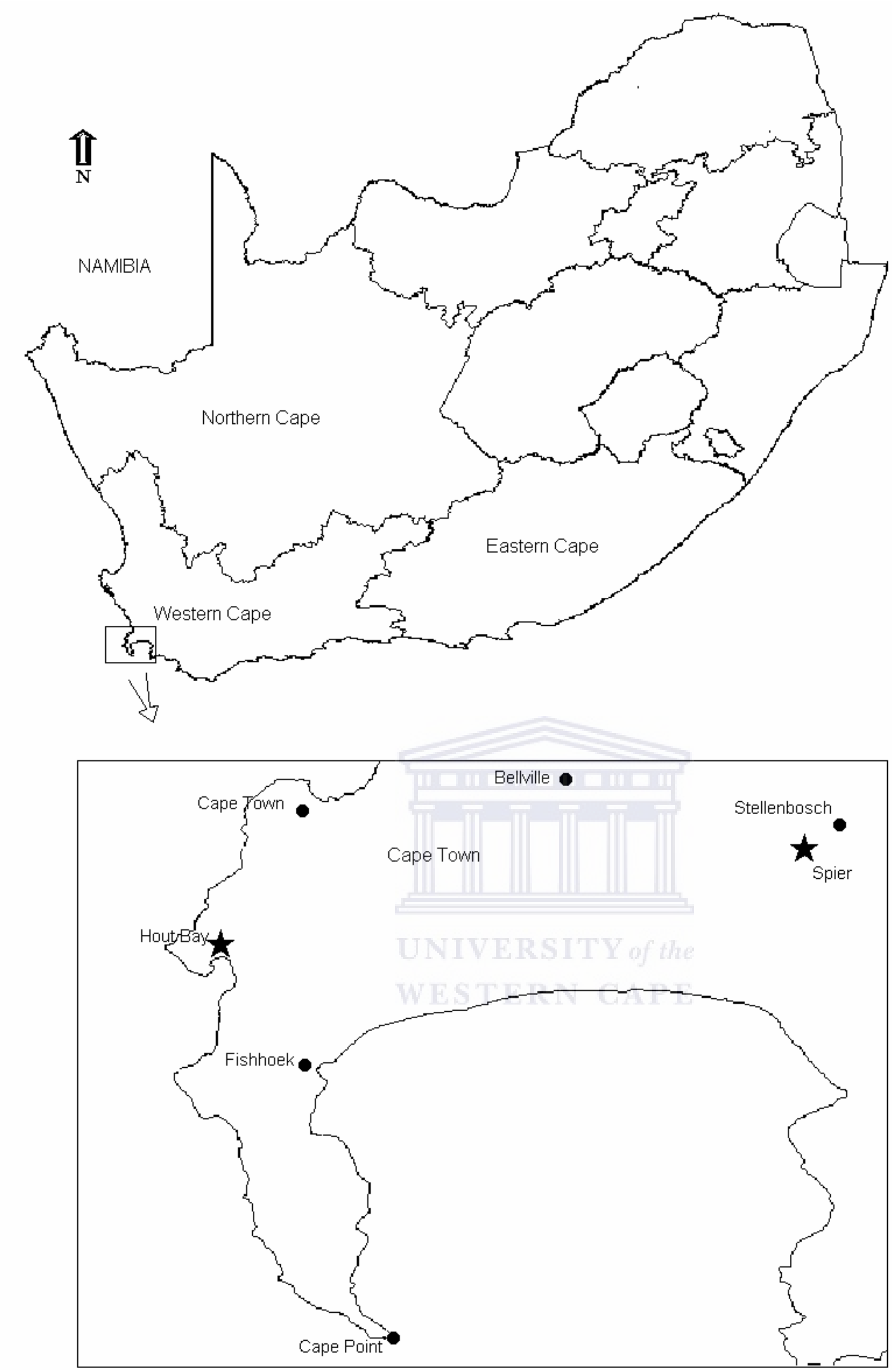


Fig. 1. Map of South Africa showing provincial boundaries. The study occurred in the Western Cape province; study sites are marked with stars; nearby towns are marked with dots.

3.4 Fuel model

The data were used in the BehavePlus fire behaviour modelling system (Andrews & Bevins 2003), and parameters set to determine fireline intensity and surface rate of spread for *Arundo* and *Phragmites*. Table 2 presents fuel models for *Arundo* and *Phragmites*. Surface area to volume ratios were determined by the estimation of 20 % leaf and 80 % stem contribution to total fuel load. Along with the fuel models, environmental conditions of wind speed, slope, and monthly moisture contents of both species were used in a fire behaviour prediction model to determine surface rate of spread (ROS) and fireline intensity (FI). Wind speeds of 0 to 50 km h^{-1} (in 5 km h^{-1} intervals) and slopes of 0 degrees were used. Only live moisture content varies throughout the year; these values were derived from monthly leaf samples. Biomass values may differ slightly between those used for the fuel model and those stated as averages in general, since different moisture contents were used - an average moisture content was used determining biomass for the fuel model values, and separate moisture contents were used for biomass values from different sites.

3.5 Statistical analysis

The Wilcoxon Rank Sum Test was used to determine whether there is a significant difference in the biomass of *Arundo* at Hout Bay and Spier (between sites), and whether there is a significant difference between the biomass of *Arundo* and *Phragmites* at Hout Bay (between species). It was also used to determine differences in biomass between the species and the sites. One-way ANOVA's were used to determine significant differences between surface rates of spread and fireline intensities per month per species.

Table 2. Fuel models of *Arundo* and *Phragmites* collected from and measured at the Disa River in Hout Bay and the Eerste River at Spier. Data were derived from five plots (plots size 4 m^2) of *Arundo* at Hout Bay and Spier (10 plots in total), and five plots of *Phragmites* at Hout Bay.

	Arundo donax	*Phragmites australis*
1-h fuel load (tons ha^{-1})	0.7 (0.53) *	2.35
10-h fuel load (tons ha^{-1})	6.17 (4.69) *	5.73
Live herbaceous fuel load (tons ha^{-1}) §	37.70 (28.65) *	8.24
1-h surface area : volume ratio (m^2 m^{-3})	3365	3348
Live herbaceous surface area : volume ratio (m^2 m^{-3})	2245	2662
Fuel bed depth (m)	4.03 (3.05) *	2.805
Dead fuel heat content (KJ kg^{-1})	15929	16815
Live fuel heat content (KJ kg^{-1})	15929	16815
Dead fuel moisture of extinction (%)	30	30

* The model allowed for a maximum fuel bed depth of 3.05 m. *Arundo* had a fuel bed depth of 4.03 m. To account for this, the fuel load and fuel bed depth were reduced by 24 % for the packing density to be a true representation. The values in brackets are the reduced values used in the fire behaviour prediction model. § All live material was classified as live herbaceous fuel since there was no live woody fuel.

4. RESULTS

4.1 Percentage moisture content

Arundo's lowest moisture content (30 %) for live herbaceous material occurred in late autumn (May 2005), increasing to maximum moisture content (380 %) in spring (October 2005), reducing slightly to 250 % in early summer (November and December 2005) and increasing in January to 300 % (Fig. 2). *Phragmites*' lowest moisture content (30 %) occurred in late autumn

(May 2005). Moisture during spring was around 230 - 250 %, decreasing in summer to between 160 and 200 %. *Arundo* has the higher moisture content in all months except May and August.

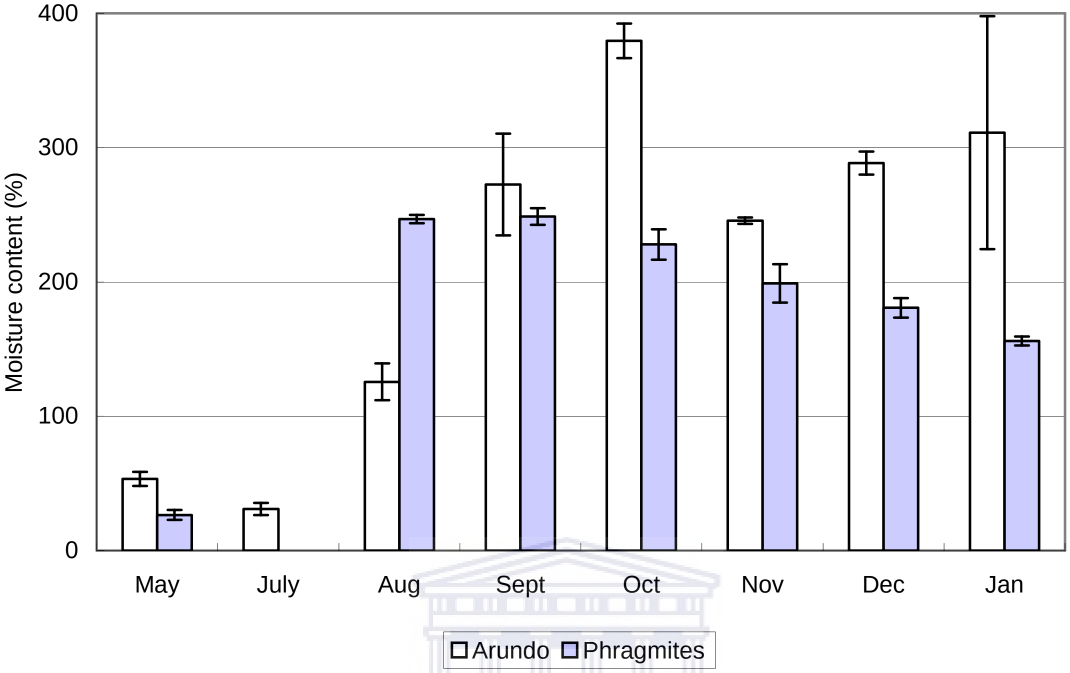


Fig. 2. Percentage moisture content taken from leaf samples of *Arundo donax* and *Phragmites australis* between May 2005 and January 2006 (n = 2). Samples were taken from along the Disa River in Hout Bay. Bars indicate minimum and maximum values.

4.2 Biomass

Total biomass of *Arundo* (average of 37.70 tons ha^{-1}) was 4.5 times higher than total biomass of *Phragmites* (8.24 tons ha^{-1}), suggesting that invasion by *Arundo* increases the biomass by 450 % (Table 2). *Arundo* at Hout Bay had significantly higher biomass (average of 43.09 tons ha^{-1}) than at Spier (27.76 tons ha^{-1}). The value of live biomass largely influenced the value of total biomass. *Phragmites* had a higher proportion of dead material to live material than did *Arundo* (Table 3).

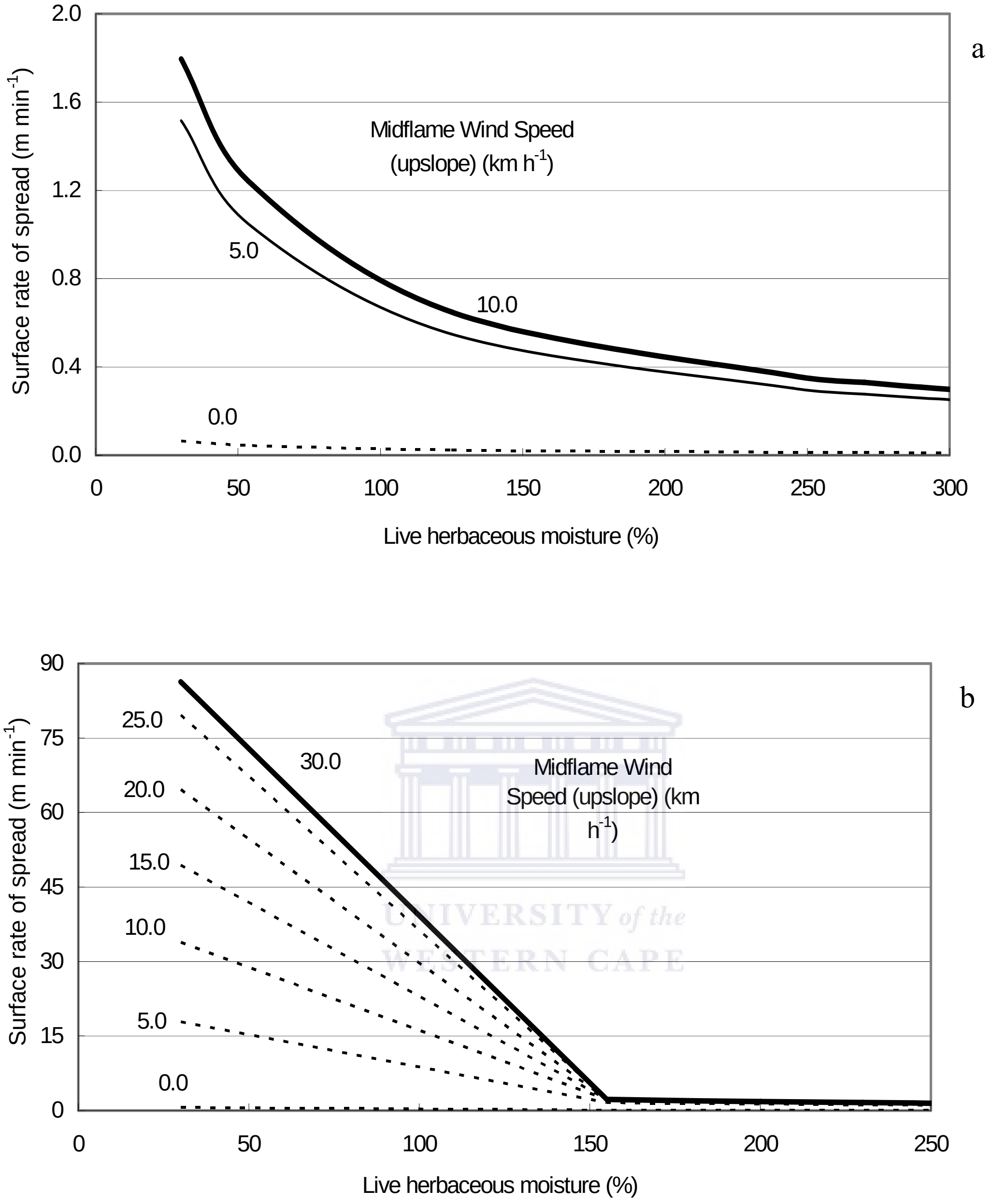
Table 3. Average phytomass, biomass and necromass (tons ha^{-1}) of *Arundo* and *Phragmites* at Hout Bay and Spier. Average values were derived from five plots each for *Arundo* from Hout Bay and Spier, and five plots for *Phragmites* at Hout Bay.

	Phytomass (live + dead)	Biomass (live)	Necromass (dead)	Proportion live / dead
Arundo donax (Hout Bay)	47.00	43.09	3.91	13.90
Arundo donax (Spier, Stellenbosch)	36.95	27.76	9.19	3.02
Phragmites australis (Hout Bay)	16.07	7.99	8.08	0.99

4.3 Predicted fire behaviour

4.3.1 Surface rate of spread

Estimated surface rate of spread (ROS) decreased with increasing herbaceous moisture content. ROS of fire through *Arundo* was highest (1.8 m min^{-1}) at wind speeds of 10 to 50 km h^{-1}, where the live herbaceous moisture was lowest (Fig. 3a). The increase between 10 and 50 km h^{-1} in wind speed did not affect estimated ROS through *Arundo*. Estimated ROS of fire through *Phragmites* was highest (86.3 m min^{-1}) at wind speeds of 30 to 50 km h^{-1}, where the live herbaceous moisture was lowest (Fig. 3b). For *Phragmites*, the estimated ROS increased with wind speed, and the maximum effect was gained at 30 km h^{-1}, after which increasing wind speed had no effect. Estimated ROS of fire through *Phragmites* was much higher (17.0 to 86.3 m min^{-1}) than through *Arundo* (maximum 1.8 m min^{-1}). Each month, *Phragmites* had significantly higher estimated ROS values than *Arundo* ($p < 0.05$). Low herbaceous moisture content and high wind speeds do not always correlate, but when they do, estimated ROS of fire will be greatest. Very low moisture content (30 %) for *Phragmites* caused estimated ROS values of 0.6 to 86.3 m min^{-1} (at different wind speeds), whereas average moisture contents of between 150 and 250 % caused ROS values of 0.04 to 2.2 m min^{-1}. Estimated ROS values did not vary as much between moisture contents for *Arundo*. Once the outlying estimated ROS value for Phragmites (May) was removed, estimated ROS averages were much lower (Fig. 4).



Figs. 3a and b. Maximum estimated surface rate of spread of fire relative to live herbaceous moisture content in stands of invasive *Arundo* (a) and *Phragmites* (b), at various midflame wind speeds. The thick line indicates the surface rate of spread of fires at maximum influential wind speeds of 10 and 30 km h^{-1}, respectively. The narrow and dotted lines are marked and represent surface rate of spread of fire at different wind speeds. Herbaceous moisture content is based on monthly sampling of *Arundo* and *Phragmites* along the Disa River in Hout Bay. BehavePlus fuel model input data in Table 2.

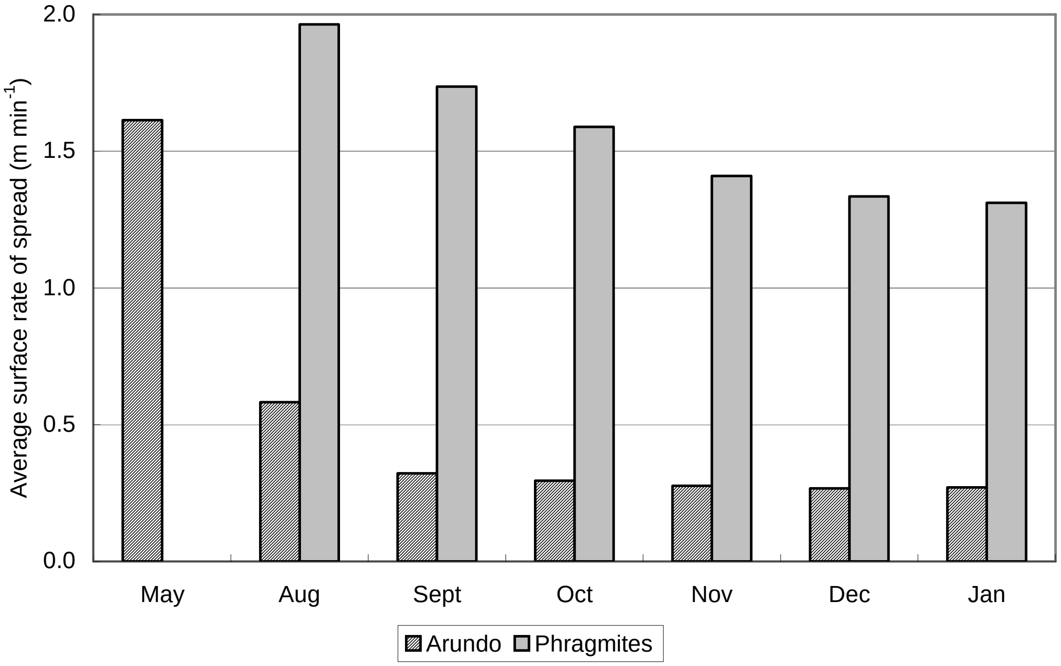
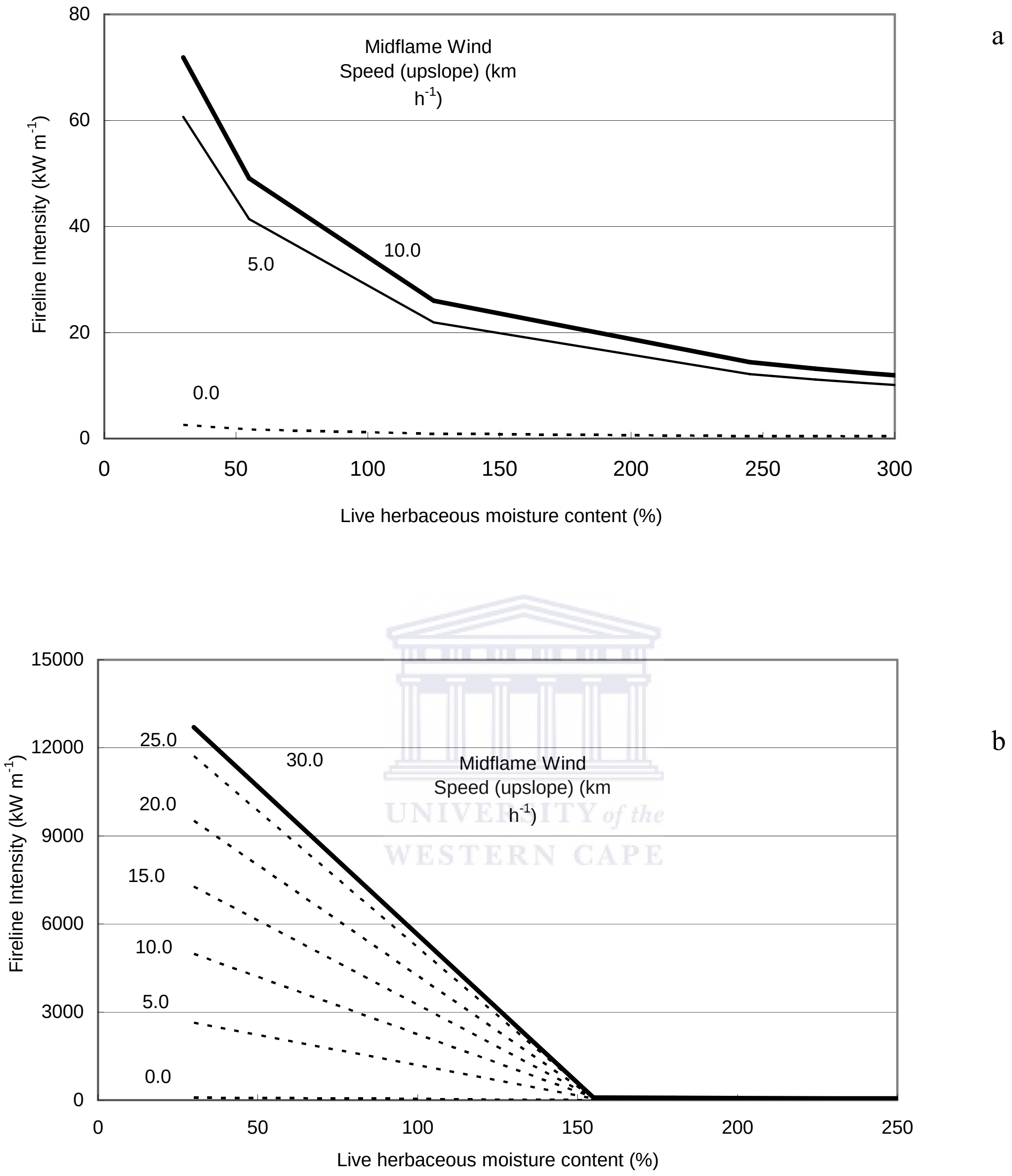


Fig. 4. Average estimated surface rate of spread of fire through *Arundo* and *Phragmites* during different months of the year. Monthly values are associated with monthly moisture contents collected from *Arundo* and *Phragmites* along the Disa River in Hout Bay. Values are averages of surface rate of spread at wind speeds of 0.0 to 50.0 km h^{-1}. BehavePlus fuel model input data in Table 2. Estimated rate of spread value of *Phragmites* for May removed (outlier).

4.3.2 Fireline intensity

Estimated fireline intensity (FI) decreased with increasing herbaceous moisture content. Maximum estimated FI in *Arundo* (71.9 kW m^{-1}) occurred at wind speeds of 10 to 50 km h^{-1}, where the live herbaceous moisture was lowest (Fig. 5a). The increase in wind speed between 10 and 50 km h^{-1} had no effect on estimated fireline intensity. Estimated FI in *Phragmites* increased with increasing wind speed (Fig. 5b). The maximum estimated FI (12 700 kW m^{-1}) was attained at 30 km h^{-1} wind speed. Increasing the wind speed to 50 km h^{-1} had no more effect than at 30 km h^{-1}. Estimated FI values for *Arundo* ranged from 0.4 to 71.9 kW m^{-1}. Estimated FI values for *Phragmites* ranged from 1.4 to 12 702 kW m^{-1}. Very low moisture content (30%) for *Phragmites* resulted in estimated FI's of between 91.7 and 12 702.1 kW m^{-1}, whereas average moisture contents of between 150 and 250 % resulted in estimated FI's of 1.4 to 84.8 kW m^{-1}. Estimated FI values for *Arundo* did not vary as much between the lowest moisture content and higher moisture contents. Once the outlying estimated FI value for *Phragmites* (May) was removed, estimated FI averages were much lower (Fig. 6). Each month, estimated FI values were significantly higher for *Phragmites* than for *Arundo* ($p < 0.05$). Very low moisture contents increased the estimated FI in *Phragmites* exponentially. Both estimated rate of spread (Fig. 4) and estimated fireline intensity (Fig. 6) in *Arundo* were highest in May, after which they were reduced by more than half for August. The values were even lower for the period September to January, each month having had similar values. Estimated rate of spread and fireline intensity in *Phragmites* were highest in August, decreasing every month until the lowest value in January.



Figs. 5a and b. Estimated fireline intensity of fire relative to live herbaceous moisture content in stands of invasive *Arundo* (a) and *Phragmites* (b), at various midflame wind speeds. The thick line represents the fireline intensity at maximum influential wind speeds of 10 and 30 km h^{-1}, respectively. The narrow and dotted lines are marked and represent fireline intensity at different wind speeds. Herbaceous moisture content is based on monthly sampling of *Arundo* and *Phragmites* along the Disa River in Hout Bay. BehavePlus fuel model input data in Table 2.

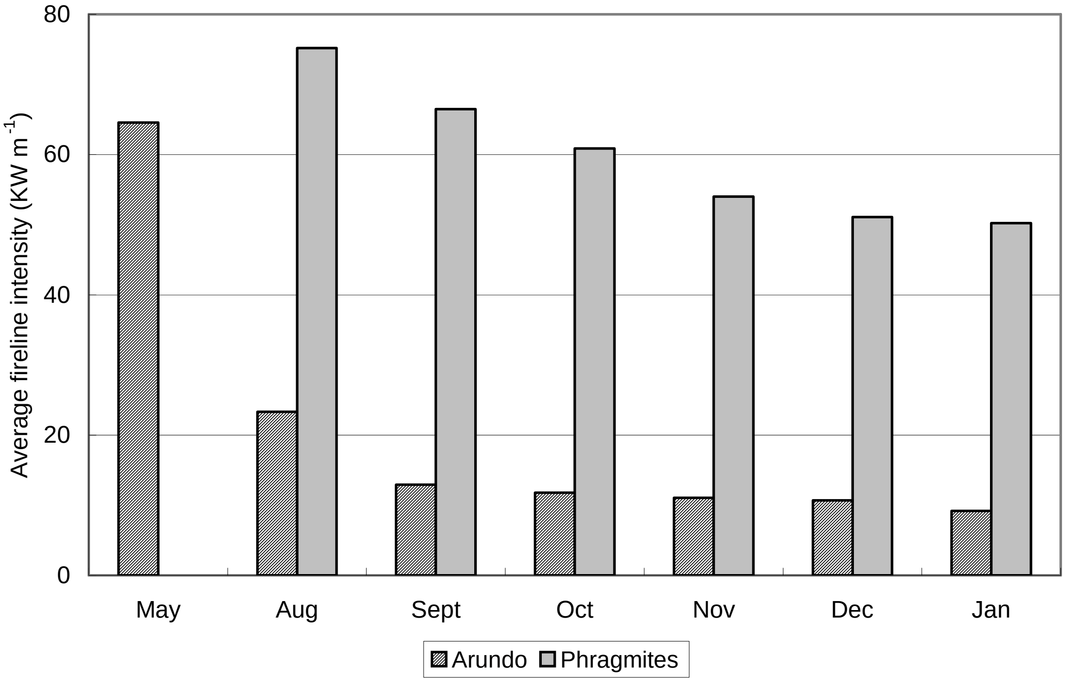


Fig. 6. Average estimated fire intensity through *Arundo* and *Phragmites* during different months of the year. Monthly values are associated with monthly moisture contents collected from *Arundo* and *Phragmites* along the Disa River in Hout Bay. Values are averages of estimated fireline intensity at wind speeds of 0 to 50 km h^{-1}. BehavePlus fuel model input data in Table 2. Estimated fireline intensity value of *Phragmites* for May removed (outlier).

5. DISCUSSION

5.1 Percentage moisture content

It is counter-intuitive that *Arundo* had the highest moisture content during summer, which is the dry season in the Western Cape, and the lowest moisture content during the rainy season. However, since *Arundo* is a user of soil water, rather than being dependent on rainfall, the results were not that unexpected or abnormal. *Arundo* may present an unseasonal fire hazard, during wet winter months, when vegetation moisture content is at its lowest. During winter there are occasionally hot days, and should a fire break out under these conditions, *Arundo* would possibly burn at higher intensity.

5.2 Biomass

Total and live biomass in stands of *Arundo* was significantly higher than total and live biomass of *Phragmites*. Dead biomass (or dry material) was lower in stands of *Arundo*. Dead biomass is most important when determining a fuel model, because it promotes burning. *Arundo* therefore effectively has a smaller fuel load than *Phragmites*. Should *Arundo* replace *Phragmites* in the Western Cape of South Africa, the ecosystem would have increased amounts of live herbaceous material, with the implied reduction in fire risk. *Arundo* has more than twenty times more live biomass than fynbos communities, and about five times more total biomass (Table 4). It has similar amounts of dead biomass, but the proportions are different. In fynbos communities, dead material constitutes 65 % of the total material, whereas in *Arundo*-dominated communities, dead material constitutes only 8 % of the total material. *Arundo* has great potential to invade fynbos systems (Rouget *et al*. 2004), increasing overall biomass. If *Arundo* were to accumulate more dry material, it would increase fuel loads of fynbos systems, with the accompanying increases in fire intensity and rate of spread.

