Soil - Plant Interactions and Establishment of Woody Perennials on Hostile Soils

A thesis submitted to the University of Adelaide

in fulfilment of the requirements for the degree of Doctor of Philosophy

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July 2013

TABLE OF CONTENTS

Acknowledgements iii

Abstract v

Declaration ix

List of Publications x

Chapter 1: Introduction **1**

Introduction 2

Objectives 3

Structure of thesis 4

References 7

Chapter 2: Review of literature **9**

Introduction 11

Establishment methods for woody perennials 13

Factors affecting reliability of direct seeding 15

Challenges and research needs 26

References 27

Chapter 3: Maximum root growth pressures of tree and pea seedlings **33**

Introduction 36

Methods and Materials 37

Results 40

Discussion 41

Conclusions 45

References 46

Chapter 4: Relative success of the primary and lateral roots of pea and different tree seedlings growing in hard soils **47**

Introduction 49

Materials and Methods 51

Results 57

Discussion 66

Conclusions 70

References 71

Chapter 5: Growth and water use by tree and barley seedlings in poorly aerated soil............ 75

Introduction.. 77

Materials and Methods.. 79

Results.. 82

Discussion... 88

Conclusions.. 91

References.. 92

Chapter 6: Field corroboration of laboratory techniques to predict successful establishment of trees on hostile soils.. 95

Introduction.. 98

Materials and Methods.. 99

Results.. 105

Discussion... 117

Conclusions.. 120

References.. 121

Chapter 7: Summary, conclusions and future research.. 125

Summary and conclusions.. 126

Future research... 129

References.. 131

Appendices.. 132

ACKNOWLEDGEMENTS

I would never be able to accomplish my PhD project without the courage and help from Almighty God. I am blessed to have my parents who sacrifice everything for me to complete my higher education. My wonderful wife Kanch who always been my consultant and loving support in any crisis that I experienced before and during my study. It is really hard to explain in words that how much your love and support mean to me. I also thank God and Kanch for making me Dad of little Saman whose lovely face always makes me proud and pushes me hard to do my best in every aspects of my life.

I am heartily grateful to my principal supervisor Dr Cameron Grant for his encouragement, guidance, and support throughout my candidature that enabled me to complete my project. Cam, your never ending support to develop my professional career was great. I really appreciate your support to publish all the manuscripts. Finally, you are a great person, very fatherly.

I express my sincere thanks to my other supervisors Dr. Ian Nuberg, Dr. Robert Murray and Dr. Jason Emms. To Ian, your support on Agoroforestry aspect of my project was wonderful; to Rob, your support in physical and mathematical problem solving was great; and to Jason, your support in developing Allometric model was fantastic.

I am also thankful to Dr. Rabindra Misra, from the University of Southern Queensland, for coming over Adelaide and helping me in designing Root Growth Pressure measuring apparatus and helping in different aspects of manuscript preparation. I express my sincere thanks to my independent advisor Associate Professor Ann McNeill for reviewing my progress reports and journal articles before submissions to the journals.

I am sincerely thankful to The University of Adelaide for ASI scholarship; to CRC-FFI for top-up scholarship and travel awards to attend *World Congress of Soil Science* in Brisbane and to present my work in *Rhizosphere3 International Conference* in Perth; to Don & Betty Foundation in association with Soil Science Society of America for travel award to present my work in *Kirkham Conference* in New Zealand; to Crawford Fund for travel award to participate in Crawford Parliamentary Conference in Canberra; and to Soil Science Australia for travel bursary to present my work in *Joint ASSSI & SSS-NZ* conference in Hobart.

I am also thankful to Mr. David Hein from *Trees For Life* to help me finding field study sites. I am thankful to Mr. Robert Ahrens, the owner of Gazania property, to allow me soil and plant sampling on his property. I am also thankful to *Monarto Zoo* authority, especially to Mr. Timothy Jenkins for his enormous support to set up my field trials and his training staffs in for their help in data collection.

To my friends and family, thank you for your loving support, encouragement and understanding my needs while staying three years away from home.

ABSTRACT

Woody perennials exist in diverse conditions across arid and semi-arid regions and they bring enormous ecological, environmental and economic benefits – yet their establishment remains unreliable and expensive. A great deal of research has gone into cultural methods to improve establishment yet the edaphic factors have been largely ignored, and this is seen as a serious limitation. Without a good understanding of the interactions between plants and (often hostile) soil conditions, improved cultural methods can generate only limited progress. This study reviewed the literature associated with establishing woody perennial species on hostile soils in arid and semi-arid regions (Chapter 2, published in *Plant and Soil* as a review paper) and concluded that two of the most important soil properties limiting woody plant growth were high soil strength and low soil aeration. It also concluded that because some species grow well in hard soils while others grow well in waterlogged soils, there must be considerable genetic variation among woody perennials in the way they adapt to edaphic conditions.

On this basis, the research reported in this thesis was conducted in four separate studies (each published or submitted for publication) to understand the variation in inherent root growth pressures that different woody species can exert on the soil (Chapter 3), the response of different species to compaction (Chapter 4), the response of different species to poor soil aeration (Chapter 5), and the response of different species to these conditions in the field (Chapter 6). Cultural methods were included as variables, and model crops (either *Pisum sativum* or *Hordium vulgare*) were included for comparison.

The establishment and survival of woody perennials on hard, dry soil was postulated to depend *inter alia* upon their ability to exert high maximum axial root growth pressures, σ_{max} (Pa), which enable them to establish deep root systems. Values of σ_{max} have been published for crop plants in the past but not for a wide range of woody perennials. In Chapter 3, six small-seeded *Eucalyptus* species from two different habitats were grown in a glasshouse for 3-4 months until their root systems developed into a root-bound ‘plug’. They were then re-potted into larger vessels to reproduce a new set of lateral roots over 3-4 days. The maximum axial root growth force, F_{max} (N), was then measured on lateral root axes using a recognized apparatus (Misra 1997, Plant Soil 188,161-170). F_{max} was also measured on the primary root

axes of 3-4-day old seedlings of the large-seeded woody perennial, *Acacia salicina*, and the crop plant, *Pisum sativum*. Values of σ_{max} were calculated from F_{max} and the corresponding root diameter (d, m) using the relation: $\sigma_{\mathrm{max}} = \frac{4F_{\mathrm{max}}}{\pi d^2}$. The primary and lateral roots of all woody perennials were found to be considerably smaller than the primary roots of *P. sativum* yet they exerted a similar mean F_{max}. The mean σ_{max} varied between 0.15 and 0.25 MPa and the species: *E. leucoxylon*, *E. loxophleba* and *A. salicina* exerted the greatest pressures among the woody perennials, which were comparable to those exerted by the crop plant, *P. sativum*. Seedling age appear to influence the value of σ_{max} for primary roots of the trees, so a separate experiment was conducted to measure F_{max} for *A. salicina* and *P. sativum* over a period of 2-10 days after germination. The value of σ_{max} for the primary roots of *A. salicina* seedlings increased with time such that it became greater than that for *P. sativum*. The value of *P. sativum* did not change with time.

In Chapter 4, four species that exerted low, medium, or high σ_{max} in Chapter 3 were selected to evaluate their performance in compacted soils containing no cracks or biopores. All species were grown by direct seeding in a loamy sand compacted to obtain a range of soil penetration resistance, SR, ranging between 0.3 and 5 MPa. The seedlings of the *Eucalyptus* species were too small to be handled so they were grown for 3-months then transplanted into soil having the same range of SR values. Root diameter, elongation rate, total length and distribution of roots with the soil depth were measured. The SR value at which the rate of root elongation was halved, $SR_{0.5}$, was determined from a plot of elongation rate versus soil resistance. The diameter of the primary roots of *A. salicina* increased more consistently and this species maintained higher rate of root elongation and had higher $SR_{0.5}$ value than those of the direct seeded eucalyptus species and *P. sativum*. However, the lateral roots of transplanted *Eucalyptus* species elongated faster and had greater values of $SR_{0.5}$ than the primary roots of all species. The lateral roots of transplanted *E. camaldulensis* were more strongly negatively affected by compaction than those of the other transplanted eucalyptus species. Irrespective of compaction, *P. sativum* grew most its roots in the top 5 cm of soil, whereas tree roots were more uniformly distributed with depth. These variations in root growth behaviour in response to varying compaction were only found to moderately correlate ($R^2 = 0.79$ and $P = 0.11$) with the ability of their roots to exert σ_{max} (measured in earlier experiments) when the soil was severely compacted.

It has been reported that many compacted and uncompacted soils in arid and semi-arid regions suffer from permanent or temporary waterlogging. Root zone of such soil lacks sufficient aeration and oxygen supply. In Chapter 5, the performance of woody perennials from previous experiments were evaluated under a range of soil aeration, ε_{air}, between totally waterlogged and highly aerated (i.e. $0 < \varepsilon_{air} < 0.20$ m^{3}m^{-3}). *Hordium vulgare* was included for comparison because it is known to survive temporary waterlogged soil conditions. All species were direct seeded and grown for 21 days. The concentration of soil oxygen was measured directly in each soil, and the diameter, total length of roots, mass of shoots and roots, as well as water use and water use efficiency were measured or calculated. The soil oxygen concentration was severely depressed in soil where $\varepsilon_{air} \leq 0.10$ m^{3}m^{-3} but there was considerable variation among plant species in their response. Root and shoot growth as well as the water use by the young seedlings of *E. camaldulensis* were virtually unaffected by soil aeration status, while the other four species showed different responses. *E. kochii*, for example, was highly sensitive to declining ε_{air}, while *H. vulgare* and *A. salicina* were somewhat less sensitive. In terms of water use efficiency, the two large seeded species, *A. salicina* and *H. vulgare*, were significantly more efficient than the eucalyptus species.

In Chapter 6, the above findings from the laboratory and glasshouse experiments, which suggested the ability of roots to either exert high σ_{max} or to maintain a high rate of root elongation might be important for establishment and survival of these woody perennials, were tested under field conditions. A field survey was conducted near Monarto, South Australia, where soil physical properties and the success of woody perennials were thought to be related to differences in land management. A planting experiment was also conducted nearby where several woody perennials were established using two different planting methods. The large-seeded acacias were more successful than the small-seeded eucalypts when both were planted from seeds. Among the small-seeded species, transplanting of 90 day-old-seedlings was more successful than direct-seeding. Differences in success rates of various tree species and planting methods in the field corroborated well with the performance of these woody perennial seedlings in the laboratory. The findings from this research can be used by land managers and revegetation agencies to select superior woody perennials and planting methods to maximize the outcomes of their revegetation efforts in arid and semi-arid regions.

The key findings from this research were:

i. There were significant differences between woody perennials in their ability to exert high root growth pressures; some tree roots exert comparable pressures to those of an annual species.

ii. Roots of older seedlings can exert higher pressures than those of younger seedlings, and when compacted conditions persist for up to 10 days, a woody perennial (i.e. *A. salicina*) can continue to exert root growth pressures that exceed those of an annual species (i.e. *P. sativum*).

iii. There are significant differences between woody perennial seedlings in their ability to penetrate soils by their roots under varying soil strength which can be justified by differences in their respective habitats. Among the direct seeded woody perennial, large-seeded species have comparatively higher $SR_{0.5}$ than those of small-seeded ones.

iv. There are significant differences in the ability of roots of young seedlings planted by different methods. The lateral roots of transplanted eucalyptus seedlings generally elongate faster at all levels of compaction and they have significantly greater $SR_{0.5}$ values than those of their direct-seeded counterparts.

v. In highly compacted soil (e.g. $SR > 4$ MPa) there is a strong correlation between the ability of species to exert high root growth pressures and their ability to continue to grow in very hard soils.

vi. The effect of soil aeration on plant growth varies widely among species. Some woody perennials are better able to grow and use water in poorly aerated soils than others (probably by moving oxygen from the shoots to the roots). There appears to be no single critical value of ε_{air} to which all woody perennials respond. Some decline as soon as $\varepsilon_{air} < 0.20$ m^3m^{-3}, while others either don’t respond at all or do not decline until $\varepsilon_{air} < 0.15$ m^3m^{-3}. Furthermore, no single plant response universally indicates plant performance under waterlogging conditions – in some cases only root or shoot growth is affected while in other cases a more integrated response occurs (e.g. water use efficiency).

vii. The laboratory and glasshouse observations can be used to predict the success of young woody perennial seedlings and planting methods in real field conditions.

DECLARATION

This work contains no material which has been accepted for the award of any other degree or diploma from any university or tertiary institution to Md Gausul Azam. To the best of my knowledge and belief, it contains no material previously published or written by any other person, except where due reference has been made in the text.

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Md Gausul Azam **Date:**

LIST OF PUBLICATIONS

Azam G, Grant CD, Nuberg IK, Murray RS, Misra RK (2011) Variability in maximum root growth pressures of selected woody perennials: A measure to establish in high strength soils. In: *Rhizosphere3 International Conference*, Perth, Australia.

Azam G, Grant CD, Nuberg IK, Murray RS, Misra RK (2012) Establishing woody perennials on hostile soils in arid and semi-arid regions – A review. *Plant and Soil* **360**, 55-76.

Azam G, Grant CD, Misra RK, Murray RS, Nuberg IK (2012) Axial growth pressure, elongation and architecture of roots of tree seedlings grown in high strength soil. In: *Kirkham Conference - Exploring Frontiers in Soil Physics*, Messy University, Palmerston North, New Zealand.

Azam G, Grant CD, Misra RK, Murray RS, Nuberg IK (2012) Maximum axial growth pressures of the primary and lateral roots of woody perennials and annual crop. In: *Joint SSA and NZSSS Soil Science Conference – Soil Solutions for Diverse Landscape*, Hobart, Australia.

Azam G, Grant CD, Misra RK, Murray RS, Nuberg IK (2013) Growth of tree roots in hostile soil: A comparison of root growth pressures of tree seedlings with peas. *Plant and Soil* **368**, 569-580.

Azam G, Nuberg IK, Grant CD, Emms J, Murray RS (2013) Field corroboration of laboratory techniques to predict the successful establishment of trees on hostile soil in degraded landscapes. *Journal of Arid Environments* (Submitted, No.JAE13-171).

Azam G, Grant CD, Murray RS, Nuberg IK, Misra RK (2013) Relative success of the primary and lateral roots of pea and different tree seedlings growing in hard soils. *Soil Research* (Accepted, No.SR13-201).

Azam G, Murray RS, Grant CD, Nuberg IK (2013) Growth and water use by tree and barley seedlings in poorly aerated soil. *Soil Research* (Accepted, No.SR13-219).

CHAPTER 1

INTRODUCTION

Introduction

A significant expansion in revegetation efforts has occurred in arid and semi-arid[1] regions in recent decades, most of it in association with either degraded agricultural landscapes or abandoned mine sites (Donohue *et al.* 2009). The revegetation movement has been supported to some extent by improved cultural practices as well as research into the important environmental and phenological factors that control establishment of woody perennials (Caldwell *et al.* 2009; Graham *et al.* 2009). Despite extensive research, however, it appears that poor plant establishment in the first growing season remains a significant limitation to successful revegetation efforts. We must ask the question "why?" A survey of the literature (both peer-reviewed and so-called 'grey' literature) suggests that the most important (edaphic) factors have been largely ignored. Given that the soil is that primary medium by which plants must secure both water and nutrients, the lack of research in this area is seen as a major deficiency.

For example, soils in arid and semi-arid regions can remain quite dry for large parts of the year (FAO 1989) so the status of soil water must play a major role in controlling plant available water and other crucial biophysical processes (Newman *et al.* 2006). Drier soils are generally harder than moist soils and when they are also compacted from anthropogenic activity, they become even harder and more impenetrable to roots (Eavis 1972; Kozlowski 1999; Masle 2002). It can reasonably be argued, therefore, that the successful establishment and survival of woody perennials depends upon the ability of their roots to penetrate the deeper subsoil horizons to draw on water and nutrients as the surface soil dries out.

