PLANT LIFE HISTORY AND THE
NATURALISATION TO INVASION PATHWAY

MEGAN LIJA PHILLIPS

Thesis submitted for the degree of Doctor of Philosophy
at the University of Technology Sydney

April 2013
DECLARATION

This is to certify that:

(i) The work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

(ii) I also certify that the thesis has been written by me.

(iii) Any help that I have received in my research work and the preparation of the thesis itself has been duly acknowledged.

(iv) In addition, I certify that all information sources and literature used are indicated in the thesis.

................................................................. Megan L. Phillips


**THESIS ABSTRACT**

Exotic plant species that become widespread and abundant in their new ranges are a worldwide environmental problem. Such invasive plant species are responsible for a growing number of ecological problems including biodiversity loss, disruptions in ecosystem function and species extinctions. Many exotic plant species introduced to new regions become naturalised, but only a small subset of these species transition from naturalisation to invasion. An important goal of invasion ecology is the identification of plant traits that enable exotic plant species to become invasive within their new ranges. The identification of such traits provides a better understanding of factors contributing to invasion success and contributes to the effective management of invasive plants. In Australia, exotic plant invasion is recognized as a serious and growing threat to native biodiversity. Yet, despite the recognition of the impacts of invasive exotic plant species, there is a paucity of information about the factors contributing to their success in Australia. Thus, identifying plant traits that promote the invasion success of exotic plant species in Australia is a research and management imperative.

This research thesis examined relationships between exotic plant species invasiveness and a range of plant life-history traits through the use of a continental-scale, target-area comparative approach. I compared plant traits between invasive and non-invasive species across multiple plant life-history stages, from seed traits in the seed bank to germination characteristics, seedling emergence and growth traits, as well as the attributes of mature plants. I first constructed a database of 468 naturalised exotic plant species in Australia, with data for four plant introduction traits. I found that residence time (the length of time an exotic plant species has been present in the introduced range) was a consistent predictor of invasion success, as was growth form with the introduction of vines significantly more likely to be linked with invasiveness within Australia. Continental origin was correlated with invasiveness, with invasive species in Australia significantly more likely to originate from North America or South America and less likely to originate from Europe or Australasia. There was no clear indication that exotic species introduced accidentally, as ornamentals or for agricultural purposes were significantly more likely to become invasive.

I then designed a novel species selection framework to closely examine life-history trait differences between invasive and non-invasive naturalised plant species.
Critical to this framework was the need to control for potentially confounding factors that might result in either the emergence of spurious life-history correlates of invasiveness or an inability to find important life-history trait relationships with invasiveness. The species selection framework controlled for the introduction traits residence time, growth form and continental origin, all found to be important correlates of invasiveness in my previous analysis, as well as geographic co-occurrence and range size differences. In the case of the latter two, it was essential to ensure that comparisons between invasive and non-invasive species involved pairs of species that occurred in the same habitats and to ensure that invasive species were substantially more widespread geographically than non-invasive species. Importantly, the framework used information about phylogenetic relationships to provide phylogenetically independent contrasts of life-history traits between invasive and non-invasive species. This species selection framework provided the foundation of all my database and experimental studies in the rest of this thesis.

Using the framework, I conducted an empirical desk-top study to analyse life-history trait relationships with species invasiveness using a complementary cross-species and phylogenetically-independent contrasts approach. The cross-species approach examined trait relationships with invasiveness without explicitly considering the phylogenetic relatedness of the study species. The contrasts approach complemented the cross-species approach by using phylogenetic information to examine patterns of correlated evolutionary divergences between life-history traits and invasiveness. Life-history traits examined in this study included seed mass, leaf size, maximum canopy height, number of dispersal mechanisms and types of dispersal mechanisms used by each species. This study detected two life-history traits linked significantly to invasiveness within the naturalised flora of Australia: an increased number of plant dispersal mechanisms and the use of water as a dispersal mechanism. Both of these traits are intimately connected with a species’ capacity to spread across a landscape, which implies enhanced dispersal may be promoting exotic species invasiveness in Australia.