5.3 Predicted fire behaviour

Fire behaviour is related to moisture content – increased rate of spread and intensity occur when vegetation is driest. According to the model, *Phragmites* will burn with greater intensity and fire will spread more rapidly in stands of *Phragmites* than in *Arundo*. *Arundo* does not appear to be increasing the fire potential of ecosystems in the Western Cape. The model predicts that *Arundo* will likely suppress fire behaviour of riparian ecosystems where it replaces *Phragmites*.

The differences between predicted fire behaviour in *Arundo* and *Phragmites* are probably due to *Phragmites* having considerably more dry material within its stands than *Arundo*. *Phragmites* generally accumulates a lot of dead material within stands (Haslam 1972). The fuel model does not take into account the full height of *Arundo*, which is taller than *Phragmites*, and may relate to discrepancies in fuel packing densities. The fire behaviour prediction is also based on physical and not physiological aspects of the individual species, such as potential volatile oils within the leaves.

Fire behaviour of *Arundo* is site-specific. In northern and drier areas of the country, which receive summer rainfall, *Arundo* may present a greater winter fire hazard. Low moisture content of

Arundo combined with low rainfall (or dry season) would present the greatest fire risk. Unseasonal fires would put other species at risk.

Table 4. Average live, dead and total biomass (tons ha^{-1}) of mature indigenous fynbos communities in the Western Cape (adapted from van Wilgen 1984). *Arundo*-dominated communities are compared with indigenous fynbos and *Phragmites*-dominated communities. *Arundo* values were derived from 10 plots (five from Hout Bay, five from Spier), and Phragmites values are derived from five plots (Hout Bay).

	Phytomass (live + dead)	Biomass (live)	Necromass (dead)	Proportion live : dead
Fynbos (Kogelberg)	7.15	3.24	3.91	0.81
Fynbos (Jonkershoek)	17.24	2.94	14.30	0.20
Fynbos (Jakkalsrivier)	10.47	7.78	2.69	2.84
Fynbos (Cape Peninsula)	9.78	1.78	8.00	0.23
Average fynbos communities	11.17	3.94	7.23	0.50
Average *Arundo* communities	41.96	35.42	6.54	5.41
Average *Phragmites* communities	16.07	7.99	8.08	0.99

Arundo creates a fire hazard and risk in other parts of the world, especially California (G. Coffman pers. comm.). In California, more dry material accumulates within stands of *Arundo*. Although California and the Western Cape both have a Mediterranean climate, California is colder and drier (Cowling *et al*. 1996), with an average rainfall of 300 – 450 mm per year, which falls mostly between January and March. The Western Cape of South Africa receives 200 – 2 000 mm rainfall per year, falling mostly between May and September. Since *Arundo* is sensitive to extreme cold (Samuels *et al*. unpublished data), more biomass dies off, and more dead material accumulates within the stands. In the northern provinces of South Africa, such as Gauteng, where it is colder than the Western Cape, there may be more dry biomass accumulating, presenting a greater fire hazard than *Arundo* presents in the Western Cape. Under extreme conditions, invasive plants could increase fire hazard and fire intensity (van Wilgen & Richardson 1985). In areas where there are extreme cold periods, and /or drought, *Arundo* would present a greater fire hazard than other areas where it is invasive.

5.4 Management implications

Fire behaviour model predictions are not always accurate. In general, fire behaviour models were designed with woody species in mind, which have different ecology and physiology to grass species. Invasive alien plants in general increase the fuel load of natural areas by 50 to 1 000 %; consequently increasing the fire hazard to property, life and the environment (Macdonald *et al.* 2004). Invaders such as *Hakea sericea* are thought to promote fire in South African fynbos, because they increase increase fuel loads and decrease herbaceous fuel moisture, but simulated fire spread rates were lower than in uninvaded shrubland due to differences in fuel-packing density (van Wilgen & Richardson 1985). Sites invaded by *Acacia saligna* also had higher fuel loads, but fuel moisture was greater, lowering the overall predicted fire spread and intensity (van Wilgen & Richardson 1985). Similarly, *Arundo* increased the biomass by 450 %, but simulated fire behaviour was less severe than in *Phragmites* stands. If *Arundo* biomass were to dry out, from cold or drought, or if stems were cut and piled (as a control method) the moisture content would reduce drastically, making *Arundo* more flammable. Piled or spread out biomass of *Arundo* creates a fire risk.

Fire behaviour model predictions should not be valued over practical experience and common sense. They are beneficial and useful where the fire behaviour and ecology of a species is well-known. Fire behaviour prediction models cannot be applied to all plant species.

6. LIMITATIONS

The fuel model does not take into account the height of *Arundo*, and as a result the packing density may have been incorrect, affecting predicted fire behaviour. It does also not take into account that some species are flammable when green. The fire behaviour model is usually applied to woody or annual grass species, and does not appear suitable for simulating conditions within stands of *Arundo*. Models require testing in order to validate them. Sampling intensity and duration could be increased. Biomass changes seasonally for many species, so it may also be useful to measure biomass of *Arundo* and *Phragmites* at different seasons, although the methods are destructive.

7. ACKNOWLEDGEMENTS

I gratefully acknowledge the DST-NRF Centre of Excellence for Invasion Biology (CIB) at Stellenbosch University for funding, and the CSIR for coordinating project expenses; Drs. Richard Knight and Brian van Wilgen as research supervisors; Jenny and Henry Nelson for initial introduction to the *Arundo donax* problem in Hout Bay; Russell Main, Bruce d'Hotman, and Isaac Crowster for assistance with fieldwork; Jeffrey Manuel and Gretchen Coffman for advice; and Prof R. Madsen for assistance with data analysis. Thanks to Spier Holdings Pty (Ltd) for permission to access study sites at Spier.

8. REFERENCES

Agee, J.K. (1993) *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, D.C.

Anderson, H.E. (1982) *Aids to determining fuel models for estimating fire behaviour*. USDA Forest Service, Gen. Tech. Report INT-122.

Andrews, P.L. & Bevins, C.D. (2003) BehavePlus fire modeling system, version 2.0: overview. *Proceedings of the Second International Wildland Fire Ecology* and *Fire Management Congress and Fifth Symposium on Fire and Forest Meteorology*, 16-20 November 2003, Orlando, Florida. American Meteorological Society, Washington, D.C.

Antonielli, M., Pasqualini, S., Batini, P., Ederli, L., Massacci, A. & Loreto, F. (2002) Physiological and anatomical characterisation of *Phragmites australis* leaves. *Aquatic Botany*, **72**, 55–66.

Bell, G.P. (1993) Biology and growth of giant reed (*Arundo donax*). *Proceedings of the* Arundo donax *workshop*, 19 November 1993, Ontario, Canada. (eds N.E. Jackson, P. Frandsen & S. Duthoit). California Exotic Pest Plant Council, Riverside.

Bell, G.P. (1997) Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in southern California. *Plant invasions: studies from North America and Europe*. (eds J.H. Brock, M. Wade, P. Pyšek & D. Green), pp. 103-113. Backhuys Publishers, Leiden, The Netherlands.

Binggeli, P., Hall, J.B. & Healey, J.R. (1998) *An overview of invasive woody plants in the tropics*. University of Wales, School of Agricultural and Forest Sciences, Publication No. 13, Bangor.

Bird, E.C.F. (1962) The river deltas of the Gippsland lakes. *Proceedings of the Royal Society of Victoria*, **75**, 65-74.

Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, **20**, 387-394.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. (2004) Effects of invasive alien plants on fire regimes. *BioScience*, **54**, 677-688.

Burdick, D.M., Buchsbaum, R. & Holt, E. (2001). Variation in soil salinity associated with expansion of *Phragmites australis* in salt marshes. *Environmental and Experimental Botany*, **46**, 247-261.

Burgan, R.E. & Rothermel, R.C. (1984) *BEHAVE: fire behavior prediction and fuel modeling system— FUEL subsystem*. USDA Forest Service Gen. Tech. Report INT-167.

Coffman, G.C., Ambrose, R.F. & Rundel, P.W. (2004) Invasion of *Arundo donax* in river ecosystems of Mediterranean climates: causes, impacts and management strategies. *Proceedings* *of the 10th MEDECOS Conference*, 25 April – 1 May 2004, Rhodes Island, Greece. (eds M. Arianoutsou & W. Papanastasis), pp. 1-8. Millpress Science Publishers, Rotterdam.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K. & Arianoutsou, M. (1996) Plant diversity in Mediterranean-climate regions. *Trends in Ecology and Evolution*, **11**, 362-366.

Cronk, Q.C.B. & Fuller, J.L. (1995) *Plant invaders: the threat to natural ecosystems*. Chapman & Hall, London.

D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63-87.

D'Antonio, C.M., Dudley, T.L. & Mack, M. (1999) Disturbance and biological invasions: direct effects and feedbacks. *Ecosystems of Disturbed Ground*. (ed L. Walker), pp. 143-452. Elsevier, Amsterdam.

Dudley, T.L. (2000) *Arundo donax*. *Invasive plants of California's wildlands*. (eds C.C. Bossard, J.M. Randall & M.C. Hoshovsky), pp. 53-58. University of California Press, Berkeley.

Duke, J.A. (1983) Handbook of Energy Crops. Unpublished. Available
http://www.hort.purdue.edu/newcrop/

Ekstam, B. (1995) Ramet size equalisation in a clonal plant, *Phragmites australis*. *Oecologia*, **104**, 440-446.

Harrod, R.J. & Reichard, S. (2001) Fire and invasive species within the temperate and boreal coniferous forests of western North America. *Proceedings of the Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management*, 27 November –1 December 2000, San Diego, California, USA. (eds K.E.M. Galley & T.P. Wilson), pp. 95-101. Miscellaneous Publication no. 11, Tall Timber Research Station, Florida.

Haslam, S.M. (1972) Biological flora of the British Isles, no. 128. *Phragmites communis* Trin. *Journal of Ecology*, **60**, 585-610.

Herrera, A.M. & Dudley, T.L. (2003) Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. *Biological Invasions*, **5**, 167-177.

Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, **6**, 324-337.

Holmes, P.M., Macdonald, I.A.W. & Juritz, J. (1987) Effects of clearing treatment on seed banks of the alien invasive shrubs *Acacia saligna* and *Acacia cyclops* in the southern and south-western Cape, South Africa. *Journal of Applied Ecology*, **24**, 1045–1051.

Hughes, F., Vitousek, P.M. & Tunison, T. (1991) Alien grass invasion and fire in the seasonal submontane zone of Hawaii. *Ecology*, **71**, 743-746.

Lippincott, C.L. (2000) Effects of *Imperata cylindrica* (L.) Beauv. (cogongrass) invasion on fire regime in Florida sandhill (USA). *Natural Areas Journal*, **20**, 140-149.

Macdonald, I.A.W., Loope, L., Usher, M. & Hamman, O. (1989) Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. *Biological Invasions: a global perspective*. (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek & M. Williamson), pp. 215-255. John Wiley & Sons, Chichester.

Macdonald, I.A.W., van Wilgen, B.W., Mgidi, T.N. & Walters, M. (2004) *Towards a national strategy for dealing with invasive alien species in South Africa*. Draft report, March 2004. Prepared for the Working for Water Programme.

Mack, M.C. & D'Antonio, C.M. (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution*, **13**, 195-198.

Meyerson, L.A., Saltonstall, K., Windham, L., Kiviat, E. & Findlay, S. (2000) A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. *Wetlands Ecology and Management*, **8**, 89-103.

Milton, S.J. (2004) Grasses as invasive alien plants in South Africa. *South African Journal of Science*, **100**, 69-75.

Perdue, R.E. (1958) *Arundo donax* – source of musical reeds and industrial cellulose. *Economic Botany*, **12**, 368-404.

Rieger, J.P. & Kreager, A. (1989) Giant reed (*Arundo donax*): a climax community of the riparian zone. *Proceedings of the California Riparian Systems Conference*, 22-24 September 1988, Davis, California, USA. (technical coordinator D.L. Abell), pp. 222-225. USDA Gen. Tech. Report PSW-110.

Rouget, M., Richardson, D.M., Nel, J.L., Le Maitre, D.C., Egoh, B. & Mgidi, T. (2004) Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climate suitability. *Diversity and Distributions*, **10**, 475-484.

Rundel, P.W. (1981) Structural and chemical components of flammability. *Proceedings of the Conference on Fire Regimes and Ecosystem Properties*, 11-15 December 1978, Honolulu, Hawaii. (eds H.A. Mooney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan & W.A. Reiners), pp. 183-207. USDA Forest Service Gen. Tech. Report WO-86.

Scott, G.D. (1993) Fire threat from *Arundo donax*. *Proceedings of the* Arundo donax *workshop*, 19 November 1993, Ontario, Canada. (eds N.E. Jackson, P. Frandsen & S. Duthoit). California Exotic Pest Plant Council, Riverside.

Smith, C.W. & Tunison, T.J. (1992) Fire and alien plants in Hawaii: research and management implications for native ecosystems. *Alien Plant Invasions in Native Ecosystems of Hawaii: Management and Research*. (eds C.P. Stone, C.W. Smith & J.T. Tunison), pp. 394-408. University of Hawaii Press, Hawaii.

van Wilgen, B.W. (1984) Adaptations of the United States Fire Danger Rating System to fynbos conditions. Part I. A fuel model for fire danger rating in the fynbos biome. *South African Forestry Journal*, **129**, 61-65.

van Wilgen, B.W. & Richardson, D.M. (1985) The effects of alien shrub invasions on vegetation structure and fire behaviour in South African Fynbos shrublands, a simulation study. *Journal of Applied Ecology*, **22**, 955-966.

van Wilgen, B.W. & Scott, W.D. (2001) Managing fires on the Cape Peninsula, South Africa: dealing with the inevitable. *Journal of Mediterranean Ecology*, **2**, 197-208.

van Wilgen, B.W. & van Hensbergen, H.J. (1992) Fuel properties of vegetation in Swartboskloof. *Fire in South African mountain fynbos. Ecosystem, community and species response at Swartboskloof.* (eds B.W. van Wilgen, D.M. Richardson, F.J. Kruger & H.J. van Hensbergen), pp. 37-52. Ecological Studies 93. Springer-Verlag, Berlin.

van Wilgen, B.W., Higgins, K.N. & Bellstedt, D.U. (1990). The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology*, **78**, 210-222.

Vilà, M., Lloret, F., Ogheri, E. & Terradas, J. (2001) Positive fire-grass feedback in Mediterranean Basin woodlands. *Forest Ecology and Management*, **147**, 3-14.

Walker, B.H. & Steffen, W.L. (1999) Interactive and integrated effects of global change on terrestrial ecosystems. *The terrestrial biosphere and global change. Implications for natural and managed ecosystems, Synthesis volume.* (eds B. Walker, W. Steffen, J. Canadell & J.S.I. Ingram), pp. 329-375. International Geosphere-Biosphere Program Book Series 4. Cambridge University Press, Cambridge.

Wells, M.J., Duggan, K. & Henderson, L. (1980) Woody plant invaders of the central Transvaal. *Proceedings of the Third National Weeds Conference*, South Africa. (eds S. Neser & A.L.P. Cairns), pp. 11-23.

Welsh, S.L., Atwood, N.D., Goodrich, S. & Higgins, L.C. (eds.) (1987) A Utah flora. *Great Basin Naturalist Memoirs* 9. Brigham Young University, Provo.

Whisenant, S.G. (1990) Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. *Proceedings of the symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management*, 5-7 April 1989, Las Vegas, USA. (eds E.D. McArthur, E.M. Romney, S.D. Smith & P.T. Tueller), pp. 4-10. USDA Forest Service Gen. Tech. Report INT-276.

Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperiled species in the United States. *BioScience*, **48**, 607-615.

CHAPTER 4

A COMPARISON OF PLANT SPECIES DIVERSITY ASSOCIATED WITH INVASIVE *ARUNDO DONAX* AND STRUCTURALLY SIMILAR INDIGENOUS SPECIES IN SOUTH AFRICA

1. SUMMARY

1. Biodiversity has a large influence on ecosystem processes, and consequently, ecosystem processes are essential to maintaining biodiversity. Plant community composition and dominant species drive ecosystem processes. Changes in plant composition and diversity affect therefore ecosystem functioning. Studies have shown that *Arundo donax* is an invasive species that reduces indigenous plant and animal species diversity. This study sought to establish the degree to which *Arundo* altered plant species diversity in Western Cape ecosystems.
2. I compared plant species data of communities dominated by *Arundo* with that of similar sites dominated by indigenous *Phragmites australis* and *Typha capensis*. Species richness, evenness, frequency, cover and height were compared. Plot similarity was estimated using TWINSPAN and PRIMER-e.
3. *Arundo*, *Phragmites* and *Typha* were dominant species in their communities in terms of height and cover. Each community had different associated species despite similar habitats.
4. *Arundo*-dominated communities had highest species richness (0.33 species m^{-2}); *Phragmites*-dominated communities had 0.19 species m^{-2}, and *Typha*-dominated communities had 0.24 species m^{-2}. *Arundo*-dominated communities had lowest average cover of 58 %; *Phragmites*-dominated communities had 72 % cover, and *Typha*-dominated communities had an average of 65 % cover.
5. Seventy per cent of the species associated with *Arundo* were alien species, compared to an average of 62 % under indigenous reeds. *Arundo* may be facilitating the establishment and spread of other invasive alien species.
6. Research was limited by the lack of undisturbed sites in habitats similar to those dominated by *Arundo* for use in comparison of invaded / uninvaded sites.
7. *Arundo* is a threat to indigenous plant species, because it has the capacity to outcompete and replace them, possibly increasing the alien species richness of the community.

2. INTRODUCTION

2.1 Biodiversity

Biodiversity broadly consists of the physical and functional components of ecosystems, and includes species, populations, their interactions and the services and functions they perform or bring about (Coleman & Whitman 2005). The primary attributes of ecosystems are their composition, structure and function (Franklin *et al*. 1981). Composition has to do with the identity and variety of elements in an ecosystem (such as species diversity, richness and identity); structure is the physical organisation of an ecosystem (such as the biomass or size of elements within an ecosystem); and ecosystem functions are the ecological or evolutionary processes taking place (Franklin *et al*. 1981; Noss 1990). Each attribute is dependent on the others, so that impacts on structure or composition, for example, will affect function.

2.2 Plant species composition

Plant community composition depends on diversity, richness and the identity of plant species present. It has been suggested that plant community composition and dominant species drive ecosystem processes (Grime 1997; Sankaran & McNaughton 1999), but the link between species diversity and ecosystem function is not one that all scientists agree upon. Some argue there is no clear link (Vitousek & Hooper 1993); while others argue that more diverse ecosystems are more capable of supporting ecosystem functions (Ehrlich & Ehrlich 1992). Most ecologists assume that the two are intimately linked (Hobbs *et al*. 1995) and that changes in plant composition and diversity affect ecosystem functioning to some extent (Tilman *et al*. 1997; Hooper *et al*. 2000; van der Putten *et al*. 2001; Zak *et al*. 2003). Changes in plant species composition can alter the abiotic environment (soil chemistry, water flow and fire), as well as the biotic environment (invertebrates, decomposer organisms, arthropods and bird species richness and diversity) (Ehrenfeld 2004). Richardson *et al*. (1995) and Coleman & Whitman (2005) believe that it is the functional types and their differences that drive and affect ecosystem functioning, rather than the species. Species identity is also in some cases a critical aspect in determining biodiversity, and hence in assessing ecosystem functioning (Hooper & Vitousek 1998).

Plant interactions (such as facilitation or competition) have complex influences on plant species distribution and abundance (Callaway & Walker 1997). Competition is a major factor in determining the composition of plant communities (Grime 1979). The competitive ability of a plant relative to others is usually a good predictor of its abundance in a plant community (Groves *et al*. 2003), and the more abundant a species is within a community, the greater its effects on the community will be (Grime 1998). More competitive species are likely to have greater effects on the community.

2.3 Disturbance

Disturbances generally have long-lasting consequences on the ecosystem (Thompson *et al*. 2002), which are reflected in the species composition and richness of most plant communities (Roem & Berendse 2000). Many alien species need disturbances to open niches for them to invade. Disturbances such as fire and eutrophication enhance the competitive ability of some species over others (Newman *et al*. 1996), and may cause changes in plant species diversity, often resulting in a loss of biodiversity (Moore *et al*. 1989). Variations in disturbance regime (intensity or frequency) can affect overall ecosystem and community structure, functioning and species composition (Hobbs & Hueneke 1992).

2.4 Invasive alien species

Invasive alien plant species affect all attributes of biodiversity: ecosystem functions (Vitousek & Walker 1989; Mack *et al*. 2001; Ehrenfeld 2003), composition (Richardson & van Wilgen 1992; Dukes & Mooney 2004; Brown & Gurevitch 2004), and structure (Gratton & Denno 2005). Invasive alien plants affect plant species composition of a community via the alteration of disturbance regimes (D'Antonio & Vitousek 1992), allelopathy (influence the growth and development of neighbouring plants by the addition of chemical compounds to the environment) (Gentle & Duggin 1997; Lavergne *et al.* 1999), competition (removal or reduction of resources such as nutrients, water and light, from the environment) and facilitation (promoting survival and establishment of other alien species (Simberloff & Von Holle 1999)).

2.5 *Arundo donax*

Arundo donax L. (Poaceae) (hereafter referred to as *Arundo*) is an invasive reed species. *Arundo* belongs to the Arundineae tribe, along with *Phragmites* species (Renvoize 1980) and is indigenous to the Indian sub-continent (Bell 1997). *Arundo* is a hydrophyte, growing along lakes, streams, drains, and other wet sites (Bell 1997), but it does not need a constant supply of water, and can grow on drier banks and roadsides. *Arundo* is a perennial C_3 grass species (Rossa *et al*. 1998). It usually grows in large stands many metres wide, and contains hundreds of stems per stand (Spencer *et al.* 2005). Stems may reach 10 metres in height (Dudley 2000). Reproduction occurs almost entirely from rhizomes and stem fragments (Boose & Holt 1999). *Arundo* rapidly colonises disturbed areas, and dominates riverbanks and estuaries (Dudley and Collins 1995). *Arundo* outcompetes and replaces indigenous riparian plants, reducing the value of riparian habitats and resources for indigenous fauna (Bell 1997). *Arundo* has in some areas begun replacing *Phragmites australis* (Grace *et al*. 2001; R. Knight pers. comm.). Gaffney & Gledhill (2003) report a reduction in vegetative structure and diversity, and an increased abundance of other alien plants associated with *Arundo* presence. It has altered plant species diversity and composition, and has reduced invertebrate, arthropod and avian species richness in some ecosystems (Dudley 2000; Herrera & Dudley 2003). The effects of *Arundo* on biodiversity are partly due to its large size and rapid growth rate (Milton 2004).

2.6 *Phragmites australis* and *Typha capensis*

Phragmites australis (Cav.) Trin. ex Steud. (Poaceae) (hereafter referred to as *Phragmites*) is also a large clonal C_3 grass species, reaching heights of two to six metres (Pearcy *et al*. 1974). It has a similar appearance to *Arundo* when young, but once the plants are mature, there are distinct differences, especially noticeable during winter months, when *Phragmites* turns brown and loses most its leaves (personal observation). *Arundo* mostly remains green (although some shades lighter) and retains most of its leaves. *Phragmites* is also shorter on average, with many more stems per area than *Arundo* (preliminary investigations). *Phragmites* reproduces mainly by vegetative reproduction, from its rhizomes (Ekstam 1995), which can reach a depth of one to two metres (Burdick *et al*. 2001). It is considered to be the most widely distributed reed species in the world (Bird 1962). It is tolerant to climate, altitude, flooding, frost, high pH, salt, a wide range of soils, and invasion by alien species (Welsh *et al*. 1987; Meyerson *et al*. 2000). *Phragmites* usually grows in open, wet areas, along streams, marshes (Meyerson *et al*. 2000), ditches, and roadsides (Chambers 1997).

Another indigenous species occurring within similar habitats in South Africa is *Typha capensis. Typha capensis* Rohrb. (Typhaceae) (hereafter referred to as *Typha*) is an indigenous bulrush species found in wetter environments, usually wetlands or lower riparian reaches. It is distinctly different in appearance from *Arundo* and *Phragmites*. It produces narrow, tapering fleshy blades from the base of a thick stem (Farnsworth & Meyerson 2003), and is green throughout the year. In common with *Arundo* and *Phragmites* is its capacity to form monocultures (Linde *et al*. 1976), resprout from rhizomes (Farnsworth & Meyerson 2003), and become invasive in some areas, especially in California, USA (Morton 1975).

In this study, I examined three dominant riparian plant species, one invasive and two indigenous, occurring within the same or similar riparian habitats. They have similar growth forms with vegetative reproduction via rhizomes. They are all C_3 species, with high growth rates and capacity to form 'monocultures'. Species diversity is estimated to be low within communities dominated by these species. *Arundo* is reported as reducing the plant species diversity within communities it dominates. Comparisons were made of plant species diversity with communities dominated by *Arundo*, *Phragmites* and *Typha*.

3. METHODS

3.1 Study areas

Selection of study sites was based on the presence of at least two of the dominant target species within 20 m of each other, in dominant or near-monoculture stands. *Arundo*, *Phragmites* and *Typha* generally occur in lower reaches of rivers. The study sites were within the lower reaches of three rivers in the Western Cape of South Africa: the Disa River in Hout Bay, the Eerste River on the Spier Wine Estate outside Stellenbosch, and the Silvermine River, downstream of the Silvermine Nature Reserve (Fig. 1). The Disa River runs through Hout Bay, a coastal town about 11 km from Cape Town. The area between the Victoria and Princess Road bridges constitutes the first study site. Residential development, agricultural use, invasive alien plants, and modifications to river geomorphology have seriously impaired the downstream reaches of the river. The Disa River was formerly a braided river system dominated by extensive stands of indigenous palmiet *Prionium serratum*. *Arundo* and *Phragmites* occur at this site. *Arundo* stands are dense and extensive, and span the entire distance between the two bridges, with fewer and less dense clumps upstream. The Eerste River is one of three rivers on the Spier Wine Estate. It is heavily impacted and polluted along most of its course. It flows through the town of Stellenbosch and is exposed to urban pollution and waste. This study site is surrounded by agricultural, grazing and open land. This site is privately owned. The *Arundo* stand at this site is extensive, but there appears to be only one major stand, spanning a distance of 300 – 400 m along the river. Smaller clumps of *Arundo* exist in other locations along the river. Many other invasive alien plants are present along the river. All three dominant species are located at this study site. The Silvermine River is the least impacted of the rivers studied, since it is located within a protected area. The study site is downstream of Silvermine Nature Reserve, and a short distance from the Sunbird Environmental Education Unit. It is relatively unimpacted and restoration has occurred primarily for flood control. The site has recently become infested with *Arundo*, probably in the last few years. There is ongoing restoration to clear the area of *Arundo* and stands have been cut in the recent past. There are stands of *Typha capensis* close to the stands of *Arundo*.

3.2 Field methods

Six plots per species were selected in total from the three study sites (Table 1). From Hout Bay, five plots were selected, two dominated by *Arundo* and three dominated by *Phragmites*. From Spier, eight plots were selected, two dominated by *Arundo*, three dominated by *Phragmites* and three dominated by *Typha*. From Silvermine, five plots were selected, three dominated by *Typha*, two dominated by *Arundo*. Plots of 5 m x 3 m were selected at least five metres apart, with each plot dominated by a stand of either *Arundo*, *Phragmites* or *Typha*. Where stands of the target species were large, plots were chosen well into the stand, removing any edge effects. All species were identified per plot; and percentage cover, functional types, and species height was recorded. Sampling was conducted during summer (January 2006) when plant cover and species flowering was at its maximum, but some ephemeral species may have been missed. Abundance (number of individuals per species) was not recorded because of the difficulty in separating individual species from one another, especially in the case of rhizomatous species such as *Arundo*, *Phragmites* and *Typha*.