Penetration of subsoils in arid and semi-arid regions, however, does not guarantee limitless access to water and nutrients. In many cases, subsoils are both saline and alkaline, which means they also become waterlogged and very dense. Only very specialized plants can cope with this sort of environment. Impacts of soil salinity on establishment, survival and growth of woody perennials have been widely investigated (Marcar *et al.* 1995; Barrett-Lennard 2002; Munns and Tester 2008). Effects of high soil strength and poor soil aeration have also been investigated but mainly for crop plants, yet our understanding of these phenomena remains inadequate (Bengough *et al.* 2011). Hence the successful establishment of woody perennials on such landscapes requires careful matching of edaphic factors with specialized

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[1] By definition, arid and semi-arid refer to the regions that either receives 100-500 mm winter rainfall or 100-800 mm summer rainfall per annum with extreme temperatures (FAO 1989).

plant characteristics. For example, it is possible that some plants are better able to cope with anaerobic conditions, while others are better able to exert high root tip pressures on the soil. There is evidence in the literature to support these possibilities for agricultural crops (e.g Bengough *et al.* 2011; Bengough 2012) yet there is virtually none associated with woody perennials.

We know there is considerable variability in the root growth characteristics for woody perennials (e.g. Kozlowski 1999) so there is clearly plenty of genetic variation to work with. An evaluation of the variation in root growth pressures of different species correlated with their ability to grow in compacted or poorly aerated soils, for example, would be of considerable value in attempts to match edaphic factors with appropriate plants.

Controlled laboratory and glasshouse experiments are called for to tease out some of the intricate and subtle species responses to different edaphic factors. However, the applicability of the findings from controlled environment studies may be restricted under real field conditions. In the field, the successful establishment of woody perennials may depend on the complex interactions between the inherent ecosystem and biophysical processes (Arnold *et al.* 2012). Therefore any laboratory based findings need to be corroborated in the field under natural conditions to evaluate their practical implications.

Objectives

Very few studies have evaluated the importance of edaphic factors such as soil hardness and aeration status on the establishment of woody perennials. This limits our ability to improve revegetation efforts on degraded landscapes. The literature indicates there is considerable genetic diversity in the growth habit of woody perennials, which suggests that specialized root characteristics such as the ability to exert high root pressures or to tolerate waterlogged conditions, may be part of this diversity. If this were the case, it may be possible to explore the role of these characteristics in helping different species develop different root systems.

No published studies have evaluated the ability of a wide range of different woody perennials to exert high root growth pressures or to elongate their roots in hard soils. To better understand the importance of root growth pressure in penetrating hard subsoils a range of woody perennials needs to be grown in soil of varying strength. Also, because poor soil aeration often accompanies high soil strength, the same range of plants needs to be evaluated for their tolerance to anoxic conditions. Furthermore, a field based study on the establishment success of different woody perennials (using different cultural methods on different soils) is also required.

The aims of this study were therefore to evaluate and explain the relative success of several woody perennials (in terms of their root and shoot growth) under a set of relevant limiting soil conditions. The specific aims of the research were:

1. To measure the extent of variability of root growth pressures exerted by primary and lateral roots of several woody perennials at a given age and by the primary roots a large-seeded woody perennial and an annual at different ages,
2. To evaluate and explain variability in the growth of primary and lateral roots of an annual and several woody perennials in soil with varying (compacted) strength and to establish relationship between root growth pressure and the rate of root elongation,
3. To evaluate and explain the relative success of several woody perennials and an annual species in terms of their total root length, biomass production and water use under a range of soil aeration conditions, and
4. To survey and evaluate field performance of a number of direct-seeded woody perennials and a number of small-seeded woody perennials established by both direct-seeding and transplanting.

Structure of thesis

This thesis comprises seven chapters: Introduction (this Chapter 1) and Concluding Chapter 7, and five chapters that have either been published or submitted for publication (Figure 1.1).

Chapter 2 was published as a review article in *Plant and Soil*, and it covers the important literature on establishment methods and relative performance of different woody perennials. It also identifies the role of different biophysical factors especially edaphic factors on the establishment, survival and growth of woody perennials in arid and semi-arid environments, which form the subjects for study in the other chapters of the thesis.

Chapter 3 was published as a research paper in *Plant and Soil* and reports the variation in root growth pressures exerted by the primary and lateral roots of different tree species. It also reports the effect of seedling age on the rate of root elongation and root growth pressure of the seedlings of a woody perennial and an annual crop.

Chapter 4 was submitted as a research paper to *Soil Research* and reports the variations in growth of primary and lateral roots of different tree species and an annual crop in compacted soil. It explains these variations in root growth using a recognized model. It also examines the relationship between root growth pressure and the rate of root elongation in highly compacted soil (soil penetration resistance > 4 MPa).

Chapter 5 was submitted as a research paper to *Soil Research* and reports the variations in below- and above-ground growth and water use of different tree species and an annual crop under varying soil aeration conditions.

Chapter 6 was submitted as a research paper to the *Journal of Arid Environments* and reports the extent of corroboration between laboratory findings and field performance in terms of tree establishment on hostile soils.

Finally, Chapter 7 provides a synthesis of the findings contained in this thesis and includes recommendations for future research.

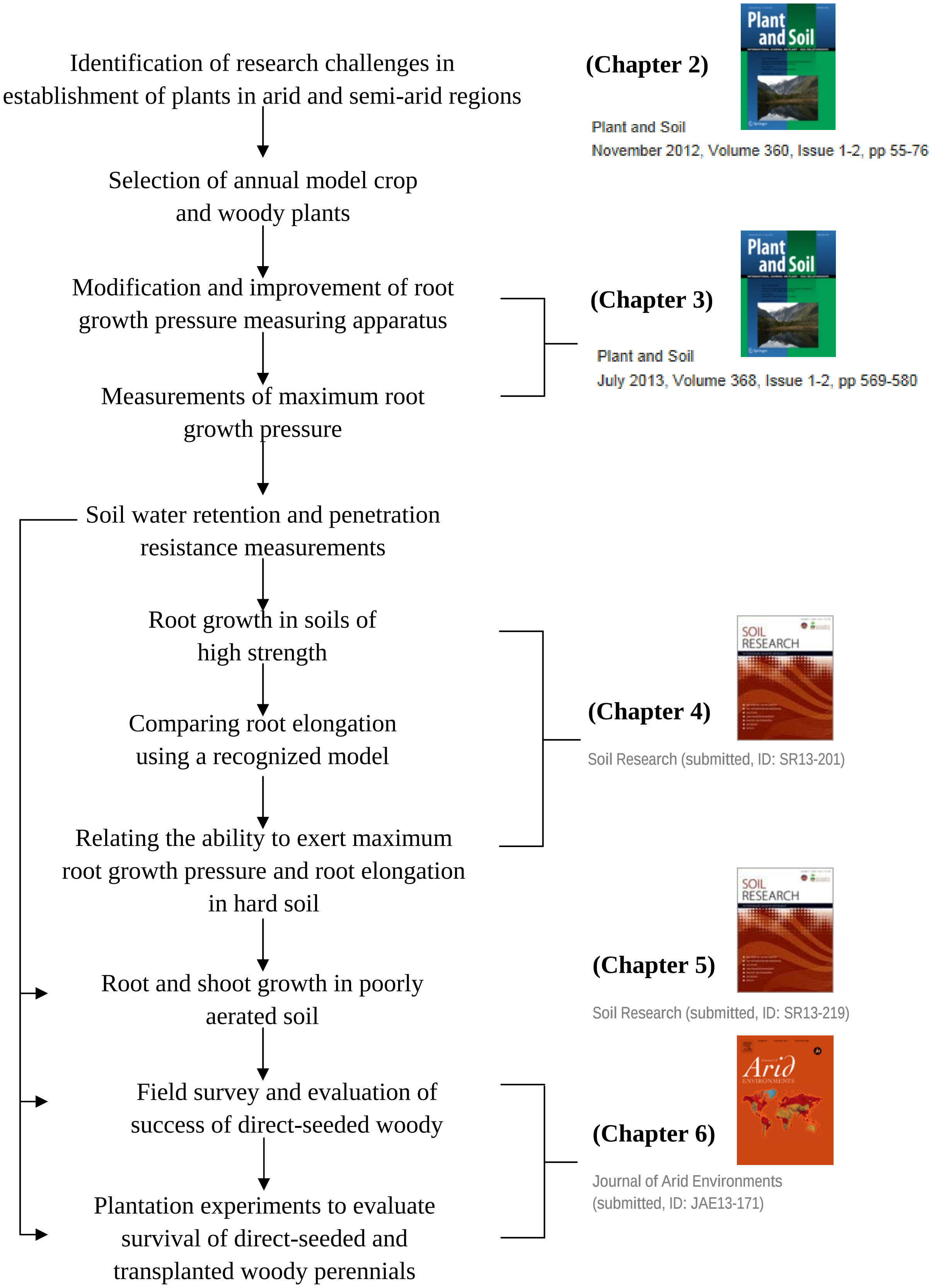

Figure 1.1. Schematic structure of the thesis

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CHAPTER 2

REVIEW OF THE LITERATUIRE

The work contained in this chapter has been published as a review paper in *Plant and Soil*.

Azam G, Grant CD, Nuberg IK, Murray RS, Misra RK (2012) Establishing woody perennials on hostile soils in arid and semi-arid regions – A review. *Plant and Soil* **360**, 55-76.

STATEMENT OF AUTHORSHIP

Establishing woody perennials on hostile soils in arid and semi-arid regions – A review. Plant Soil 360, 55-76.

AZAM G (Candidate)

Collected, analysed and interpreted literature, wrote manuscript. I hereby certify that the statement of the contribution is accurate.

Signed Date 26/7/2013

GRANT CD

Supervised writing, reviewed and edited manuscript. I hereby certify that the statement of the contribution is accurate.

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NUBERG IK

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MURRAY RS

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MISRA RK

Reviewed and edited manuscript. I hereby certify that the statement of the contribution is accurate.

Signed Date 5·7·13

Azam, G., Grant, C.D., Nuberg, I.K., Murray, R.S. & Misra, R.K. (2012) Establishing woody perennials on hostile soils in arid and semi-arid regions – A review.
Plant and Soil, v. 360 (1), pp. 55-76.

CHAPTER 3

MAXIMUM ROOT GROWTH PRESSURES OF TREE AND PEA SEEDLINGS

The work contained in this chapter has been published as a research paper in *Plant and Soil*.

Azam G, Grant CD, Misra RK, Murray RS, Nuberg IK (2012) Growth of tree roots in hostile soil: A comparison of root growth pressures of tree seedlings with peas. *Plant and Soil* **368**, 79-80.

STATEMENT OF AUTHORSHIP

Growth of tree roots in hostile soil: A comparison of root growth pressures of tree seedlings with peas. Plant and Soil 368, 79-80.

AZAM G (Candidate)

Experimental development, measured root growth pressures for all species, data analysis and critical interpretation, wrote manuscript. I hereby certify that the statement of the contribution is accurate.

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GRANT CD

Supervised development of work, data analysis and interpretation, reviewed and edited manuscript. I hereby certify that the statement of the contribution is accurate.

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MISRA RK

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MURRAY RS

Supervised development of work, reviewed and edited manuscript. I hereby certify that the statement of the contribution is accurate.

Signed Date 30/7/13

NUBERG IK

Supervised development of work, reviewed and edited manuscript. I hereby certify that the statement of the contribution is accurate.

Signed Date 26/7/2013

Azam, G., Grant, C.D., Misra, R.K., Murray, R.S., & Nuberg, I.K. (2012) Growth of tree roots in hostile soil: A comparison of root growth pressures of tree seedlings with peas.
Plant and Soil, v. 368 (1), pp. 569-580.

CHAPTER 4

RELATIVE SUCCESS OF THE PRIMARY AND LATERAL ROOTS OF PEA AND DIFFERENT TREE SEEDLINGS GROWING IN HARD SOILS

The work contained in this chapter has been submitted as a research paper to *Soil Research.*

Azam G, Grant CD, Murray RS, Nuberg IK, Misra RK (2013). Relative success of the primary or lateral roots of pea and different tree seedlings growing in hard soils. *Soil Research* (Submitted No. SR13-201).

Abstract

Establishment and survival of tree seedlings in hard soils depends on producing deep root systems. This study evaluated the primary and lateral roots of an annual (*Pisum sativum*) and several tree species (*Acacia salicina, Eucalyptus camaldulensis, E. leucoxylon* and *E. kochii*) growing in soil of varying strength. We grew peas and acacias by direct seeding, plus three eucalypts by direct seeding and transplanting, and measured various root characteristics.

At all levels of soil compaction, the primary roots of acacia were relatively thicker and they elongated faster than those of the eucalypts. However, lateral roots of transplanted eucalypts elongated faster than their primary roots, and the rate of root elongation was negatively correlated with soil penetration resistance, especially for *E. camaldulensis*. The primary root diameters for all plants increased with increasing penetration resistance but acacia roots continued to elongate faster than those of peas. Peas produced most of their roots in the top 5 cm, whereas tree roots were more uniformly distributed with depth. Although it was not statistically significant at $P = 0.05$, the relative rate of root elongation in very hard soil correlated modestly ($P = 0.11$) with the maximum root growth pressure for the four tree species. These variations in root growth behaviour can be related to the intrinsic variability of root characteristics (e.g. architecture and size roots) for each plant species and the natural abundance of each species in different environments.

STATEMENT OF AUTHORSHIP

Relative success of the primary or lateral roots of pea and different tree seedlings growing in hard soils. Soil Research (submitted No. SR13-201).

AZAM G (Candidate)

Experimental development, measured root growth pressures for all species, data analysis and critical interpretation, wrote manuscript. I hereby certify that the statement of the contribution is accurate.

Signed Date 26/7/2013

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Introduction

Revegetation of agricultural landscapes with trees has attracted much attention over the last three decades (e.g., Simpfendorfer 1975; Hillis and Brown 1984; Stirzaker et al. 2002; Donohue et al. 2009). Plant establishment, however, remains highly variable especially in lower rainfall regions where seasonally dry environments often coincide with hard soils (Azam et al. 2012). High soil strength (i.e., > 2 MPa penetration resistance) is one of the greatest limiting factors for tree establishment (Kozlowski 1999). In these situations, plant roots (especially the primary axes) must be able to grow rapidly and take advantage of the temporal availability of water and nutrients before the topsoil becomes dry and impenetrable (Lloret et al. 1999). It could therefore be argued that trees having roots that can ramify and explore the subsoil quickly during the first growing season may have an ecological advantage over those that grow more slowly (Grime 1977).

The ability of roots to penetrate hard soils varies among tree species (Kozlowski 1999; Alameda and Villar 2009). Azam et al. (2012, 2013a) argued that the natural spatial distribution of trees growing in low rainfall zones could be related to genetic variations in the important root characteristics shown in Table 1. Plants that can exert large axial root growth pressures, for example, can elongate their roots faster without significant root thickening (Bengough 2012).

The question arises as to whether variations in root growth characteristics can be used to identify more robust trees for planting on hard soils in seasonally dry regions. Other factors, of course, also need to be taken into account in any such analysis. For example, seed size is known to correlate positively with root growth rate (Lloret et al. 1999) but it is still a matter of supposition that larger seeds and growth rates might coincide with greater penetration of hard soils. Planting method is also important here because it controls which roots (primary or lateral) are exposed to the soil first. When trees are direct seeded, for example, the primary roots must do the initial soil exploration, whereas transplanted seedlings use their lateral roots for exploration. Although we know that both primary and lateral roots respond to soil compaction (Misra and Gibbons1996; Zou et al.2001) we do not understand the extent to which the predominance of one type of root or the other might confer an advantage in hard soils. A better understanding of the effects of seed size, plant species and planting method on early plant establishment would increase the chances of successful revegetation on hard soils exposed to seasonally dry conditions.

Table 1. Variation in root characteristics of various plant species that may affect their ability to penetrate hard soils

Important root characteristic for penetrating hard soil	**Species**	**Reference**
High turgor pressure of root cells High extensibility of root cell walls (rapid growth rate)	*Zea mays* (L.)	Barlow 1987
Ability to circum-nutate impenetrable objects	Several annual crops and trees	Barlow et al. 1994
Ability to explore biopores and cracks	*Avena sativa* (L.)	Ehlers et al. 1983
Ability to lubricate soil to reduce friction	*Zea mays* (L.)	Bengough and Mullins 1991
Ability to thicken behind root tip to exert radial pressure	Several annual crops	Clark et al. 2003; Lipiec et al. 2012; Materechera et al. 1991
Ability to exert high axial tip pressure to displace soil	Several annual crops and trees	Azam et al. 2013a;Barley 1962; Bengough 2012; Cockroft et al. 1969

The present paper follows work conducted by Azam et al.(2013a) which found significant variation in root growth rates and maximum axial root growth pressures (σ_{max}) exerted by young roots of several different tree species. The extent to which this variation correlates with the performance of these species in terms of root growth in hard soils is the subject of the current paper. We compacted soil to varying extents and grew four tree species (one Acacia and three Eucalyptus species) and an annual reference crop (*P. sativum*) in experiments designed to account for the effects of variation in seed size, root growth pressure, and planting method on root diameter, total root length, root elongation rate and root distribution with depth.