Using a subset of plant species from the desk-top dataset, I performed three separate experiments. In the first experiment, I found evidence on a local scale that the survival of seeds of invasive species in the soil seed bank was significantly higher than seed survival in non-invasive species (in six out of seven congeneric contrasts). I also
found that the application of a fungicide treatment led to a larger increase in seed survival in the non-invasive compared with the invasive species, suggesting that poorer seed survival in the non-invasive species could be attributed to seed-deteriorating soil-borne pathogenic fungi present in the new range. In the second experiment, I compared a range of seed germination characteristics between invasive and non-invasive species. I found that the seeds of invasive species germinated significantly more rapidly (in five out of seven contrasts), but were also more likely to exhibit a ‘bet-hedging’ strategy by staggering seed germination over a longer period of time (in four out of seven contrasts), as well as retaining a higher proportion of dormant but viable seeds after a germination-triggering event occurred (in five out of seven contrasts). In the third experiment, I compared seedling traits between invasive and non-invasive plant species using four congenic pairs to determine whether there were any consistent trait correlations with species invasiveness. The study explored five seedling traits including time to seedling emergence from the soil, seedling height, leaf production, specific leaf area and biomass. I found evidence that some invasive species differed from non-invasives during the seedling stage, but I found no consistent seedling trait explicitly linked to species invasiveness.

The work presented in this thesis contributes to the quest to identify plant traits facilitating the naturalisation to invasion transition. This thesis used a comparative approach to successfully link exotic plant species invasiveness within the introduced range to plant introduction and life-history traits across a range of plant life stages. The approach and findings of this thesis were built on an important historical and growing body of work examining plant species invasiveness. Given the relative paucity of work specifically focusing on the shift from naturalisation to invasion, this thesis provides information crucial for our understanding and management of the global problem of biological invasions.
ACKNOWLEDGEMENTS

I wish to acknowledge the Australian Research Council for providing the scholarship that funded my PhD and enabled this research to happen. I also wish to thank the School of the Environment, the Faculty of Science and UTS for providing me with a scholarship top-up and support funds for my projects including the many thousands of seeds used in my research. My thanks to the Faculty for providing travel funding that allowed me to present my research findings at the ESA 2010 and ESA 2011 conferences.

I owe much gratitude and thanks to my supervisor, Greg Skilbeck. I am fortunate to have had his sound, practical advice and guidance through my time as a PhD student. Greg is the sort of supervisor a research student dreams of – calm, level-headed and a problem-solver. My thanks go to him for all of his help over these last few years. I’d also like to thank him for crafting Mabel, the Patterson’s-curse-munching bovine for me, who (in my eyes) was the real star of the UTS 3 Minute Thesis competition.

I want to give my deepest thanks to amazing Lyndle Hardstaff for being the best field, lab and glasshouse assistant any PhD student could ask for, as well as an amazing friend and comrade in all things nerdy and wonderful. Lyndle is one of those people who, instead of constantly talking about change, actually goes out and makes the world a better place to live in, one day at a time. Her optimism and tenacity are utterly unsinkable. I’d like to acknowledge her as being a lifeboat of support for me over all of these years and thank her for the loan of the ‘Captain Safety’ vest for field work.

I’d also like to thank Tara Konarzewski for being such an inspiring friend and sharing my all my joys and troubles as a card-holding member of Team PhD. They say some of the most stressful things you can do in life are organise a wedding, move into a new house and write a thesis. Tara has done all three, almost all at once. In times of sheer, unbridled madness she handles it all with such extraordinary grace and good humour. I completely admire her for it. She’s been a generous wellspring of understanding and of empathy for me and I will never be able to thank her enough for it. I know that when we’re old ladies, we’ll still be friends and look back at now and smile.

My thanks go to everyone in the Murray Research Lab – I’d like to thank Leigh Martin for all the insightful chats about the environment, invasive species and politics over the last few years, as well as putting me on to single-malt scotch and for keeping me good-humoured about life’s sporadic absurdities. My thanks also to Kien Nguyen for
the research chats about invasive species and for the ridiculously epic spring rolls. My thanks and good luck go to Kien who is, as I write this, at the start of his surely brilliant PhD and also the same to Matt Hinge who is just beginning his post-grad research journey, diving headfirst into R statistics!

I’d like to thank Andy Leigh for being a ball of positive energy and a truly inspiring role model for me. She knows exactly how to keep people sane and positive – intuitively sending me advice, positive thoughts, photos and cat videos whenever I needed a laugh or a lift. I’d like to thank her for helping me design my seedling growth project and for the years of continual encouragement.