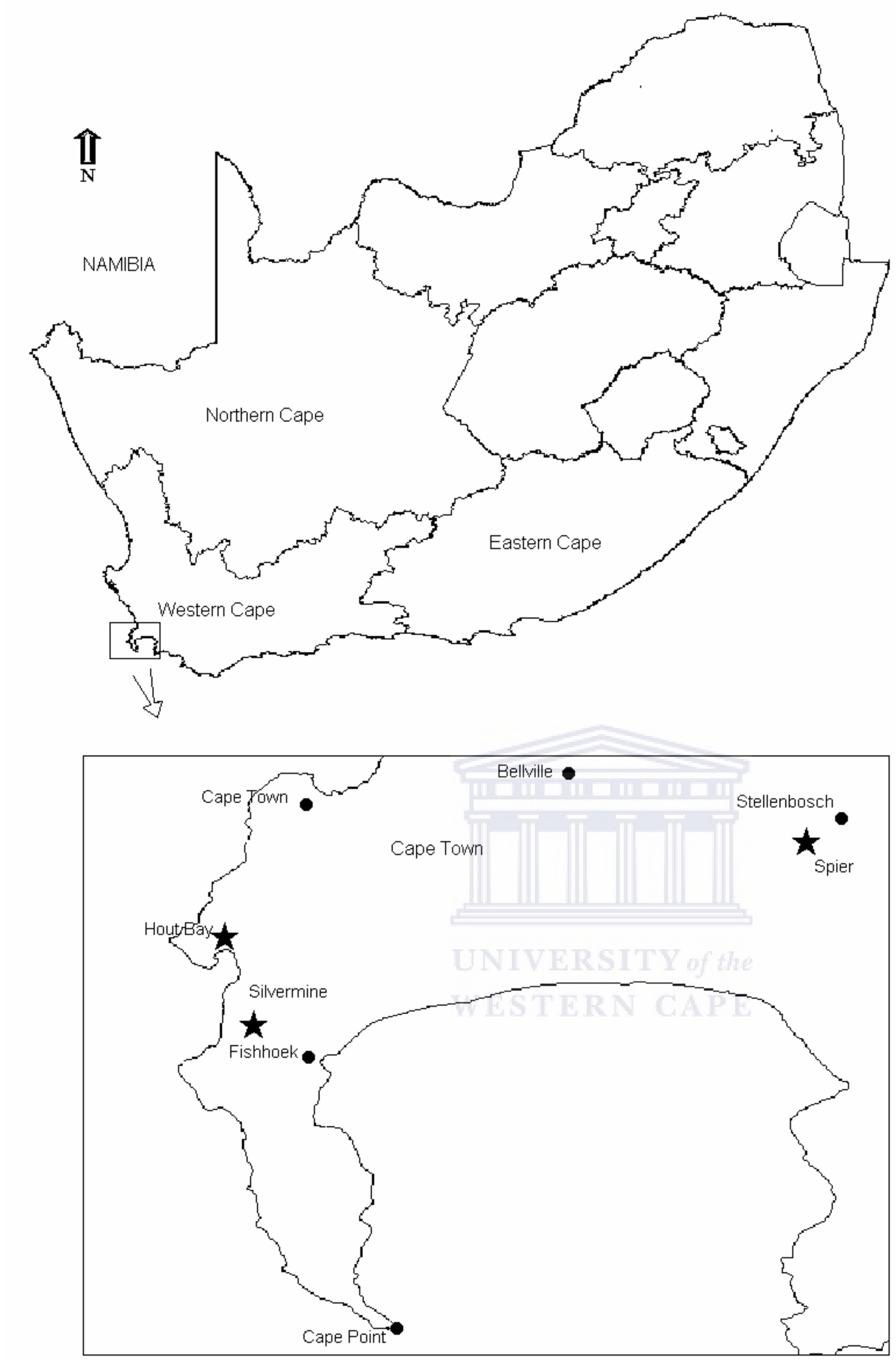


Fig. 1. Map of South Africa showing provincial boundaries. The study occurred in the Western Cape province; study sites are marked with stars; nearby towns are marked with dots.

Table 1. Plot location for *Arundo*, *Phragmites* and *Typha*. Six plots were selected per species from the sites Hout Bay, Spier and Silvermine.

Arundo	*Phragmites*	*Typha*
S 34° 01' 58.4" E 18° 21' 12.8" (Hout Bay)	S 34° 01' 49.4" E 18° 21' 15.6" (Hout Bay)	S 33° 59' 12.8" E 18° 47' 34.7" (Spier)
S 34° 02' 01.7" E 18° 21' 13.2" (Hout Bay)	S 34° 01' 50.6" E 18° 21' 14.8" (Hout Bay)	S 33° 59' 12.0" E 18° 47' 32.4" (Spier)
S 33° 59' 13.2" E 18° 47' 33.4" (Spier)	S 34° 01' 52.0" E 18° 21' 14.4" (Hout Bay)	S 33° 58' 36.1" E 18° 46' 43.1" (Spier)
S 33° 59' 10.8" E 18° 47' 32.3" (Spier)	S 33° 59' 07.7" E 18° 47' 26.2" (Spier)	S 34° 06' 43.4" E 18° 24' 34.7" (Silvermine)
S 34° 06' 41.7" E 18° 24' 34.6" (Silvermine)	S 33° 59' 06.3" E 18° 47' 24.2" (Spier)	S 34° 06' 44.2" E 18° 24' 29.3" (Silvermine)
S 34° 06' 43.0" E 18° 24' 34.2" (Silvermine)	S 33° 58' 36.6" E 18° 46' 42.4" (Spier)	S 34° 06' 39.6" E 18° 24' 32.7" (Silvermine)

3.3 Statistical analysis

TWINSPAN is a programme for classifying species and samples, producing an ordered two-way table of their occurrence. The process is hierarchical; samples (plots) are divided into categories, and species divided into categories on the basis of sample classification. Using TWINSPAN, I compared plots on the basis of species presence / absence and percentage cover (Hill & Šmilauer 2005). Alien and indigenous species data were compared. Plant species richness was determined per plot, and per dominant species. PRIMER-e is a statistical programme used for analysing species / sample abundance matrices. Using PRIMER-e, I constructed ordination plots (by non-metric multidimensional scaling) and similarity clusters (hierarchical clustering into species groups) (Clarke & Warwick 2001), using species presence / absence and percentage cover data.

Communities were compared in terms of plants' height, percentage cover and functional types. Frequency of species occurrence within plots was determined.

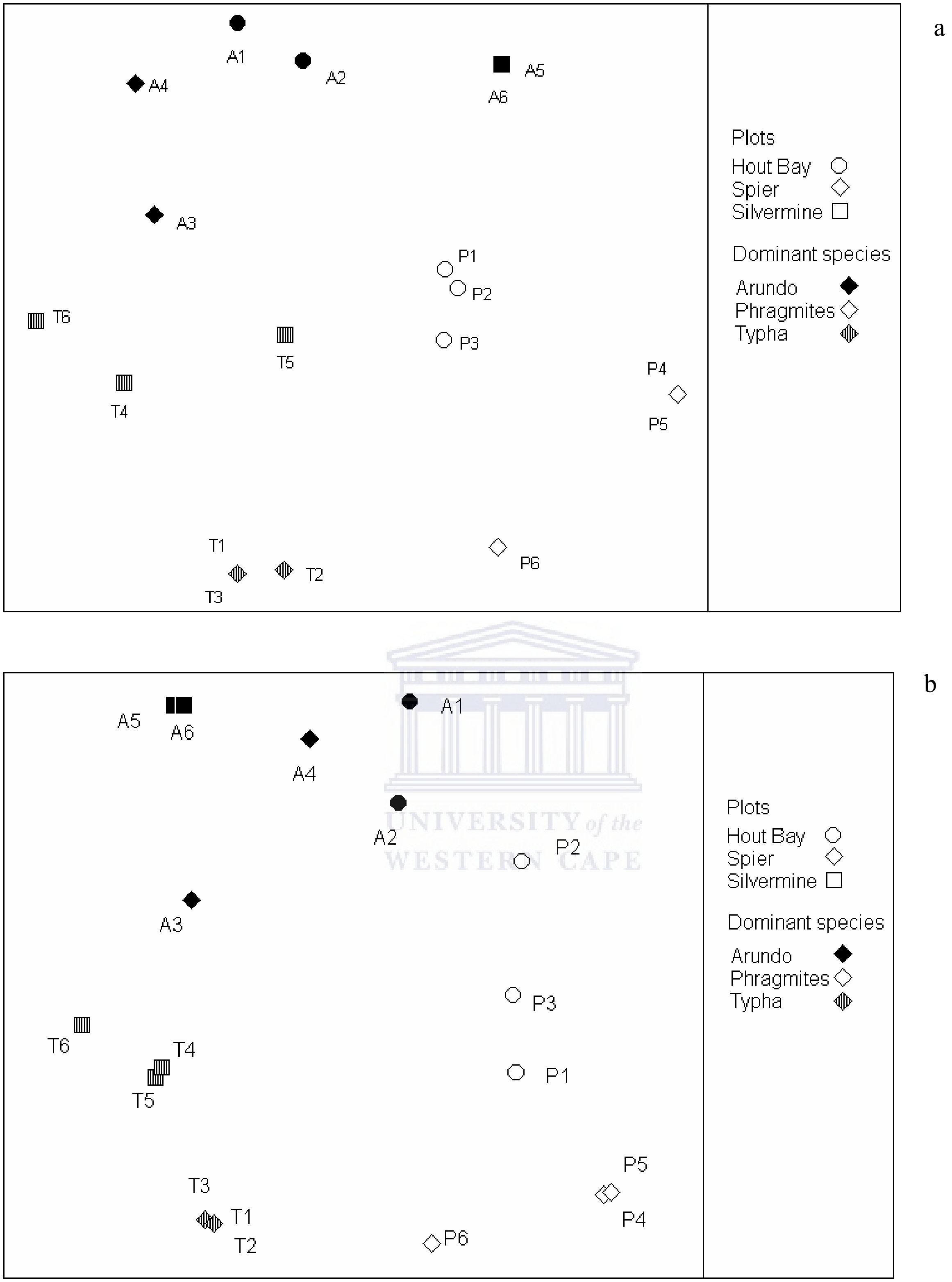
4. RESULTS

4.1 Similarity

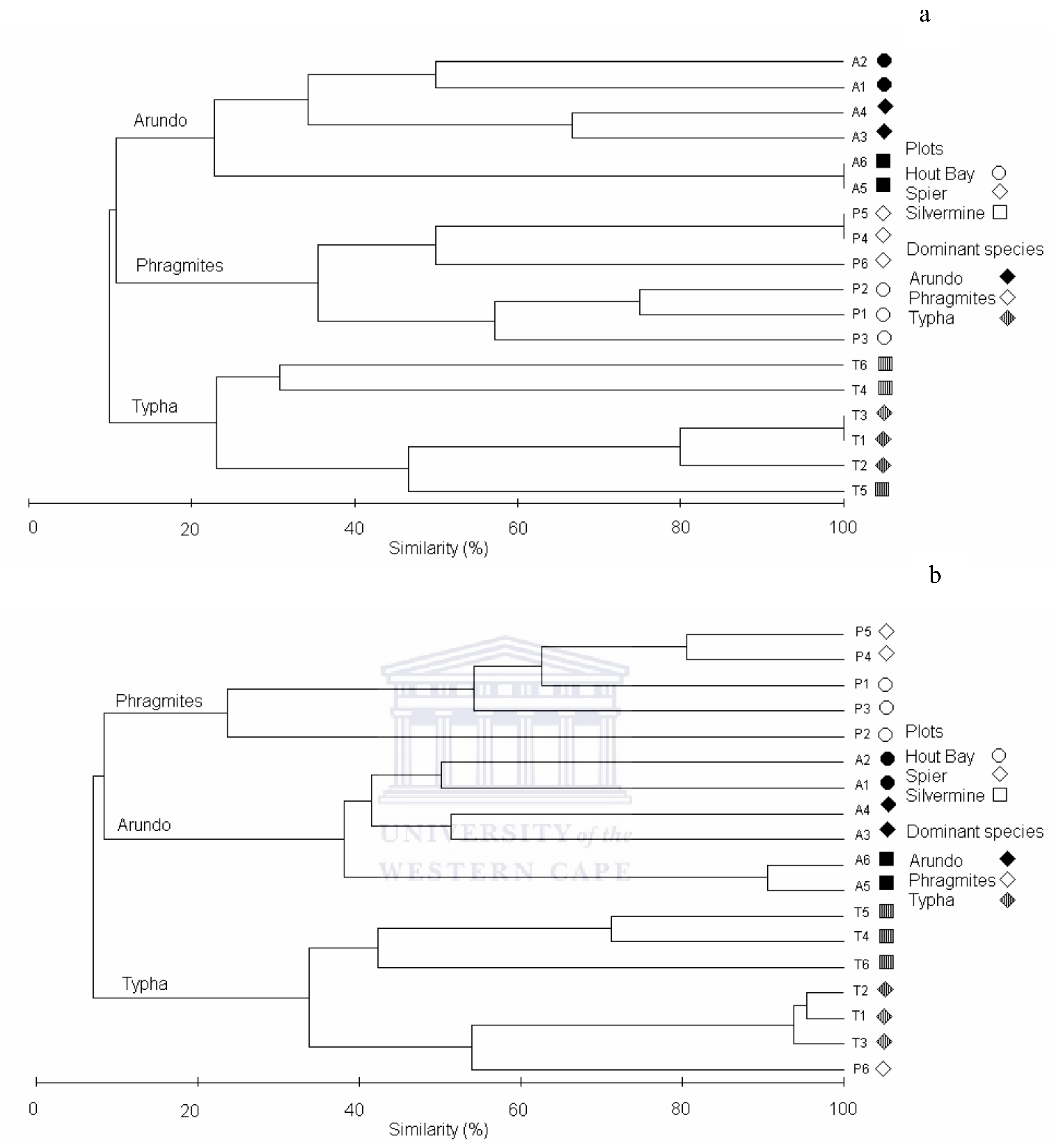
TWINSPAN analysis groups similar plots and species according to the percentage cover of species within the plots (Table 2). Plot similarity is also expressed in ordination graphs (Figs. 2a and b). Despite the graphs representing different data (Fig. 2a represents presence / absence data, Fig. 2b represents percentage cover data), *Arundo*, *Phragmites* and *Typha* were clearly separated in both graphs. There was no overlap between any of the dominant species, showing that they were considerably dissimilar. Similarity clusters indicate the degree of similarity between the plots (Figs. 3a and b). Similarity based on presence absence separated the dominant species into three distinct groups (A1 to A6, P1 to P6, and T1 to T6) (Fig. 3a). The three groups were 10 % similar to each other. Plots from the *Arundo* group were 25 % similar to each other, as were plots from the *Typha* group, while those of *Phragmites* were 35 % similar to each other. In general, similarity between plots and groups was low. One set of identical plots (in terms of presence / absence data) existed for each dominant species (A5 and A6, P4 and P5, T1 and T3). Dominant species were separated entirely and showed no overlap with each other in terms of presence / absence data (Fig. 3a). Similarity in terms of percentage cover data showed a slightly different pattern, but the three groups of dominant species were still mostly separated from each other (Fig. 3b), with one outlying plot, namely P6. Sites were also separated out and quite distinct from each other, especially Hout Bay and Silvermine (Fig. 3b). Overall, the three groups shared about 5 % similarity with each other, less than when using the presence / absence data. However, individual groups shared a lot more similarity than individual groups separated by presence / absence data. The *Phragmites* group consisted of only five plots, with P4 and P5 being the most similar, but only about 80 % similar. The *Arundo* group had six plots more similar to each other than either the *Phragmites* or *Typha* groups. Plots A5 and A6 were the most similar, with approximately 90 % similarity. The *Typha* group had seven plots, six *Typha*-dominated plots, as well as P6 (a *Phragmites*-dominated plot). Plots T1, T2 and T3 were all similar, between 90 and 95 % similar to each other.

Table 2. An ordered two-way table derived from percentage cover data in plots at Hout Bay, Spier and Silvermine, dominated by *Arundo*, *Phragmites* and *Typha*, and ordered by TWINSPAN. Invasive alien species are indicated in bold type. Vertical lines separate similar groups of plots in terms of species. Horizontal lines delimit groups of species associated with particular groups of plots. Numbers within tables indicate a ranking of the percentage cover, with 5 being the highest (highest percentage cover of a particular species in a particular plot), and 1 the lowest. A = plots dominated by *Arundo*; P = plots dominated by *Phragmites*; T = plots dominated by *Typha*.

	Plots																	
Species	A 5	A 6	A 1	A 2	A 4	P 2	P 1	P 3	P 4	P 5	P 6	A 3	T 4	T 1	T 2	T 3	T 5	T 6
Cliffortia odorata					5							2						
Pennisetum clandestinum			5	5	5	5	2	5				1	1					3
Polygonum salicifolium					3							1						
Arundo donax	5	5	5	5	5							5						
Avena fatua			1															
Chenopodium ambrosioides			1	5														
Cirsium vulgare					1													
Convolvulus arvensis				1														
Conyza bonariensis			1															
Hypochaeris radicata			1															
Populus x canescens						2												
Ricinus communis					3													
Sonchus arvensis			4															
Pteridium aquilinum	5	5																
Tropaeolum majus			5				3											
Zantedeschia aethiopica	3	1				5	2										1	
Phragmites australis						2	5	5	5	5	5							
Phytolacca octandra									3	5								
Sesbania punicea								2							1			
Commelina benghalensis											5			5	5	5		
Typha capensis												5	5	5	5	5	5	5
Anagallis arvensis													1					
Cyperus sp.													3					
Juncus sp.													1					
Scirpus sp.												1	2					
Chrysanthemoides monilifera																		5
Delairea odorata																		4
Ipomoea purpurea																		4
Rubus fruticosus																		1
Sonchus oleraceus																		2



Figs. 2a and b. Ordination plots (non-metric multi-dimensional scaling) of species similarity between plots at Hout Bay, Spier and Silvermine, in terms of presence / absence data (a), and percentage cover data (b).



Figs. 3a and b. Similarity cluster of plots based on presence / absence data (a), and percentage cover data (b), of species from plots at Hout Bay, Spier and Silvermine.

4.2 Plant species richness

Arundo-dominated plots had 17 species in total, five indigenous (29 %) and 12 alien species (71 %), including *Arundo*. These plots had an average species richness of 5.00 species per plot (plot size 15 m^2, n = 6). Species richness was 0.33 species m^{-2}. Indigenous species had an average richness of 0.09 species m^{-2}, and alien species had a richness of 0.24 species m^{-2} (Fig. 4). *Phragmites*-dominated plots had eight species, two indigenous (25 %) and six alien species (75 %). These plots had an average species richness of 2.83 species per plot (n = 6). Species richness was 0.19 species m^{-2}. Indigenous species had an average species richness of 0.09 species m^{-2}, and alien species had a richness of 0.10 species m^{-2} (Fig. 4). *Typha*-dominated plots had 14 species, seven indigenous (50 %) and seven alien species (50 %). These plots had an average species richness of 3.67 species per plot (n = 6). Species richness was 0.24 species m^{-2}. Indigenous species had an average species richness of 0.13 species m^{-2}, and alien species had a richness of 0.11 species m^{-2} (Fig. 4).

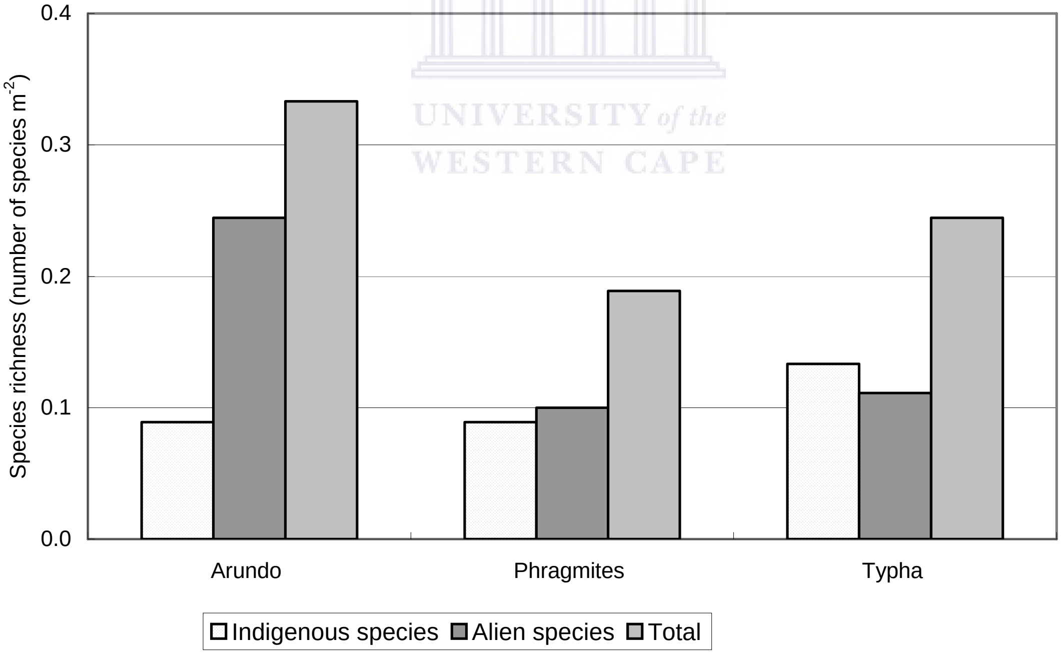
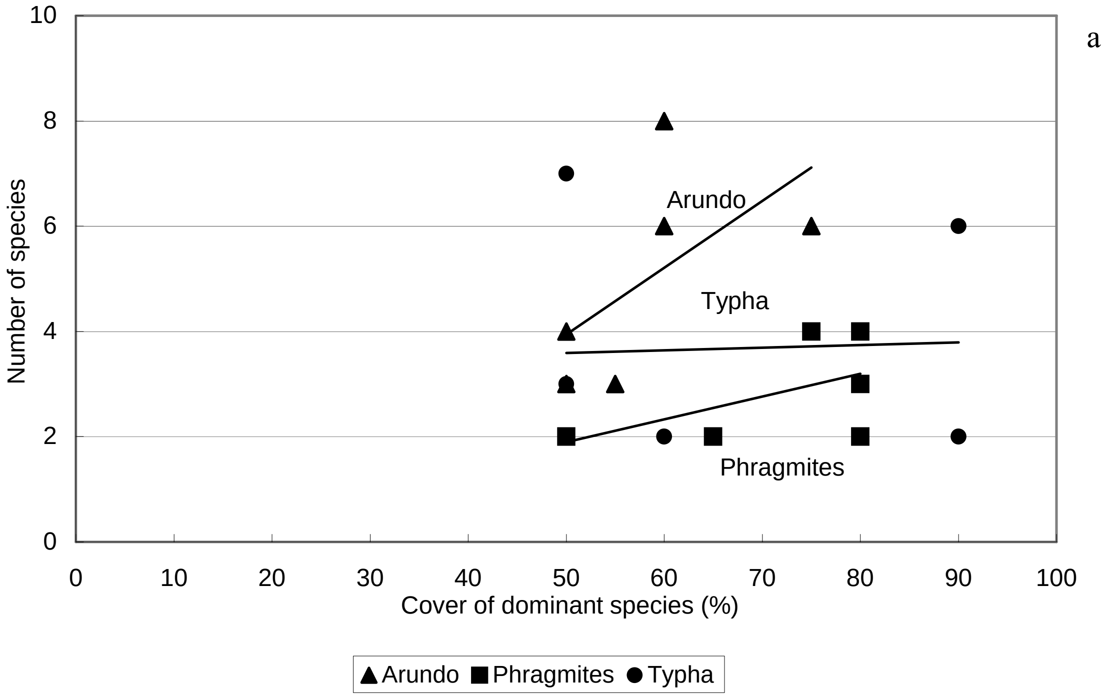


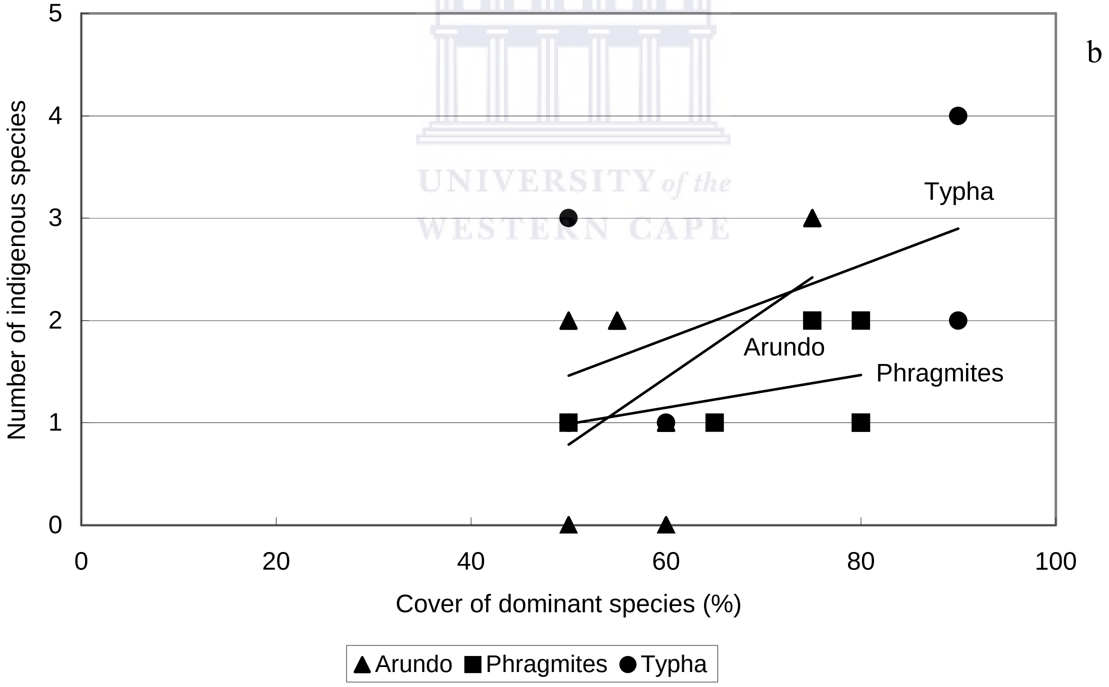
Fig. 4. Plant species richness (species m^{-2}) for *Arundo*, *Phragmites* and *Typha*, from six plots each at Hout Bay, Spier and Silvermine.

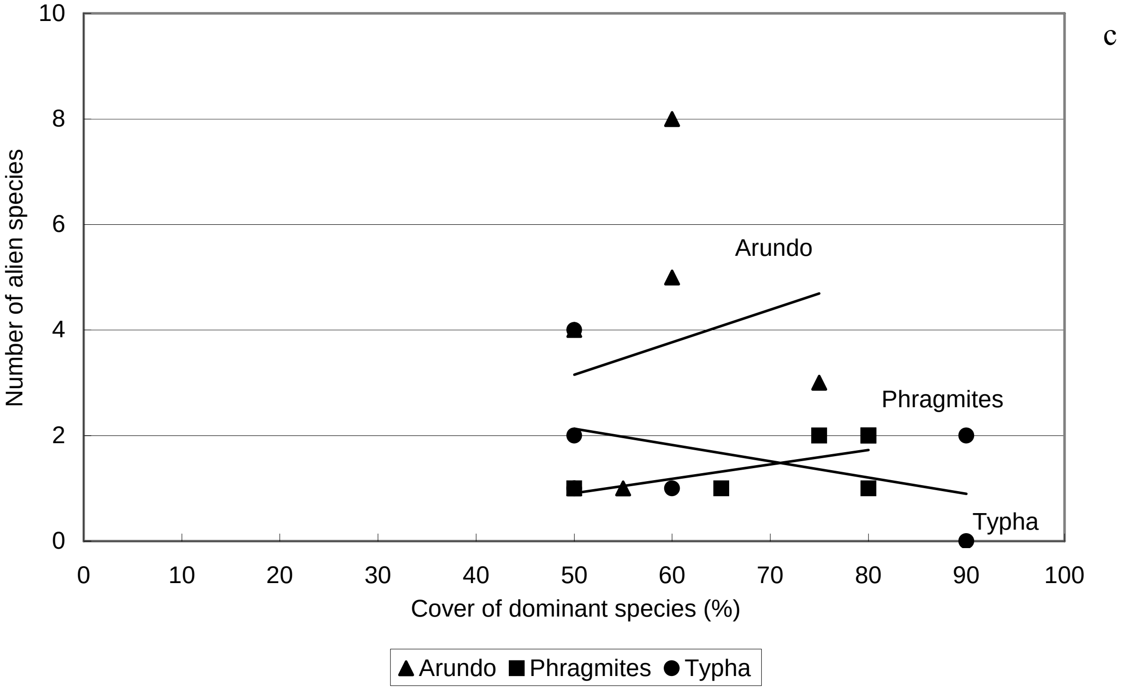
4.3 Percentage cover

Arundo contributed an average of 58 % of the percentage cover per plot, ranging from 50 to 75 % cover. Other species in *Arundo*-dominated plots that contributed considerably (an average of more than 20 %) to percentage cover were *P. clandestinum* (53 %), *C. arvensis* (40 %), *T. majus* (30 %), *P. aquilinum* (25 %) and *C. odorata* (23 %). In 75 % of the plots where *Arundo* and *P. clandestinum* co-occur, the latter species had a greater percentage cover. *Phragmites* contributed an average of 72 % of the percentage cover per plot, ranging from 50 to 80 % cover. It often co-occurred with one other species that had considerable percentage cover, such as *C. benghalensis* (85 %), *P. clandestinum* (57 %) or *P. octandra* (23 %). During the study, there were no more than three species recorded co-occurring with *Phragmites*. Approximately 50 % of species associated with *Arundo* and *Phragmites* had less than 5 % cover. *Typha* had an average of 65 % percentage cover per plot, ranging from 50 to 90 %. Other dominant species in terms of percentage cover were *C. benghalensis* (80 %) and *I.purpurea* (20 %). When *Typha* and *C. benghalensis* co-occurred, *C. benghalensis* had the greater percentage cover. Sixty-four percent of species in *Typha*-dominated plots had less than 5 % cover. *Pennisetum clandestinum* was a dominant weedy species, co-occurring in at least two plots each with *Arundo*, *Phragmites* and *Typha*. Each dominant species covered no less than 50 % in each plot it occupied.