Materials and methods

Soil characterization

A non-saline (electrical conductivity of saturated paste extract = 0.49 ± 0.05 dS m^{-1}), slightly alkaline (pH of saturated paste extract = 7.6 ± 0.2), loamy sand (87% of 200-20 μm, 7% of 20-2 μm and 6% of < 2μm) was collected from Monarto, South Australia (latitude 35° 5' S, longitude 139°4'E), air-dried and sieved through a 2 mm mesh. It was a top soil (5-20 cm depth) that contained 1.30% organic carbon, 53 mg kg^{-1} total N and 230 mg kg^{-1} P. A simple compaction test (Proctor 1933) was conducted to determine the optimum gravimetric water content (θ) for efficient compaction (found to be 0.14 kg kg^{-1}). To ensure the volumetric air content of the most densely-packed soil (i.e., 1750 kg m^{-3}) did not impose poor soil aeration (Wesseling and van Wijk 1957) the soil was wetted at a slightly lower water content of θ = 0.12 kg kg^{-1} before packing; this ensured the volumetric air content of the soil was always ε_{air} > 0.10 m^3m^{-3} (Table 2).

Table 2. Total porosity (ε, m^3 m^{-3}), volumetric air content ($\varepsilon_{air,}$ m^3 m^{-3}) and penetration resistance (SR, MPa) of soil calculated from soil water retention and soil penetration resistance curves for five bulk densities. SR was calculated at a constant volumetric water content of 0.22 m^3m^{-3}. Mean values are followed by the standard error (SE, *n* = 3) of the variables.

Bulk density (kg m^{-3})	ε ± SE (m^3 m^{-3})	ε_{air} ± SE (m^3 m^{-3})	SR ± SE (MPa)
1350	0.49 ± 0.00	0.27 ± 0.00	0.3 ± 0.1
1450	0.45 ± 0.01	0.23 ± 0.01	0.7 ± 0.1
1550	0.41 ± 0.00	0.20 ± 0.00	1.1 ± 0.1
1650	0.38 ± 0.00	0.16 ± 0.00	2.3 ± 0.3
1750	0.35 ± 0.00	0.13 ± 0.00	4.8 ± 0.6

Soil volumetric water retention curves were determined at five different bulk densities (1350, 1450, 1550, 1650 and 1750 kg m^{-3}) using three replicated soil samples. Soil was moistened and packed incrementally in stainless steel cylindrical rings (70 mm internal diameter, 50 mm height) to the required bulk densities using five hydraulically controlled piston pressures (Fig. 1). The packed soil samples were then saturated and placed on porous ceramic plates connected to either hanging columns of water (0.001, 0.0033 and 0.01 MPa) for 48 hours, then sealed in pressure chambers (models 1500F1 and 1600, Soilmoisture Equipment Corp., Santa Barbara, California) set at 0.033 MPa for 2 weeks, then 0.1 and 0.5 MPa for 3 weeks, and finally 1.5 MPa for 5 weeks. When samples came to equilibrium, which was checked by repeated weighing until constant weight at the given pressure, the final weight was recorded. The resistance to a penetrometer (SR) was then measured using an automated cone-penetrometer having a recessed shaft and cone-base diameter of 2.38 mm with tip semi-angle 30° (model Lloyd LFPlus 1 kN, CSC Force Measurement Inc, Agawam, Massachusetts, USA); the penetrometer advanced at a constant speed of 3 mm min^{-1}. The force required to push the cone into the hardest soils exceeded the capacity of the Lloyd instrument (5.5 MPa) so it was not possible to measure SR for the two driest and greatest bulk densities. For the SR profile in each soil sample, the penetration force was averaged over 25 to 45 mm depth then divided by the cross sectional area of the penetrometer cone to obtain a mean SR (MPa) at each matric suction and bulk density (Fig. 2). The five curves in Fig. 2 were used to select appropriate packing densities and watering regimes for the plant growth experiments. The mean saturated hydraulic conductivity (K_s) was measured on the soil samples and found to range from 2 mm h^{-1} (most compacted soil) up to 53 mm h^{-1} (least compacted soil), which indicated that hydraulic restrictions were not a problem even in the most compacted soil.

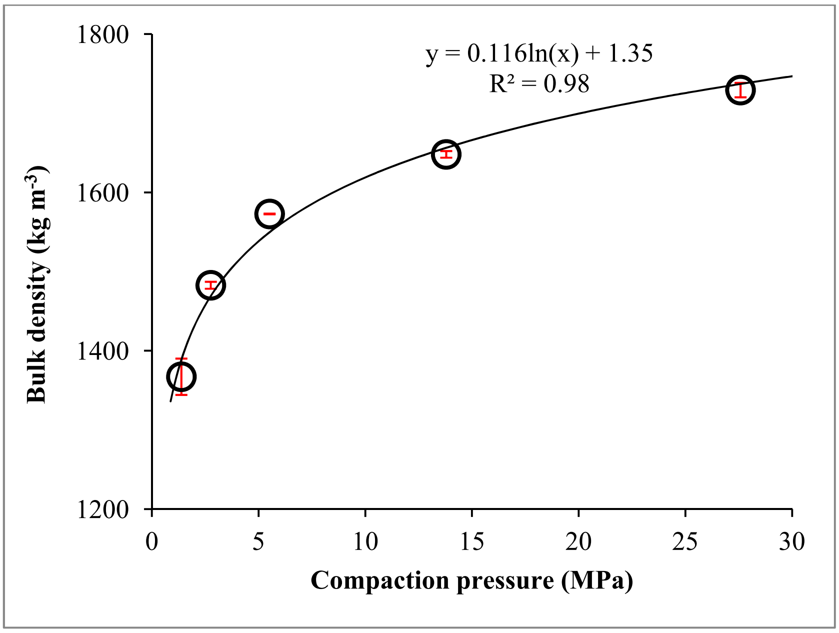

Fig. 1. Bulk density (kg m^{-3}) of soil samples as a function of the hydraulic pressure (MPa) applied to compact them at a fixed gravimetric water content of 0.12 kg kg^{-1}. Vertical bars represent standard errors of the mean bulk density.

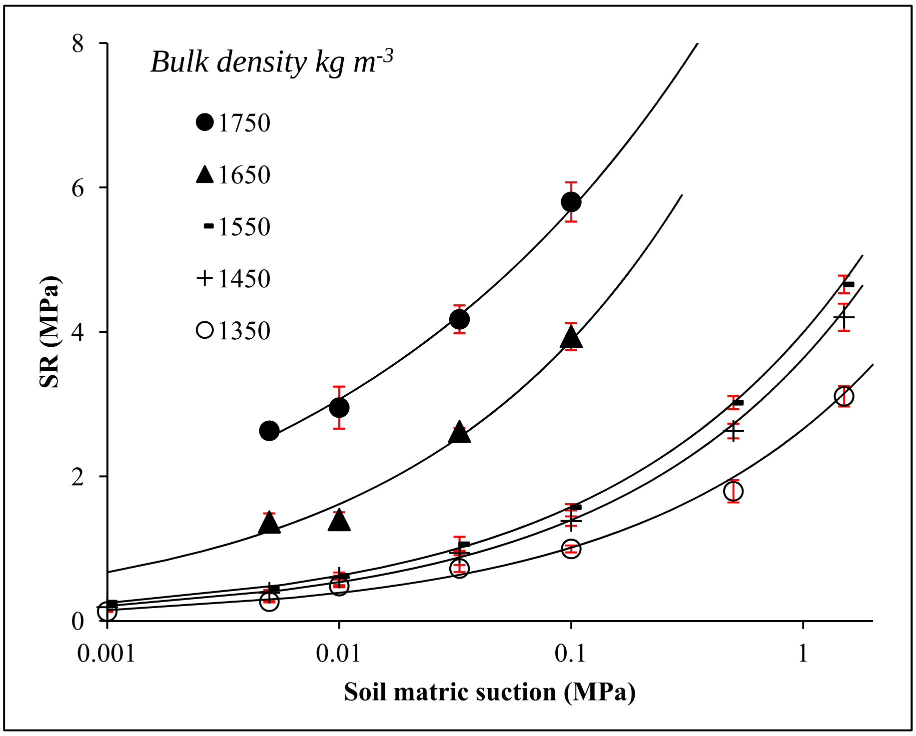

Fig. 2. Mean soil penetration resistance, SR, (MPa) as a function of the soil matric suction (MPa) at different bulk densities (kg m^{-3}). Vertical bars represent standard errors of the mean SR.

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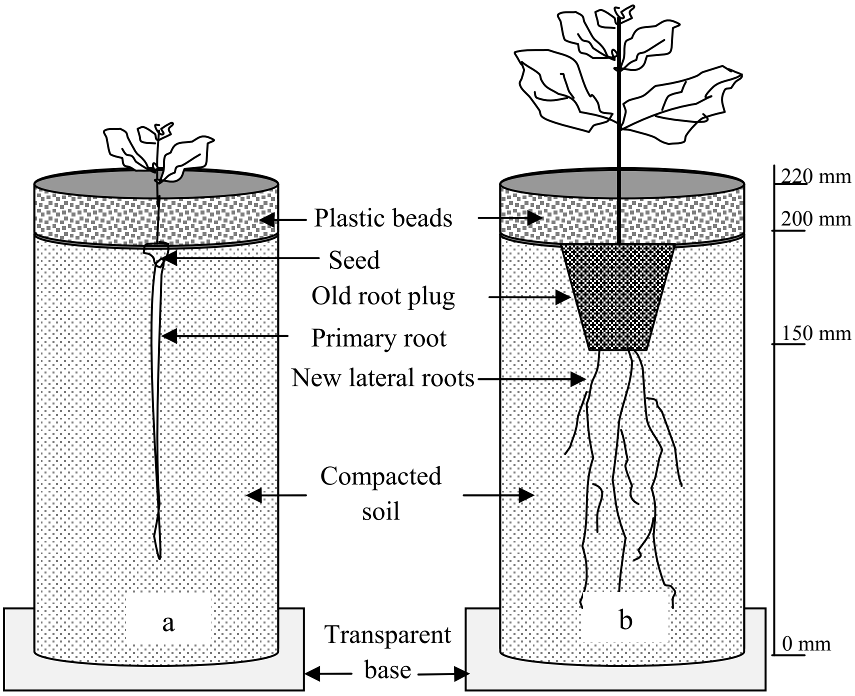


Fig. 3. Schematic view of a planting pot used in (a) direct seeding, and (b) transplanting experiments.

Preparation of PVC containers for plants

Moist soil (θ = 0.12 kg kg^{-1}) was packed into rigid PVC pots (220 mm height, 70 mm diameter) having transparent plexiglass bases, which enable us to observe the average time it took for roots to approach the bottom of each pot (Figs 3a and 3b). Soil was packed to the five bulk densities mentioned above by adding small increments of moist soil under the appropriate hydraulic compaction pressure. Soil was added until its height was 20 mm from the top of the pots (i.e., soil sample height = 200 mm) as shown in Figures 3a and 3b. All pots were fertilized with 5 mL of a nutrient solution containing 5.0 mM N, 0.29 mM P and 1.2 mM K plus essential micronutrients according to Ingestad and Lund (1986). Additional water was added to each pot so its volumetric water content was never greater than 0.22 m^3m^{-3}, which ensured sufficient aeration at all times (Table 2). The pots were then sealed and stored for one week in a dark, constant-temperature chamber to allow hydraulic equilibrium and age hardening to occur (Utomo and Dexter 1981).

Planting and maintenance of seedlings

The experiments were conducted in a controlled temperature glasshouse having respective day and night temperatures of 25 ± 2 °C and 18 ± 2 °C. Five plant species, *Pisum sativum* (L.), *Acacia salicina* (Lindl.), *Eucalyptus camaldulensis* (Dehnh.), *E. leucoxylon* (F.Muell) and *E. kochii* (Maiden & Blakely), were selected from those used by Azam et al. (2013a) for use in three different experiments (Table 3). Direct seeding experiments, i.e., experiments 1 and 2, had five compaction treatments; the transplanting experiment, i.e., experiment 3, had four compaction treatments (there was no significant difference between soil penetration resistances of the two lowest compaction treatments, so the lowest compaction treatment was eliminated). The reason for growing Eucalyptus species using two planting methods was that the fine roots of Eucalyptus species were too small to get reliable measurements of root growth pressure (Azam et al. 2013a) so the lateral (larger) roots of transplanted seedlings had to be used instead.

In experiment 1, the two large-seeded species, i.e., *P. sativum* and *A. salicina*, were planted from pre-germinated seeds (direct seeded) and observations were collected on all (i.e., primary and lateral) roots (Table 3). Similarly, in experiment 2, three small-seeded Eucalyptus species, i.e., *E. camaldulensis*, *E. leucoxylon*, and *E. kochii*, were planted from pre-germinated seeds (direct seeded) and observations were also collected on their primary and lateral roots (Table 3). In experiment 3, the same three small-seeded Eucalyptus species were transplanted using 90 day-old seedlings grown from the same seed lot, and data were collected on their newly regenerated lateral roots only (i.e., roots from the early-growth root plug were excluded, Table 3).

For the direct-seeded experiments, three pre-germinated seeds were planted in a circle in each of the three replicated pots. For the transplanting experiment, only one seedling was transplanted into the centre of each pot (three replicates) by packing identical soil around the root plug (50 mm long) at the appropriate bulk density (Fig. 3b). After the seeds or seedlings were planted, 20 mm of polyethylene beads were poured onto the top of each pot (Figs 3a and 3b), which reduced evaporation by 82 ± 2%. Plants were watered to predetermined weight at sunset, daily, and if hot weather was forecast an additional watering was made at 0900 h that day. The large-direct-seeded species and the transplanted species were harvested 14 days after planting or transplanting, whereas the small-direct-seeded species grew much more slowly and had to be harvested later, 35 days after planting.

Table 3. Overview of the three experiments in factorial design

Experiment	Treatment and replication	Measurements					
		R	L	L_{Depth}	D_{Prim}	D_{Lat}	SR
1. Direct seeding	2 Species (*P. sativum*, *A. salicina*) × 5 bulk densities × 3 replicates	x	x	x	x	x	x
2. Direct seeding	3 Species (*E. camaldulensis, E. leucoxylon*, *E. kochii*) × 5 bulk densities × 3 replicates	x	x	x	ND	x	x
3. Transplanting	3 Species (*E. camaldulensis, E. leucoxylon*, *E. kochii*) × 4 bulk densities × 3 replicates	x	x	ND	ND	x	x

SR, soil penetration resistance; D_{Prim}, diameter of primary roots; D_{Lat}, diameter of lateral roots; R, rate of root elongation; L, total root length per plant; L_{Depth}, total root length per plant by depth; x, determined; ND, not determined.

Measurement of penetration resistance and plant growth

At multiple intervals each day the transparent base of each pot was observed to determine whether the roots had reached the bottom of the pot. When roots appeared at the bottom, the time was noted and the root elongation rate, R, was estimated from the length of the soil sample (200 mm) divided by the time at which the first roots appeared at the bottom of the pot. The length of the soil sample used in the transplanting experiments was only 150 mm because the newly grown lateral roots regenerated from the bottom of the (50 mm long) root plug (see Fig. 3b). In the two most compacted treatments, no roots reached the bottom of the pots; for these treatments, roots were simply washed from the soil using a 0.5 mm sieve and the length of their main axes was measured directly with a ruler (± 0.5 mm accuracy); the root elongation rate for these pots was calculated by dividing the length of the main root axis by the duration of experiment.

At the nominated harvest time shoots were clipped at their bases and then soil penetration resistance was measured to a depth of 50 mm on each of the three replicated undisturbed pots. For the direct seeding experiments, the soil sample was divided into four equal horizontal layers (5 cm thick) to quantify the vertical distribution of roots in each layer. Roots were separated from the soil in each of the three experiments using a gentle jet of water over a 0.5 mm sieve. For experiment 1, the primary root (of the large-seeded species) was separated from its lateral roots to measure its mean diameter and length using a high-resolution scanner (600 dpi) combined with WinRhizo image analysis software (v. 2005c; Régent Instruments 2005, Sainte-Foy, Quebec City). For experiment 2, the primary and lateral roots were sufficiently similar in size that they could not be separated from each other, so all roots were scanned together to measure the mean diameter and length of all roots. For experiment 3, all root measurements were taken on all the roots in whole soil sample rather than subdividing the soil into layers.