My thanks also to Alex Pulkownik for all of the wisdom and friendship she shared with me throughout my research. If it weren’t for Alex’s belief in me and my abilities, I would never have had the great start in teaching that I was fortunate enough to have.

Thanks to my Head of School, Bill Gladstone, for his excellent mentorship as well as his practical advice and support. Bill is genuinely committed to ensuring the wellbeing and success of staff and students. He took the time to support me in all my endeavours and made sure I was looked after. I also extend my thanks to the staff and students of the UTS School of the Environment and Faculty of Science for always being so unfailingly helpful and friendly. People here are genuinely nice and want to help and I’m glad to have interacted with so many of them. I feel very fortunate to have done my PhD research in the company of such wonderful and brilliant scientists.

I’d like to thank my extremely capable research volunteers, Danielle Jones and Alex Gale, for taking time and care to help me with all my seed-based projects. Seeds aren’t the easiest things to measure. They’re small, fiddly and seemingly-endless in number. Helping me cumulatively count and measure many thousands of the little things as well as staying cheerful and interested in my work absolutely deserves due credit.

I’d like to thank the UTS technical crew Andrew Malecki, Rod Hungerford, Jane Easton and Peter Jones in particular for all the project support and technical assistance they’ve given me over the last few years. Thanks especially to Gemma Armstrong for lending me the Tetrazolium Handbook. I’m grateful for her generous help and understanding when the invasive herbs, shrubs and grasses I kept in the glasshouse (that started out as small and cute plants) morphed in to a horde of rampaging triffids.
My thanks to Emanuelle Paradis and Campbell Webb for giving me helpful pointers when I was ironing out the intricacies of phylogenetic analyses in R (the ‘APE’ package) and Phylocom. My thanks also to Petr Pyšek, Jan Pergl, Votja Jarošík, Milan Chytrý, Ingolf Kühn, Michelle Leishman and Robert Ingram for their interest in my research, collegiality and collaborative spirit.

A big thanks to all of my friends and colleagues (who are too many to list here!) for their encouragement, friendship and support during my time as a research student. My thanks to my lovely cats Bert and Ernie for giving me so much joy while keeping my lap warm and my perspective balanced.

I know the best outcome from these past four years has been sharing this journey with my best friend, soul-mate and husband: Brad Murray. I married the best person out there for me. Kind, sweet, funny and completely brilliant: Brad is the only person who fully appreciates all of my eccentricities and off-beat sense of humour. He has been a true and steadfast supporter of all my quests in life and has unconditionally loved me during the best of times and the worst of times. He has always been there for me - always supportive of my life’s choices and truly instrumental in instilling confidence in my work as a scientist. I’ll never be able to thank him enough for all the happiness that he brings into my world. What we’ve both learned from these last few years has strengthened our passion for environmental conservation as well as our commitment to each other and determination to live life to the fullest.

Thank you for everything, my Obi-Wan.
Preface

All research presented here was completed for my PhD thesis.

A version of Chapter 2 has been published in the journal Austral Ecology.

A version of Chapter 4 has been published in the journal Evolutionary Ecology Research.

A version of Chapter 7 has been published in the journal Preslia.

Versions of Chapters 3 and 4 have been presented as posters at the Ecological Society of Australia’s annual national conference in 2010 and 2011 respectively.
# Table of Contents

Declaration ................................................................................................................................. ii
Thesis Abstract ............................................................................................................................ iii
Acknowledgements ....................................................................................................................... vi
Preface........................................................................................................................................ ix
Table of contents ......................................................................................................................... x
List of figures and boxes............................................................................................................... xiv
List of tables................................................................................................................................ xviii

## Chapter 1 – General Introduction ....................................................................................... 1-10

- Invasion ecology and its inception ......................................................................................... 1
- The problem of invasive exotic plant species ....................................................................... 2
  - The naturalisation to invasion transition ........................................................................... 2
- The value of trait information for understanding invasiveness ........................................... 4
  - Introduction-history traits ................................................................................................. 5
  - Life-history traits ............................................................................................................... 5
- The ‘target-area’ approach: Application to Australia ............................................................ 5
- Research overview .............................................................................................................. 8
  - Thesis objectives ............................................................................................................... 8
  - Thesis structure .................................................................................................................. 9