A positive relationship existed between percentage cover of dominant species (*Arundo*, *Phragmites*, and *Typha*) and the number of species (both total and indigenous) present in each plot (Figs. 5a and b). Positive relationships existed between percentage cover of *Arundo* and *Phragmites* with the number of alien species (Fig. 5c). A negative relationship existed between percentage cover of *Typha* and the number of alien species. The relationships are not significant in terms of p-value, but do show a trend.


a
Number of species
10
8
6
4
2
0
Arundo
Typha
Phragmites
0
10
20
30
40
50
60
70
80
90
100
Cover of dominant species (%)
▲ Arundo ■ Phragmites ● Typha


b
Number of indigenous species
5
4
3
2
1
0
Typha
Arundo
Phragmites
0
20
40
60
80
100
Cover of dominant species (%)
▲ Arundo ■ Phragmites ● Typha



Figs. 5a, b and c. Relationship between the number of species, total (a), indigenous (b), and alien (c), and the percentage cover of dominant species (*Arundo*, *Phragmites* or *Typha*) per plot (15 m^2) (n = 6). Linear trendlines indicate positive correlations for *Arundo* and *Phragmites*; each trendline is marked with the relevant dominant species.

4.4 Plant functional types

From the 30 species, five functional types were assigned to species co-occurring with *Arundo*, *Phragmites* and *Typha*: grass (G), herb (H), sedge / rush (S / R), shrub (S) and tree (T). This produced two species each of grasses, reeds and trees; as well as fourteen herb species, four sedge / rush species, and six shrub species. *Arundo* was associated with four functional types (Fig. 6), more herb species than the other dominant species, and a greater herb representation than from the other functional types. *Arundo* had no tree species recorded within its plots. *Phragmites* had four functional types associated with it, and no sedges / rushes (Fig. 6). *Typha* was associated with all five functional types. It had more sedges / rushes and shrubs than the other dominant species. *Typha*-dominated communities were richer in terms of functional types than *Arundo* and *Phragmites* (Fig. 6).

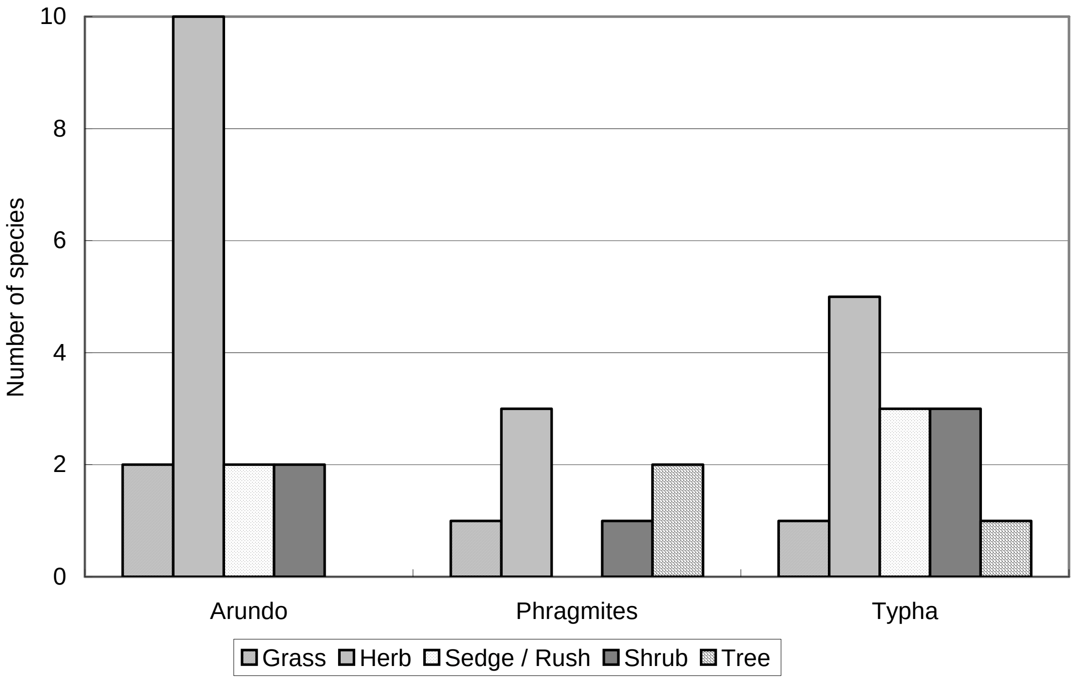


Fig. 6. Number of species per functional type associated with *Arundo*, *Phragmites*, and *Typha*, from six plots per dominant species at Hout Bay, Spier and Silvermine.

4.5 Plant species height

Arundo had an average height of 3.7 m, greater than that of *Phragmites* and *Typha*, at 3.1 m and 2.1 m respectively. *Arundo* was 1.5 m taller than any of the species with which it co-existed (Fig. 7a). *Phragmites* was only slightly taller than the tree species it co-existed with (*S. punicea,* 3.0 m) but was 1.2 m taller than any of the other species (Fig. 7b). *Typha* was also relatively similar in height to *S. punicea* recorded co-occurring with it (2.0 m) and 1 m taller than the other species (Fig. 7c).

Figs. 7a, b, and c. Plant species (illustrated as functional type) within communities dominated by *Arundo*, *Phragmites* and *Typha*, using data from plots at Hout Bay, Spier and Silvermine, with key alongside illustrating species and functional types referred to. All species are represented in terms of their average height and their functional type. For the purpose of these diagrams (to show differences in species height), the ‘herb’ category was subdivided into ‘herb’ and ‘creeper’.

4.6 Frequency

Only *Arundo* occurred in each plot where *Arundo* was the dominant species. Species co-occuring with *Arundo* in more than one plot were *P. clandestinum* (in 67 % of the plots), *C. ambrosioides* (33 %), *C. odorata* (33 %), *P. salicifolium* (33 %), *P. aquilinum* (33 %) and *Z. aethiopica* (33 %). Only *Phragmites* occurred in each plot where it was dominant. Co-occurring species included *P. clandestinum* (in 50 % of the plots), *P. octandra* (33 %) and *Z. aethiopica* (33 %). Only *Typha* occurred in each plot where it was dominant. Co-occurring species were *C. benghalensis* (50 %) and *P. clandestinum* (33 %). *Arundo* had more co-occurring species with higher frequency of occurrence than did *Phragmites* and *Typha*.

5. DISCUSSION

Some studies have looked at the impacts of invasion on indigenous plant species diversity and composition (e.g. Houlahan & Findlay 2004; Hejda & Pysek 2006). This is the first to investigate plant species diversity associated with invasive alien species within wetland or riparian habitats.

5.1 Similarity

The lack of similarity between plots and groups can possibly be attributed to the high amount of disturbance at these sites, including development, pollution and eutrophication, agriculture and restoration efforts. Disturbance encourages the establishment and spread of invasive alien species (Smith & Knapp 1999), and species composition in disturbed areas consists mainly of pioneer species (Hobbs & Huenneke 1992).

5.2 Cover

Arundo had the lowest average percentage cover, as well as the most co-occurring species, indicating the potential for its co-existence with other species, albeit alien species.

5.3 Species richness

Arundo has been associated with lower plant species diversity, and lower animal (invertebrates, arthropods and birds) species richness and diversity (Scott 1993; Herrera 1997; Herrera & Dudley 2003). These authors report that invertebrate and bird species richness concomitant with indigenous vegetation was higher than that associated with *Arundo*.

Arundo-dominated communities had the greatest species richness, most of it made up by alien species. High alien species richness may reduce the capacity for ecosystem functioning (Tilman 1999). *Arundo*-dominated communities had low indigenous species richness (0.09 species m^{-2}). Richardson *et al*. (1989) found that dense stands of invasive alien trees and shrubs reduce indigenous plant species richness. The loss of species after invasion by alien species is likely to have implications for ecosystem functioning (Richardson *et al*. 1997). Macdonald *et al*. (1988) state that the reduced indigenous plant species diversity associated with plant invasions is unique to the fynbos biome. This study demonstrates the potential for invasive species to reduce indigenous species diversity in riparian biomes as well.

Communities dominated by *Phragmites* had low species richness. Meyerson *et al*. (2000) found that *Phragmites* may inhibit or limit the establishment and growth of other plants because of its height, stem density, and large volumes of decomposing matter, which reduces light and air temperatures within the stands. *Arundo* and *Typha* are also much taller than their co-occurring species and have high densities, but do not accumulate much dead matter. The accumulation of dead matter rather than greater height or density, or perhaps in combination with them, may be more of a factor contributing towards reduced species richness.

Richardson & van Wilgen (1986) likened invasion by alien species to afforestation. Plant species cover and density were reduced by 54 and 70 %, respectively, after afforestation with *Pinus radiata* (Richardson & van Wilgen 1986). Species richness was also reduced after invasion. After afforestation some new species were found that were not recorded prior to afforestation. Most of these were small herbaceous plants or cosmopolitan weeds (Richardson & van Wilgen 1986). Similarly, *Arundo* had many small herbs or cosmopolitan weeds growing within the communities it dominated. More invasive alien species were present under *Arundo* than beneath the indigenous dominant species. Invasion by *Arundo* has created a new community with properties and attributes different to indigenous communities.

Increased percentage cover of indigenous *Typha* appeared to reduce the number of alien species and increase the number of indigenous plant species. Mature, dense stands of *Typha* may be more resistant to invasion by alien species. Increased percentage cover (canopy cover) of alien *Pinus pinaster* was associated with a decrease in the number of indigenous species (Richardson *et al*. 1989). Conversely, increased percentage cover of *Arundo* does not reduce the number of indigenous species, but does appear to correlate with increased numbers of alien species. *Arundo* may be facilitating the establishment and growth of alien species rather than inhibiting the growth of indigenous species ('invasional meltdown').

5.4 'Invasional meltdown'

The biotic resistance model states that species-rich communities are less vulnerable to invasion than species-poor ones, because of competition for limiting resources (Elton 1958). *Arundo*-dominated communities, according to this theory, would have lower vulnerability to further invasion by alien species than would indigenous communities (Ricciardi 2001). Simberloff & Von Holle (1999) introduced the 'invasional meltdown' theory, which states that alien species facilitate one another's invasion in various ways, increasing the likelihood of survival, and potentially leading to an increase in the number of introduced species, and consequently, their impacts (Simberloff 2006). New introductions cause greater threats either by their continuous disturbance of an ecosystem, or by further altering habitat conditions in favour of themselves and other invaders (Ricciardi 2001). This creates a positive feedback system that increases the rate and accumulation of alien species (Simberloff & Von Holle 1999). According to this theory, *Arundo* invasion would promote future invasions by alien plants. Invasive plants can facilitate further invasions by altering the soil to suit invasive plant requirements (Klironomos 2002). Facilitation increases an area's susceptibility to invasion. This theory better suits results for *Arundo* found in this study. *Arundo* may facilitate invasions by other alien species by altering habitat conditions with its large size, high density, fast growth rate, and possibly altered nutrient cycling (Chapter 5).

5.5 Competitive performance of alien versus indigenous species

The relative competitive performance of indigenous versus alien species often depends on environmental conditions (Daehler 2003). These conditions could be favoured to suit alien species, such as with global change, which may enhance the competitive success of biological invaders (Huenneke 1997; Dukes & Mooney 1999). Ecosystems may become more suitable to the growth and spread of invader species, since alien species generally fare well in disturbed conditions (Mack & D'Antonio 1998). *Arundo* mostly invades disturbed areas (Bell 1997), but it is also one of the few alien species that invade undisturbed or naturally disturbed systems (Rejmánek 1989). Eutrophication in particular appears to enhance the success of *Arundo* (di Castri 1991; Coffman & Knight 2004). *Arundo* is also adapted to drought and fire (Chapter 3).

Indigenous species (such as *Phragmites* and *Typha*) in riparian habitats are more water-restricted than *Arundo* (R. Knight pers. comm.). Disturbance (e.g. eutrophication, drought, fire) will not affect *Arundo* negatively, but habitat quality would be reduced for indigenous species. *Arundo's* tolerance to various climatic and habitat conditions, as well as its high growth rate and lack of natural predators, allow *Arundo* to outcompete and replace indigenous species, especially under times of stress or disturbance. *Arundo*'s potential capacity to facilitate the success of other invasive species could further negatively impact sensitive riparian ecosystems.

6. LIMITATIONS

The lack of pristine study sites to compare pre- and post-invasion dynamics in similar habitats limited the study to comparisons of plant species composition and richness within alien and indigenous species stands. All the study sites were affected to a large degree by some disturbance, such as development, eutrophication, agriculture, clearing, restoration attempts and / or other invasive species. The sites therefore do not represent ideal conditions for comparison. The results cannot specifically be attributed to species dominance, and could be attributed to site disturbance.

7. ACKNOWLEDGEMENTS

I gratefully acknowledge the DST-NRF Centre of Excellence for Invasion Biology (CIB) at Stellenbosch University for funding, and the CSIR for coordinating project expenses; Drs. Richard Knight and Brian van Wilgen as research supervisors; Jenny and Henry Nelson for initial introduction to the *Arundo donax* problem in Hout Bay; Russell Main, Bruce d'Hotman, and Isaac Crowster for assistance with fieldwork; Igshaan Samuels for advice; and Prof R. Madsen for assistance with data analysis. Thanks to Spier Holdings Pty (Ltd) and CapeNature for permission to access study sites at Spier and Silvermine respectively.

8. REFERENCES

Bardgett, R.D. (2002) Causes and consequences of biological diversity in soil. *Zoology*, **105**, 367-374.

Bell, G.P. (1997) Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in southern California. *Plant invasions: studies from North America and Europe*. (eds J.H. Brock, M. Wade, P. Pyšek & D. Green), pp. 103-113. Backhuys Publishers, Leiden, The Netherlands.

Bird, E.C.F. (1962) The river deltas of the Gippsland lakes. *Proceedings of the Royal Society of Victoria*, **75**, 65-74.

Boose, A.B. & Holt, J.S. (1999) Environmental effects on asexual reproduction in *Arundo donax*. *Weed Research*, **39**, 117-127.

Brown, K.A. & Gurevitch, J. (2004) Long-term impacts of logging on forest diversity in Madagascar. *Proceedings of the National Academy of Sciences*, **101**, 6045-6049.

Burdick, D.M., Buchsbaum, R. & Holt, E. (2001). Variation in soil salinity associated with expansion of *Phragmites australis* in salt marshes. *Environmental and Experimental Botany*, **46**, 247-261.

Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958-1965.

Chambers, R.M. (1997) Porewater chemistry associated with *Phragmites* and *Spartina* in a Connecticut tidal marsh. *Wetlands*, **17**, 360-367.

Clarke, K.R. & Warwick, R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition*. PRIMER-E. Natural Environment Research Council, Plymouth.

Coffman, G.C. & Knight, R.S. (2004) Giant reed eradication project would provide economic benefits to impoverished communities (South Africa). *Ecological Restoration*, **22**, 146-147.

Coleman, D.C. & Whitman, W.B. (2005) Linking species richness, biodiversity and ecosystem function in soil systems. *Pedobiologia*, **49**, 479-497.

D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63-87.

Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 183-211.

di Castri, F. (1991) An ecological overview of the five regions with a Mediterranean climate. *Biogeography of Mediterranean Invasions*. (eds R.H. Groves & F. di Castri), pp 3-16. Cambridge University Press, Cambridge.

Dudley, T.L. (2000) *Arundo donax*. *Invasive plants of California's wildlands*. (eds C.C. Bossard, J.M. Randall & M.C. Hoshovsky), pp. 53-58. University of California Press, Berkeley.

Dudley, T.L. & Collins, B. (1995) *Biological invasions in California wetlands: the impacts and control of non-indigenous species in natural areas*. Pacific Institute for Studies in Development, Environment and Security, Oakland.

Dukes, J. S. & Mooney, H.A. (1999) Does global change increase the success of biological invaders? *Trends in Ecology and Evolution*, **14**, 135–139.

Dukes, J.S. & Mooney, H.A. (2004) Disruption of ecosystem processes in western North America by invasive species. *Revista Chilena de Historia Natural*, **77**, 411-437.

Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503-523.

Ehrenfeld, J.G. (2004) Implications of invasive species for belowground community and nutrient processes. *Weed Technology*, **18**, 1232-1235.

Ehrlich, P.R. & Ehrlich, A.H. (1992) The value of biodiversity. *Ambio*, **21**, 219-226.

Ekstam, B. (1995) Ramet size equalisation in a clonal plant, *Phragmites australis*. *Oecologia*, **104**, 440-446.

Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.

Farnsworth, E.J. & Meyerson, L.A. (2003) Comparative ecophysiology of four wetland plant species along a continuum of invasiveness. *Wetlands*, **23**, 750-762.

Franklin, J.F., Cromack, K., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F. & Juday, G. (1981). *Ecological characteristics of old-growth Douglas-fir forests*. USDA Forest Service Gen. Tech. Report PNW-118.

Gentle, C.B. & Duggin, J. A. (1997) Allelopathy as a competitive strategy in persistent thickets of *Lantana camara* L. in three Australian forest communities. *Plant Ecology*, **132**, 85–95.

Gaffney, K.A. & Gledhill, K. (2003) Influence of giant reed on floodplain riparian plant communities: implications for invasive plant control and habitat restoration at the watershed level. *Proceedings of the Riparian Habitat and Floodplains Conference*, 12-25 March 2001, Sacramento, USA. (ed P.M. Faber). University of California Press, Sacramento.

Grace, J.B., Smith, M.D., Grace, S.L., Collins, S.L. & Stohlgren, T.J. (2001) Interactions between fire and invasive plants in temperate grasslands of North America. *Proceedings of the Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management*, 27 November –1 December 2000, San Diego, California, USA. (eds K.E.M. Galley & T.P. Wilson), pp. 40-65. Miscellaneous Publication no. 11, Tall Timber Research Station, Florida.

Gratton, C. & Denno, R.F. (2005) Restoration of arthropod assemblages in a *Spartina* salt marsh following removal of the invasive plant *Phragmites australis*. *Restoration Ecology*, **13**, 358-372.

Grime, J.P. (1979) *Plant strategies and vegetation processes*. John Wiley, Chichester.

Grime, J.P. (1997) Biodiversity and ecosystem function: the debate depends. *Science*, **277**, 1260-1261.

Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–10.

Groves, R.H., Austin, M.P. & Kaye, P.E. (2003) Competition between Australian native and introduced grasses along a nutrient gradient. *Austral Ecology*, **28**, 491-498.

Hansen, R.A. (2000) Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology*, **81**, 1120-1132.

Hejda, M. & Pysek, P. (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biological Conservation*, **132**, 143-152.

Herrera, A.M. (1997) Invertebrate community reduction in response to *Arundo donax* invasion at Sonoma Creek. *The science and policy of environmental impacts and recovery.* (eds T. Dudley, J. Reynolds & M. Poteet), pp. 94-105. Berkeley, California.

Herrera, A.M. & Dudley, T.L. (2003) Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. *Biological Invasions*, **5**, 167-177.

Hill, M.O. & Šmilauer, P. (2005) *TWINSPAN for Windows Version 2.3*. Centre for Ecology and Hydrology & University of South Bohemia, Huntingdon & Ceske Budejovice.

Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, **6**, 324-337.

Hobbs, R.J., Richardson, D.M. & Davis, G.W. (1995) Mediterranean-type ecosystems: opportunities and constraints for studying the function of biodiversity. *Mediterranean-type ecosystems. The function of biodiversity*. (eds G.W. Davis & D.M. Richardson). Ecological Studies 109. Springer-Verlag, Berlin.

Hooper, D.U. & Vitousek, P.M. (1998) Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs*, **68**, 121-149.

Hooper, D.U., Bignell, D.E., Brown, V.K., Brussaard, L., Dangerfield, J.M., Wall, D.H., Wardle, D.A., Coleman, D.C., Giller, K.E., Lavelle, P., van der Putten, W.H., De Ruiter, P.C., Rusek, J., Silver, W.L., Tiedje, J.M. & Wolters, V. (2000) Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms and feedbacks. *BioScience*, **50**, 1049-1061.

Houlahan, J.E. & Findlay, C.S. (2004) Effect of invasive plant species on temperate wetland plant diversity. *Conservation Biology*, **18**, 1132-1138.

Huenneke, L.F. (1997) Outlook for plant invasions: interactions with other agents of global change. *Assessment and Management of Plant Invasions*. (eds Luken, J.O. & J.W. Thieret), pp. 95–103. Springer-Verlag, Berlin.

Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417**, 67-70.

Lavergne, C., Rameau, J. & Figier, J. (1999) The invasive woody weed *Ligustrum robustum* subsp. *walkeri* threatens native forests on La Reunion. *Biological Invasions*, **1**, 377–392.

Linde, A.F., Janisch, T. & Smith, D. (1976) Cattail: the significance of its growth, phenology and carbohydrate storage to its control and management. *Wisconsin Department of Natural Resources Technical Bulletin*, **94**, 1-25.

Macdonald, I.A.W., Graber, D.M., Debenedetti, S., Groves, R.H. & Fuentes, E.R. (1988) Introduced species in nature reserves in Mediterranean-type climate regions of the world. *Biological Conservation*, **44**, 37-66.

Mack, M.C. & D'Antonio, C.M. (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution*, **13**, 195-198.

Mack, M.C., D'Antonio, C.M. & Ley, R.E. (2001) Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C_4 grasses in Hawaii. *Ecological Applications*, **11**, 1323-1335.

Meyerson, L.A., Saltonstall, K., Windham, L., Kiviat, E. & Findlay, S. (2000) A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. *Wetlands Ecology and Management*, **8**, 89-103.

Milton, S.J. (2004) Grasses as invasive alien plants in South Africa. *South African Journal of Science*, **100**, 69-75.

Moore, D.R.J., Keddy, P.A., Gaudet, C.L. & Wisheu, I.C. (1989) Conservation of wetlands: do infertile wetlands deserve a higher priority? *Biological Conservation*, **47**, 203-217.

Morton, J.F. (1975) Cattails (*Typha* spp.): weed problem or potential crop? *Economic Botany*, **29**, 7–29.

Newman, S., Grace, J.B. & Koebel, J.W. (1996) Effects of nutrients and hydroperiod on *Typha*, *Cladium* and *Eleocharis*: implications for Everglades restoration. *Ecological Applications*, **6**, 774-783.

Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**, 355-364.

Pearcy, R.W., Berry, J.A. & Bartholomew, B. (1974) Field photosynthetic performance and leaf temperatures of *Phragmites communis* under summer conditions in Death Valley, California. *Photosynthetica*, **8**, 104-108.

Rejmánek, M. (1989) Invasibility of plant communities. *Biological Invasions: a global perspective.* (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek & M. Williamson), pp. 369-388. John Wiley & Sons, Chichester.

Renvoize, S.A. (1980) The sub-family Arundinoideae and its position in relation to a general classification of the Gramineae. *Kew Bulletin*, **36**, 85-102.

Ricciardi, A. (2001) Facilitative interactions among aquatic invaders: is an “invasional meltdown” occurring in the Great Lakes? *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 2513-2525.

Richardson, D.M. & van Wilgen, B.W. (1986) Effects of thirty-five years of afforestation with *Pinus radiata* on the composition of mesic mountain fynbos near Stellenbosch. *South African Journal of Botany*, **52**, 309-315.

Richardson, D.M. & van Wilgen, B.W. (1992) Ecosystem, community and species response to fire in mountain fynbos: conclusions from the Swartboskloof experiment. *Fire in South African mountain fynbos. Ecosystem, community and species response at Swartboskloof.* (eds B.W. van Wilgen, D.M. Richardson, F.J. Kruger & H.J. van Hensbergen), pp. 273-284. Ecological Studies 93. Springer-Verlag, Berlin.

Richardson, D.M., Macdonald, I.A.W. & Forsyth, G.G. (1989) Reductions in plant species richness under stands of alien trees and shrubs in the fynbos biome. *South African Forestry Journal*, **149**, 1-8.

Richardson, D.M., Cowling, R.M., Bond, W.J., Stock, W.D. & Davis, G.W. (1995) Links between biodiversity and ecosystem function in the Cape Floristic Region. *Mediterranean-type ecosystems: the function of biodiversity*. (eds G.D. Davis & D.M. Richardson), pp. 285-333. Ecological Studies 109. Springer-Verlag, Berlin.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., & Henderson, L. (1997) Alien plant invasions. *The vegetation of Southern Africa.* (eds R.M. Cowling, D.M. Richardson & S.M. Pierce), pp. 535-570. Cambridge University Press, Cambridge.

Roem, W.J. & Berendse, F. (2000) Soil acidity and nutrient supply ratio as possible factors determining changes in plant species diversity in grassland and heathland communities. *Biological Conservation*, **92**, 151-161.

Rossa, B., Tuffers, A.V., Naidoo, G. & von Willert, D.J. (1998) *Arundo donax* L. (Poaceae) – a C_3 species with unusually high photosynthetic capacity. *Botanica Acta*, **111**, 216-221.

Sankaran, M. & McNaughton, S.J. (1999) Determinants of biodiversity regulate compositional stability of communities. *Nature*, **401**, 691-693.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21-32.

Simberloff, D. (2006). Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters*, **9**, 912-919.

Smith, M.D. & Knapp, A.K. (1999) Exotic plant species in a C_4-dominated grassland: invasibility, disturbance, and community structure. *Oecologia*, **120**, 605-612.

Spencer, D.F., Ksander, G.G. & Whitehand, L.C. (2005) Spatial and temporal variation in RGR and leaf quality of a clonal riparian plant: *Arundo donax*. *Aquatic Botany*, **81**, 27-36.

Thompson, J., Brokaw, N., Zimmerman, J.K., Waide, R.B., Everham III, E.M., Lodge, D.J., Taylor, C.M., García-Montiel, D. & Fluet, M. (2002) Land use history, environment, and tree composition in a tropical forest. *Ecological Applications*, **12**, 1344-1363.

Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, **80**, 1455-1474.

Tilman, D., Knopps, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300-1302.

van der Putten, W.H., Vet, L.E.M., Harvey, J.A. & Wackers, F.L. (2001) Linking above- and belowground miltitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends in Ecology and Evolution*, **16**, 547-554.

Vitousek, P.M. & Hooper, D.U. (1993) Biological diversity and terrestrial ecosystem biogeochemistry. *Ecosystem function of biodiversity.* (eds E. Schulze & H.A. Mooney), pp. 3-14. Springer, Heidelberg.

Vitousek, P.M. & Walker, L.R. (1989) Biological invasion by *Myrica faya* in Hawaii: Plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs*, **59**, 247-266.

Welsh, S.L., Atwood, N.D., Goodrich, S. & Higgins, L.C. (eds.) (1987) A Utah flora. *Great Basin Naturalist Memoirs* 9. Brigham Young University, Provo.

Zak, D.R., Holmes, W.E., White, D.C., Peacock, A.D. & Tilman, D. (2003) Plant diversity, soil microbial communities, and ecosystem function: are there any links? *Ecology*, **84**, 2042-2050.

CHAPTER 5

IMPACTS OF THE INVASIVE ALIEN SPECIES *ARUNDO DONAX* ON THE NUTRIENT DYNAMICS OF RIPARIAN AREAS

1. SUMMARY

1. Invasive alien plants impact on all attributes of ecosystems, including ecosystem functions. They may alter fire and water regimes, nutrient cycling, and soil generation, among others. *Arundo* is an aggressive invader in many biomes of South Africa, where it may be altering the soil nutrient status of ecosystems. There is further potential for it to do so upon burning or piling biomass.
2. Invasive *Arundo* and indigenous *Phragmites australis*, being morphologically similar and occurring within similar habitats, were compared in terms of decomposition rates, vegetation nutrient concentration, vegetation nutrient pools and associated soil nutrient content.
3. *Arundo* decomposed up to twice as fast as *Phragmites*, and leaf material decomposed faster than stem material in both *Arundo* and *Phragmites*.
4. Nutrient content within above-ground vegetation of *Arundo* was significantly higher than that of *Phragmites* for all nutrients.
5. Sites supporting *Arundo* had relatively similar soil nutrient concentrations as sites supporting *Phragmites*.
6. Faster rates of decomposition only alter soil nutrient status if large amounts of leaf litter are produced. *Arundo* accumulates little dry material, and binds nutrients in its living material. *Phragmites* produces large amounts of refractory dry material, binding nutrients in its dead material. Neither species contribute significantly to nutrient cycling via decomposition in these climatic conditions.
7. *Arundo* has the potential to change nutrient regimes because of its rapid decomposition rates. This has implications for areas where more dry biomass accumulates within stands of *Arundo*, or where burning or piling cut biomass is used as a method of *Arundo* control. Invasion of *Arundo* may then alter soil nutrient cycling.

2. INTRODUCTION

2.1 Biodiversity

Biodiversity encompasses the functional and physical attributes of ecosystems, such as the provision of goods and services, and the presence and interactions of species constituting that ecosystem (Coleman & Whitman 2005). The primary attributes of ecosystems are their composition, structure and function (Franklin *et al*. 1981). Composition has to do with the identity and variety of elements in an ecosystem; structure is the physical organisation of an ecosystem; and ecosystem functions are the ecological or evolutionary processes taking place (Franklin *et al.* 1981; Noss 1990). Ecosystem functions include water purification, decomposition, nutrient cycling, and soil generation (Kremen 2005).

2.2 Nutrient cycling and decomposition

Decomposition is one of the main elements of nutrient cycling in terrestrial systems (Zimmer 2002). It involves the mechanical break down of litter, leaching of soluble compounds and chemical deterioration of plant tissue (Lavelle *et al.* 1996). Decomposition and nutrient cycling are regulated by climate and soil (Swift *et al.* 1979; Johansson *et al.* 1995; Trofymow *et al*. 2002), chemical composition of litter (Aerts 1997), and by interactions between organisms (Cortez 1998; Schädler & Brandl 2005).