Statistical analyses

Factorial designs were used for all the experiments (see Table 3). Data were first subjected to a normality test of the variance to verify the requirement for analyses of variance (ANOVA). Data on soil penetration resistance, SR, diameter of roots, DR, total root length, L, and rate of root elongation, R, were all found to be normally distributed and were thus subjected to a two-way ANOVA with the factors: plant species, compaction levels and their interactions at a significance level of $P = 0.05$ using GenStat for Windows (ed 14, VSN International, Hemel Hempstead, Hertfordshire, UK). The distribution of root lengths in the four layers for experiments 1 and 2 was skewed toward much greater root lengths in the top layer, so the data for each layer was log-transformed using $\ln(1+ L_{Depth})$ to achieve a normal distribution. This enabled the data to be subjected to a three-way ANOVA with the factors: plant species, soil compaction, soil depth and their interactions at a significance level of P = 0.05 using GenStat. Mean L_{Depth} values for each depth were back-transformed using procedures outlined in Misra et al. (1998).

Results

Table 4 summarizes the effects of plant species (S), soil compaction (C), and the interaction of S × C on various root growth parameters in three different experiments. Obviously, soil resistance increased significantly (P = 0.05) with increasing bulk density (Fig. 4) although there was no significant difference in SR for the two lowest bulk densities, so the lowest density (1350 kg m^{-3}) was eliminated in experiment 3.

Table 4. Summary of the analyses of variance to evaluate the effect of plant species, S, soil compaction, C, and their interaction, S × C, on rate of root elongation, R, total root length per plant, L, diameter of primary and lateral roots, D_{Prim} and D_{Lat}, and soil penetration resistance, SR, of five plant species in three different experiments.

Experiment	Factor	Parameters				
		R	L	D_{Prim}	D_{Lat}	SR
1	Species	*	***	***	**	NS
	Compaction	***	NS	***	**	***
	S × C interaction	NS	NS	***	NS	NS
2	Species	NS	***	ND	***	NS
	Compaction	***	***	ND	***	***
	S × C interaction	NS	NS	ND	NS	NS
3	Species	***	***	ND	***	NS
	Compaction	***	***	ND	***	***
	S × C interaction	***	NS	ND	NS	NS

Significant treatment effects at $P \leq 0.001$, $P \leq 0.01$ and $P \leq 0.05$ are indicated as ***, ** and *, respectively; no significant treatment effect at $P = 0.05$ is indicated as NS.

ND = not determined.

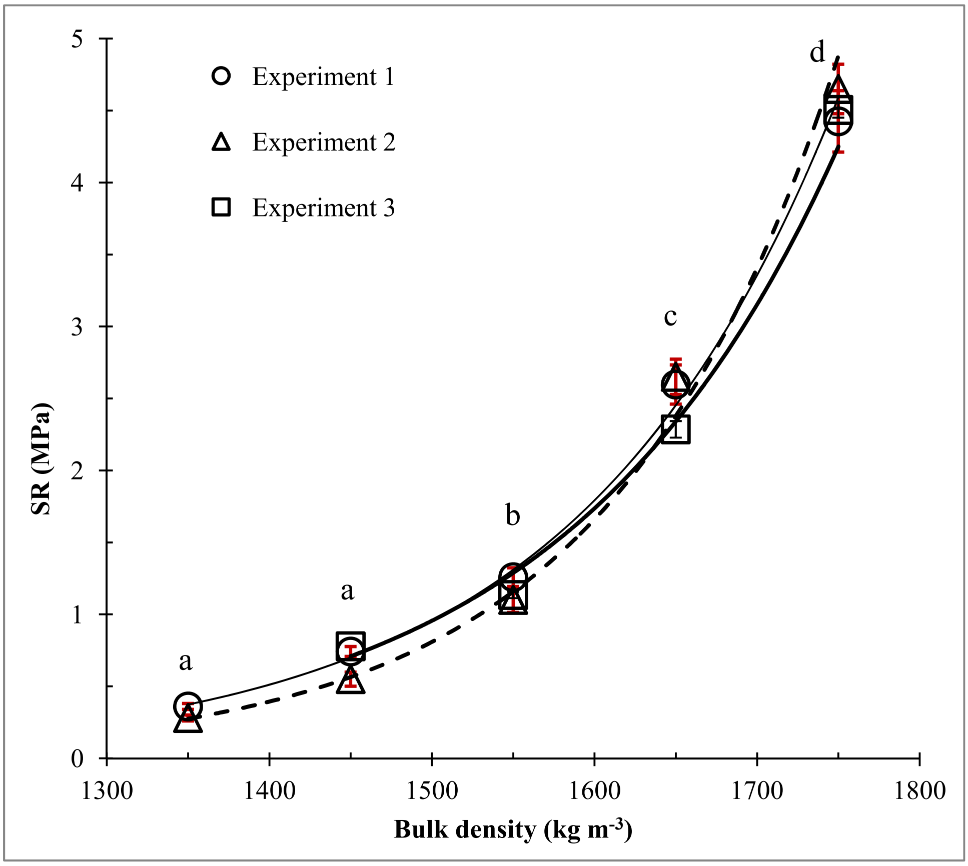


Fig. 4. Soil penetration resistance, SR, (MPa) at harvest as a function of the soil bulk density (kg m^{-3}). Mean values with a different letter are significantly different ($P \leq 0.05$) when compared with the least significant difference, LSD. Vertical bars represent standard errors of the mean SR.

Rate of root elongation

For the two large-seeded species (experiment 1), the rate of root elongation, R , depended significantly on plant species at all levels of compaction (Table 4). The mean values of R for the two large-seeded species decreased significantly as bulk density increased ($P = 0.05$, Table 5). Overall, roots of *A. salicina* elongated significantly faster (0.89 ± 0.11 cm d^{-1}) than those of *P. sativum* (0.78 ± 0.11 cm d^{-1}). Among the direct-seeded Eucalyptus species (experiment 2), the mean elongation rates of primary roots were similar for all species (Table 4) and declined significantly with increasing compaction ($P = 0.05$, Table 5). Among the transplanted Eucalyptus species (experiment 3), the mean elongation rate of lateral roots also declined significantly with increasing compaction ($P = 0.05$) but the effects were more pronounced in some species (as indicated by a significant interaction for S × C in Table 4). For example, R declined significantly with each incremental increase in bulk density for the species in the order *E. camaldulensis* > *E. leucoxylon* > *E. kochii*. At the highest bulk density of ≥ 1650 kg m^{-3} there was no significant difference in R between these species (P = 0.05, Table 5).

Table 5. Mean rate of root elongation, R, as influenced by bulk density and plant species in all 3 experiments. Significant interaction between plant species and soil compaction is shown for experiment 3 only. For first 2 experiments, mean values with a different superscripted letter are significantly different ($P \leq 0.05$) when compared with the least significant difference, LSD. For experiment 3, different letters denote significantly different ($P \leq 0.05$) values in both rows and columns when compared with the LSD. ND means the measurement was not made at the given bulk density.

Experiment	Species	R (cm d^{-1}) at different bulk density (kg m^{-3})					LSD
		1350	1450	1550	1650	1750	(cm d^{-1})
1	Mean of two species	1.35^{a}	1.41^{a}	1.00^{b}	0.29^{c}	0.13^{c}	0.17
2	Mean of three species	0.70^{a}	0.67^{a}	0.62^{a}	0.13^{b}	0.08^{b}	0.08
3	*E. camaldulensis*	ND	2.67^{a}	2.17^{b}	1.30^{d}	0.53^{f}	0.27
	E. leucoxylon	ND	1.98^{bc}	1.77^{c}	1.23^{d}	0.60^{ef}	
	E. kochii	ND	1.40^{d}	1.43^{d}	0.86^{e}	0.37^{f}	

In all three experiments the rate of root elongation relative to its maximum rate, R/R_{max}, (Dexter 1987) declined exponentially with increasing soil penetration resistance (SR). The effect of compaction on the different species is shown in Figs 5a, 5b, and 5c and can be quantified using the relation of Misra and Gibbons (1996):

$$\frac{R}{R_{\max}} = e^{-\alpha\, SR} \qquad (1)$$

where α is a freely adjustable fitting parameter (MPa^{-1}). Equation (1) can be equated to Dexter's (1987) relation to describe the effects of compaction on root growth relative to a critical point, $SR_{0.5}$:

$$\frac{R}{R_{\max}} = e^{-0.6931 \frac{SR}{SR_{0.5}}} \qquad (2)$$

where $SR_{0.5}$ is the soil penetration resistance at which the relative root elongation rate is halved, $\frac{R}{R_{\max}} = 0.5$ and where -0.6931 = ln(0.5).

By equating and rearranging Equations (1) and (2) we can obtain values of $SR_{0.5}$ for each species and these are shown in Table 6:

$$SR_{0.5} = \frac{0.6931}{\propto} \qquad (3)$$

Table 6. Soil penetration resistance at which the relative rate of root elongation was halved ($SR_{0.5}$) as calculated from Equations (1) and (3) for each species

Experiment	Species	Fitting parameter, α (MPa^{-1}) from Equation (1)	Mean α (MPa^{-1})	$SR_{0.5}$ (MPa^{-1}) from Equation (3)	Mean $SR_{0.5}$ (MPa^{-1})
1	*P. sativum*	0.6502	-	1.07	-
	A. salicina	0.4433		1.56	
2	*E. camaldulensis*	0.5042	0.5	1.37	1.5
	E. leucoxylon	0.4862		1.43	
	E. kochii	0.4457		1.56	
3	*E. camaldulensis*	0.3482	0.3	1.99	2.5
	E. leucoxylon	0.2514		2.76	
	E. kochii	0.2519		2.75	

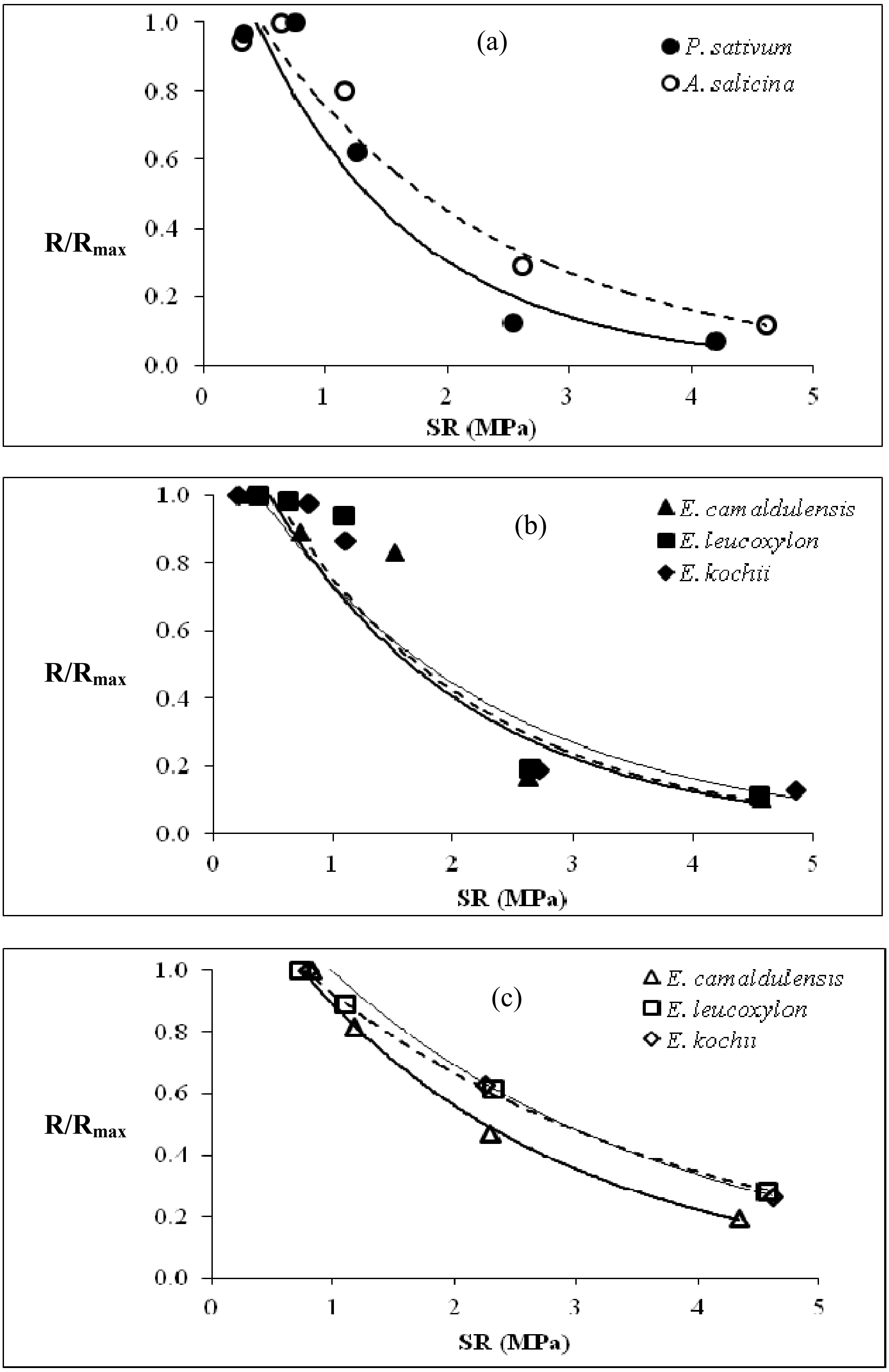


Fig. 5. Relative rate of root elongation, $\frac{R}{R_{\max}}$, as a function of soil penetration resistance, SR, (MPa) for (a) primary roots of direct-seeded *P. sativum* and *A. salicina*, (b) primary roots of direct-seeded *Eucalyptus* species, and (c) lateral roots of transplanted *Eucalyptus* species.

Total length of roots

In experiment 1, the total length of roots, L, was significantly affected by plant species, and it depended on neither soil compaction nor the interaction between plant species and soil compaction (Table 4). At all levels of compaction the mean total root length was significantly greater for *P. sativum* (1.28 ± 0.15 m) than for *A. salicina* (0.33 ± 0.06 m).

Table 7. Mean total root length, L, in experiments 1, 2 and 3 as influenced by soil bulk density (compaction). Mean values with a different superscript letter for a given experiment (data row) are significantly different ($P \leq 0.05$) when compared with the least significant difference, LSD. ND means the measurement was not made at the given bulk density

Experiment	L (m plant^{-1}) at different bulk density (kg m^{-3})					LSD
	1350	1450	1550	1650	1750	(m plant^{-1})
1	1.35^{a}	1.41^{a}	1.00^{a}	0.29^{b}	0.13^{b}	0.46
2	2.96^{a}	2.52^{ab}	1.83^{bc}	1.20^{c}	0.88^{c}	0.96
3	ND	17.6^{a}	14.6^{a}	9.91^{b}	8.34^{b}	3.10

For the direct-seeded and transplanted Eucalyptus seedlings (i.e., experiments 2 and 3), there were significant compaction- and plant species-effects but no interactions at P = 0.05 (Table 4). For example, in experiment 2, *E. camaldulensis* seedlings produced significantly (P = 0.05) greater mean total root length (3.04 ± 0.47 m) than did *E. leucoxylon* (1.44 ± 0.23 m) and *E. kochii* (1.15± 0.18 m). Similarly, in experiment 3, *E. camaldulensis* seedlings produced significantly (P = 0.05) greater mean total root length (16.42 ± 2.01 m) than those of *E. leucoxylon* (10.56 ± 0.87 m) and *E. kochii* (10.83 ± 0.74 m).

Mean total root length decreased significantly for all species with increasing compaction (P = 0.05) but the level of compaction at which total root length declined varied among species. For example, significant reductions in total root length occurred for *E. camaldulensis* when bulk density increased to 1550 kg m^{-3} whereas significant reductions (P = 0.05) only occurred for *E. leucoxylon* and *E. kochii* only when bulk density exceeded 1650 kg m^{-3}. In experiment

3 differences among species were not statistically significant once bulk density exceeded 1550 kg m^{-3}.