## Chapter 2 – The naturalisation to invasion transition: Introduction-history correlates of invasiveness in the exotic flora of Australia ........................................ 11-22

- Introduction .......................................................................................................................... 11
  - The target area approach: Australia .................................................................................. 12
  - Research questions .......................................................................................................... 13
- Methods ................................................................................................................................ 14
  - Introduction-history traits ............................................................................................... 14
  - Study species and dataset compilation ......................................................................... 14
  - Statistical analyses ......................................................................................................... 15
- Results ................................................................................................................................... 16
- Discussion ............................................................................................................................ 19
Conclusions .......................................................................................................................... 22
Coda .................................................................................................................................... 22

CHAPTER 3 – The role of plant traits in the naturalisation to invasion transition: a framework and Australian case study ................................................................. 23-53

Introduction ........................................................................................................................ 23
Species selection framework ............................................................................................. 23
Quantifying interspecific trait relationships in plant ecology ........................................... 23
A complementary ‘CS’ and ‘PIC’ approach ....................................................................... 25
Criteria for species selection ............................................................................................ 28
  Consistency in the definition of invasiveness ................................................................. 28
  Phylogenetically-independent contrasts ....................................................................... 29
  Residence time in the introduced range ....................................................................... 30
  Habitat co-occurrence ................................................................................................. 30
  Growth form ................................................................................................................. 31
An empirical test of the framework ................................................................................. 32

Materials and Methods .................................................................................................... 34
Study species and dataset compilation ........................................................................... 34
Plant life-history traits ...................................................................................................... 42
Statistical analyses ......................................................................................................... 42

Results ................................................................................................................................ 45
Cross-species analyses ..................................................................................................... 45
Correlated divergence analyses ....................................................................................... 47

Discussion ........................................................................................................................ 49

CHAPTER 4 – Investigating relationships between seed bank survival and invasion success in exotic plant species within the introduced range ........................................ 54-66

Introduction ...................................................................................................................... 54

Methods ............................................................................................................................ 56
  Invasive vs. non-invasive congeneric contrasts ......................................................... 56
  Seed survival measurements ....................................................................................... 58
  Statistical analyses ....................................................................................................... 60

Results ................................................................................................................................ 61
CHAPTER 5 – Relationships between seed germination and plant species invasiveness

Introduction .................................................................................................................. 67

Methods ....................................................................................................................... 70
  Species selection ........................................................................................................ 70
  Seed viability assessment at the beginning of the experiment ................................... 70
  Dormancy-breaking procedures ............................................................................... 70
  Germination traits and their measurement ............................................................... 72
  Seed viability assessment at the end of the experiment ........................................... 73
  Statistical analysis ..................................................................................................... 74
    Data normality ......................................................................................................... 74
    The potential influence of seed mass on germination ............................................. 75

Results ......................................................................................................................... 78
  Time to first germination ......................................................................................... 78
  Germination period .................................................................................................. 78
  Total seed germination ............................................................................................ 80
  Seed dormancy ......................................................................................................... 82

Discussion ..................................................................................................................... 85

CHAPTER 6 – Relationships between seedling emergence, growth variation and species invasiveness

Introduction .................................................................................................................. 89

Methods ....................................................................................................................... 91
  Glasshouse experiment ............................................................................................ 91
  Seedling measurements ............................................................................................ 95
  Statistical analyses .................................................................................................. 95

Results ......................................................................................................................... 96
  Time to seedling emergence .................................................................................... 96
  Seedling height at 12 weeks ................................................................................... 98

Conclusion ..................................................................................................................... 66
Leaf production after 12 weeks ................................................................. 99
Specific leaf area..................................................................................... 99
Biomass...................................................................................................... 100
Discussion................................................................................................ 101

Chapter 7 – Plant species of the Central European flora as exotic species in

Australia.................................................................................................... 105-121

Introduction............................................................................................. 105

Materials and Methods .......................................................................... 108
  Source species pool................................................................................ 108
  Target region data.................................................................................. 109
  Statistical analyses................................................................................ 111

Results...................................................................................................... 111
  Central European species in Australia: a summary.............................. 111
  Accidental and deliberate introductions over time.............................. 112
  Current status of Central European plants in Australia in relation to
  introduction periods............................................................................ 114
  Introductions of plant families over time............................................ 114
  Introductions of plant growth forms over time................................... 114