Plant species have different effects on nutrient cycling because of their differential nutrient uptake, loss and retention (Hobbie 1992; Knops *et al*. 2002), and different effects on decomposition due to productivity and leaf litter (Mack & D'Antonio 2003). Increased productivity usually leads to increased resource use, increased leaf litter, and increased rates of decomposition. Interactions among plant species may alter the quantity or quality of leaf litter produced (Mack & D'Antonio 2003). High plant species diversity may lead to high litter diversity, which in turn supports a greater diversity of decomposers and detritivores (Jones *et al*. 1997; Hansen 2000), and in turn this may lead to an increased variety of food resources and greater habitat complexity (Bardgett 2002).

2.3 Disturbance

Species vary in their response to disturbance, so disturbance may favour one species over another (Hobbs & Huenneke 1992). Ecosystem disturbances have long lasting consequences, which can often be seen in the species composition of a disturbed area (Roem & Berendse 2000; Thompson *et al*. 2002). Some important ecosystem disturbances include fire and invasion by alien species.

2.3.1 Fire

Fire affects the nutrient status of the soil (Rundel 1983; Stock & Lewis 1986). There is usually a temporary increase in nutrient availability to the soil after fire (Day 1983), but an overall nutrient loss, occurring via volatilisation, erosion and leaching (De Bano & Conrad 1978). Nutrients not lost through volatilisation will be deposited in ash, which is usually high in available nutrients, promoting rapid regrowth after fire (Day 1983).

2.3.2 Invasive alien species

Invasive alien species out-compete indigenous species for resources and space, alter fire and water regimes, and alter soil nutrient status (Macdonald *et al.* 1989; Cronk & Fuller 1995). They also impact on the ecosystem functions of decomposition, nutrient cycling, and soil generation (D'Antonio & Vitousek 1992; Walker & Smith 1997; Standish *et al*. 2004). The most damaging species transform ecosystems by using or adding excessive amounts of resources, such as water, light, oxygen, and nutrients (Richardson *et al*. 2000).

Invasive alien species often establish in high-nutrient areas, and some can alter soil nutrients to suit their own requirements (Huenneke *et al*. 1990; Ostertag & Verville 2002), suggesting possible feedbacks between nutrient cycling and plant species composition (Simberloff & Von Holle 1999; Ehrenfeld *et al*. 2001). Invasive plant species usually increase biomass and net primary production, and produce litter with higher decomposition rates than co-occurring indigenous species (Ehrenfeld 2003). They usually enhance soil nutrients by their elevated litterfall or elevated litter nutrient concentration (Ehrenfeld 2003).

2.4 *Arundo donax*

Arundo donax L. (hereafter referred to as *Arundo*) belongs to the Arundineae tribe, along with *Phragmites* species (Renvoize 1980). *Arundo* is indigenous to the Indian sub-continent (Bell 1997), and invasive in many regions of the world, including South Africa. *Arundo* is a hydrophyte, growing along lakes, streams, drains, and other wet sites (Bell 1997). *Arundo* is a perennial C_3 grass species (Rossa *et al*. 1998), resembling the indigenous common reed *Phragmites australis* when young. *Arundo* usually grows in large stands, containing hundreds of stems per stand (Spencer *et al.* 2005). Stems may reach 10 metres in height (Dudley 2000). Reproduction occurs almost entirely from rhizomes and stem fragments (Boose & Holt 1999), which are usually carried by floodwaters into new habitats (Else 1996). *Arundo* can tolerate a wide variety of ecological conditions (Perdue 1958), mostly due to its deep rhizomes and roots (Mackenzie 2004). It survives in all types of soils (Perdue 1958), and is usually associated with higher soil nutrient levels than indigenous plants (Coffman *et al.* 2004). *Arundo* is usually associated with rivers that have been physically disturbed (Bell 1997), but may invade undisturbed or naturally disturbed systems (Rejmánek 1989). Recent nutrient loading of rivers is hypothesized to be a major factor contributing to *Arundo* invasion in California (di Castri 1991).

Iverson (1993) and Zimmerman (1999) report that *Arundo* uses and transpires three times more water than indigenous riparian tree species in the USA. *Arundo* is competitive, and once established, it physically inhibits and replaces indigenous plant communities (Bell 1997), forming extensive stands or monocultures. It is partly due to its size and rapid growth rate that *Arundo* can reduce the diversity of riparian fauna and flora (Milton 2004). *Arundo* produces large quantities of biomass that increase the available fuel for unseasonal and higher intensity fires (Coffman *et al*. 2004). It is highly adapted to fires and flammable throughout most of the year (Bell 1997). *Arundo* appears to use more soil nutrients (especially nitrogen) than indigenous species (Coffman *et al.* 2004). It also invades more readily in areas where soil nitrogen is high, growing rapidly with elevated nutrients (Decruyenaere 2000). It decomposes at rates similar to indigenous litter in riparian environments in the USA, but changes the structure of the soil, making it unsuitable for decomposer organisms (B. Lichtman, unpublished data, in Herrera & Dudley 2003). Indigenous vegetation has a larger and more complex litter layer than *Arundo* (Herrera & Dudley 2003).

2.5 *Phragmites australis*

Common reed *Phragmites australis* (Cav.) Trin. ex Steud. (hereafter referred to as *Phragmites*) is a large clonal C_3 grass species, reaching heights of two to six metres (Pearcy *et al*. 1974). It has a similar appearance to *Arundo* when young, but once the plants are mature, there are distinct differences, especially noticeable during winter months, when *Phragmites* turns brown and loses most of its leaves (personal observation). *Arundo* remains green (although some shades lighter during winter) and retains most its leaves. *Phragmites* is also shorter on average, with more stems per area than *Arundo* (preliminary investigations). *Phragmites* reproduces mainly by vegetative reproduction, via rhizomes (Ekstam 1995). It is tolerant to climate, altitude, flooding, frost, high pH, salt, a wide range of soils, and invasion by many other species (Welsh *et al*. 1987; Meyerson *et al*. 2000). *Phragmites* usually grows in open, wet areas, along streams, marshes (Meyerson *et al*. 2000), ditches, and roadsides (Chambers 1997). Studies show that increased nutrient loads increase *Phragmites* growth (Haslam 1965; Marks *et al*. 1994). *Phragmites* is an invasive species in the USA (Meyerson 2000; Meyerson *et al*. 2000).

The purpose of this research was to determine whether invasion by *Arundo* would alter nutrient dynamics of ecosystems. Invasive *Arundo* and indigenous *Phragmites* were compared in terms of rates of decomposition, vegetation nutrient concentrations and content, and soil nutrient concentrations of sites dominated by these species.

3. METHODS

3.1 Study areas

The Western Cape of South Africa has a Mediterranean-type climate: warm, dry summers and wet, temperate winters. Rainfall varies from 200 to 2000 mm per year, and falls mainly during the winter months. Strong south-easterly winds blow primarily during summer, from November to February. The study sites are within the lower reaches of three rivers in the Western Cape of South Africa: the Disa River in Hout Bay (S 34° 01' 56.2", E 18° 21' 13.1"), the Eerste River on the Spier Wine Estate outside Stellenbosch (S 33° 59' 12.6", E 18° 47' 34.6"), and the Silvermine River, downstream of the Silvermine Nature Reserve (S 34° 06' 41.7", E 18° 24' 34.6"). The last site was used only for collection of *Phragmites* plant material, and is a marsh situated on the campus of the University of the Western Cape, Bellville (S 33° 56' 09.3", E 18° 37' 43.4"). The Disa River runs through Hout Bay, a coastal town about 11 km from Cape Town. This study site was limited to the area between the Victoria and Princess Road bridges, along the Disa River. Residential development, agricultural use, invasive alien plants, and modifications to river geomorphology have seriously altered much of the downstream reaches of the river. The Disa River was formerly a braided river system dominated by extensive stands of indigenous palmiet *Prionium serratum*. *Arundo* stands are dense and extensive, and span the entire distance between the Victoria and Princess Road bridges, with fewer and less dense clumps upstream. The lower reach of the Disa River is characterised by a broad floodplain and most of it falls within residential or commercial zoning. The Eerste River is one of three rivers on the Spier Wine

Estate. It is heavily impacted and polluted along most of its course. It flows through the town of Stellenbosch and is exposed to urban pollution and waste. This study site is surrounded by agricultural, grazing and open land. The public have little or no access to this site since the wine estate is a privately owned enterprise. The *Arundo* stand at this site is extensive, but there appears to be only one major stand, spanning a distance of 300 – 400 m along the river. Smaller clumps of *Arundo* exist in other locations along the river. Many other invasive plants are present along the river and there have been no formal eradication or control plans for any of them. The Silvermine River is located within a protected area. The study site however, is downstream of the Nature Reserve, and a short distance from the Sunbird Environmental Education Unit near Clovelly. It is relatively and comparatively unimpacted. The site has recently become infested with *Arundo*, probably in the last few years. There is ongoing restoration to clear the area of *Arundo* – stands of *Arundo* have been cut in the recent past. There is limited development and no agriculture (hence likely no nutrient enrichment) on or near the site. Vegetation dominating the marsh on the University campus consists mainly of *Phragmites australis* and *Typha capensis*.

3.2 Decomposition experiment

Leaf and stem samples of *Arundo* and *Phragmites* were collected in Hout Bay. Plant material was cut to similar dimensions: leaf material to pieces of similar length (80 – 100 mm) and width (15 – 20 mm), and stem material to 40 – 50 mm sections of internode material with similar diameters (8 – 15 mm). Material was air-dried at room temperature for three weeks until constant weight was achieved. The plant material was not artificially dried as this could have affected microbial activity, and consequently the decomposition rate (Tanner 1981). Litterbags were made from shade cloth material, and had inside measurements of 150 mm x 150 mm. Each bag was filled with approximately 5 g of dried leaf or stem material. Mesh size was sufficiently small (1 mm x 5 mm) to minimize losses of litter due to breakage, while large enough to allow access of most litter-dwelling invertebrates into the bags (Loranger *et al*. 2002). Each bag was individually marked and tagged with a bright orange strip of linen tied to the bag (0.5 m in length), as well as aluminium tags inside the bags. No further site marking was deemed necessary since there was little groundcover at preliminary site visits, and upon burial of the litterbags. All litterbags were buried between 100 and 200 mm below the surface, at random sites, but within close proximity to stands of *Arundo* (no further than 1 m) in Hout Bay, in April 2005. There was an initial sample size of 36 litterbags (Table 1), sufficient for three replicates per collection. However, at the time of the first collection (three months after burial), many litterbags had been lost despite marking and tagging. The site had become considerably overgrown by *Tropaeolum majus* and *Pennisetum clandestinum*. To allow for at least one sample to be collected per category per retrieval date, only one sample per category was collected at each three-month interval. Sample size was reduced from n = 3 to n = 1. The results therefore are not statistically robust but do give an indication of possible trends.

The litterbags were collected over a nine-month period. One litterbag per species material was collected (random selection) at each three-month interval. Sample retrieval occurred during July 2005, October 2005 and January 2006. Retrieved bags were placed inside ziplock bags until laboratory analysis. Litterbag material was carefully transferred onto white sheets of paper. Invertebrates were first removed. *Arundo* and *Phragmites* material were separated from other plant material (moss, mould, roots), debris and soil. In cases where further removal of other material would cause damage to the sample, the sample was analysed without removal of that material. Once material was cleaned and weighed, it was oven-dried at 60 ºC for 24 hours, and re-weighed to determine mass loss due to decomposition.

3.3 Plant material nutrient analysis

Five samples each of stem and leaf material per species were collected early in August 2006. *Arundo* material was collected from Hout Bay, and *Phragmites* material was collected from Bellville, since the leaves on *Phragmites* plants in Hout Bay had senesced shortly before plant material collection, whereas the stand at Bellville had not. Plant material was cut to similar dimensions: leaf material to pieces of similar length (80 – 100 mm) and width (15 – 20 mm), and stem material to 40 – 50 mm sections of internode material with similar diameters (8 – 15 mm). The plant material was oven-dried at 60 – 70 ºC for 72 hours until constant weight. Stem and leaf material per species was analysed for NH_4 nitrogen, phosphorus, potassium, calcium, magnesium, sodium, iron, copper, zinc, manganese, boron and aluminium content, at Western Cape Department of Agriculture at Elsenburg. Methods of analysis comply with procedures used by member laboratories of the inter-laboratory control scheme AgriLASA (Agri Laboratory Association of Southern Africa) and official methods of the AOAC (Association of Official Analytical Chemists). The values for average biomass were taken from Chapter 3 of this thesis to estimate above-ground nutrient pools in the vegetation. Leaf and stem material was estimated to constitute 20 % and 80 % of the total biomass, respectively.

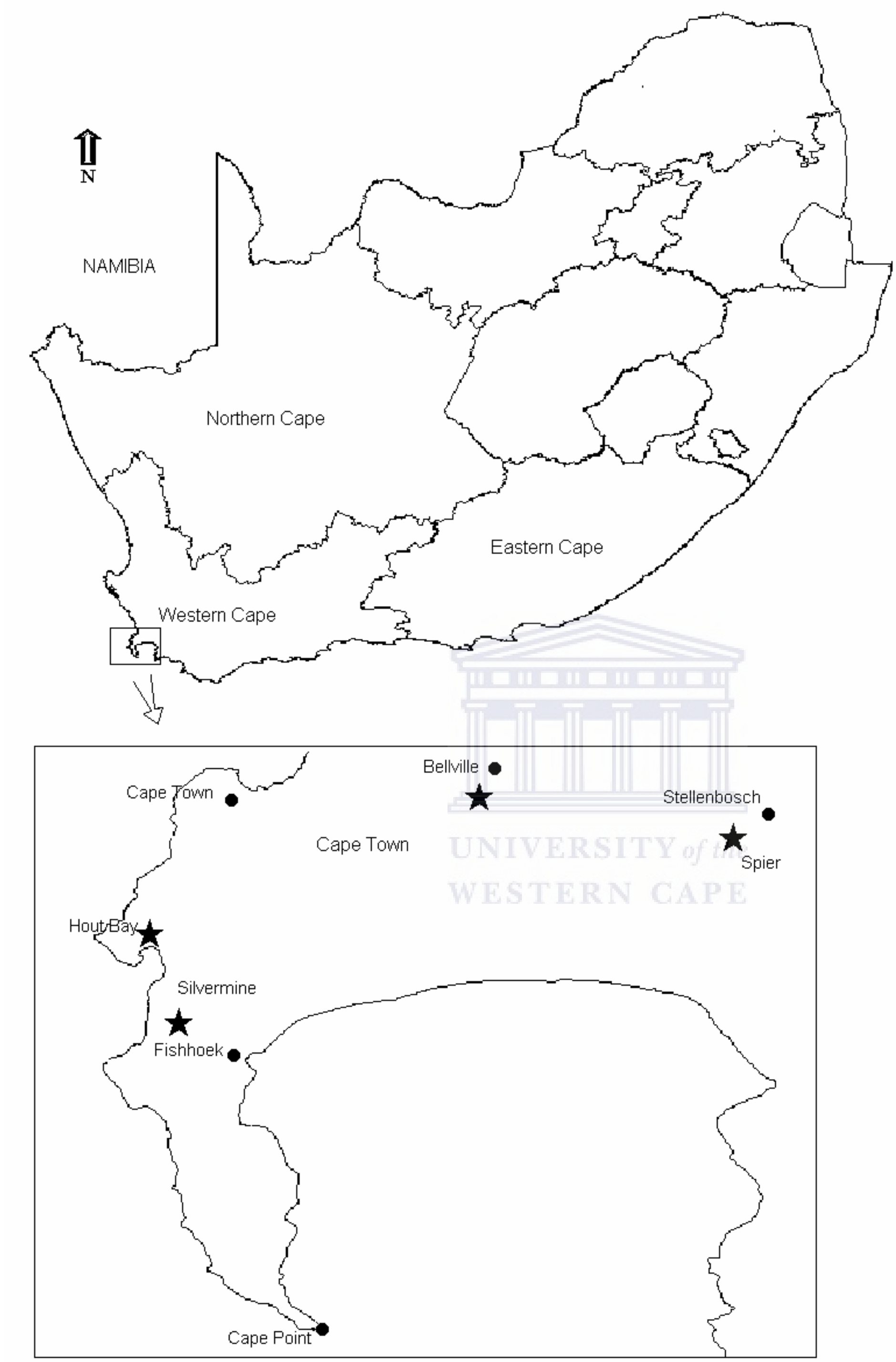


Fig. 1. Map of South Africa showing provincial boundaries. The study occurred in the Western Cape province; study sites are marked with stars; nearby towns are marked with dots.

Table 1. The design of an experiment to assess the rate of decomposition of *Arundo* and *Phragmites* stem and leaf material. Data show the number of replicates; months indicate duration of burial.

	Arundo stem	*Arundo* leaf	*Phragmites* stem	*Phragmites* leaf
Three months	3	3	3	3
Six months	3	3	3	3
Nine months	3	3	3	3
Total	9	9	9	9
	18		18	
	36			

3.4 Soil nutrient analysis

Twenty-two soil samples were collected in January 2006 (dry season) from stands of *Arundo* and *Phragmites* from Hout Bay, Spier and Silvermine. Eleven samples were collected from *Arundo* stands (seven from Hout Bay, two from Spier, two from Silvermine) and eleven from *Phragmites* stands (eight from Hout Bay, three from Spier). Samples were collected from various sites to separate sites effects from species effects. Samples were collected from 150 mm deep at the base of *Arundo* and *Phragmites* stands. Soil was analysed at Western Cape Department of Agriculture at Elsenburg, for nitrogen, phosphorus, potassium, calcium, magnesium, sodium and carbon. Nitrogen content was determined using the Kjeldahl method (Bremner & Mulvaney 1982), and phosphorus, potassium, calcium, magnesium, sodium and carbon were determined using 1 % citric acid.

3.5 Statistical analysis

Mass loss and rate of mass loss was determined on a percentage basis, since litterbags did not all have the same initial weight. Nutrient concentrations were applied to five average biomass values (kg ha^{-1}) of live material from Hout Bay (Chapter 3) to determine nutrient pools within vegetation. Soil nutrients were analysed per plot and per species, and applied to non-metric multidimensional scaling analysis in PRIMER-e (Clarke & Warwick 2001). One-way ANOVA's were used to determine significant differences between stem and leaf nutrient content of *Arundo* and *Phragmites*, and between soil nutrient concentrations associated with the species various sites.

4. RESULTS

4.1 Percentage mass lost during decomposition

Percentage mass loss of stem and leaf material after three, six, and nine months, was higher for *Arundo* than for *Phragmites*. Overall, *Arundo* lost a greater percentage of mass to decomposition than did *Phragmites*. Percentage mass loss of leaf material after three, six and nine months, was greater than that of stem material, for both species. Mass loss was greatest between three and six months, after which it decreased, with the exception of *Arundo* leaf material, which continued its mass loss after six months (Figs. 2a and b).

4.2 Rate of mass loss during decomposition

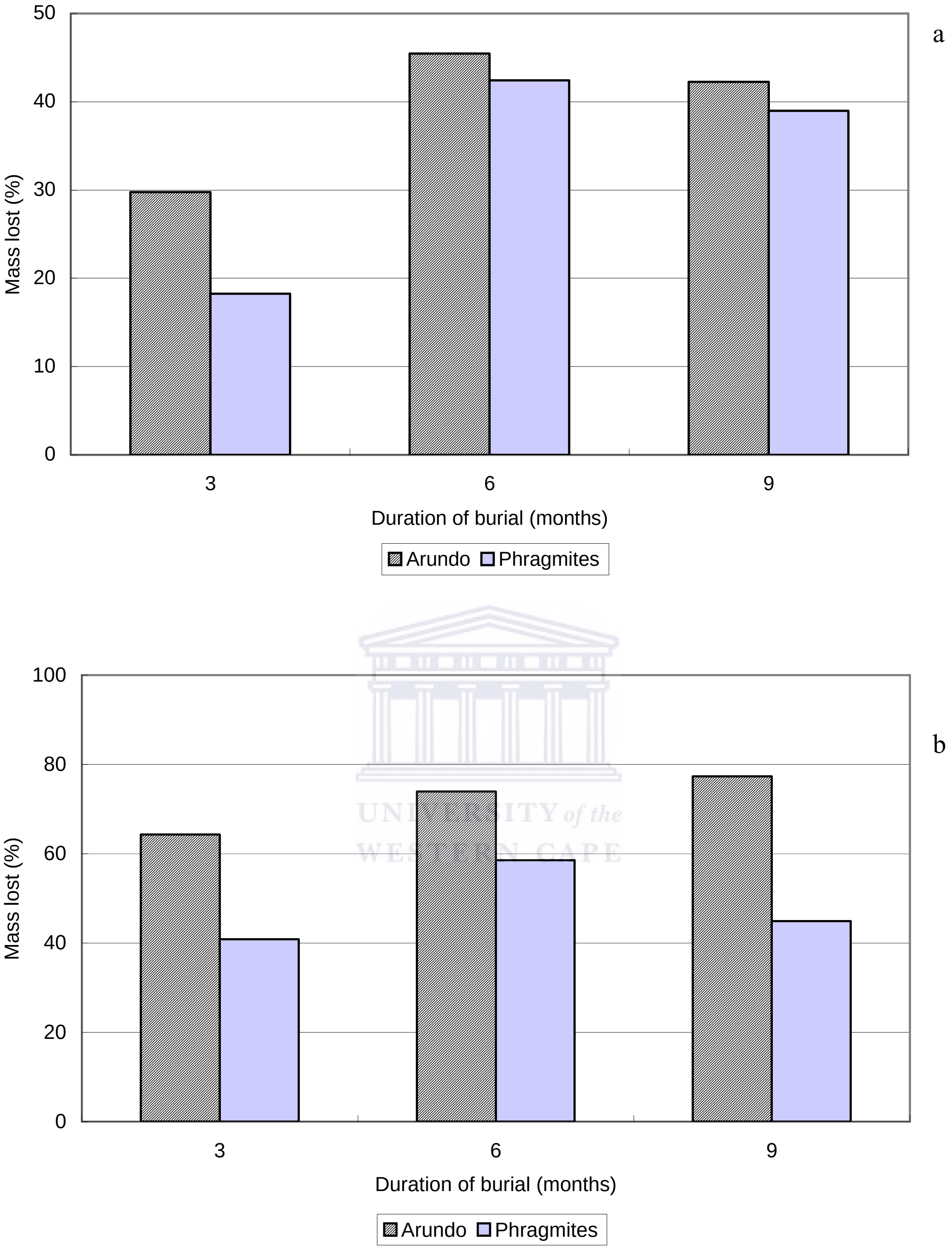
Arundo decomposed faster than *Phragmites*. Rate of mass loss was greater for *Arundo* stem and leaf material than for *Phragmites* material, at three, six, and nine months. Leaf material decomposed faster than stem material. Rate of mass loss of leaf material was greater than that of stem material, at three, six, and nine months, for both species. The rate of mass loss decreased over time for *Arundo* and *Phragmites* stem and leaf material (Figs. 3a and b).

4.3 Plant material nutrient concentration

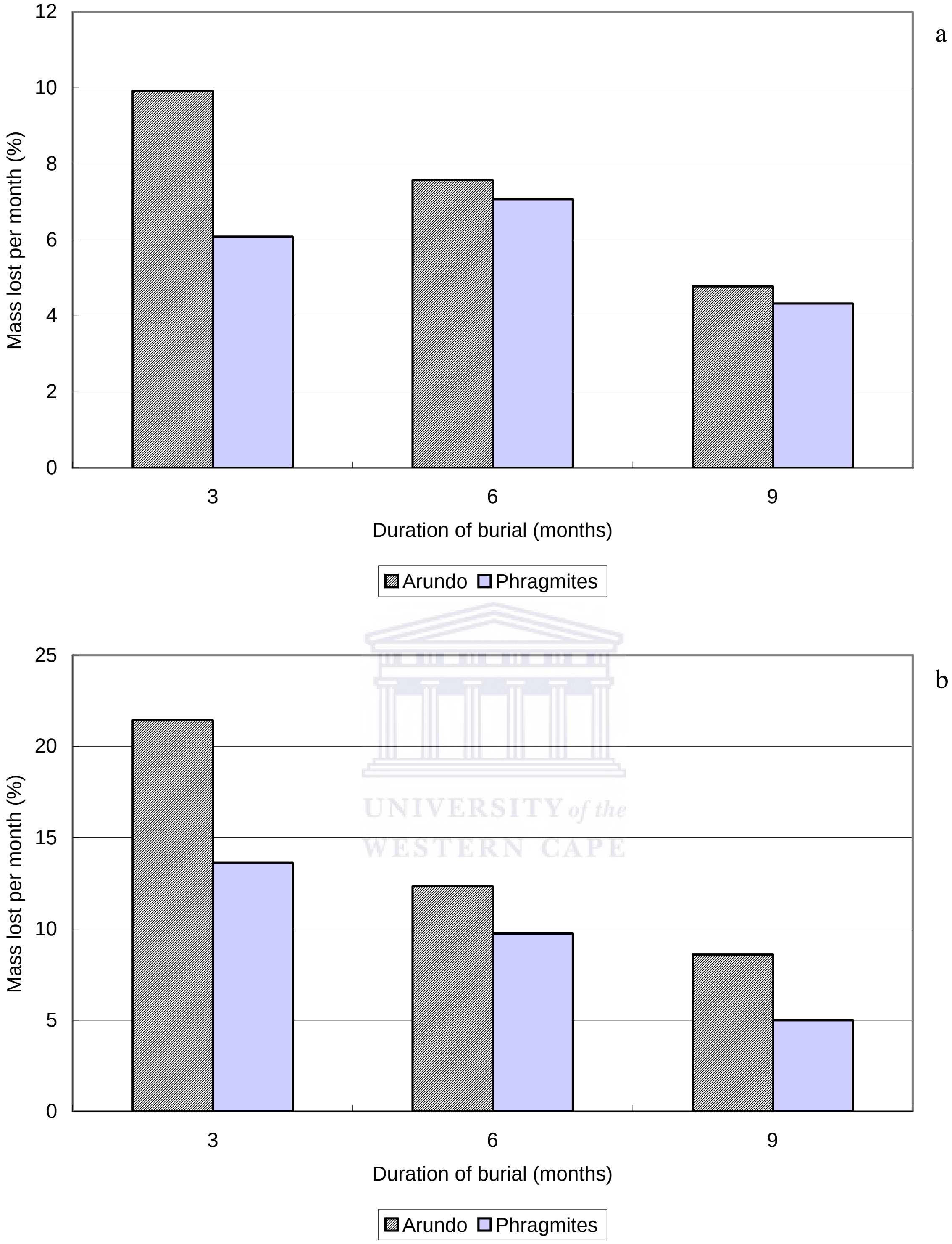
In most instances, nutrient concentration was significantly higher in *Arundo* material than in *Phragmites* material (Table 2). Leaves usually had higher nutrient concentrations than stems. According to Marschner (2002), *Arundo* and *Phragmites* are deficient in NH4, K, Zn, Cu and Bo, in terms of the range suitable for crop plants.

4.4 Nutrient pools in vegetation

The total above-ground biomass nutrient pool (combined stem and leaf material values) was significantly higher in *Arundo* than *Phragmites* for all nutrients (Figs. 4a, b, c, and d) ($p < 0.05$). This is largely due to the biomass of *Arundo* being that much greater than *Phragmites*.



Figs. 2a and b. Percentage mass loss of *Arundo* and *Phragmites* stem (a) and leaf (b) material collected from and buried at Hout Bay for the decomposition experiment. The months indicate the duration for which the litterbags (n = 1) were buried. Note different scales for Fig. 2a and b.



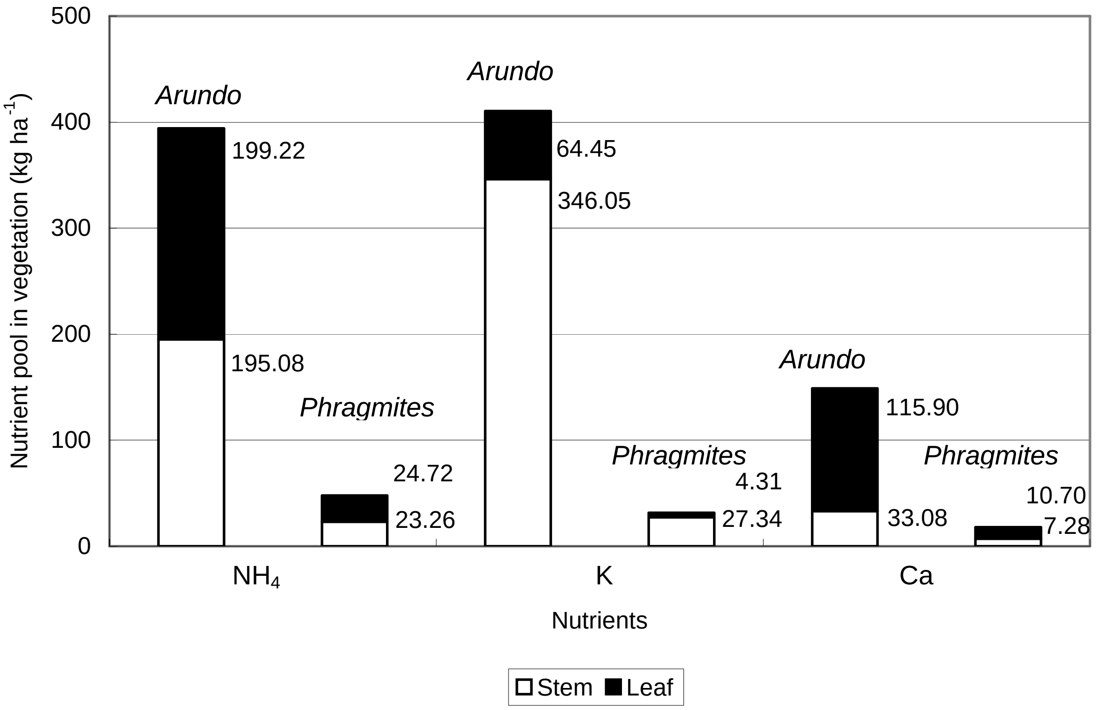
Figs. 3a and b. Rate of mass loss per month of *Arundo* and *Phragmites* stem (a) and leaf (b) material collected from and buried at Hout Bay. Rate of mass loss is determined by percentage mass loss divided by duration of burial in months. The months indicate the duration for which the litterbags (n = 1) were buried. Note the different scales for Figs. 3a and b.