Root diameter

In experiment 1 (involving *Pisum* and *Acacia*), the diameter of the primary roots, D_{Prim}, increased significantly (P = 0.05) with compaction, C, and differed according to plant species, S; the significant interaction term, S × C, in Table 4 suggests the magnitude of the compaction effect depended on plant species. *P. sativum* produced significantly thicker (P = 0.05) primary roots (1.72 ± 0.11 mm) than those of *A. salicina* (1.09 ± 0.06 mm).

In all three experiments, the diameter of the lateral roots, D_{Lat} increased significantly (P = 0.05) with compaction and this differed for each plant species but there were no interaction effects (i.e., none of the S × C interaction terms for D_{Lat} in Table 4 was significant at P = 0.05). For example, *P. sativum* produced significantly thicker (P = 0.05) lateral roots (0.84 ± 0.03 mm) than *A. salicina* (0.72 ± 0.03 mm) in experiment 1. Direct-seeded *Eucalyptus camaldulensis* produced significantly thicker (P = 0.05) roots (0.50 ± 0.02 mm) than both *E. leucoxylon* (0.41 ± 0.02 mm) and *E. kochii* (0.45± 0.03 mm) in experiment 2. Finally, the transplanted *E. camaldulensis* (0.62 ± 0.02 mm) and *E. leucoxylon* (0.65 ± 0.02 mm) produced significantly thicker (P = 0.05) lateral roots than *E. kochii* (0.51 ± 0.02 mm) in experiment 3.

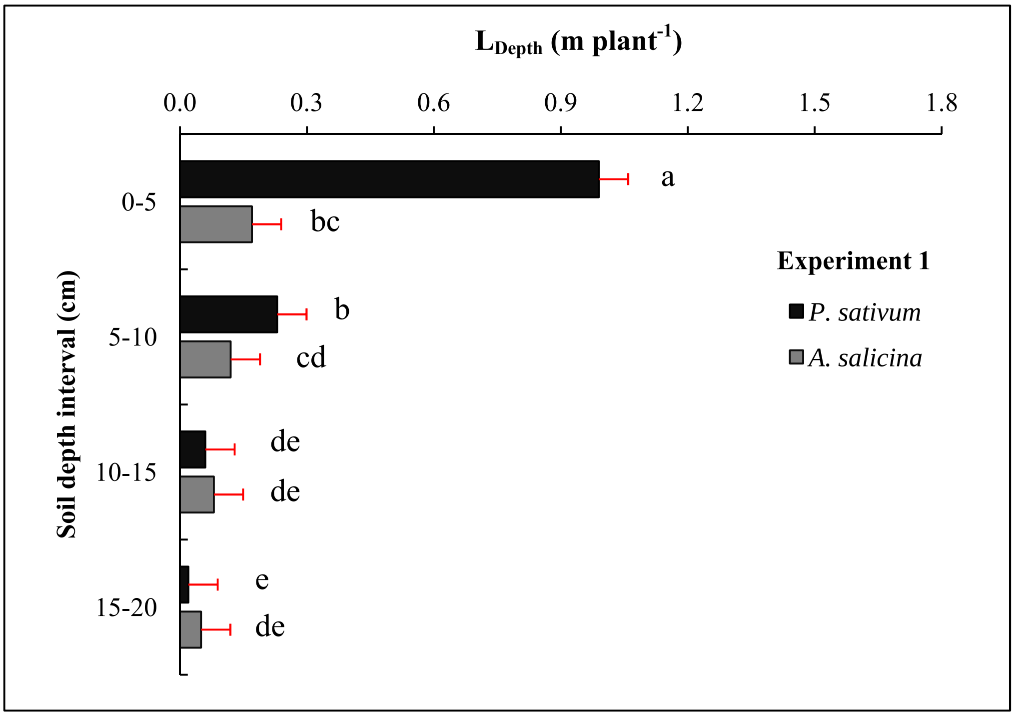
Distribution of roots with depth (direct seeded only)

The statistical significance of the variables and their interactions on root distribution with depth are summarized in Table 8. In both experiments 1 and 2, there were significant interactions ($P \leq 0.05$) between species and soil depth which influenced the distribution of roots with depth. Figure 6 shows that most of the roots for all species grew in the top few centimetres of soil (0-5 cm layer); this was especially so for the more compacted soils. In particular, the 14-day old *P. sativum* plants (experiment 1) and the 35-day old seedlings of *E. camaldulensis* (experiment 2) had a greater proportion of their roots in the top 5 cm compared to other species, whose roots were more uniformly distributed with depth (Figure 6). In experiment 2 however *E. camaldulensis* produced significantly greater total root length than those of other Eucalyptus species. At the relatively high bulk density of 1650 kg m^{-3}, *A. salicina* roots grew into the 5-10 cm layer within only two weeks (experiment 1) whereas none of the Eucalyptus species used in experiment 2 produced any roots in that soil depth at the same level of compaction, even after five weeks following germination (data not presented). Furthermore, there were no significant differences in the distribution of roots among the three direct-seeded Eucalyptus species (Figure 6).

Table 8. Summary of the analyses of variance to evaluate the effect of plant species, S, soil compaction, C, soil depth, D, and their interactions on total root length per plant in experiment 1 and 2.

Factor	Total root length, L (m plant^{-1})	
	Experiment 1	Experiment 2
Species	***	***
Compaction	**	***
Depth	***	***
Interactions		
S × C	NS	***
S × D	***	***
C × D	NS	***
S × C × D	NS	NS

Significant treatment effects at $P \leq 0.001$ and $P \leq 0.01$ are indicated as *** and **, respectively; no significant treatment effect at $P = 0.05$ is indicated as NS.



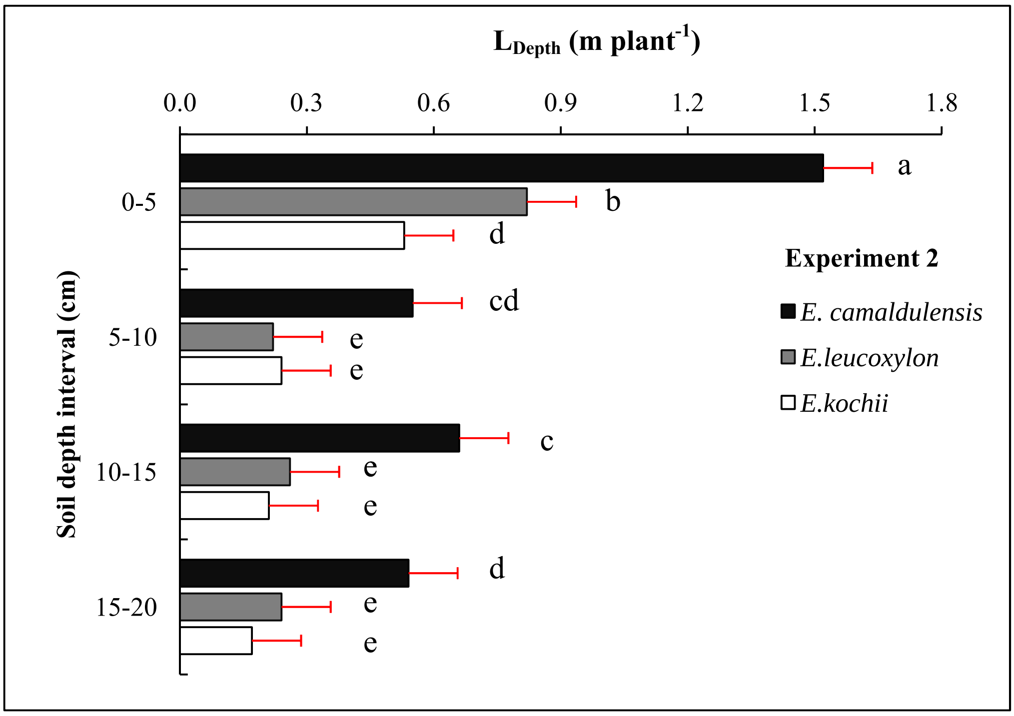


Fig. 6. Mean total root length L (m plant^{-1}) as influenced by the interaction between plant species and soil depth in experiment 1 and 2. Significant interaction between plant species and soil depth is shown for both experiments. Mean values with a different letter are significantly different ($P \leq 0.05$) when compared with the least significant difference, LSD. Horizontal bars represent the LSD values for the interactions.

Discussion

Root elongation rate

The magnitudes of α and $SR_{0.5}$ shown in Table 6 suggest the relative growth rate of *P. sativum* roots is more sensitive to compaction than that of the trees, although there is insufficient data at present to assign statistical significance. Table 6 shows that $\frac{R}{R_{\max}}$ was halved for *P. sativum* by soil compaction in the order of only 1 MPa ($SR_{0.5}$ = 1.07 MPa), whereas it took over 1.5 MPa to halve the relative growth rate of *A. salicina* roots ($SR_{0.5}$ = 1.56 MPa) and 2 to 2.8 MPa to halve the relative rates for the lateral roots of the transplanted trees.

Among the three direct-seeded Eucalyptus species (experiment 2) there were no significant differences in $\frac{R}{R_{\max}}$ (Fig. 5b); their α values averaged 0.5 MPa^{-1}, and their $SR_{0.5}$ values averaged 1.5 MPa, which was similar to *A. salicina* and greater than *P. sativum* (Table 6). For the transplanted Eucalyptus species (experiment 3) the values of $\frac{R}{R_{\max}}$ responded in a similar manner to the direct seeded Eucalyptus species except that the lateral roots involved here (being larger) showed somewhat less sensitivity to compaction than the (primary) roots of the direct-seeded trees (Fig 5c); their α values were somewhat smaller (mean α = 0.3 MPa^{-1}) and their $SR_{0.5}$values were all greater (mean $SR_{0.5}$ = 2.5 MPa) than those by direct-seeding (Table 6).

The greater elongation rates at low soil compaction for the fast-growing tree, *E. camaldulensis*, relative to those of *E. leucoxylon* and *E. kochii* (Table 5) are consistent with the domination of *E. camaldulensis* in regions that have wetter (i.e., softer) soils (Marcar *et al.* 1995) and thus becomes established faster than other trees. By contrast, *E. leucoxylon* and *E. kochii* have higher $SR_{0.5}$ values than *E. camaldulensis* (Table 6) so they tend to thrive on harder, drier soils than *E. camaldulensis*. For example, *E. kochii* is a small, slow-growing tree that occurs most commonly in the drier regions of Western Australia (Robinson *et al.* 2006). Similarly, in South Australian woodlands where *E. leucoxylon* occurs with *E. camaldulensis*, *E. leucoxylon* is found on shallower, high-altitude areas of the same soil catena (Boomsma and Lewis 1980).

Total root length

In experiment 1, total root length was significantly greater for *P. sativum* than for *A. salicina* because *P. sativum* is highly sensitive to compaction (Hebblethwaite and McGowan 1980) so it produces lateral roots close to the soil surface as an early response (Goss 1977). By contrast, *A. salicina* does not generate laterals so quickly; rather it directs resources into generating large axial root growth pressures over time (Azam *et al.* 2013a) to maintain its root growth rate (Table 5) and continue pushing through the harder soil (Fig. 5a).

Among the three *Eucalyptus* species, *E. camaldulensis* had significantly greater total root length at all levels of soil compaction compared to all other species, regardless of planting method (Table 7). This is presumably why *E. camaldulensis* trees are so much larger than either *E. leucoxylon* or *E. kochii* when they have access to plenty of water and nutrients (Marcar *et al.* 1995).

Although the root lengths of the transplanted *E. leucoxylon* and *E kochii* were somewhat less than for *E. camaldulensis*, they appear to be less sensitive to compaction because their root lengths declined by only 53% (14.4 to 6.8 m plant^{-1}) and 33% (12.5 to 8.4 m plant^{-1}) respectively from the least to the most compacted soil, whereas root lengths for *E. camaldulensis* declined by 62% (25.8 to 9.8 m plant^{-1}) under the same conditions. This is perhaps not surprising in light of the fact that *E. leucoxylon* and *E kochii* both can exert significantly greater axial root growth pressures than for *E. camaldulensis* (Azam et al. 2013a) and they naturally thrive on shallower, drier (i.e., harder) soils than *E. camaldulensis* (Boomsma and Lewis 1980; Robinson *et al.* 2006). The significantly greater total root lengths for the three transplanted *Eucalyptus* species supports the practical finding in the field that transplanted, small-seeded species tend to establish more successfully than those of the direct-seeded trees of the same species with adequate watering and weed control (Clemens 1980;Young and Evans 2000; Azam *et al.* 2013b).

Root thickening

Table 8 suggests that the investment in primary root thickening as a response to compaction was greater for *P. sativum* (D_{Prim} increased from 1.34 to 2.23 mm) than it was for the tree species, *A. salicina* (D_{Prim} increased from 0.83 to 1.37 mm). Materechera *et al.* (1991) suggested that root thickening comes at a cost in terms of soil exploration. On the one hand, thickening may help weaken the soil by opening cracks for further root development but it may also reduce root elongation rates, which can be critical to maintain for survival. In our experiment 1, the difference in root thickening corresponded with a 93% reduction in the root growth rate for *P. sativum* (R dropped from 1.35 to 0.09 cm d^{-1}) versus an 87% reduction in root growth rate for *A. salicina* (R dropped from 1.34 to 0.17 cm d^{-1}) when exposed to bulk densities ranging from 1350 to 1750 kg m^{-3}. This is because tree species such as *A. salicina* develop several layers of suberised cells behind the root tip (Steudle 2000), which makes them less susceptable to cell deformation with increasing soil strength and this allowed them to maintain a greater relative root elongation rate (Lipiec *et al.* 2012).The greater thickening of *P. sativum* roots, by contrast, caused them to invest more energy in thickening (especially at the two higher compaction levels), which left them with less stored energy to maintain elongation rates (Thaler and Pages 1996).

Root distribution

The heavy concentration of *P. sativum* roots in the top 5 cm at all levels of compaction suggests that peas are more sensitive to compaction (Goss 1977; Hebblethwaite and McGowan 1980) than most of the tree species (Fig 6). This was especially so in our experiments at the lower levels of compaction: > 60% of the pea roots were restricted to the top 5 cm, whereas at the same levels of compaction the tree root systems were more uniformly distributed with depth.

Among the tree species, at comparatively high levels of compaction (e.g., bulk density = 1650 kg m^{-3}), *A. salicina* roots grew down into the 5-10 cm layer within only 14 days, whereas none of the Eucalyptus species produced any roots in that layer at the same level of compaction even after 35 days. This suggests that if direct seeding is the only option in the field, large seeded Acacias are better able to penetrate hard soils than small seeded Eucalyptus trees. This also supports the observation that when species of Acacia and Eucalyptus are mixed-seeded, the Acacias establish themselves first as pioneer species during the first 2-3 years and thereby creates a favorable microclimate for the subsequent establishment of Eucalyptus species (Richardson *et al.* 2011; Azam *et al.* 2013b). Lack of any significant difference in root distribution of three direct-seeded Eucalyptus species implies no superiority of one Eucalyptus species over another, especially immediately after germination.

Relation between root growth pressure and root growth rate

Figures 5a, 5b and 5c and Table 5 suggest there is species variation in the way root elongation rates decline in response to soil compaction. It has been postulated that sustained high axial root growth pressures may play a crucial role in maintaining root elongation rates of plants growing in hard soils (Bengough 2012; Azam *et al*. 2013a). This idea can be at least partly evaluated by plotting the relative root growth rates (3 replicates) found in the most compacted soils (bulk density 1750 kg m^{-3}) against the maximum axial root growth pressures (≥ 9 replicates) reported for the same species by Azam *et al*. (2013a). Only four species are currently available for this analysis (Fig. 7) but the linear dependency was fair ($R^2 = 0.79$) and the relationship was significant at $P = 0.11$. While this level of significance is not strong, it is still possible to speculate that in very hard soils (particularly in the absence of biopores and cracks) species that can exert greater axial root growth pressures may be able to maintain somewhat greater root elongation rates (Fig. 7). Given that only 4 points (i.e., 4 species) were used in this analysis, the veracity of this idea requires further testing using a wider range of plant species.