Discussion................................................................................................ 117

Chapter 8 – Synthesis.............................................................................. 122-131

Thesis overview....................................................................................... 122

Were the aims of this thesis met?............................................................. 123

The ongoing search for plant species traits driving invasiveness........... 126

Exotic species invasions: the outlook for Australia................................. 127

Conclusion................................................................................................ 131

Thesis reference list.................................................................................. 132-165
LIST OF FIGURES AND BOXES

Box 1.1 The introduction to invasion pathway ................................................................. 3

Figure 2.1 The percentage of naturalised invasive and non-invasive exotic plant species in Australia originating from different continents ......................................................... 17

Figure 2.2 The percentage of naturalised invasive and non-invasive exotic plant species introduced into Australia unintentionally or for ornamental or agricultural purposes .............................................................................................................................. 17

Figure 2.3 Residence times (mean ± SE) of naturalised invasive and non-invasive exotic plants in Australia ................................................................................................................. 18

Figure 2.4 The percentage of naturalised invasive and non-invasive exotic plant species in Australia in each primary growth form .................................................................................. 18

Figure 2.5 Residence times (mean ± SE) of naturalised invasive and non-invasive exotic plants in Australia as a function of continent of origin ..................................................................... 19

Figure 3.1 Phylogenetic tree of the study species. Internal nodes were dated based on clade age estimates provided by Wikström et al. (2001) .................................................................................. 44

Figure 3.2 Box plots comparing a) seed mass and b) leaf size between invasive and non-invasive species. The box plots reveal the distribution and skew of the life-history trait data, from the smallest observation (i.e. lower error bar) to the largest observation (i.e. upper error bar). The data median is indicated as the line within the grey box. Data outliers are represented by the symbols ° and * ............................................................................................... 45

Figure 3.3 Box plots comparing maximum canopy height between invasive and non-invasive species ................................................................................................................................. 46
Figure 3.4  The number of invasive (dark blue bars) and non-invasive species (light blue bars) as a function of the total number of propagule dispersal mechanisms used. 47

Figure 3.5  The proportions of invasive and non-invasive species that utilize each dispersal mechanism: (a) adhesion, (b) endozoochory, (c) water dispersal and (d) wind dispersal. ................................................................................................................................. 48

Figure 4.1  Comparison of mean seed survival (±SE) between (a) invasive and non-invasive species, (b) control group (no fungicide) and treatment group (fungicide addition), and (c) invasive and non-invasive species separated into the treatment (●) and the control (○) groups. ......................................................................................................................... 62

Figure 4.2  Comparison of mean seed survival (±SE) between the invasive and non-invasive species of each congeneric contrast, separated into the control (○) and treatment (●) groups ........................................................................................................................................ 63

Figure 4.3  Comparison of mean seed mass (±SE) between the invasive (dark bars) and non-invasive (light bars) species of each congeneric contrast. Species with low variation in seed mass do not show error bars. ........................................................................................................................................ 64

Figure 5.1  First germination as a function of mean seed mass ...................................................... 76

Figure 5.2  Germination period as a function of mean seed mass .................................................... 76

Figure 5.3  Total seed germination as a function of mean seed mass ............................................... 77

Figure 5.4  Seed dormancy as a function of mean seed mass .......................................................... 77

Figure 5.5  First germination (mean ± S.E.) compared across plant genera and as a function of invasiveness. Dark blue circles represent invasive species; light blue circles represent non-invasive species ............................................................................................................................. 79
Figure 5.6  Length of germination period (mean ± S.E.) compared across plant genera and as a function of invasiveness. Dark blue circles represent invasive species; light blue circles represent non-invasive species ................................................................. 81

Figure 5.7  First germination (mean ± S.E.) compared across plant genera and as a function of invasiveness. Dark blue circles represent invasive species; light blue circles represent non-invasive species ................................................................. 83

Figure 5.8  First germination (mean ± S.E.) compared across plant genera and as a function of invasiveness. Dark blue circles represent invasive species; light blue circles represent non-invasive species ................................................................. 84

Figure 6.1  Time to seedling emergence (mean ± S.E.) of Coreopsis seedlings compared across nutrient conditions and as a function of invasiveness. Dark blue circles represent the invasive Coreopsis lanceolata which had a shorter time to emergence; light blue circles represent the non-invasive C. grandiflora .................................................................................. 98