Table 2. Nutrient concentration of stem and leaf material of *Arundo* and *Phragmites*, from samples (n = 5) collected in August 2006. Underlined values are significantly different between species; **bold type** indicates the higher value ($p < 0.05$). Optimum range of values is in the same units as the column they are in. D, U, and W abbreviate nutrient status of deficiency, unknown, and within range (Marschner 2002).

	%					mg kg^{-1}						
Arundo	NH_4	K	Ca	P	Mg	Na	Fe	Mn	Al	Zn	Cu	Bo
Stem	**0.6**	**1.0**	0.1	**0.1**	0.2	438.0	253.9	12.8	27.6	9.0	2.5	1.0
Leaf	**2.3**	**0.8**	**1.4**	**0.1**	**0.7**	145.8	322.6	132.2	12.0	**13.0**	3.5	3.5
Average	1.4	**0.9**	0.7	**0.1**	**0.4**	291.9	288.3	72.5	19.8	11.0	3.0	2.3

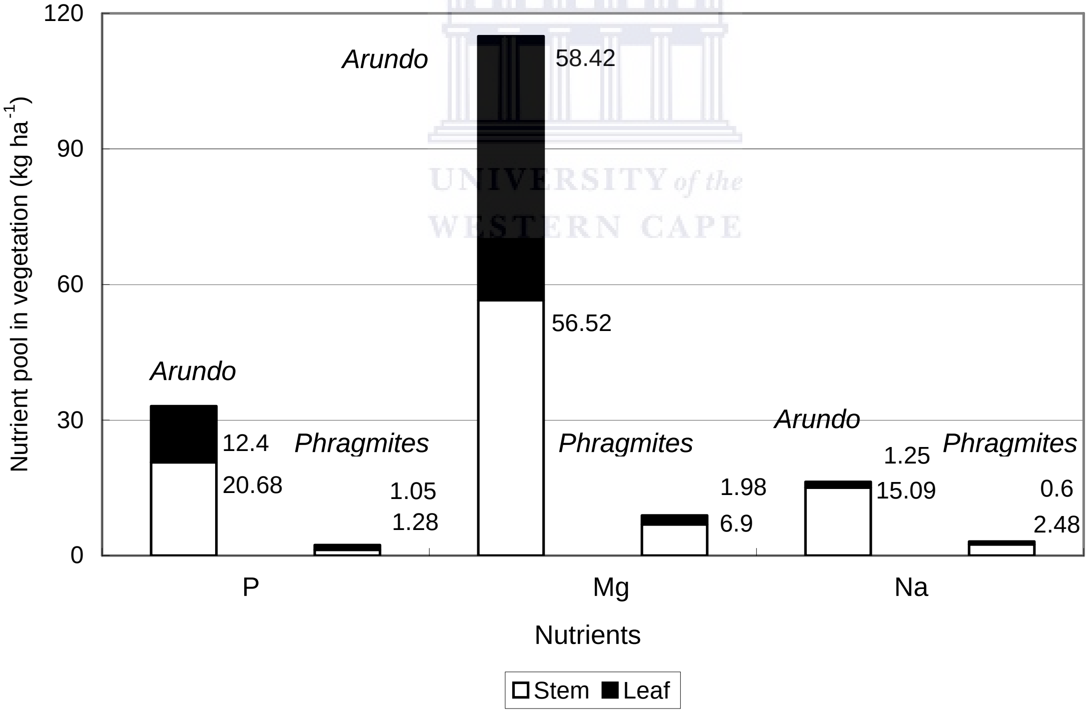
Phragmites	NH_4	K	Ca	P	Mg	Na	Fe	Mn	Al	Zn	Cu	Bo
Stem	0.4	0.4	0.1	0.0	0.1	387.6	542.7	7.8	19.5	8.6	1.8	1.1
Leaf	1.6	0.3	0.7	0.1	0.1	**374.8**	239.0	93.7	28.1	7.3	3.8	**11.0**
Average	1.0	0.4	0.4	0.1	0.1	381.2	390.8	50.8	23.8	7.9	2.8	6.1

Optimum range (Marschner 2002)	2-5	2-5	-	-	-	-	100 - 500	20 - 200	-	20 - 100	5 - 20	10 - 100
Status	D	D	U	U	U	U	W	W	U	D	D	D



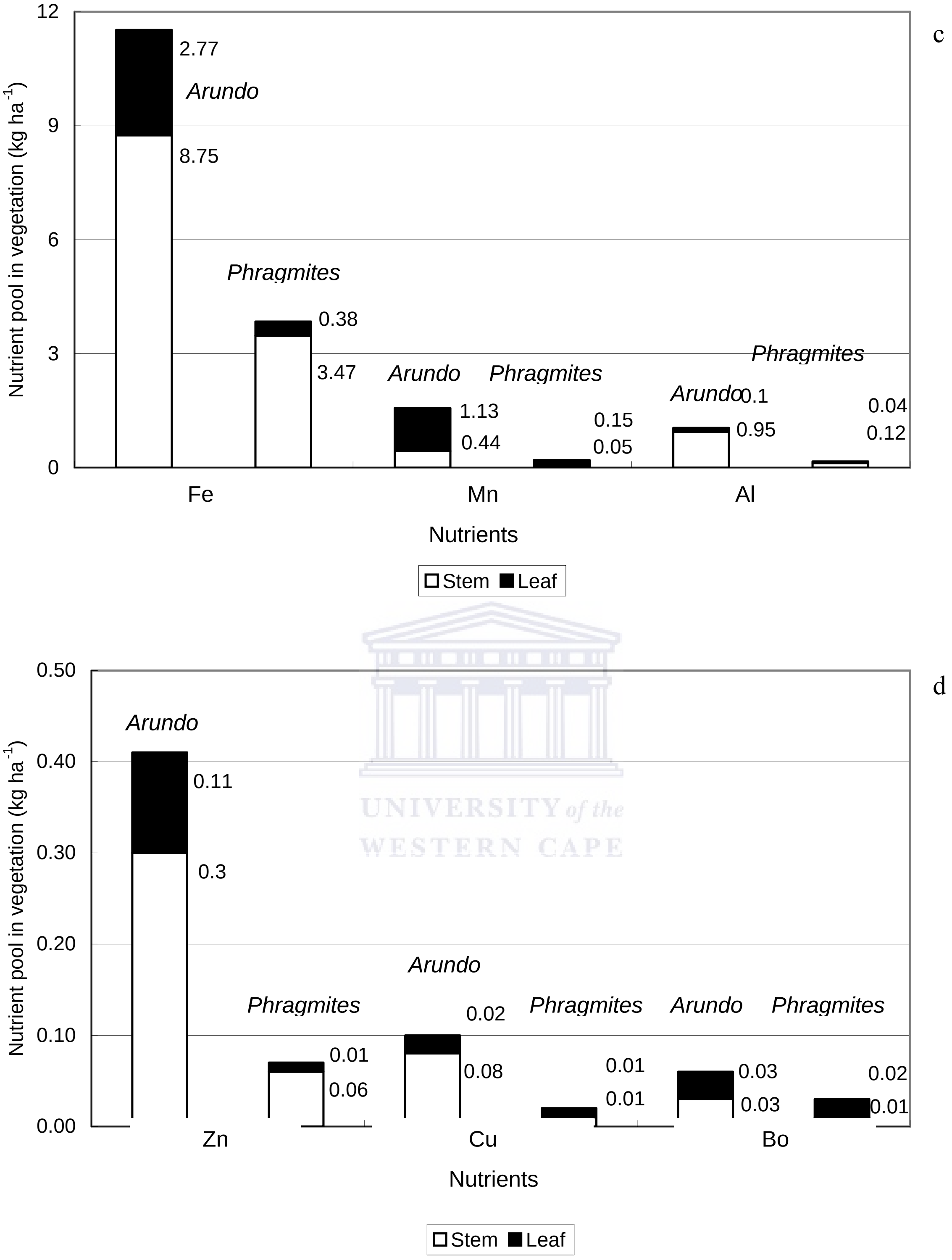
500
400
300
200
100
0
Nutrient pool in vegetation (kg ha^{-1})
Arundo
199.22
195.08
Phragmites
24.72
23.26
Arundo
64.45
346.05
Phragmites
4.31
27.34
Arundo
115.90
33.08
Phragmites
10.70
7.28
NH$_4$
K
Ca
Nutrients
☐ Stem ■ Leaf

a



120
90
60
30
0
Nutrient pool in vegetation (kg ha^{-1})
Arundo
12.4
20.68
Phragmites
1.05
1.28
Arundo
58.42
56.52
Phragmites
1.98
6.9
Arundo
1.25
15.09
Phragmites
0.6
2.48
P
Mg
Na
Nutrients
☐ Stem ■ Leaf

b



Figs. 4a, b, c and d. Leaf, stem and total biomass nutrient pools (kg ha^{-1}) of NH_4, K, Ca (a), P, Mg, Na (b), Fe, Mn, Al (c), Zn, Cu, Bo (d), of *Arundo* and *Phragmites*. Nutrient pools determined using estimated biomass values (n = 5) from Hout Bay (Chapter 3 of thesis), and nutrient concentrations from plants sampled at Hout Bay and Bellville in August 2006.

4.5 Soil nutrients

Most soil nutrients associated with *Arundo* increase in value from Hout Bay to Spier to Silvermine (Table 3). Soil associated with *Arundo* and *Phragmites* at Hout Bay separate out quite well in the non-metric multidimensional scaling (Fig. 5). The exception is K, which is highest at Spier and lowest at Silvermine. The soil nutrients associated with *Phragmites* do not show the same pattern – higher values occur at Hout Bay for C, N, Mg, K, and P. Spier has higher values of Ca and Na. Comparing species per site shows that *Phragmites* at Spier is associated with lower nutrients than *Arundo* at Spier, except for Ca, which is higher for *Phragmites*. At Hout Bay, *Phragmites* is associated with higher soil nutrients than *Arundo*, except for Mg, which is marginally higher for *Phragmites*. Overall, most of the values are quite similar for *Arundo* and *Phragmites*. *Arundo* has higher soil nutrients of C, N, Mg and Na. *Phragmites* has higher soil nutrient contents of Ca, K and P. Only Mg is significantly higher in soil associated with *Arundo* than in soil associated with *Phragmites*.

Table 3. Average soil nutrient content of soil taken from within *Arundo* stands at Hout Bay, Spier and Silvermine. The overall averages are per plot from all the sites (and not an average of those preceding them in the table). n represents the number of replicates. Underlined values are significantly different between species; **bold type** indicates the higher value ($p < 0.05$).

	%		cmol kg^{-1}		mg kg^{-1}			
Arundo donax	N	C	Ca	Mg	K	Na	P	n
Hout Bay	0.2	2.1	5.4	1.6	117.9	17.9	50.7	7
Spier	0.3	3.4	6.8	2.6	285.0	69.0	242.5	2
Silvermine	0.5	5.3	9.8	3.7	67.0	70.0	383.0	2
Overall average	0.2	2.9	6.4	**2.2**	139.0	36.6	146.0	11

Phragmites australis	N	C	Ca	Mg	K	Na	P	n
Hout Bay	0.2	2.8	7.1	1.6	167.5	28.0	242.0	8
Spier	0.1	1.5	12.0	1.0	142.7	31.0	69.3	3
Overall average	0.2	2.5	8.4	1.4	160.7	28.8	194.9	11

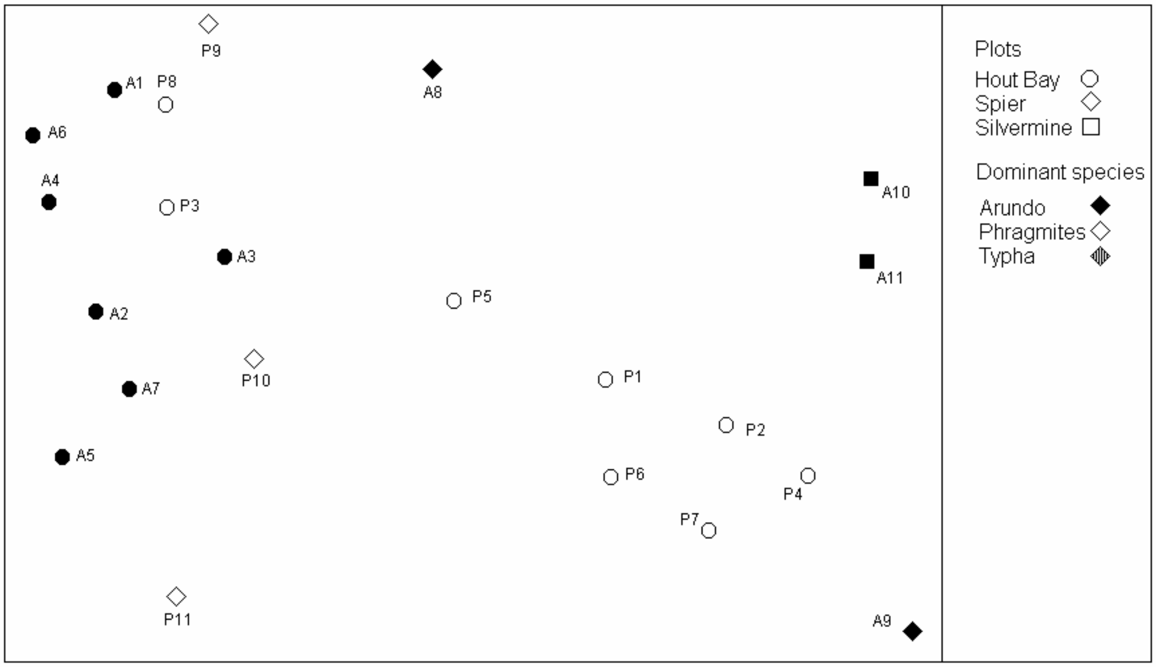


Fig. 5. Ordination plot (non-metric multi-dimensional scaling) of similarity in soil nutrient concentrations (Table 2) from plots dominated by *Arundo* and *Phragmites* at Hout Bay, Spier and Silvermine.

5. DISCUSSION

5.1 Invasive plant species and nutrient cycling

Plant species have different effects on nutrient cycling due to differential nutrient uptake, loss and retention (Hobbie 1992; Knops *et al*. 2002), and altered nutrient pools can affect plant community composition and species diversity (Levine *et al*. 1998). Nitrogen mineralization and nitrification rates usually increase in response to invasions (Ehrenfeld 2003). Vitousek *et al*. (1987) found that the invasion of *Myrica faya* (a nitrogen-fixer) into an Hawaiian ecosystem increased the rate of nitrogen accumulation more than fourfold (Dukes & Mooney 2004), in an originally nutrient-poor system. *Acacia saligna* increased soil nutrients of fynbos systems in South Africa (Musil & Midgely 1990) through its higher leaf fall and decomposition rates (Witkowski 1991).

5.2 Nutrient pools in vegetation

Arundo has higher nutrient concentrations (of most nutrients), greater amounts of biomass (Chapter 3), and consequently higher nutrient pools in vegetation than *Phragmites* and other indigenous vegetation (Table 4). *Arundo* biomass has between six and ten times more phosphorus, potassium, magnesium, calcium and nitrogen than *Phragmites* biomass, and between three and 17 times more of the same nutrients than fynbos biomass. Larger nutrient pools in vegetation relate to greater input of nutrients from vegetation upon decomposition (i.e. the greater potential for increased soil nutrient availability).

Table 4. Average plant material nutrient pools (kg ha^{-1}) for living material (biomass) of different vegetation types in the Western Cape, South Africa (van Wyk *et al*. 1992).

	UNINVADED SITES				INVADED
	11 year old fynbos [1]	21 year old fynbos [2]	29 year old fynbos [3]	*Phragmites* communities	*Arundo* communities
K	36.7	86.47	111.70	91.57	824.17
Ca	174.7	69.92	31.96	52.02	299.38
Mg	10.9	15.57	13.87	25.69	230.78
N	76.7	105.17	107.50	138.78	791.65
P	7.2	6.35	6.67	6.75	66.43

[1] Low (1983)

[2] van Wilgen & Le Maitre (1981)

[3] van Wyk *et al*. (1992)

5.3 Rates of decomposition and consequent nutrient cycling

Invasive alien plants usually alter soil nutrient dynamics by increasing litter quantity, rates of decomposition and nutrient cycling (Ehrenfeld 2003). Rates of decomposition determine the rate at which nutrients cycle within an ecosystem (Facelli & Pickett 1991; Hobbie 1992). *Arundo* decomposed faster than *Phragmites*, and therefore may recycle nutrients in a system faster than *Phragmites*. In order for invasions to alter nutrient fluxes, invasive plants must not only displace indigenous species (Chapter 4), but must also produce significant amounts of litter (Allison & Vitousek 2004). *Arundo*-dominated communities had less leaf litter and other dry or dead material than *Phragmites*-dominated communities (Chapter 3). Many of the nutrients in above-ground biomass of *Arundo* will be bound in the living material and not returned to the soil via decomposition, since there is little dead material in stands of *Arundo*. The material that does decompose will do so rapidly, but there is not sufficient material to significantly enrich the soil. In colder and more arid areas, such as California (G. Coffman pers. comm.), more *Arundo* material dies off and accumulates within stands. In these regions, invasion by *Arundo* may increase nutrient cycling, since rates of decomposition and amounts of leaf litter will possibly be higher than that of indigenous species.

In general, leaves decompose more rapidly than stems and branches (Berg *et al*. 1996). The experiment confirms the trend with *Arundo* and *Phragmites*. Leaves, roots and rhizomes of *Phragmites* are known to decompose relatively rapidly (Wrubelski *et al*. 1997), whereas stems decompose more slowly (Emery & Perry 1996; Meyerson 2000). Because of the slow decomposition of stem material, *Phragmites* builds up a large amount of refractory (decomposition-resistant) material. This is thought to impoverish *Phragmites*-dominated sites by binding nutrients in organic material and making them unavailable to other plants (Meyerson *et al*. 2000). It seems that *Phragmites* binds nutrients in its dead material and *Arundo* binds nutrients in its living material. Both species therefore contribute little to nutrient cycling as a direct result of decomposition, in these conditions. This has implications for areas where more dry material accumulates within stands of *Arundo*, for areas where *Arundo* may be burnt either accidentally or in an attempt to control its spread, and for areas where cut *Arundo* biomass is piled on site. Greater amounts of dry, burnt or piled *Arundo* biomass may enhance nutrient cycling.

5.4 Plant species composition

Plant species composition (and consequently leaf litter composition) and functional types, have important influences on decomposition (Melillo *et al.* 1982; Perreira *et al.* 1998; Conn & Dighton 2000). Zimmer (2002) found that higher diversity of plant species (providing a higher diversity of leaf litter) had faster rates of decomposition. However, Blair *et al.* (1990) found no difference between decomposition rates of single-species litter and mixed-species litter. Wardle & Lavelle (1997) found that species identity was more important than species richness or diversity to decomposition. Many invasive plants form monocultures and yet have higher rates of decomposition than indigenous plant species (Allison & Vitousek 2004). Both *Arundo* and *Phragmites* form near-monocultures (Chapter 4). Since *Arundo* and *Phragmites* are so dominant in the ecosystems where they occur, species identity is possibly more important than species diversity in terms of decomposition and nutrient cycling.

5.5 Soil nutrients and soil development

There is no evidence from this study to conclusively state that *Arundo* either depletes or enhances the soil nutrient status. Litter from invasive species usually decomposes rapidly, immediately releasing nutrients (Allison & Vitousek 2004). This has implications for soil development, since the substrate beneath invasive species is unlikely to accumulate organic matter if it decays rapidly (Allison & Vitousek 2004). High rates of decomposition in *Arundo*, as well as limited leaf litter, may reduce organic matter content of soil beneath *Arundo*.

Soil nutrients associated with *Arundo* and *Phragmites* are relatively similar (only magnesium is significantly higher in soil associated with *Arundo*). Despite the greater nutrient content in *Arundo* material, the soil nutrients are not elevated. *Arundo* may use soil nutrients more efficiently, and retain them in the living material by not dropping leaves during the winter.

Soil nutrients appear to be site-specific rather than related to the dominant plant species. The more impacted site in terms of development, pollution and other invasive species (Hout Bay) had lower soil nutrients. Nutrient-rich sites within ecosystems may promote invasions (Huenneke *et al*. 1990; Ostertag & Verville 2002), since invaders are more successful under high nutrient conditions (Halpern *et al*. 1997). *Arundo* has been present in Hout Bay for a longer time period than at Spier or Silvermine. *Arundo* may have established in Hout Bay under high nutrient conditions and over time depleted the soil of nutrients. This is mere conjecture, and there is no confirmation of this.

5.6 Fire and nutrients

Burning piled or standing *Arundo* is a fire risk under certain climatic conditions. It also provides the soil with an instant increase in nutrients for regrowth (White & Gartner 1975). Increased nutrient levels may stimulate the already enhanced growth rates of *Arundo*. Since *Arundo* burns easily, even when green (Bell 1997), increased intensity or frequency of unseasonal fires is possible. This can lead to loss of soil nutrients from the ecosystem in the long term (van Wilgen & Le Maitre 1981), since nutrients may be volatilised (nitrogen and sulphur), lost via leaching, or lost via windswept ash (Vogl 1974; De Bano & Conrad 1978; van Wyk *et al*. 1992).

5.7 Global warming

Global warming may enhance decomposition rates (Coûteaux *et al*. 1995). Carbon and nitrogen mineralisation rates would increase, making more nutrients available to plants (Coûteaux *et al*. 1995). With greater cycling of nutrients, nutrient-rich species, and those functioning best under high nutrient conditions, are likely to replace those that are adapted to nutrient-poor conditions, such as fynbos species. *Arundo* is more successful where groundwater and soil nitrogen is higher (Coffman *et al.* 2004). *Arundo* and other invasive alien species often establish and dominate under high nutrient conditions (Huenneke *et al*. 1990; Coffman *et al*. 2004).

6. LIMITATIONS

This study covered only the early phase of decomposition (Salamanca *et al*. 1998). The study was of limited duration and intensity. In order to obtain a complete picture, sampling should be undertaken over many years, and at much greater intensity. Results are based on a single replicate for the decomposition experiment, since many buried samples were lost. Results could therefore not be statistically tested for significance, and merely provide an indication of possible trends. Sample sites should have been labelled in a more permanent fashion with stakes, but since it was public land, this may have compromised the experiment by drawing too much undue attention. The best option would have been to find privately owned land on which to establish this experimental study. Decomposition could have been studied in a way that is possibly more representative of natural decomposition (Bärlocher 1997), which occurs on the plant and not necessarily in the soil. Instead of disconnecting live leaves from the plant, one could follow the decay dynamics of tagged leaves that are left attached to the shoot in their natural position (Newell & Fallon 1989). However, decaying leaves are difficult to age so comparison between species would have been difficult. Litterbags could also have been attached to the soil surface and not buried, but again, this may have drawn undue attention. Leaf litter per species could have been measured, collected and analysed.

7. ACKNOWLEDGEMENTS

I gratefully acknowledge the DST-NRF Centre of Excellence for Invasion Biology (CIB) at Stellenbosch University for funding, and the CSIR for coordinating project expenses; Drs. Richard Knight and Brian van Wilgen as research supervisors; Jenny and Henry Nelson for initial introduction to the *Arundo donax* problem in Hout Bay; Russell Main and Isaac Crowster for assistance with fieldwork; and Dr. L. Raitt for advice. Thanks to Spier Holdings Pty (Ltd) and CapeNature for permission to access study sites at Spier and Silvermine respectively.

8. REFERENCES

Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos*, **79**, 439-449.

Allison, S.D. & Vitousek, P.M. (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawaii. *Oecologia,* **141**, 612-619.

Bärlocher, F. (1997) Pitfalls of traditional techniques when studying decomposition of vascular plant remains in aquatic habitats. *Limnetica*, **13**, 1-11.

Bell, G.P. (1997) Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in southern California. *Plant invasions: studies from North America and Europe*. (eds J.H. Brock, M. Wade, P. Pyšek & D. Green), pp. 103-113. Backhuys Publishers, Leiden, The Netherlands.

Berg, B., Ekbohm, G., Johansson, M., McClaugherty, C., Rutigliano, F.A. & Virzo De Santo, A. (1996) Maximum decomposition limits of forest litter types: a synthesis. *Canadian Journal of Botany*, **74**, 659-672.

Blair, J.M., Parmelee, R.W. & Beare, M.H. (1990) Decay rates, nitrogen fluxes, and decomposer communities of single- and mixed-species foliar litter. *Ecology*, **71**, 1976-1985.

Boose, A.B. & Holt, J.S. (1999) Environmental effects on asexual reproduction in *Arundo donax*. *Weed Research*, **39**, 117-127.

Bremner, J.M. & Mulvaney, C.S. 1982. Nitrogen-total. *Methods of Soil Analysis: Part 2 Chemical and Microbial Properties*. (eds Page, A.L., Miller, R.H. & Keeney, D.R.), pp. 595-624. ASA Monograph number 9.

Chambers, R.M. (1997) Porewater chemistry associated with *Phragmites* and *Spartina* in a Connecticut tidal marsh. *Wetlands*, **17**, 360-367.

Clarke, K.R. & Warwick, R.M. (2001) *Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition*. PRIMER-E. Natural Environment Research Council, Plymouth.

Coffman, G.C., Ambrose, R.F. & Rundel, P.W. (2004) Invasion of *Arundo donax* in river ecosystems of Mediterranean climates: causes, impacts and management strategies. *Proceedings of the 10th MEDECOS Conference*, 25 April – 1 May 2004, Rhodes Island, Greece. (eds M. Arianoutsou & W. Papanastasis), pp. 1-8. Millpress Science Publishers, Rotterdam.

Coleman, D.C. & Whitman, W.B. (2005) Linking species richness, biodiversity and ecosystem function in soil systems. *Pedobiologia*, **49**, 479-497.

Conn, C. & Dighton, J. (2000) Litter quality influences on decomposition, ectomycorrhizal community structure and mycorrhizal root surface acid phosphatase activity. *Soil Biology & Biochemistry*, **32**, 489–496.

Cortez, J. (1998) Field decomposition of leaf litters: relationships between decomposition rates and soil moisture, soil temperature and earthworm activity. *Soil Biology & Biochemistry*, **30**, 783-793.

Coûteaux, M., Bottner, P. & Berg, B. (1995) Litter decomposition, climate and litter quality. *Trends in Ecology and Evolution*, **10**, 63-66.

Cronk, Q.C.B. & Fuller, J.L. (1995) *Plant invaders: the threat to natural ecosystems*. Chapman & Hall, London.

D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63-87.

Day, J.A. (1983) Mineral nutrients in Mediterranean ecosystems. *South African National Scientific Programmes Report No. 71*. (ed J. Day). Report on the workshop meeting of the Third International Conference on Mediterranean-Type Ecosystems, Hermanus, 1980. CSIR, Pretoria.

De Bano, L.F. & Conrad, C.E. (1978) The effect of fire on nutrients in a chaparral ecosystem. *Ecology*, **59**, 487-497.

Decruyenaere, J.G. (2000) Seasonal and site effects on the vegetative reproduction and demography of *Arundo donax* L. (Poaceae). MSc thesis, University of California.

di Castri, F. (1991) An ecological overview of the five regions with a Mediterranean climate. *Biogeography of Mediterranean Invasions*. (eds R.H. Groves & F. di Castri), pp 3-16. Cambridge University Press, Cambridge.

Dudley, T.L. (2000) *Arundo donax*. *Invasive plants of California's wildlands*. (eds C.C. Bossard, J.M. Randall & M.C. Hoshovsky), pp. 53-58. University of California Press, Berkeley.

Dukes, J.S. & Mooney, H.A. (2004) Disruption of ecosystem processes in western North America by invasive species. *Revista Chilena de Historia Natural*, **77**, 411-437.

Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503-523.

Ehrenfeld, J.G., Kourtev, P. & Haung, W. (2001) Changes in soil functions following invasions of exotic understorey plants in deciduous forests. *Ecological Applications*, **11**, 1287-1300.

Ekstam, B. (1995) Ramet size equalisation in a clonal plant, *Phragmites australis*. *Oecologia*, **104**, 440-446.

Else, J.A. (1996) Post-flood establishment of native woody species and an exotic, *Arundo donax*, in a southern Californian riparian system. MSc thesis, San Diego State University.

Emery, S.L & Perry, J.A. (1996) Decomposition rates and phosphorus concentrations of purple loosestrife (*Lythrum salicaria*) and cattail (*Typha* spp.) in fourteen Minnesota wetlands. *Hydrobiologia*, **323**, 129–38.

Facelli, J.M. & Pickett, S.T.A. (1991) Plant litter: its dynamics and effects on plant community structure. *Botanical Review*, **57**, 1-32.