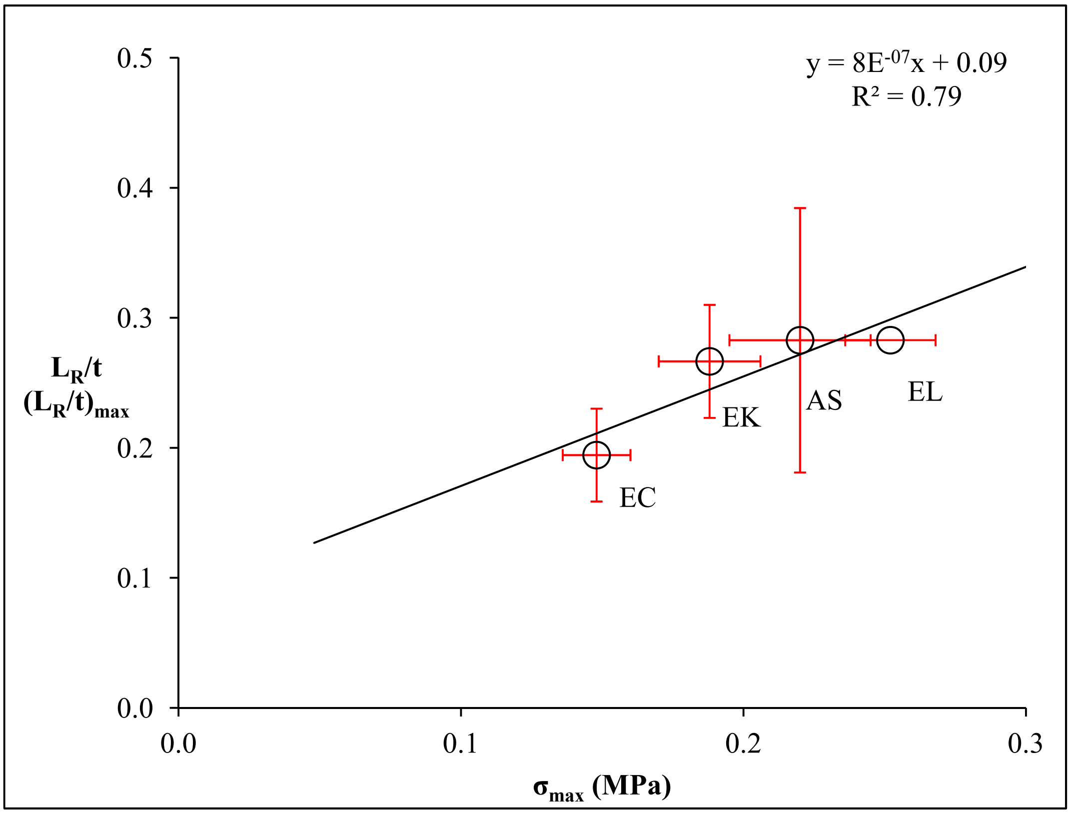


Fig. 7. Relationship between maximum axial root growth pressure, σ_{max}, (MPa) and the relative rate of root elongation, $\frac{R}{R_{max}}$, for the lowest and highest levels of soil compaction. The values of σ_{max} of *E. camaldulensis* (EC), *E. leucoxylon* (EL), *E. kochii* (EK) and *A.salicina* (AS) were reported in Azam et al. (2013a). Horizontal and vertical bars represent the standard errors of the means.

Conclusions

We conclude that root growth rates of tree seedlings (e.g., *A. salicina*) are considerably less sensitive to soil compaction than those of the annual species, *P. sativum*. Furthermore, tree roots are able to penetrate hard soils and distribute their roots more uniformly with depth than the annual, *P. sativum*, which expends more resources on root thickening. This confers an obvious advantage in terms of survival in seasonally dry environments: roots growing to greater depths can sustain plant life longer by accessing a greater volume of soil before the surface soil dries out.

Soil compaction causes an increase in root diameter as well as a decrease in elongation rate and total length of roots. When compaction is very severe, some tree species such as *A. salicina*, *E. leucoxylon* and *E. kochii* are able to maintain root growth more successfully than an annual or another tree (e.g., *E. camaldulensis*). Given that significant variation in root responses to compaction have been demonstrated here among only a few tree species and an annual, it is reasonable to expect considerably more variation among other species, both annual and perennial.

The lateral roots of transplanted Eucalyptus are able to elongate faster than the primary roots of direct-seeded *Eucalyptus* and *A. salicina* at all levels of soil compaction. This has implications for species selection and tree planting methods in revegetation programmes. If a dry season is anticipated, for example, it may be better to invest in transplanting to get faster establishment, rather than risk losing direct-seeded plants even though they may appear to be more economical.

A modest relationship was observed between the relative root elongation rate in very hard soils and the maximum root growth pressure that four different tree species can exert. However, because of the limited number of species examined, we consider this relationship to be speculative until additional work on other species comes to light.

Finally, the ability of established trees to maintain high root growth rates, or to distribute roots uniformly in a larger volume of soil, or to increase the diameter of roots may all be important mechanisms for sustaining mature trees whose roots grow in urban soils that become compacted (e.g., parkland and street trees).

Acknowledgments

The senior author acknowledges the support from the University of Adelaide in the form of an International Postgraduate Student Scholarship and the Cooperative Research Centre for Future Farm Industries for a supplementary scholarship and research support.

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CHAPTER 5

GROWTH AND WATER USE BY TREE AND BARLEY SEEDLINGS IN POORLY AERATED SOIL

The work contained in this chapter has been submitted as a research paper to *Soil Research*.

Azam G, Murray RS, Grant CD, Nuberg IK (2012) Growth and water use by tree and barley seedlings in poorly aerated soil. *Soil Research* (Submitted, SR13-219).

Abstract

Poor soil aeration restricts the establishment of plants, yet some species used in revegetation programs are more tolerant of waterlogging than others. This study evaluated the sensitivity to poor soil aeration of young seedlings of *Acacia salicina*, *Eucalyptus camaldulensis*, *E. leucoxylon*, and *E. kochii* plus a reference cereal crop, barley (*Hordeum vulgare* var. Keel). Seedlings were grown for 21 days in a loamy sand under a range of controlled volumetric air contents of the soil, ε_{air}, between 0 and 0.2 m^3m^{-3} then the diameter and total length of roots, plus the dry masses of shoots and roots were measured, and water use and water use efficiency were calculated.

All plants had some degree of sensitivity to poor soil aeration but their tolerance varied widely. Seedlings of *E. camaldulensis* were highly tolerant of waterlogging while seedlings of *E. kochii* were highly sensitive. Seedlings of *H. vulgare* and *A. salicina* showed moderate tolerance and had significantly greater water use efficiencies than any of the eucalypts. Among the more sensitive plants there was no single universal aeration state that caused a consistent reduction in all plant parameters; some species responded to any restriction in aeration whatsoever by reducing water use efficiency, while others only declined when aeration declined below 0.15 m^3m^{-3}. No single early-growth parameter adequately described a species sensitivity to waterlogging; some were simple (e.g., shoot mass) while others were more integrated (e.g., water use efficiency). Differences in growth rate and water use by the different species under low ε_{air} suggest that land managers and revegetation agencies have scope to select superior tree species for improving the establishment of trees on waterlogged soils. Furthermore the wide variation in tolerance to poor soil aeration among the trees relative to the cereal crop, barley, suggests there is considerable scope for genetic improvement of cereals using material from native trees.

STATEMENT OF AUTHORSHIP

Growth and water use by tree and barley seedlings in poorly aerated soil. ***Soil Research.*** **(*Submitted, SR13-219*).**

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Experimental development, data collection, analysis and critical interpretation, wrote manuscript.

I hereby certify that the statement of the contribution is accurate.

Signed Date 26/7/2013

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Supervised development of work, data analysis and interpretation, reviewed and edited manuscript.

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Introduction

The main soil conditions that limit plant establishment in low rainfall regions include high soil salinity, high soil strength and poor soil aeration, especially for trees (Marcar 1993; Misra and Gibbons 1996; Cook *et al.* 2004). Soil salinity and its impact on tree establishment as well as the role of native trees as biological tools for salinity management, have been thoroughly investigated (Marcar *et al.* 1995; Barrett-Lennard 2002; Munns and Tester 2008). High soil strength and poor soil aeration and their impacts on plant growth have also been investigated, yet our understanding of them remains inadequate (Bengough *et al.* 2011). We know that high soil strength can severely reduce root elongation (Cockroft *et al.* 1969) but that the roots of some plant species have ways to explore strong soils better than others (Materechera *et al.* 1991; Azam *et al.* 2013c). Among the *Eucalyptus* tree species, for example, Azam *et al.* (2013c) found that seedlings *E. leucoxylon* and *E. kochii* were less sensitive to high soil strength than *E. camaldulensis*. Azam *et al.* (2013c) found that this correlated well with their ability to exert higher maximum axial root growth pressures.

Arid and semi-arid regions not only receive low rainfall (considered to be 100 to 500 mm per year in winter or 100 to 800 mm per year in summer) but also the rainfall is erratic. These areas also experience seasonally extreme temperatures and soils remain dry for extended parts of the year, which restricts opportunities for plant establishment (FAO 1989). Poor soil aeration therefore is a problem not generally associated with semi-arid regions but it commonly occurs where water tables are shallow and capillary action brings excess water and salt into the root zone (Northey *et al.* 2006). Poor soil aeration also occurs in riparian zones (Merrill and Benning 2006) or where soil profiles have restricted hydraulic properties (Gardner *et al.* 1992) and it often coincides with high soil strength, especially in dense subsoils (e.g., texture contrast soils). In waterlogged conditions, water excludes soil air and hence oxygen in the root zone (Gliński and Stępniewski 1985). Lack of soil oxygen is detrimental to various plant physiological processes and it also mediates the microbial transformation of mineral and organic substances into phytotoxic compounds (Armstrong and Drew 2002).

Early literature suggests that physiological processes in plants can be restricted when the volumetric air content of the soil, ε_{air}, falls below 0.10 m^3 air m^{-3} total soil (Grable and Siemer 1968). There is some doubt, however, about whether a single universal value of ε_{air} such as 0.10 m^3m^{-3} exists and indeed, Cook *et al.* (2004) proposed such value of ε_{air} to be only an indicator. Under such restricted soil aeration some plants can maintain a supply of oxygen internally from shoot to root and some species can cope with high concentrations of toxic substances (e.g., sulphides), which can occur in waterlogged soils (Gliński and Stępniewski 1985, Colmer and Voesenek 2009). Moreover, Cook *et al.* (2004) argued that oxygen supply to roots is a complex process in which microbial population, root-length density itself, and depth-position in the soil profile all influence the relative importance of soil oxygen. The sensitivity of root- and plant-growth as a whole to poor soil aeration would appear to be rather species specific, and this provides an opportunity to evaluate the relative performance of different tree species to poor soil aeration. Such an evaluation is essential to guide the selection of species to revegetate poorly aerated soils in arid and semi-arid landscapes.

Sensitivity to poor soil aeration depends on plant age as well. Many mature Australian native plants, for example, are known to tolerate waterlogging (Marcar *et al.* 1995; Marshall *et al.* 1997). In fact, flooding of semi-arid landscapes has been observed to improve the general health and water use of some eucalypts, e.g., *Eucalyptus largiflorens* in the post-flooding period (Akeroyd *et al.* 1998). Furthermore, some nursery raised eucalypts such as *E. camaldulensis* and *E. globulus* are also relatively tolerant of poor soil aeration (Sena-Gomes and Kozlowski 1980; Marcar 1993) but these trees are well established by the time they are exposed to such conditions upon transplanting. Young seedlings, however, are often exposed to waterlogging from a very early stage (due to shallow water tables), yet we know little about how different tree species cope with poor soil aeration from germination onward.

Azam *et al.* (2013c) related the relative success of some recently germinated tree species growing in low-strength soils to their natural abundance in wet landscapes relative to other species. Although the correlation did not necessarily imply that the successful species would grow better when direct-seeded in waterlogged soils, it suggested they would be suitable subjects for comparative evaluation of the tolerance of different tree species exposed to extended periods of wet conditions. The objective of this study was to evaluate the relative success of the young seedlings of four different tree species (*Acacia salicina, Eucalyptus camaldulensis, E. leucoxylon* and *E. kochii*) plus a barley crop (*Hordeum vulgare* var. Keel) under varying degrees of waterlogging. Barley has previously been used as a reference plant in waterlogging studies (e.g., Harris *et al.* 2010) so it was considered an ideal species for comparison.

Materials and Methods

Bulk soil was collected from 5-20 cm below the surface under native vegetation near Monarto, South Australia (latitude 35° 05' S, longitude 139°04'E). The soil texture was a loamy sand, with 87% sand (200-20 μm), 7% silt (20-2 μm) and 6% clay (< 2 μm). The field bulk density was 1410 ± 5 kg m^{-3} and the particle density, measured using pycnometers (Blake and Hartge 1986), was found to be 2670 ± 12 kg m^{-3}. The particle density was used to calculate the total porosity of samples, from which the volumetric water contents were subtracted to calculate the volumetric air contents, ε_{air}. The soil was non-saline (electrical conductivity of saturated paste extract = 0.49 ± 0.05 dS m^{-1}) and slightly alkaline (pH of saturated paste extract = 7.6 ± 0.2). The soil contained 1.3% total organic carbon (Walkey-Black method, Nelson and Sommers, 1982), 530 mg kg^{-1} total N (Kjeldahl method, Bremner and Mulvaney, 1982) and 230 mg kg^{-1} total P (digestion with nitric acid - perchloric acid, Olsen and Sommers, 1982) and was classified in Isbell's (2002) Australian Soil Classification as a Grey Orthic Tenosol. All soil was air-dried and passed through a 2 mm sieve. All soil was air-dried and passed through a 2 mm sieve.

Subsamples were moistened to a water content of 0.14 kg kg^{-1} then packed incrementally (ca. 120 g soil per increment) to reach field bulk density in three stainless steel cylindrical rings (70 mm inside diameter, 50 mm height); these were used to measure the volumetric water retention (and volumetric air content) curves (Figure 1). Samples were saturated and placed onto porous ceramic plates connected to either hanging columns of water or sealed in pressure chambers (Soil Moisture Equipment Co., California). Samples were progressively weighed at 10 different matric suctions (i.e., saturation, 0.001, 0.003, 0.005, 0.01, 0.033, 0.1, 0.5, 1 and 1.5 MPa) and the volumetric water and air contents calculated. The water retention (and air content) curves shown in Figure 1 were used to select appropriate watering regimes to maintain five levels of soil aeration (Table 1).

Bulk soil was wetted to a gravimetric water content of 0.14 kg kg^{-1} and was then packed to a bulk density of 1450 kg m^{-3} by adding increments (2 cm each time) of moist soil into tapered plastic pots (1144 mL capacity; 12 cm height, 12 cm top diameter, 10 cm basal diameter). Each pot had three holes in the base, which allowed air to escape during soil packing. Each pot was fertilized with 10 mL of nutrient solution containing 5.0 mM N, 0.3 mM P and 1.2 mM K plus other essential micronutrients recommended by Ingestad and Lund (1986). The potted soil had a total porosity of 0.46 m^3m^{-3} (1 - bulk density/particle density). When additional water was added to each pot to bring the volumetric water content up to…

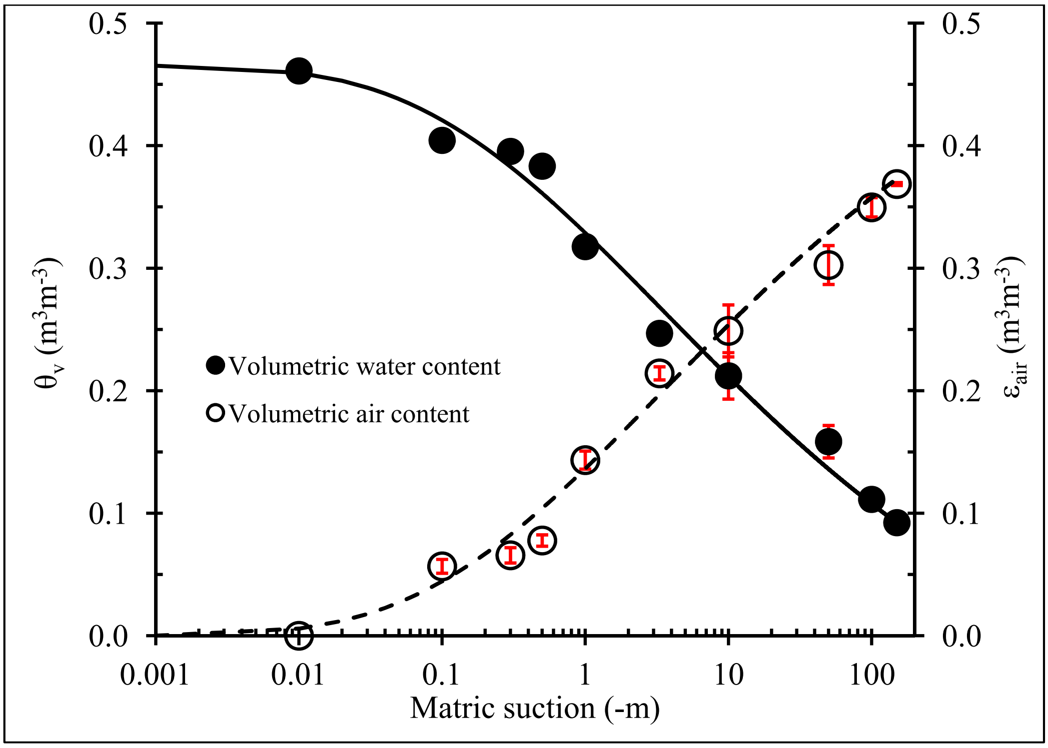

Fig. 1. Experimentally measured volumetric water retention curve $\theta_v(h)$ (solid line) and its corresponding (calculated) volumetric air content curve, $\varepsilon_{air}(h)$ (dashed line) of soil packed to a bulk density of 1450 kg m^{-3}. Vertical bars represent the standard errors of the means of the two variables.