Figure 6.2  Seedling height (mean ± S.E.) of Passiflora seedlings at 12 weeks compared across nutrient conditions and as a function of invasiveness. Dark blue circles represent invasive Passiflora foetida; light blue circles represent non-invasive P. coccinea .......... 99

Figure 6.3  Specific leaf area (mean ± S.E.) of Salvia seedlings compared across nutrient conditions and as a function of invasiveness. Dark blue circles represent invasive Salvia coccinea; light blue circles represent non-invasive S. splendens .................................................................................................................. 100

Figure 7.1  Frequency distribution of introduction times for all Central European plant species that have been introduced to Australia ................................................................. 112

Figure 7.2  Frequency distributions of introduction times for species that were introduced (a) accidentally or (b) deliberately .................................................................................. 113
Figure 7.3  Frequency distributions of introduction times for species that are currently classed as (a) casual or (b) naturalised ................................................................. 115

Figure 7.4  Distribution of earliest years of introduction for families with more than 15 species. The median, upper and lower quartile, smallest and largest non-outlier observations and outliers are presented. Outliers are those further away than 1.5 times the interquartile range (box) .................................................................................................................. 116

Figure 7.5  Distribution of earliest years of introduction for species in each of the four plant growth forms. The median, upper and lower quartile, smallest and largest non-outlier observations and outliers are presented. Outliers are those further away than 1.5 times the interquartile range (box) .................................................................................................................. 117

Figure 8.1  Available information on the legal status to import to Australia each of the 133 invasive exotic species listed in Randall (2007) (Source: AQIS ICON database; accessed July 2012) .................................................................................................................................................. 130

Figure 8.2  Legal status to import (a) seeds and (b) live seedlings to Australia for each the 82 invasive exotic species listed in AQIS ICON (Source: AQIS ICON database; accessed July 2012) .................................................................................................................................................. 130
**LIST OF TABLES**

**Table 2.1** Two-way ANOVA examining differences in residence time (response variable) as a function of both invasion success (two-level explanatory variable, invasive and non-invasive) and continent of origin (five-level explanatory level, South America, North America, Europe, Australasia and Africa)................................................................. 19

**Table 3.1** Congeneric contrasts established for the study following the species selection process. MRT represents a species’ minimum residence time within Australia. MAO represents the minimum area of continental occupancy of the species within Australia. The symbol (*) indicates that the species precise native is obscure .................... 35

**Table 3.2** Life-history traits of the congeneric contrasts of plant invasiveness. .......... 38

**Table 4.1** Invasive and non-invasive exotic plant species in each of the seven congeneric contrasts. Time is minimum residence time (years) ................................................................. 57

**Table 5.1** Invasive and non-invasive exotic plant species in each of the seven congeneric contrasts used in this study................................................................................................................................. 71

**Table 5.2** Linear regressions examining the effect of seed mass on the germination responses of exotic species.................................................................................................................. 75

**Table 5.3** Generalized linear model relating first germination to species invasiveness and taxonomy (genus) ........................................................................................................................................... 78

**Table 5.4** Generalized linear model relating germination period to species invasiveness and taxonomy (genus) ........................................................................................................................................... 80

**Table 5.5** Generalized linear model relating total seed germination to species invasiveness and taxonomy (genus) ........................................................................................................................................... 80
**Table 5.6** Generalized linear model relating seed dormancy to species invasiveness and taxonomy (genus) .....................................................................................................................................................82

**Table 5.7** Summary of germination responses across plant genera. The ‘†’ symbol indicates response higher value for invasive species compared with non-invasive species, the ‘†’ symbol indicates a lower value for invasive species, and the ‘=’ symbol indicates the invasive and non-invasive species had qualitatively the same response.) .................................................................................................................................................................82

**Table 6.1** Invasive and non-invasive exotic plant species in each of the four congeneric contrasts used in this study ........................................................................................................................................................................92

**Table 6.2** General linear models relating seedling emergence and growth traits (along the first row of the table) to invasive status and soil nutrient enrichment separately within each congeneric pair. ‘Interaction’ is that between invasive status and soil nutrient enrichment ..................................................................................................................................................................................97