Franklin, J.F., Cromack, K., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F. & Juday, G. (1981). *Ecological characteristics of old-growth Douglas-fir forests*. USDA Forest Service Gen. Tech. Report PNW-118.

Halpern, C.B., Antos, J.A., Geyer, M.A. & Olson, A.M. (1997) Species replacement during early secondary succession: the abrupt decline of a winter annual. *Ecology*, **78**, 621-631.

Haslam, S.M. (1965) Ecological studies in the Breck fens, I. Vegetation in relation to habitat. *Journal of Ecology*, **53**, 599-619.

Herrera, A.M. & Dudley, T.L. (2003) Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. *Biological Invasions*, **5**, 167-177.

Hobbie, S.E. (1992) Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution*, **7**, 336-339.

Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, **6**, 324-337.

Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A. & Vitousek, P.M. (1990) Effects of soil resources on plant invasion and community structure in Californian [USA] serpentine grassland. *Ecology*, **71**, 478-491.

Iverson, M. (1993) The impact of *Arundo donax* on water resources. Proceedings of the *Arundo donax* workshop, 19 November 1993, Ontario, Canada. (eds N.E. Jackson, P. Frandsen & S. Duthoit). California Exotic Pest Plant Council, Riverside.

Johansson M., Berg, B. & Meentemeyer, V. (1995) Litter mass-loss rates in late stages of decomposition in a climatic transect of pine forests: long-term decomposition in Scots pine forest. *Canadian Journal of Botany*, **73**, 1509-1521.

Jones, C.G., Lawton, J.H. & Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**, 1946-1957.

Knops, J.M.H., Bradley, K.L. & Wedin, D.A. (2002) Mechanisms of plant species impacts on ecosystem nitrogen cycling. *Ecology Letters*, **5**, 454–466.

Kremen, C. (2005) Managing ecosystem service: what do we need to know about their ecology? *Ecology Letters*, **8**, 468-479.

Lavelle, P., Blanchart, E., Anges, M., Martin, S., Spain, A., Toutain, F., Barois, I. & Schaefer, R. (1996) A hierarchical model for decomposition in terrestrial ecosystems: application to soils in the humid tropics. *Biotropica*, **24**, 130-150.

Levine, J.M., Brewer, J.S. & Bertness, M.D. (1998) Nutrients, competition and plant zonation in a New England salt marsh. *Journal of Ecology*, **86**, 285-292.

Loranger, G., Ponge, J.F., Imbert, D. & Lavelle, P. (2002) Leaf litter decomposition in two semi-evergreen tropical forests: influence of litter quality. *Biology and Fertility of Soils*, **35**, 247-252.

Low, A.B. (1983) Phytomass and major nutrient pools in an 11 year post-fire coastal fynbos community. *South African Journal of Botany*, **2**, 98-104.

Macdonald, I.A.W., Loope, L., Usher, M. & Hamman, O. (1989) Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. *Biological Invasions: a global perspective*. (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek & M. Williamson), pp. 215-255. John Wiley & Sons, Chichester.

Mack, M.C. & D'Antonio, C.M. (2003). The effects of exotic grasses on litter decomposition in a Hawaiian woodland: the importance of indirect effects. *Ecosystems*, **6**, 723-738.

Mackenzie, A. (2004) Giant Reed. *The Weed Workers' Handbook*. (eds C. Harrington & A. Hayes), pp. 92-93. The Watershed Project and California Invasive Plant Council, California.

Marks, M., Lapin, B. & Randall, J. (1994) *Phragmites australis* (*P. communis*): threats, management and monitoring. *Natural Areas Journal*, **14**, 285–294.

Marschner, H. 2002. *Mineral nutrition of higher plants*, 2nd edn. Academic Press, New York.

Melillo, J.M., Aber, J.B. & Muratore, J.F. (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, **63**, 621–626.

Meyerson, L.A. (2000) Ecosystem-level effects of invasive species: a *Phragmites* case study in two freshwater tidal marsh ecosystems on the Connecticut River. PhD thesis, Yale University.

Meyerson, L.A., Saltonstall, K., Windham, L., Kiviat, E. & Findlay, S. (2000) A comparison of *Phragmites australis* in freshwater and brackish marsh environments in North America. *Wetlands Ecology and Management*, **8**, 89-103.

Milton, S.J. (2004) Grasses as invasive alien plants in South Africa. *South African Journal of Science*, **100**, 69-75.

Musil, C.F. & Midgely, G.F. (1990) The relative impact of invasive Australian acacias fire and season on the soil chemistry status of a sand plant lowland fynbos community. *South African Journal of Botany*, **56,** 419-427.

Newell, S.Y. & Fallon, R.D. (1989) Litterbags, leaftags, and decay of nonabscised intertidal leaves. *Canadian Journal of Botany*, **67**, 2324-2327.

Ostertag, R. & Verville, J.H. (2002) Fertilization with nitrogen and phosphorous increases abundance of non-native species in Hawaiian montane forests. *Plant Ecology*, **162**, 77-90.

Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**, 355-364.

Pearcy, R.W., Berry, J.A. & Bartholomew, B. (1974) Field photosynthetic performance and leaf temperatures of *Phragmites communis* under summer conditions in Death Valley, California. *Photosynthetica*, **8**, 104-108.

Perdue, R.E. (1958) *Arundo donax* – source of musical reeds and industrial cellulose. *Economic Botany*, **12**, 368-404.

Perreira, A.P., Graca, M.A.S. & Molles, M. (1998) Leaf litter decomposition in relation to litter physio-chemical properties, fungal biomass, arthropod colonization, and geographical origin of plant species. *Pedobiologia*, **42**, 316-327.

Rejmánek, M. (1989) Invasibility of plant communities. *Biological Invasions: a global perspective.* (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek & M. Williamson), pp. 369-388. John Wiley & Sons, Chichester.

Renvoize, S.A. (1980) The sub-family Arundinoideae and its position in relation to a general classification of the Gramineae. *Kew Bulletin*, **36**, 85-102.

Richardson, D.M., Bond, W.J., Dean. W.R.J., Higgins, S.I., Midgley, G.F., Milton, S.J., Powrie, L.W., Rutherford, M.C., Samways, M.J. & Schulze, R.E. (2000). Invasive alien organisms and global change: a South African perspective. *Invasive species in a changing world*. (eds H.A. Mooney & R.J. Hobbs), pp. 303-349. Island Press, Washington, D.C.

Roem, W.J. & Berendse, F. (2000) Soil acidity and nutrient supply ratio as possible factors determining changes in plant species diversity in grassland and heathland communities. *Biological Conservation*, **92**, 151-161.

Rossa, B., Tuffers, A.V., Naidoo, G. & von Willert, D.J. (1998) *Arundo donax* L. (Poaceae) – a C_3 species with unusually high photosynthetic capacity. *Botanica Acta*, **111**, 216-221.

Rundel, P.W. (1983) Impact of fire on nutrient cycles in Mediterranean-type ecosystems with reference to chapparal. *Mediterranean-Type Ecosystems: The Role of Nutrients* (eds F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis), pp. 192-207. Springer-Verlag, Berlin.

Salamanca, E.F., Kaneko, N. & Katagiri, S. (1998) Effects of leaf litter mixtures on the decomposition of *Quercus serrata* and *Pinus densiflora* using field and laboratory microcosm methods. *Ecological Engineering*, **10**, 53–73.

Schädler, M. & Brandl, R. (2005) Do invertebrate decomposers affect the disappearance rate of litter mixtures? *Soil Biology & Biochemistry*, **37**, 329-337.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21-32.

Spencer, D.F., Ksander, G.G. & Whitehand, L.C. (2005) Spatial and temporal variation in RGR and leaf quality of a clonal riparian plant: *Arundo donax*. *Aquatic Botany*, **81**, 27-36.

Standish, R.J., Williams, P.A., Robertson, A.W., Scott, N.A. & Hedderley, D.I. (2004) Invasion by a perennial herb increases decomposition rate and alters nutrient availability in warm temperate lowland forest remnants. *Biological Invasions*, **6**, 71-81.

Stock, W.D. & Lewis, O.A.M. (1986) Soil nitrogen and the role of fire as a mineralizing agent in a South African coastal fynbos ecosystem. *Journal of Ecology*, **74**, 317-328.

Swift, M.J., Heal, O.W. & Anderson, J.M. (1979) *Decomposition in terrestrial ecosystems*. Studies in Ecology 5. Blackwell, Oxford.

Tanner, E.V.J. (1981) The decomposition of leaf litter in Jamaican Montane rain forests. *Journal of Ecology*, **69**, 263-275.

Thompson, J., Brokaw, N., Zimmerman, J.K., Waide, R.B., Everham III, E.M., Lodge, D.J., Taylor, C.M., García-Montiel, D. & Fluet, M. (2002) Land use history, environment, and tree composition in a tropical forest. *Ecological Applications*, **12**, 1344-1363.

Trofymow, J.A., Moore, T.R., Titus, B., Prescott, C., Morrison, I., Siltanen, M., Smith, S., Fyles, J., Wein, R., Camiré, C., Duschene, L., Kozak, L., Kranabetter, M. & Visser, S. (2002) Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. *Canadian Journal of Forest Research*, **32**, 789-804.

van Wilgen, B.W. & Le Maitre, D.C. (1981) Preliminary estimates of nutrient levels in fynbos vegetation and the role of fire in nutrient cycling. *South African Forestry Journal*, **119**, 24-28.

van Wyk, D.B, Lesch, W. & Stock, W.D. (1992) Fire and Catchment Chemical Budgets. *Fire in South African mountain fynbos. Ecosystem, community and species response at Swartboskloof.* (eds B.W. van Wilgen, D.M. Richardson, F.J. Kruger & H.J. van Hensbergen), pp. 240-257. Ecological Studies 93. Springer-Verlag, Berlin.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dumbois, D. & Matson, P.A. (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science*, **238**, 802-804.

Vogl, R.J. (1974) Effects of fire on grasslands. *Fire and Ecosystems*. (eds T.T. Koslowski & C.E. Ahlgren.), pp. 139-194. Academic Press, New York.

Walker, L.R. & Smith, S.D. (1997) Impacts of invasive plants on community and ecosystem properties. *Assessment and management of plant invasions*. (eds J.O. Luken & J. Thierret), pp. 69-86. Springer-Verlag, New York.

Wardle, D.A. & Lavelle, P. (1997) Linkages between soil biota, plant litter quality and decomposition. *Driven by nature – plant litter quality and decomposition*. (eds G. Cadish & K.E. Giller), pp. 107-124. CAB International, Wallingford.

Welsh, S.L., Atwood, N.D., Goodrich, S. & Higgins, L.C. (eds.) (1987) A Utah flora. *Great Basin Naturalist Memoirs* 9. Brigham Young University, Provo.

White, E.M., & Gartner, F.R. (1975) Immediate effects of prairie fire on the soil nitrate, ammonium, available phosphorous and total N content. *Proceedings of the South Dakota Academy of Science*, **54**, 188-193.

Witkowski, E.T.F. (1991) Growth and competition between seedlings of *Protea repens* (L.) L. and the alien invasive, *Acacia saligna* (Labill.) Wendl. in relation to nutrient availability. *Functional Ecology*, **5**, 101-110.

Wrubelski, D.A., Murkin, H.R., van der Valk, A.G. & Nelson, J.W. (1997) Decomposition of emergent macrophyte roots and rhizomes in a northern prairie marsh. *Aquatic Botany*, **58**, 121-134.

Zimmer, M. (2002) Is decomposition of woodland leaf litter influenced by its species richness? *Soil Biology & Biochemistry*, **34**, 277-284.

Zimmerman, P. (1999) Rates of transpiration by a native willow, *Salix exigua*, and by a non-native invasive, *Arundo donax*, in a riparian corridor of northern California. *Proceedings of the California Exotic Pest Plant Council*, October 1999, Sacramento, California.

CHAPTER 6

SYNTHESIS

1. BRIEF SUMMARY: INVASIVE ALIEN SPECIES

Maintenance of biodiversity is important for the protection of ecosystems against future losses of functionally important components (Richardson *et al*. 1995). Since invasive alien species are the second highest threat to biodiversity (after direct habitat destruction), they are cause for concern. Invasive alien species affect all components of the ecosystems, including functions (Mack *et al*. 2001; Ehrenfeld 2003), structure (Brown & Gurevitch 2004) and composition (Gratton & Denno 2005). Invasive alien species out-compete indigenous species for resources and space (Macdonald *et al*. 1989). They change vegetation and soil structure, by dominating, and by altering soil nutrient concentrations (Cronk & Fuller 1995). Ecosystem functions affected by invasive alien species include decomposition, nutrient cycling, soil development, and fire and water regimes (D'Antonio & Vitousek 1992; Walker & Smith 1997; Standish *et al*. 2004).

Arundo is poorly researched in South Africa, and hence, poorly understood in terms of its ecology and impacts. Most of the data available on *Arundo* is a result of studies undertaken in the USA. In the USA, *Arundo* has been studied more intensely, and has been labelled a high priority species in terms of its actual and potential ecological and economic costs. It is a highly productive species, producing up to 20 tons of biomass per hectare in the USA (Perdue 1958). It threatens indigenous plant and animal species diversity by dominating, and consequently displacing indigenous plant species (Bell 1997). It increases fire hazards in riparian areas, which are sometimes in urban / rural fringes, placing human health and safety at risk. There are associated increases in flood damage because biomass is often washed downstream, against bridges or culverts during storms, causing blockages and damaging infrastructure (Coffman *et al*. 2004). *Arundo* increases bank erosion and instream sedimentation, alters soil nutrient status, and uses three times more water than indigenous species (Iverson 1993). It is exceptionally difficult to eradicate and is mostly resistant to herbicide treatment (unless used in conjunction with other control methods). Most of its impacts are due to its large height and biomass, and rapid growth rate (Milton 2004).

2. RESEARCH FINDINGS

This study investigated potential control methods, as well as impacts of an invasive alien plant, *Arundo donax*, on aspects of biodiversity in the Western Cape of South Africa. For simplicity, I used Noss (1990)'s definition of biodiversity: briefly, that it consists of three major attributes, composition, structure and function, operating at different levels. Results of the study are discussed below in terms of new information generated by this study.

2.1 Control

Herbicide reduced the height, growth rate and density of *Arundo* stands. Over time, density increased to levels surpassing that of the control. Cutting alone is not a viable option since it increases the density of *Arundo* stands with each cut. Local application of herbicide is effective to some extent but not sufficient to control *Arundo* in the long term.

2.2 Composition

I investigated plant species composition and richness of *Arundo*-dominated communities, and compared the results with those from communities dominated by indigenous *Phragmites australis* and *Typha capensis*. This is the first study to look at plant species diversity beneath *Arundo* in South Africa. It is also the first to look at impacts of invasion by alien species on indigenous plant species diversity and richness in riparian or wetland areas in South Africa. *Arundo* had lower cover within communities than did the indigenous species, contrary to expectations. *Arundo* is well-known in the USA to be a 'monoculture' (Bell 1997; Coffman *et al*. 2004). *Arundo*-dominated communities had higher species richness, and a greater number of alien species co-occurring with it than did communities dominated by indigenous species. Gaffney & Gledhill (2003) also found increased numbers of alien species co-occurring with *Arundo*.

2.3 Structure

I compared height and biomass of *Arundo* stands with that of *Phragmites*. I also investigated vegetation nutrient concentrations and associated soil nutrient concentrations of *Arundo* and *Phragmites*. Biomass and nutrient concentrations affect the ecosystem functions of fire behaviour and nutrient cycling.

2.3.1 Height

On average, stem heights of *Arundo* and *Phragmites* are 4.03 m and 2.81 m, respectively.

2.3.2 Biomass

Arundo stands produce between 37 and 47 tons / ha biomass (total above-ground material). This biomass consists largely of live material (76 to 92 % live material). Moisture content of *Arundo* ranges from 30 to 380 %. *Phragmites* stands produces approximately 16 tons / ha above-ground biomass. *Phragmites* has an even distribution of live and dead material within its biomass (50 %). *Arundo* had a lower fuel load than *Phragmites* despite higher biomass, because of the small amount of dry material in its stands. Moisture content varied from 30 to 250 %. Invasion by *Arundo* will increase biomass by 450 %.

2.3.3 Vegetation nutrient pools

Arundo has higher nutrient pools in vegetation than *Phragmites*, because of its elevated nutrient concentrations and greater biomass.

2.3.4 Soil nutrient concentrations

Soil nutrient concentrations associated with *Arundo* and *Phragmites* are similar. This implies that neither *Arundo* nor *Phragmites* contribute more significantly than the other towards nutrient cycling via decomposition. Neither species appears to be enhancing the nutrient status of the soil.

2.4 Function

Impacts on the ecosystem functions of fire behaviour and nutrient cycling are derived from impacts on community composition and vegetative structure. Fire behaviour is dependent on biomass for fuel properties, and nutrient cycling is affected by biomass and nutrient concentrations of vegetation.

2.4.1 Fire behaviour

Fire behaviour was estimated using a fire behaviour prediction model (BehavePlus). The model uses biomass values and specifically relies on percentage values of dead material, which determine the fuel load. Fire intensity and rates of spread are estimated to be higher in *Phragmites* than in *Arundo*. Estimated maximum rate of spread of fire in *Arundo* is 1.8 m min^{-1} at wind speeds of 10 to 50 km h^{-1}, and 86.3 m min^{-1} at wind speeds of 30 to 50 km h^{-1} in

Phragmites. Estimated maximum fireline intensity in *Arundo* is 71.9 kW m^{-1} at wind speeds of 10 to 50 km h^{-1}, and 12 700 kW m^{-1} at wind speed of 30 km h^{-1} in *Phragmites*. *Arundo* may reduce fire intensity and rates of spread in the ecosystems it invades in the Western Cape. *Arundo* is likely to have greater fire potential (danger) in drier or colder regions, where more dry material accumulates within stands. *Arundo* possibly presents an unseasonal fire hazard, since plant moisture is lowest and estimated fire behaviour highest during winter months.

2.4.2 Nutrient cycling

Arundo has higher decomposition rates than *Phragmites*. Leaf material decomposes faster than stems material for both *Arundo* and *Phragmites*. *Arundo* has great potential to alter soil nutrient cycling by increasing soil nutrients as a result of its rapid rate of decomposition. In these climatic conditions, where little dry material accumulates, *Arundo* is unlikely to increase soil nutrients, but where biomass dried out and accumulates, nutrient cycling will be enhanced. Nutrients are stored in the living material of *Arundo*, and in the dead, refractory (decomposition-resistant) material of *Phragmites*.

3. LIMITATIONS

3.1 Availability of suitable sites for study

The lack of uninvaded study sites in similar habitats to those invaded by *Arundo*, resulted in a comparison being made of indigenous species and *Arundo*, instead of the initial intention of comparing invaded and uninvaded riparian systems. The lack of study sites can be attributed to most downstream sites being invaded by at least one alien species, or being highly impacted on by agriculture or development. Other potential study sites were on private land, which I was unable to gain access to, or were isolated and unsafe for unaccompanied research.

It is difficult to separate whether species diversity and soil nutrients are related to *Arundo* invasion, or to the many disturbances at the selected study sites. Nonetheless, species diversity and soil nutrient data has been generated for sites dominated indigenous and alien plant species in riparian areas of the Western Cape.

3.2 Unanticipated practical problems

Loss of litterbags (decomposition experiment) limited the results to one replicate per analysis. Results are therefore not conclusive, but do provide indications of possible and probable trends in terms of decomposition and nutrient cycling of *Arundo* and *Phragmites* in the Western Cape.

The loss of plastic sheeting (tarpaulin) hampered the project to some extent but this is a reality when working within windy coastal areas or near impoverished communities. Tarping is not a suitable or practical method of control in these areas.

3.3 Fire behaviour prediction model

The fire behaviour model BehavePlus is limited and unsuitable for predicting fire behaviour in *Arundo*. It does not take into account the full height (or fuel depth) of *Arundo*, which could complicate fuel-packing densities. It does also not simulate fire behaviour under extreme weather conditions very well. Fire behaviour models in general do not take into account physiological aspects of the vegetation being modelled, such as volatile oils present in plant material.

4. MANAGEMENT IMPLICATIONS

4.1 Control

Cutting alone is not an effective solution for control or management of *Arundo*. Herbicide must be used to some extent. The effects of herbicide are small when compared to the long-term environmental damage (and subsequent economic costs) of *Arundo* (Bell 1997; Monheit 2003). Burning is also not a viable control option, since (a) *Arundo* is highly flammable, posing a fire risk, and (b) burning piled or standing *Arundo* (or any high-nutrient alien species) provides the soil with an instant increase in nutrient levels for regrowth (White & Gartner 1975). Since *Arundo* burns easily, even when green (Bell 1997), increased intensity or frequency of unseasonal fires is possible, and can lead to loss of soil nutrients from the ecosystem in the long term (van Wilgen & Le Maitre 1981), since nutrients may be volatilised (nitrogen and sulphur), lost via leaching, or lost via windswept ash (Vogl 1974; De Bano & Conrad 1978; van Wyk *et al*. 1992). Alternative methods to control *Arundo* in South Africa must be researched or extrapolated from the USA.

4.2 Species diversity

Reduced indigenous species diversity beneath *Arundo*, confirms the need control *Arundo* and prevent its further establishment and spread. If invasive alien species such as *Arundo* are not controlled, then we are allowing the establishment and spread of a species that we know has negative ecological impacts, as well as allowing the establishment and spread of other alien species possibly facilitated by *Arundo*. High alien species richness further complicates the matter of control and management, and the greater number of alien species associated with *Arundo* implies greater and possibly synergistic impacts.

4.3 Fire behaviour

Fire behaviour of *Arundo* is context- and site-specific. Invasion by *Arundo* will alter fuel properties and complicate fire management in invaded areas. Wildfires could become more difficult to control, especially under conditions of extreme fire weather. There are likely to be unseasonal fire risks. Prescribed burning, as a potential control method, will be made more difficult. *Arundo* stands in different climatic regions need to be considered as independent, since climate (temperature and rainfall) has such as great influence on fuel loads of *Arundo*. Increased fuel loads (associated with colder and drier areas) will increase fire intensity and rates of spread. Fire behaviour models have limitations and should not be valued over practical experience and common sense.

5. RESEARCH NEEDS

Although it is convenient to extrapolate impacts, ecology and behaviour of species between areas (justifed on the basis of climatic and habitat similarity), some species such as *Arundo* have context-specific impacts, ecology and behaviour. Although both the Western Cape and California have Mediterranean-type climates, there are differences in morphology and behaviour of *Arundo*. Research needs to be within the context of its application.

There are a number of unanswered questions concerning the ecology and management of *Arundo*. They are listed below, starting with the most important.

1. **Water use**. South Africa is a water-scarce country. Public awareness of major alien plant species is largely a result of campaigns based on their water use. *Arundo* has already been listed as a large user of water in both the USA and South Africa. The results of such an experiment to determine water use might increase public awareness (e.g. landowners, conservation officers, and the general public) of *Arundo*, as well as increase possible funding for research into control and management of this species. If *Arundo* is relegated as less important following such as study, then more focus can be given to alien species that are large consumers of water.

2. **Fire behaviour**. *Arundo* is hardly known in South Africa as creating potential fire hazards, yet in California it is widely known and even notorious, similar to *Hakea* and *Acacia* species in South Africa. Biomass and fuel loads of *Arundo* should be investigated around the country, since climate has a large impact on fuel loads of this species. Fire behaviour models should be compared and tested against practical knowledge. It is important to determine whether this species is indeed creating greater fire hazards, or whether it has the potential to under certain conditions.

3. **Social aspects**. Many people make use of *Arundo* products, some without being aware of it. Impoverished households can support themselves by using plant parts to make products such as baskets, fences, screens, frames, blinds and ceilings, among others. Cost-benefit analyses need to be undertaken to determine best methods of control or management to suit users as well as landowners and conservationists.

4. **Control and management**. Prescribed burning and cutting are the two methods most used in South Africa to control *Arundo*. Burning is dangerous and difficult, and *Arundo* often grows back within days. Cutting increases density over time. A more effective control method needs to be implemented almost immediately to prevent the spread of this species. Biological control is also an avenue to explore, and collaboration with international experts is essential. A likely candidate for biological control is the stem-boring wasp *Tetramesa romana*, which is being investigated in California (T. Dudley & A. Lambert pers. comm.) and has possibly been seen Hout Bay, Western Cape.

5. **Growth and spread rate.** It may be interesting to determine how *Arundo* has spread over the last few decades. Aerial photos and interviews with relevant landowners could be helpful in determining this. We know that *Arundo* has a very high growth rate and is very productive. It is important also to determine how *Arundo* will react to climate change. Current thoughts and predictions are that *Arundo* will thrive better under conditions of climate change, and that global warming and increased nitrogen in the soil will assist in spreading *Arundo* further.

6. **Impacts on invertebrate and aquatic fauna.** *Arundo* is mainly a riparian invader, where it reduces plant species diversity and richness. It has impacts on aerial, terrestrial and aquatic invertebrates in the USA. Little is known about its impacts on those invertebrates in South African ecosystems.

CHAPTER 7

REFERENCES

Ahmed, M., Jabbar, A. & Samad, K. (1977) Ecology and behavior of *Zyginidia guyumi* (Typhlocyloinae: Cicadellidae) in Pakistan. *Pakistan Journal of Zoology,* **9**, 79-85.

Anon. (2002) *The Working for Water Annual Reports for the years 1996/97 to 2001/02*. Department of Water Affairs and Forestry, Cape Town.

Bardgett, R.D. (2002) Causes and consequences of biological diversity in soil. *Zoology*, **105**, 367-374.

Bell, C.E. (1996) *Saltcedar: a non-native invasive plant in the western United States*. University of California Cooperative Extension Service. University of California, Berkeley.

Bell, G.P. (1997) Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in southern California. *Plant invasions: studies from North America and Europe*. (eds J.H. Brock, M. Wade, P. Pyšek & D. Green), pp. 103-113. Backhuys Publishers, Leiden, The Netherlands.

Boose, A.B. & Holt, J.S. (1999) Environmental effects on asexual reproduction in *Arundo donax*. *Weed Research*, **39**, 117-127.

Braithwaite, R.W., Lonsdale, W.M. & Estbergs, J.A. (1989) Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. *Biological Conservation*, **48**, 189-210.

Breytenbach, G.J. (1986) Impacts of alien organisms on terrestrial communities with emphasis on communities of the south-western cape. *The ecology and management of biological invasions in Southern Africa.* (eds I.A.W MacDonald, F.J. Kruger & A.A. Ferrar), pp. 229-238. Oxford University Press, Cape Town.

Bromilow, C. (2001) *Problem plants of South Africa – a guide to identification and control of more than 300 invasive plants and other weeds.* Briza Publications, Pretoria.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. (2004) Effects of invasive alien plants on fire regimes. *BioScience*, **54**, 677-688.

Brown, K.A. & Gurevitch, J. (2004) Long-term impacts of logging on forest diversity in Madagascar. *Proceedings of the National Academy of Sciences*, **101**, 6045-6049.

Chadwick & Associates (1992) *Santa Ana River use attainability analysis. Volume 2: Aquatic biology, habitat and toxicity analysis*. Santa Ana Watershed Project Authority, Riverside.

Chiej, R. (1984) *Encyclopaedia of Medicinal Plants*. MacDonald, London.

Christou, M. (2001) Giant Reed in Europe. *Proceedings of the First World Conference on Biomass for Energy and Industry*, Sevilla, Spain, 5–9 June 2000. (eds K. Beenackers, A.A.C.M. Helm, P. Grassi & A. Chiaramonti), pp. 2092–2094. James & James (Science Publishers) Ltd., London.

Cilliers, C.D., Esler, K.J. & Boucher, C. (2004) Effects of alien plant management and fire on soil seed banks and regeneration in the Cape Peninsula National Park, South Africa. *South African Journal of Botany*, **70**, 705-712.

Coffman, G.C., Ambrose, R.F. & Rundel, P.W. (2004) Invasion of *Arundo donax* in river ecosystems of Mediterranean climates: causes, impacts and management strategies. *Proceedings of the 10th MEDECOS Conference*, 25 April – 1 May 2004, Rhodes Island, Greece. (eds M. Arianoutsou & W. Papanastasis), pp. 1-8. Millpress Science Publishers, Rotterdam.

Cory, J.S. & Myers, J.H. (2000) Direct and indirect ecological effects of biological control. *Trends in Ecology and Evolution*, **15**, 137-139.

Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K. & Arianoutsou, M. (1996) Plant diversity in Mediterranean-climate regions. *Trends in Ecology and Evolution*, **11**, 362-366.

Coyle, J. & Roberts, N.C. (1975) *A field guide to the common and interesting plants of Baja California*. Natural History Publishing Co., California.

Crawley, M.J. (1987) What makes a community invasible? *Colonisation, Succession and Stability*. (eds M.J. Crawley, P.J. Edwards and A.J. Gray), pp. 429-454. Blackwell Scientific, Oxford.

Cronk, Q.C.B. & Fuller, J.L. (1995) *Plant invaders: the threat to natural ecosystems*. Chapman & Hall, London.

Culvenor, C.C.J. (1956) The alkaloids of *Echium plantagineum* L. Echiumine and Echimidine. *Australian Journal of Chemistry*, **9**, 512–520.

Cummins, G.B. (1971) *The rust fungi of Cereals, Grasses and Bamboos*. Springer-Verlag, New York.

D'Antonio, C.M. (2000) Fire, plant invasions, and global changes. *Invasive Species in a Changing World*. (H.A. Mooney & R.J. Hobbs), pp. 65-93. Island Press, Washington, D.C.