Table 1. Experimental treatments and measurements.

Treatments	**Measurements**
5 plant species x 3 replicates: o *Acacia salicina* (Lindl.) o *Eucalyptus camaldulensis* (Dehnh.) o *E. leucoxylon* (F.Muell) o *E. kochii* (Maiden & Blakely) o *Hordeum vulgare* (L. var. Keel)	Oxygen concentration Soil penetration resistance Root diameter and length Dry biomass of shoots and roots Plant water use
5 levels of soil aeration (ε_{air}): o 0.00, 0.05, 0.10, 0.15 and 0.20 cm^3cm^{-3}	

…0.26 m^3 water m^{-3} soil, it provided a volumetric air content, ε_{air}, of 0.20 m^3 air m^{-3} soil for all treatments at the start. All pots were wrapped in plastic and stored in a dark, constant-temperature chamber (25 °C) for one week to allow hydraulic equilibrium and age hardening to occur (Utomo and Dexter 1981).The pots were then moved to a controlled temperature glasshouse (day and night temperatures of 25 ± 2 °C and 18 ± 2 °C, respectively). Three seedlings (one-day old) of each of the plant species shown in Table 1 were planted equidistant from one another in each of three pots for the imposed aeration treatments. An additional replicate pot for the barley plants was included solely for the purpose of measuring the soil oxygen concentration. The volumetric water content of the soil in all pots at planting time was 0.26 m^3m^{-3} and this water status was maintained for three days to allow plant emergence in all treatments. Prescribed amounts of water were then added to the pots to achieve five different volumetric water- and air-contents. The two lowest volumetric air contents, ε_{air} = 0 and 0.05 m^3m^{-3}, were achieved by resting each pot in another plastic pot of same size containing water; this forced water up the gap between the pots to establish matric suctions within the soil of 0 and 7 cm, respectively, relative to the soil surface (the water level was corrected twice a day using a syringe down the gap between the pots). For ε_{air} of 0.05 m^3m^{-3} treatment the soil in the bottom half of the pot was thus completely saturated while the upper half (where oxygen concentration was measured) maintained an ε_{air} of 0.05 m^3m^{-3} determined from Figure 1. The other three volumetric air contents, 0.10, 0.15 and 0.20 m^3m^{-3}, were achieved by watering each pot from the top twice per day to maintain masses corresponding to volumetric water contents determined from the water retention curve (Figure 1). A two-centimetre-thick layer of polyethylene beads was added to the top of each pot to reduce evaporative water losses to 18 ± 2% of that from control pots having no polyethylene beads. It was assumed to within experimental error that plant extraction of water from the soil accounted for any changes in pot weight to be regarded as plant water use. The 3 holes in the base of these pots were covered with plastic to prevent air diffusion back into the soil from below. All the plants were harvested 21 days after planting.

An estimate of the soil oxygen concentration for the different aeration treatments was made by inserting an oxygen sensor (model ICT02, manufactured by ICT International, Armidale, NSW, Australia) to a depth of 5 cm below the soil surface in one, randomly selected pot of soil for each of the five aeration treatments from the second day for seven consecutive days. We had a limited number of oxygen probes available so only the pots containing barley were equipped with the sensors; all other things being equal, the oxygen status in the barley pots was considered to be similar to that in the pots containing other species.

The soil penetration resistance, SR, was measured for each treatment at harvest using an automated laboratory penetrometer (recessed shaft, cone-base diameter 2.38 mm, tip semi-angle 30°, model Lloyd LFPlus 1 kN, manufactured by C.S.C. Force Measurement, Inc., Agawam, Massachusetts, USA). SR was measured on only three randomly selected pots from each aeration treatment irrespective of plant species as soils were packed uniformly plus all SR values remained below 0.5 MP. The harvested shoots were dried at 70 °C for one week and weighed. The soil from each pot was then washed through a 0.5 mm sieve to separate and collect the roots. Total length of roots in each pot was measured digitally using a high resolution scanner (600 dpi) combined with WinRhizo image analysis software (version 2005c; Régent Instruments 2005). After scanning, all the roots were collected, dried at 70 °C for one week and weighed. Total lengths (m per plant), plant dry masses (mg per plant), total water use (mm water used per plant) and water use efficiency (mm water used per plant divided by total dry shoot and root mass) were calculated.

Data on root diameter, total root length, shoot dry mass, total shoot+root dry mass, total water use and water use efficiency were subjected to a two-way ANOVA with the factors plant species, ε_{air} and their interaction, at a significance level of $P = 0.05$ using the statistical software package GenStat for Windows, edition 14 (VSN International, Hemel Hempstead, UK). When confirming a statistically significant *P* value, the post hoc Tukey multiple-range test was applied ($P = 0.05$) as a multiple comparison procedure (Snedecor and Cochran 1980). Correlation analyses were subsequently performed to evaluate relationships between factors and measured variables.

Results

Soil penetration resistance, SR, remained in the non-restricting range 0.10-0.35 MPa depending on the levels of volumetric water content (Figure 2b), and ε_{air} all fell in the range between 0 and 0.20 $cm^3\ cm^{-3}$ as expected from the water retention curve (Figure 1). Immediately before the different volumetric air contents were imposed on day 3, the concentration of oxygen the soil was approximately 20.9%, which was equal to the ambient concentration in the air. For the completely waterlogged treatment (i.e., $\varepsilon_{air} = 0\ m^3m^{-3}$), the concentration of oxygen approached to zero within 1-2 days due to its limited diffusion in water (Gliński and Stępniewski 1985) and the large demand for oxygen by the plant roots and other soil biota in the rhizosphere (Armstrong and Drew 2002). The concentration of O_2 also dropped to zero within 2 days for the soil having $\varepsilon_{air} = 0.05\ m^3m^{-3}$ (Figure 2a), and for the treatment having $\varepsilon_{air} = 0.10$ m^3m^{-3}, it took 5 days to decline to approximately 2%. For the other two treatments, there was little difference in the concentration of oxygen over time; for $\varepsilon_{air} = 0.15$ m^3m^{-3} the oxygen concentration was 19.3 ± 1.17% and for $\varepsilon_{air} = 0.20$ m^3m^{-3} it was 19.9 ± 0.77%. For these two treatments, a distinct diurnal variation was observed in the concentration of oxygen in accordance with the greater demand for soil oxygen by the plants at night (Figure 2a).

A two-way ANOVA showed that plant species, ε_{air}, and the interaction between plant species and aeration, significantly influenced all the plant growth parameters at $P < 0.001$ except the water use efficiency, WUE, ($P = 0.091$). Water use efficiency was significantly affected by both ε_{air} and plant species at $P < 0.001$. Further analysis using Tukey's multiple-range test showed a significant increase in root diameter under completely waterlogged conditions (i.e., $\varepsilon_{air} = 0$ m^3m^{-3}) for three of the four tree species, i.e., *Acacia salicina, Eucalyptus camaldulensis* and *E. kochii* at $P = 0.05$ (Table 2). No significant changes in root diameter, however, were observed for *E. leucoxylon* and *Hordeum vulgare*. The diameter of *A. salicina* roots was significantly greater ($P = 0.05$) than that for all other species at all levels of ε_{air}. By contrast, *H. vulgare* had significantly smaller root diameter in the range of aeration ε_{air} between 0 and 0.15 m^3m^{-3} than all other species. Among the three Eucalyptus species, E. kochii produced significantly thicker roots (P = 0.05) under completely waterlogged conditions as well as at $\varepsilon_{air} = 0.05$ and $\varepsilon_{air} = 0.10$ m^3m^{-3} than the other two Eucalyptus species, however there were no differences among the eucalypts once ε_{air} exceeded 0.15 m^3m^{-3} (Table 2).

H. vulgare produced significantly greater (P = 0.05) total root length than any of the tree species at all states of soil aeration (Table 3). Among the *Eucalyptus* species, *E. camaldulensis* had significantly greater total root length than both *E. leucoxylon* and *E. kochii* at all levels of ε_{air}. Total root length decreased significantly with decreasing aeration (P = 0.05) for all species except *E. camaldulensis*. The species *H. vulgare, A. salicina* and *E. kochii* all produced significantly shorter roots when ε_{air} dropped below 0.10 m^3m^{-3}, whereas *E. leucoxylon* produced significantly shorter roots ($P = 0.05$) only when ε_{air} dropped below 0.05 m^3m^{-3} (Table 3).

Shoot dry mass generally decreased with decreasing ε_{air} and differences were observed among the plant species at $P = 0.05$ (Table 4). For example, a reduction in shoot dry mass ($P = 0.05$) occurred for *H. vulgare* and *E. kochii* when aeration declined below $\varepsilon_{air} \leq 0.10$ m^3m^{-3}, whereas shoot dry mass only declined significantly at $P = 0.05$ for *E. camaldulensis, E. leucoxylon* and *A. salicina* when $\varepsilon_{air} \leq 0.05$ m^{3}m^{-3} (Table 4).

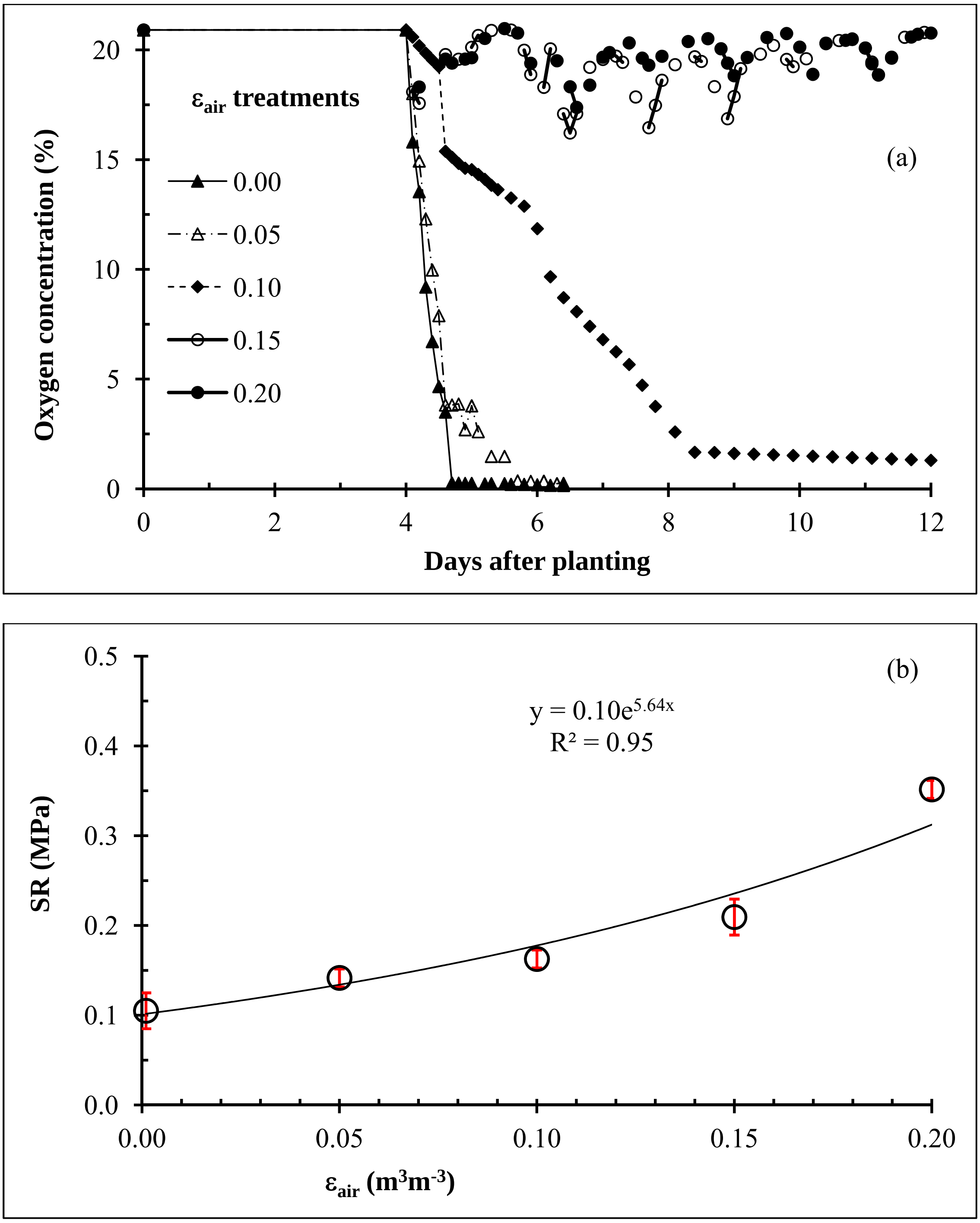

Fig. 2. (a) Concentration of soil oxygen as a function of time in pots of soils having different volumetric air contents ranging from $\varepsilon_{air} = 0.00$ to 0.20 m^3 m^{-3}. (Measurements were taken in the pots of soil in which *H. vulgare* grew), and (b) mean soil penetration resistance (SR, MPa), in potted soil as function of soil volumetric air content (ε_{air}, m^{3}m^{-3}). Vertical bars represent standard errors of the mean SR.

Table 2. Mean root diameter (D_R, mm) for different plant species grown in soil having a typical range of soil volumetric air contents, ε_{air}.

Species	D_R (mm) for soil with different ε_{air} , m^3m^{-3}				
	0.00	**0.05**	**0.10**	**0.15**	**0.20**
H. vulgare	$0.33^{a,D}$	$0.29^{a,D}$	$0.32^{ab,C}$	$0.33^{a,C}$	$0.34^{a,B}$
A. salicina	$0.69^{a,A}$	$0.57^{b,A}$	$0.51^{b,A}$	$0.47^{b,A}$	$0.46^{b,A}$
E. camaldulensis	$0.42^{a,C}$	$0.39^{b,BC}$	$0.35^{b,BC}$	$0.34^{b,B}$	$0.36^{b,B}$
E. leucoxylon	$0.37^{a,C}$	$0.35^{a,C}$	$0.33^{a,C}$	$0.34^{a,B}$	$0.35^{a,B}$
E. kochii	$0.52^{a,B}$	$0.44^{b,B}$	$0.40^{b,B}$	$0.38^{b,B}$	$0.36^{b,B}$

Within rows and columns, mean values followed by the same superscripted small letter and capital letter, respectively, are not significantly different (P = 0.05) by Tukey's multiple-range test.

Table 3. Mean total root length (L_R, m per plant) for different plant species grown in soil having a typical range of soil volumetric air contents, ε_{air}.

Species	L_R ($m\ plant^{-1}$) for soil with different ε_{air} , m^3m^{-3}				
	0.00	**0.05**	**0.10**	**0.15**	**0.20**
H. vulgare	$6.44^{b,A}$	$7.76^{b,A}$	$9.56^{b,A}$	$17.83^{a,A}$	$19.47^{a,A}$
A. salicina	$0.73^{c,C}$	$1.08^{bc,C}$	$1.87^{b,BC}$	$3.12^{a,B}$	$3.30^{a,C}$
E. camaldulensis	$3.22^{a,B}$	$4.00^{a,B}$	$4.33^{a,B}$	$5.10^{a,B}$	$4.46^{a,B}$
E. leucoxylon	$0.76^{b,C}$	$1.14^{b,C}$	$2.09^{a,BC}$	$2.38^{a,C}$	$2.53^{a,CD}$
E. kochii	$0.39^{b,C}$	$0.68^{b,C}$	$0.97^{b,C}$	$1.90^{a,C}$	$2.04^{a,D}$

Within rows and columns, mean values followed by the same superscripted small letter and capital letter, respectively, are not significantly different (P = 0.05) by Tukey's multiple-range test.