D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63-87.

D'Antonio, C.M., Dudley, T.L. & Mack, M. (1999) Disturbance and biological invasions: direct effects and feedbacks. *Ecosystems of Disturbed Ground*. (ed L. Walker), pp. 143-452. Elsevier, Amsterdam.

Daar, S. (1983) Using goats for brush control. *The IPM Practitioneer*, **5**, 4-6.

De Bano, L.F. & Conrad, C.E. (1978) The effect of fire on nutrients in a chaparral ecosystem. *Ecology*, **59**, 487-497.

Decruyenaere, J.G. & Holt, J.S. (2001) Seasonality of clonal propagation in giant reed. *Weed Science*, **49**, 760-767.

di Castri, F. (1991) An ecological overview of the five regions with a Mediterranean climate. *Biogeography of Mediterranean Invasions*. (eds R.H. Groves & F. di Castri), pp 3-16. Cambridge University Press, Cambridge.

Douce, R.S. (1993) The biological pollution of *Arundo donax* in river estuaries and beaches. *Proceedings of the* Arundo donax *workshop*, 19 November 1993, Ontario, Canada. (eds N.E. Jackson, P. Frandsen & S. Duthoit). California Exotic Pest Plant Council, Riverside.

Dudley, T.L. (2000) *Arundo donax*. *Invasive plants of California's wildlands*. (eds C.C. Bossard, J.M. Randall & M.C. Hoshovsky), pp. 53-58. University of California Press, Berkeley.

Dudley, T.L. & Collins, B. (1995) *Biological invasions in California wetlands: the impacts and control of non-indigenous species in natural areas*. Pacific Institute for Studies in Development, Environment and Security, Oakland.

Duke, J.A. (1983) Handbook of Energy Crops. Unpublished. Available http://www.hort.purdue.edu/newcrop/. Accessed 22/08/2006.

Duke, J.A. & Wain, K.K. (1981) *Medicinal plants of the world*. Computer index with more than 85,000 entries and three volumes.

Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, **6**, 503-523.

Ehrlich, P.R. & Ehrlich, A.H. (1992) The value of biodiversity. *Ambio*, **21**, 219-226.

Eiswerth, M.E. & Johnson, W.S. (2002) Managing non-indigenous invasive species: insights from dynamic analysis. *Environmental and Resource Economics*, **23**, 319-342.

Elmore, C.L. (1990) Use of solarization for weed control. *Soil Solarization*. (eds J.E. DeVay, J.J. Stapleton & C.L. Elmore), pp. 61-72. United Nations, Rome.

Else, J.A. (1996) Post-flood establishment of native woody species and an exotic, *Arundo donax*, in a southern Californian riparian system. MSc thesis, San Diego State University.

Enright, W.D. (2000) The effect of terrestrial invasive alien plants on water scarcity in South Africa. *Physics and Chemistry of the Earth (B)*, **25**, 237-242.

Evans R.C., Tingey, D.T., Gumpertz, M.L. & Burns, W.F. (1982) Estimates of isoprene and monoterpene emission rates in plants. *Botanical Gazette*, **143**, 304-310.

Ewel, J.J. (1986) Invasibility: lessons from South Florida. *Ecology of biological invasions of North America and Hawaii*. (eds H.A. Mooney & J.A. Drake), pp. 214-230. Springer-Verlag, New York.

Fornell, T.C. (1990) Widespread adventive plants in Catalonia. *Biological Invasions in Europe and the Mediterranean basin.* (eds F. di Castri, A.J. Hansen & M. Debussche), pp. 85-104. Kluwer Academic Publishers, Boston.

Frandsen, P. & Jackson, N. (1993) Impact of *Arundo donax* on flood control and endangered species. *Proceedings of the* Arundo donax *workshop*, 19 November 1993, Ontario, Canada. (eds N.E. Jackson, P. Frandsen & S. Duthoit). California Exotic Pest Plant Council, Riverside.

Franklin, J.F., Cromack, K., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F. & Juday, G. (1981). *Ecological characteristics of old-growth Douglas-fir forests*. USDA Forest Service Gen. Tech. Report PNW-118.

Gaffney, K.A. & Gledhill, K. (2003) Influence of giant reed on floodplain riparian plant communities: implications for invasive plant control and habitat restoration at the watershed level. *Proceedings of the Riparian Habitat and Floodplains Conference*, 12-25 March 2001, Sacramento, USA. (ed P.M. Faber). University of California Press, Sacramento.

Giesy, J.P., Dobson, S. & Solomon, K.R. (2000) Ecotoxicological risk assessment for Roundup herbicide. *Reviews of Environmental Contamination & Toxicology*, **167**, 35-120.

Gordon, A.J. (1999) A review of established and new insect agents for the biological control of *Hakea sericea* Schrader (Proteaceae) in South Africa. Biological control of weeds in South Africa (1990-1998). (eds T. Olckers & M.P.Hill). *African Entomology Memoir*, **1**, 35-43.

Gratton, C. & Denno, R.F. (2005) Restoration of arthropod assemblages in a *Spartina* salt marsh following removal of the invasive plant *Phragmites australis*. *Restoration Ecology*, 13, 358-372.

Grossinger, R., Alexander, J., Cohen, A.N. & Collins, J.N. (1998) *Introduced tidal marsh plants in the San Francisco Estuary. Regional distribution and priorities for control.* San Francisco Estuary Institute, CALFED Category III Steering Committee. California

Hafliger, E. & Scholz, H. (1981) Grass Weeds 2. Documenta, Ciba-Geigy Ltd., Basle, Switzerland.

Hansen, R.A. (2000) Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology*, 81, 1120-1132.

Hejda, M. & Pysek, P. (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biological Conservation*, **132**, 143-152.

Henderson, L. (1998) South African Plant Invaders Atlas (SAPIA). *Applied Plant Sciences*, 12, 31-32.

Henderson, L. (2001) *Alien Weeds and Invasive Plants. A complete guide to declared weeds and invaders in South Africa*. Plant Protection Research Institute Handbook No. 12. Agricultural Research Council, Pretoria.

Herrera, A.M. & Dudley, T.L. (2003) Reduction of riparian arthropod abundance and diversity as a consequence of giant reed (*Arundo donax*) invasion. *Biological Invasions*, **5**, 167-177.

Hewitt, C.N., Monson, R.K. & Fall, R. (1990) Isoprene emissions from the grass *Arundo donax* L. are not linked to photorespiration. *Plant Science*, **66**, 139-144.

Hickman, J.C. (ed.). (1993) *The Jepson manual: higher plants of California*. University of California Press, Berkeley, California.

Hobbs, R.J. (1989) The nature and effects of disturbance relative to invasions. *Biological Invasions: a global perspective.* (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek & M. Williamson), pp. 389-405. John Wiley & Sons, New York.

Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, **6**, 324-337.

Hobbs, R.J. & Humphries, S.E. (1995) An integrated approach to the ecology and management of plant invasions. *Conservation Biology*, **9**, 761 - 770.

Hobbs, R.J., Richardson, D.M. & Davis, G.W. (1995) Mediterranean-type ecosystems: opportunities and constraints for studying the function of biodiversity. *Mediterranean-type ecosystems. The function of biodiversity.* (eds G.W. Davis & D.M. Richardson). Ecological Studies 109. Springer-Verlag, Berlin.

Hoffmann, J.H., Moran, V.C. & Zimmermann, H. (1999). Integrated management of *Opuntia stricta* (Haworth) Haworth (Cactaceae) in South Africa: an enhanced role for two, renowned, insect agents. Biological control of weeds in South Africa (1990 - 1998). (eds T. Olckers & M.P. Hill). *African Entomology Memoir*, **1**, 15-20.

Holling, C.S. (1978) *Adaptive environmental assessment and management*. John Wiley & Sons, Chichester.

Holmes, P.M. & Cowling, R.M. (1997) The effects of invasion by *Acacia saligna* on the guild structure and regeneration capabilities of South African fynbos shrublands. *Journal of Applied Ecology*, **34**, 317-332.

Houlahan, J.E. & Findlay, C.S. (2004) Effect of invasive plant species on temperate wetland plant diversity. *Conservation Biology*, **18**, 1132-1138.

IUCN / SSC / ISSG (2004) Global Invasive Species database. World Conservation Union, Species Survival Commission, Invasive Species Specialist Group. Available http://www.issg.org/database/species/search.asp?st=100ss&fr=1&sts. Accessed 22/08/2006.

Iverson, M. (1993) The impact of *Arundo donax* on water resources. *Proceedings of the* Arundo donax *workshop*, 19 November 1993, Ontario, Canada. (eds N.E. Jackson, P. Frandsen & S. Duthoit). California Exotic Pest Plant Council, Riverside.

Jackson, N.E. (1993) The story of Team Arundo. *California EPPC News* (United States), **1**, 6-7.

Katan, J., Grinstein, A., Greenberger, A., Yarden, O. & DeVay, J.E. (1987) First decade (1976-1986) of soil solarization (solar heating)-A chronological bibliography. *Phytoparasitica*, **15**, 229-255.

Keeley, J.E., Lubin, D. & Fotheringham, C.J. (2003) Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications*, **13**, 1355–1374.

Kirk, A.A., Widmer, T., Campobasso, G., Carruthers, R.I. & Dudley, T. (2003) The potential contribution of natural enemies from Mediterranean Europe to the management of the invasive weed *Arundo donax* (Graminae; Arundinae) in the U.S. *Proceedings of the California Invasive Plant Council Symposium, Volume 7*. (ed C. Pirosko), pp. 62-68.

Langeland, K.A. & Burks, K.C. (1998) *Identification and biology of non-native plants in Florida's natural areas*. IFAS Distribution Centre, University of Gainesville, Florida.

Le Maitre, D.C., Versfeld, D.B. & Chapman, R.A. (2000) The impact of invading alien plants on surface water resources in South Africa: A preliminary assessment. *Water SA*, **26**, 397-408.

Lee, J.A. (1999) The calcicole-calcifuge problem revisited. *Advances in Botanical Research*, **29**, 1-30.

Loreau, M., Naeem, S. & Inchausti, P. (2002) *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford.

Lotter, W.D. & Hoffmann, J.H. 1998. An integrated management plan for the control of *Opuntia stricta* (Cactaceae) in the Kruger National Park, South Africa. *Koedoe*, **48**, 241 - 255.

Macdonald, I.A.W., Loope, L., Usher, M. & Hamman, O. (1989) Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. *Biological Invasions: a global perspective*. (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek & M. Williamson), pp. 215-255. John Wiley & Sons, Chichester.

Mack, M.C. & D'Antonio, C.M. (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution*, **13**, 195-198.

Mack, M.C., D'Antonio, C.M. & Ley, R.E. (2001) Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C_4 grasses in Hawaii. *Ecological Applications*, **11**, 1323-1335.

Mackenzie, A. (2004) Giant Reed. *The Weed Workers' Handbook*. (eds C. Harrington & A. Hayes), pp. 92-93. The Watershed Project and California Invasive Plant Council, California.

Marais, C., van Wilgen, B.W. & Stevens, D. (2004) The clearing of invasive alien plants in South Africa: a preliminary assessment of costs and progress. *South African Journal of Science*, **100**, 97-103.

Miles, D.H, Tunsuwan, K., Chittawong, V., Kokpol, U., Choudhary, M.I. & Clardy, J. (1993) Boll weevil antifeedants from *Arundo donax*. *Phytochemistry* (Oxford), **34**, 1277-1279.

Milton, S.J. (1981a). Above-ground biomass of Australian acacias in the southern Cape, South Africa. *South African Journal of Botany*, **47**, 701-716.

Milton, S.J. (1981b). Litterfall of the exotic acacias in the south-western Cape. *South African Journal of Botany*, **47**, 147-155.

Milton, S.J. (2004) Grasses as invasive alien plants in South Africa. *South African Journal of Science*, **100**, 69-75.

Moerman, D. (1998) *Native American Ethnobotany*. Timber Press, Oregon.

Monheit, S. (2003) Glyphosate-based aquatic herbicides – an overview of risk. California Department of Food & Agriculture, Integrated Pest Control. *Noxious Times*, **Summer 2002**, 5-9.

Musil, C.F. (1993) Effect of invasive Australian acacias on the regeneration, growth and nutrient chemistry of South African lowland fynbos. *Journal of Applied Ecology*, **30**, 361-371.

Myers, J.H., Simberloff, D., Kuris, A.M. & Carey, J.R. (2000) Eradication revisited: dealing with exotic species. *Trends in Ecology and Evolution*, **15**, 316-320.

Nel, J.L., Richardson, D.M., Rouget, M., Mgidi, T.N., Mdzeke, N., Le Maitre, D.C., van Wilgen, B.W., Schonegevel, L., Henderson, L. & Neser, S. (2004) A proposed classification of invasive alien plant species in South Africa: towards prioritising species and areas for management action. *South African Journal of Science*, **100**, 53-64.

Nordblom, T.L., Smyth, M.J., Swirepik, A., Sheppard, A.W. & Briese, D.T. (2002) Spatial economics of biological control: investing in new releases of insects for earlier limitation of Paterson's curse in Australia. *Agricultural Economics*, **27**, 403-424.

Noss, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology*, **4**, 355-364.

Olson, B.E. (1999) Impacts of noxious weeds on ecologic and economic systems. *Biology and management of noxious rangeland weeds* (eds R.L. Sheley & J.K. Petroff), pp. 4-18. Corvallis, Oregon State University Press.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E. & Goldwasser, L. (1999) Impact: towards a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3-9.

Parsons, W.T. & Cuthbertson, E.G. (1992) *Noxious Weeds of Australia*. Inkata Press, Melbourne.

Perdue, R.E. (1958) *Arundo donax* – source of musical reeds and industrial cellulose. *Economic Botany*, **12**, 368-404.

Perkins, T.E. & Wilson, M.V. (2005) The impacts of *Phalaris arundinacea* (reed canarygrass) invasion on wetland plant richness in the Oregon Coast Range, USA depend on beavers. *Biological Conservation*, **124**, 291-295.

Perrings, C., Williamson, M., Barbier, E., Delfino, D., Dalmazzone, S., Shogren, J., Simmons, P. & Watkinson, A. (2002) Biological invasion risks and the public good: An economic perspective. *Conservation Ecology*, **6**, 1.

Piggin, C.M. & Sheppard, A.W. (1995) *Echium plantagineum* L. *The Biology of Australian Weeds. Volume 1* (eds R.H. Groves, R.C.H. Shepherd & R.G. Richardson), pp. 87–110. Richardson, Melbourne.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems & Environment*, **84**, 1-20.

Poiani, K.A, Richter, B.D., Anderson, M.G. & Richter, H.E. (2000) Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. *BioScience*, **50**, 133-146.

Polunin, O. & Huxley, A. (1987) *Flowers of the Mediterranean*. Hogarth Press, London.

Pyšek P., Richardson D.M., Rejmánek M., Webster G.L., Williamson M. & Kirschner J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**, 131-143.

Rejmánek, M. (1989) Invasibility of plant communities. *Biological Invasions: a global perspective.* (eds J.A. Drake, H.A. Mooney, F. di Castri, R.H. Groves, F.J. Kruger, M. Rejmánek & M. Williamson), pp. 369-388. John Wiley & Sons, Chichester.

Renvoize, S.A. (1980) The sub-family Arundinoideae and its position in relation to a general classification of the Gramineae. *Kew Bulletin*, **36**, 85-102.

Richardson, D.M. & van Wilgen, B.W. (1986) The effects of fire in felled *Hakea sericea* and natural fynbos and implications for weed control in mountain catchments. *South African Forestry Journal*, **139**, 4-14.

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.

Richardson, D.M. (2001) Plant invasions. *Encyclopedia of Biodiversity. Volume 4.* (ed S. Levin), pp. 677-688. Academic Press, San Diego.

Richardson, D.M., Macdonald, I.A.W. & Forsyth, G.G. (1989) Reductions in plant species richness under stands of alien trees and shrubs in the fynbos biome. *South African Forestry Journal*, **149**, 1-8.

Richardson, D.M., Cowling, R.M., Bond, W.J., Stock, W.D. & Davis, G.W. (1995) Links between biodiversity and ecosystem function in the Cape Floristic Region. *Mediterranean-type ecosystems: the function of biodiversity*. (eds G.D. Davis & D.M. Richardson), pp. 285-333. Ecological Studies 109. Springer-Verlag, Berlin.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., & Henderson, L. (1997) Alien plant invasions. *The vegetation of Southern Africa.* (eds R.M. Cowling, D.M. Richardson & S.M. Pierce), pp. 535-570. Cambridge University Press, Cambridge.

Richardson, D.M., Bond, W.J., Dean. W.R.J., Higgins, S.I., Midgley, G.F., Milton, S.J., Powrie, L.W., Rutherford, M.C., Samways, M.J. & Schulze, R.E. (2000). Invasive alien organisms and global change: a South African perspective. *Invasive species in a changing world*. (eds H.A. Mooney & R.J. Hobbs), pp. 303-349. Island Press, Washington, D.C.

Richardson, D.M., Rouget, M., Ralston, S.J., Cowling, R.M., van Rensburg, B.J. & Thuiller, W. (2005) Species richness of alien plants in South Africa: environmental correlates and the relationship with indigenous plant species richness. *Ecoscience*, **12**, 391-402.

Rieger, J.P. & Kreager, A. (1989) Giant reed (*Arundo donax*): a climax community of the riparian zone. *Proceedings of the California Riparian Systems Conference*, 22-24 September 1988, Davis, California, USA. (technical coordinator D.L. Abell), pp. 222-225. USDA Gen. Tech. Report PSW-110.

Robbins, W.W., Bellue, M.K. & Ball, W.S. (1951) *Weeds of California*. Department of Agriculture, Sacramento.

Robertson, M.P., Villet, M.H., Fairbanks, D.H.K., Henderson, L., Higgins, S.I., Hoffmann, J.H., Le Maitre, D.C., Palmer, A.R., Riggs, I., Shackleton, C.M. & Zimmerman, H.G. (2003) A proposed prioritisation system for the management of invasive alien plants in South Africa. *South African Journal of Science*, **99**, 37-43.

Rossa, B., Tuffers, A.V., Naidoo, G. & von Willert, D.J. (1998) *Arundo donax* L. (Poaceae) – a C_3 species with unusually high photosynthetic capacity. *Botanica Acta*, **111**, 216-221.

Rouget, M., Richardson, D.M., Nel, J.L., Le Maitre, D.C., Egoh, B. & Mgidi, T. (2004) Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climate suitability. *Diversity and Distributions*, **10**, 475-484.

Samways, M.J., Caldwell, P.M. & Osborn, R. (1996) Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agriculture, Ecosystems and Environment*, **59**, 19-32.

Schmid, B., Joshi, J. & Schläpfer, F. (2002) Empirical evidence for biodiversity-ecosystem functioning relationships. *Functional consequences of biodiversity: experimental progress and theoretical extensions*. (eds A. Kinzig, S. Pacala & D. Tilman), pp. 120-150. Princeton University Press, Princeton.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21-32.

Solbrig, O.T. (1991) Biodiversity: scientific issues and collaborative research proposals. MAB Digest 9, UNESCO, Paris.

Solbrig, O.T. (1992) Biodiversity: an introduction. *Biodiversity and global change*. (eds O.T. Solbrig, H.M. van Emden & P.G.W.J. van Oordt), pp. 13-20. International Union of Biological Sciences, Paris.

Spencer, D.F., Ksander, G.G. & Whitehand, L.C. (2005) Spatial and temporal variation in RGR and leaf quality of a clonal riparian plant: *Arundo donax*. *Aquatic Botany*, **81**, 27-36.

Standish, R.J., Williams, P.A., Robertson, A.W., Scott, N.A. & Hedderley, D.I. (2004) Invasion by a perennial herb increases decomposition rate and alters nutrient availability in warm temperate lowland forest remnants. *Biological Invasions*, **6**, 71-81.

Stirton, C.H. (1978) Plant *invaders: beautiful but dangerous*. Department of Nature and Environmental Conservation, Cape Town.

Stock, W.D., Wienand, K.T. & Baker, A.C. (1995) Impacts of invading N_2-fixing Acacia species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and ^{15}N natural abundance values. *Oecologia*, **101**, 375-382.

Team Arundo del Norte (1999a) *Controlling Arundo in your watershed: a guide for organizations*. US Environmental Protection Agency and California Department of Fish and Game. Available http://teamarundo/org/education/org_guide.pdf. Accessed 22/08/2006.

Team Arundo del Norte (1999b) *Arundo donax: Status and management needs in the CALFED Bay-Delta Watershed*. Available http://teamarundo.org/control_manage/whitepaper.txt. Accessed 22/08/2006.

Tilman, D., Knopps, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300-1302.

Tracy, J.L. & DeLoach, C.J. (1999) Suitability of classical biological control for giant reed (*Arundo donax*) in the United States. Arundo and Saltcedar: The Deadly Duo. *Proceedings of the Arundo and Saltcedar Workshop*, 18 June 1998. Ontario, Canada. (ed C.R. Bell), pp. 73-109. UC Cooperative Extension, California.

Tu, M., Hurd, C. & Randall, J.M. (2001) *Weed Control Methods Handbook: Tools and Techniques for Use in Natural Areas*. The Nature Conservancy, California.

Turpie, J. (2004) The role of resource economics in the control of invasive alien plants in South Africa. *South African Journal of Science*, **100**, 87-93.

United States Environmental Protection Agency (1997) *Control of Giant Cane in Riparian and Wetland Areas of Northern and Central California*. US EPA Grant, Gray Lodge Wildlife Area, Butte County.

United States Department of Agriculture, Forest Service (1993) *Eradication of* Arundo donax*: San Francisquito and Soledad Canyons*. Environmental Assessment. Arcadia, California.

Usher, G. (1974) *A dictionary of plants used by man*. Haffner Press, New York.

van den Berckt, T. (2000) The ecological effect of *Acacia saligna* in a Sand Plain Fynbos ecosystem of the Western Cape, South Africa. MSc thesis, University of Stellenbosch.

van Wilgen, B.W. & Le Maitre, D.C. (1981) Preliminary estimates of nutrient levels in fynbos vegetation and the role of fire in nutrient cycling. *South African Forestry Journal*, **119**, 24-28.

van Wilgen, B.W., Little, P.R., Chapman, R.A., Görgens, A.H.M., Willems, T. & Marais, C. (1997) The sustainable development of water resources: history, financial costs, and benefits of alien plant control programmes. *South African Journal of Science*, **93**, 404-411.

van Wilgen, B.W., Le Maitre, D.C. & Cowling, R.M. (1998) Ecosystem services, efficiency, sustainability and equity: South Africa's working for water programme. *Trends in Ecology & Evolution*, **13**, 378.

van Wilgen, B.W., Richardson, D.M. & Higgins, S. (2000) Integrated control of invasive alien plants in terrestrial ecosystems. *Best management practices for preventing and controlling invasive alien species.* (eds G. Preston, G. Brown & E. van Wyk), pp. 118-128. Working for Water Programme, Cape Town.

van Wilgen, B.W., Richardson, D.M., Le Maitre, D.C., Marais, C. & Magadlela, D. (2001) The economic consequences on alien plant invasions: examples of impacts and approaches to sustainable management in South Africa. *Environment, Development and Sustainability*, **3**, 145-168.

van Wilgen, B.W., Marais, C., Magadlela, D., Jezele, N. & Stevens, D. (2002) Win-win-win: South Africa's Working for Water Programme. *Mainstreaming biodiversity in development. Case studies from South Africa*. (eds S.M. Pierce, R.M. Cowling, T. Sandwith & K. MacKinnon), pp. 5-20. The World Bank Environment Department, Washington, D.C.

van Wyk, D.B, Lesch, W. & Stock, W.D. (1992) Fire and Catchment Chemical Budgets. *Fire in South African mountain fynbos. Ecosystem, community and species response at Swartboskloof.*

(eds B.W. van Wilgen, D.M. Richardson, F.J. Kruger & H.J. van Hensbergen), pp. 240-257. Ecological Studies 93. Springer-Verlag, Berlin.

Versfeld, D.B. & van Wilgen, B.W. (1986) Impact of woody aliens on ecosystem properties. *The ecology and management of biological invasions in South Africa*. (eds I.A.W. Macdonald, F.J. Kruger & A.A. Ferrar), pp. 239-246. Oxford University Press, Cape Town.

Versfeld, D.B., Le Maitre, D.C. & Chapman, R.A. (1998) *Alien invading plants and water resources in South Africa: a preliminary assessment*. Water Research Commission Report No TT 99/98. Water Research Commission, Pretoria.

Vilà, M., Lloret, F., Ogheri, E. & Terradas, J. (2001) Positive fire-grass feedback in Mediterranean Basin woodlands. *Forest Ecology and Management*, **147**, 3-14.

Vitousek, P.M. (1986) Effects of alien plants on native ecosystems. *Ecology of Biological invasions of North America and Hawaii*. (eds H.A. Mooney & J.A. Drake), pp. 163-176. Springer-Verlag, New York.

Vitousek, P.M. & Hooper, D.U. (1993) Biological diversity and terrestrial ecosystem biogeochemistry. *Ecosystem function of biodiversity*. (eds E. Schulze & H.A. Mooney), pp. 3-14. Springer, Heidelberg.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M. & Westbrooks, R. (1997) Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology*, **21**, 1-16.

Vogl, R.J. (1974) Effects of fire on grasslands. *Fire and Ecosystems*. (eds T.T. Koslowski & C.E. Ahlgren.), pp. 139-194. Academic Press, New York.

Walker, B.H. & Steffen, W.L. (1999) Interactive and integrated effects of global change on terrestrial ecosystems. *The terrestrial biosphere and global change. Implications for natural and managed ecosystems, Synthesis volume*. (eds B. Walker, W. Steffen, J. Canadell & J.S.I. Ingram), pp. 329-375. International Geosphere-Biosphere Program Book Series 4. Cambridge University Press, Cambridge.

Walker, L.R. & Smith, S.D. (1997) Impacts of invasive plants on community and ecosystem properties. *Assessment and management of plant invasions*. (eds J.O. Luken & J. Thierret), pp. 69-86. Springer-Verlag, New York.

Wardle, D.A., Bonner, K.I. & Barker, G.M. (2002) Linkages between plant litter decomposition, litter quality, and vegetation responses to herbivores. *Functional Ecology*, **16**, 585-595.

Wedin, D.A. (1999) Nitrogen availability, plant-soil feedbacks and grassland stability. *Proceedings of the VI International Rangeland Congress on People and Rangelands Building the Future*, 19-23 July 1999, Townsville, Australia. (eds D. Eldridge & D. Freudenberger), pp. 193-197.

Wells, M.J., Duggan, K. & Henderson, L. (1980) Woody plant invaders of the central Transvaal. *Proceedings of the Third National Weeds Conference*, South Africa. (eds S. Neser & A.L.P. Cairns), pp. 11-23.

White, E.M., & Gartner, F.R. (1975) Immediate effects of prairie fire on the soil nitrate, ammonium, available phosphorous and total N content. *Proceedings of the South Dakota Academy of Science*, **54**, 188-193.

Whisenant, S.G. (1990) Changing fire frequencies on Idaho's Snake River plains: ecological and management implications. *Proceedings of the symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management*, 5-7 April 1989, Las Vegas, USA. (eds E.D. McArthur, E.M. Romney, S.D. Smith & P.T. Tueller), pp. 4-10. USDA Forest Service Gen. Tech. Report INT-276.

Wiesenborn, W.D. (1996) Saltcedar impacts on salinity, water, fire frequency and flooding. *Proceedings of the Saltcedar Management Workshop*, 12 June 1996, Rancho Mirage, California, USA. (eds J. DiTomaso & C.E.Bell), pp. 9-12.

Williams, G.M., Kroes, R. & Munro, I.C. (2000) Safety evaluation and risk assessment of the herbicide Roundup and its active ingredient, glyphosate, for humans. *Regulatory Toxicology and Pharmacology*, **31**, 117-165.

Wilson, D.E., Cole, R.F. & Nichols, J.D., Rudran, R. & Foster, M.S. (1996) *Measuring and monitoring biological diversity: standard methods for mammals*. Smithsonian Institution Press, Washington, D.C.

Woodward, F.I. (1993) How many species are required for a functional ecosystem? *Ecosystem function of biodiversity*. (eds E-D. Schulze & H.A. Mooney). Ecological studies 99. Springer, Berlin.

Wynd, F.L., Steinbauer, G.P. & Diaz, N.R. (1948) *Arundo donax* as a forage grass in sandy soils. *Lloydia*, **11**, 181-184.

Yelenik, S., Stock, W.D. & Richardson, D.M. (2004) Ecosystem-level impacts of invasive alien nitrogen-fixing plants. Ecosystem and community-level impacts of invasive alien *Acacia saligna* in the fynbos vegetation of South Africa. *Restoration Ecology*, **12**, 44-51.

Zedler, P.H., Gautier, C.R. & McMaster, G.S. (1983) Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. *Ecology*, **64**, 809-818.

Zimmerman, P. (1999) Rates of transpiration by a native willow, *Salix exigua*, and by a non-native invasive, *Arundo donax*, in a riparian corridor of northern California. *Proceedings of the California Exotic Pest Plant Council*, October 1999, Sacramento, California.

Zohary, M. & Willis, A.J. (1992) *The vegetation of Egypt*. Chapman & Hall, London.

Zuňiga, G.E., Argandona, V.H., Niemeyer, H.M. & Corcuera, L.J. (1983) Hyroxamic content in wild and cultivated Gramineae. *Phytochemistry*, **22**, 2665-266.