Table 4. Mean shoot dry mass (M_S, mg per plant) for different plant species grown in soil having a typical range of soil volumetric air contents, ε_{air}.

Species	M_S (mg plant^{-1}) for soil with different ε_{air}, m^{3}m^{-3}				
	0.00	**0.05**	**0.10**	**0.15**	**0.20**
H. vulgare	$77.6^{b,A}$	$88.6^{b,A}$	$132^{b,A}$	$162^{ab,A}$	$203^{a,A}$
A. salicina	$59.6^{b,B}$	$68.7^{b,A}$	$88.9^{ab,B}$	$93.4^{ab,B}$	$106^{a,B}$
E. camaldulensis	$29.4^{b,C}$	$32.7^{b,B}$	$43.3^{a,C}$	$49.1^{a,C}$	$46.6^{a,C}$
E. leucoxylon	$11.2^{b,D}$	$13.1^{b,BC}$	$24.3^{a,C}$	$28.0^{a,C}$	$26.9^{a,C}$
E. kochii	$3.67^{b,D}$	$9.33^{b,C}$	$10.9^{b,D}$	$30.9^{a,C}$	$24.9^{a,C}$

Within rows and columns, mean values followed by the same superscripted small letter and capital letter, respectively, are not significantly different (P = 0.05) by Tukey's multiple-range test.

Table 5. Mean total water use (WU, mm water used per plant) for different plant species grown in soil having a typical range of soil volumetric air contents, ε_{air}.

Species	WU (mm plant^{-1}) for soil with different ε_{air}, m^{3}m^{-3}				
	0.00	**0.05**	**0.10**	**0.15**	**0.20**
H. vulgare	$6.30^{c,A}$	$7.27^{bc,A}$	$8.93^{b,A}$	$10.92^{a,A}$	$10.75^{a,A}$
A. salicina	$3.39^{c,CD}$	$4.13^{bc,BC}$	$4.37^{b,BC}$	$5.00^{a,B}$	$5.39^{a,B}$
E. camaldulensis	$4.73^{a,B}$	$4.89^{a,B}$	$5.10^{a,B}$	$5.20^{a,B}$	$5.20^{a,B}$
E. leucoxylon	$3.67^{b,C}$	$3.90^{b,BC}$	$3.97^{b,C}$	$4.88^{ab,B}$	$5.44^{a,B}$
E. kochii	$2.88^{b,D}$	$3.42^{b,C}$	$3.56^{b,C}$	$4.94^{a,B}$	$4.80^{a,B}$

Within rows and columns, mean values followed by the same superscripted small letter and capital letter, respectively, are not significantly different (P = 0.05) by Tukey's multiple-range test.

H. vulgare used significantly greater amount of water at all levels of aeration than any of the tree species at $P = 0.05$ (Table 5). For $\varepsilon_{air} \leq 0.10$ m^{3}m^{-3} water use generally declined with decreasing ε_{air} for all plant species except *E. camaldulensis* – for this species there was no significant reduction in water use per plant as ε_{air} declined (Table 5). *E. camaldulensis* used significantly more water than any of the other trees. A further ($P = 0.05$) decrease in water use was also observed under completely waterlogged conditions for only *H. vulgare* and *A. salicina* (Table 5).

A preliminary estimate of the water use efficiency, WUE, of each plant species under different soil aeration conditions can be obtained by dividing the total dry mass per plant (mg shoots + roots) by the amount of water used per plant from Table 5. A Tukey's multiple range test of this data shows that at each aeration state the WUE was greatest for *H. vulgare* and *A. salicina*, than *E. camaldulensis, E. leucoxylon* and *E. kochii* (Table 6). Furthermore, it shows that WUE for the different plant species was influenced to varying degrees by soil aeration. The most sensitive plants were *H. vulgare* and *A. salicina*, and the least sensitive plant was *E. camaldulensis*. The WUE of *E. leucoxylon* and *E. kochii* was intermediate in its sensitivity to soil aeration.

A more integrated estimate of WUE can be obtained by evaluating the correlation between total dry mass per plant (mg shoots + roots) and total amount of water used per plant (mm) shown in Figure 3a. Fitting quadratic polynomials to these data and taking their first derivatives allows the change in dry matter per mm water to be calculated using the water consumed at each volumetric air content from Table 5 (mg mm^{-1}). Plotting WUE calculated this way against the volumetric air content of the soil (Figure 3b) reveals that the different plant species have quite different sensitivities to soil aeration. For example, within the range of soil aeration used in this study, WUE for the tree species *Acacia salicina* and *Eucalyptus leucoxylon* declined continuously with decreasing soil aeration as soon as the volumetric air content dropped below the maximum value used here ($\varepsilon_{air} = 0.20\ m^3m^{-3}$), whereas WUE for *H. vulgare* and *E. kochii* did not start declining until ε_{air} dropped below 0.15 m^3m^{-3}. The WUE of *E. camaldulensis* was completely insensitive to soil aeration and did not change as ε_{air} declined from 0.20 to 0.00 m^3m^{-3}.

Table 6. Mean water use efficiency (WUE, mg dry shoot+root per plant per mm water used per plant) for different plant species grown in soil having a typical range of soil volumetric air contents, ε_{air}.

Species	WUE (mg mm^{-1}) for soil with different ε_{air} , m^{3}m^{-3}				
	0.00	**0.05**	**0.10**	**0.15**	**0.20**
H. vulgare	$16.44^{b,AB}$	$16.32^{b,A}$	$18.87^{b,A}$	$20.80^{b,A}$	$26.71^{a,A}$
A. salicina	$19.98^{a,A}$	$19.65^{a,A}$	$21.22^{a,A}$	$23.59^{a,A}$	$25.78^{a,A}$
E. camaldulensis	$12.80^{a,B}$	$13.14^{a,B}$	$14.85^{a,B}$	$14.48^{a,B}$	$12.30^{a,B}$
E. leucoxylon	$3.79^{b,C}$	$4.56^{b,C}$	$8.30^{a,C}$	$8.17^{a,C}$	$9.29^{a,B}$
E. kochii	$2.07^{b,C}$	$2.52^{b,C}$	$4.55^{b,D}$	$8.26^{a,C}$	$8.65^{a,B}$

Within rows and columns, mean values followed by the same superscripted small letter and capital letter, respectively, are not significantly different (P = 0.05) by Tukey's multiple-range test.

Discussion

Roots of agricultural crops growing in poorly aerated soil are generally thicker and shorter (Eavis 1972) and the growth response of shoots is closely linked to that of the roots (Gliński and Stępniewski 1985). In the present study significant negative root and shoot responses also occurred but they were not universal in effect and they were species-specific. For example the tree *E. camaldulensis* was consistently the least sensitive to poor soil aeration as ε_{air} declined from 0.20 to 0.00 m^{3}m^{-3} of any plant examined in this study (as measured by smaller changes in root diameter and total root length, shoot dry mass, water use and water use efficiency). The remarkable insensitivity of this species to waterlogging is consistent with its reported ability to draw oxygen down from the shoots into the roots (Colmer and Voesenek 2009) as well as its ability to produce specialised roots with aerenchyma (van der Moezel et al. 1988). Although it is speculative to extend the findings from the 21-day experiments reported here to longer time frames in the field, the flexibility of this species under poorly drained and well aerated conditions may explain why it is the dominant eucalypt species across the Mediterranean landscapes of the Australian continent (Butcher *et al.* 2009).

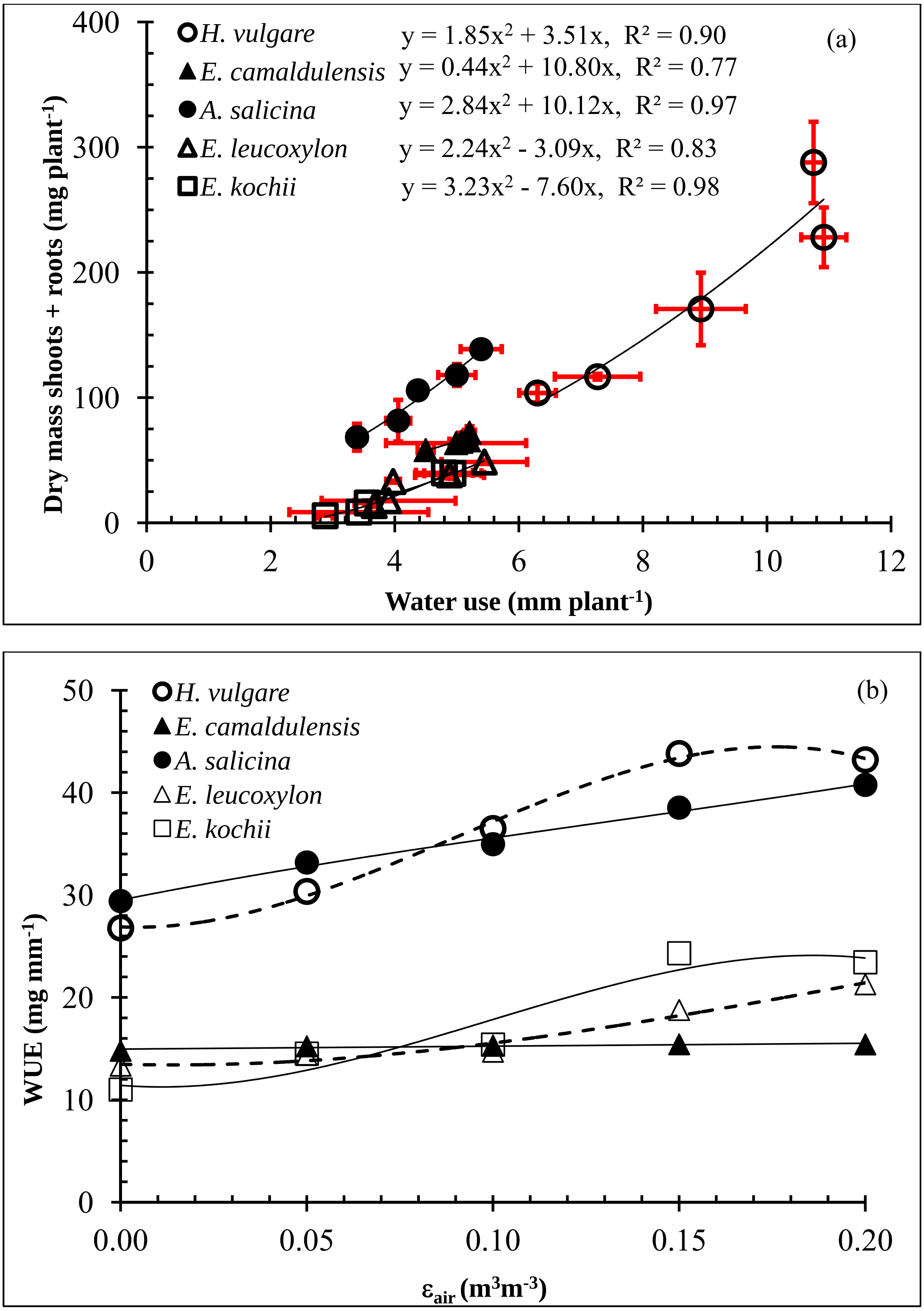

Fig. 3. (a) Mean total dry matter production (shoots + roots, M_T) of different plant species as (quadratic) functions of their mean total water use WU; correlations forced through the origin. Vertical and horizontal red bars represent 1 standard error of the mean parameter, and (b) water use efficiency (WUE, dM_T/dWU, mg mm^{-1}) of different plant species as a function of the soil volumetric air content, ε_{air} (m^3 m^{-3}).

By contrast, ε_{air} declined from 0.20 m^3m^{-3} to complete waterlogging, *E. kochii* and *A. salicina* experienced the greatest relative increases in root diameter of all species (+47% and +51% respectively; Table 2) and the greatest relative decreases in root length (-81% and -78% respectively; Table 3). However, it was *E. kochii* and *E. leucoxylon* that experienced the greatest relative decreases in shoot dry mass as ε_{air} declined from 0.20 m^3m^{-3} to complete waterlogging (-88% and -67% respectively; Table 4), whereas *A. salicina* and *E. camaldulensis* responded similarly to each other in terms of shoot dry mass. In this connection, it is interesting that *A. salicina* and *E. camaldulensis* co-dominate open woodland communities along (wet) creek banks and flood plains (Whibley and Symon 1992)), where their root and shoot systems have adapted accordingly. Furthermore, it was *E. kochii* and *H. vulgare* that experienced the greatest relative reductions in water use (-40% and -41% respectively, Table 5) and in WUE (-53% and -38% respectively, Table 6) as ε_{air} declined from 0.20 to 0 m^3m^{-3}. The higher sensitivity of *E. kochii* to waterlogging is consistent with this species being confined largely to the drier regions of Western Australia (Robinson *et al.*, 2006) where extended periods of waterlogging are less common. Similarly, *H. vulgare*'s greater relative sensitivity than some of the tree seedlings examined may reflect its origins as a grassland species where flooding is less common. Furthermore, our results suggest there is scope to improve the waterlogging tolerance of barley. For example, genetic profiling of the highly tolerant *E. camaldulensis* along with promising lines of barley (e.g. Pang *et al.* 2004) may reveal new mechanisms by which agriculturally important crops can be bred for use in wetter (and possibly more saline) soils.

Finally, the tree species, *A. salicina*, had the highest WUE of all plant species at all states of aeration (Table 6), which is consistent with that fact that when acacias and eucalypts are mixed-seeded, acacias become 'pioneer' plants in both wet and dry conditions, which create a favorable niche for the later establishment of the eucalypts (Richardson *et al.* 2011; Azam *et al.* 2013b).). An examination of the traits responsible for the high tolerance of *A. salicina* to waterlogging combined with those responsible for high tolerance to salinity (e.g. Rehman *et al.* 1998) might identify lines of acacia that are suitable for use in re-vegetating regions of rising saline water tables such as the Salic Hydrosols in Western Australian.

Plants in this study were grown in moist, relatively soft soil (i.e., soil compaction was not a limiting factor) containing plenty of nutrients. All variations in plant growth and water use were therefore attributed to variations in soil aeration status alone, plus the relative sensitivity of the different plant species. In reality, of course, waterlogged soils are often saline, low in nutrients and can be highly compacted, so the findings reported here may not reflect what occurs in the field. A more realistic evaluation of the effects of waterlogging would therefore need to be conducted with plants grown in different soils having multiple stresses on top of poor soil aeration (e.g. salinity, compaction, nutrient deficiencies).

Conclusions

Although all plants examined in this study had some degree of sensitivity to poor soil aeration, their waterlogging tolerance varied widely within the range of ε_{air} used here. The seedlings of *E. camaldulensis* were particularly tolerant of water-logging while *E. kochii* was highly sensitive to it particularly when ε_{air} was < 0.10 m^3m^{-3}. The cereal crop *H. vulgare* showed intermediate tolerance to poor soil aeration and was able to maintain nearly 40-50% of its relative root and shoot growth under completely waterlogged conditions.

Among the plants that were sensitive to soil aeration, there was no single critical value of ε_{air} that caused a consistent reduction in all plant parameters examined here. Some species (e.g., *A. salicina* and *E. leucoxylon*) responded negatively in terms of WUE to any reduction in ε_{air} < 0.20 m^3m^{-3}, whereas WUE for other species (e.g., *H. vulgare* and *E. kochii*) only started to decline when ε_{air} fell below 0.15 m^3m^{-3}. The widely used critical volumetric air content of 0.10 m^3m^{-3} (Grable and Seimer 1968) has been shown here to not be universally applicable to all plants in terms of plant available water (e.g., Groenevelt *et al.* 2001).

The wide range in tolerance to waterlogging shown by the five different plant species examined in this study plus the many different ways in which they express their sensitivity suggest there is plenty of genetic variation that can be manipulated to extend the range of crops that can grow on soils exposed to periodic waterlogging. It also suggests there is no single early-growth parameter that can universally indicate a plant's sensitivity to waterlogging; for some it will be a simple measure of shoot mass, while for others it will be a more difficult or integrated set of measurements (e.g., root diameter, root length, water use or water use efficiency). This study has evaluated the effect of a single soil problem, i.e., ε_{air}, on plant performance at early stage of establishment using one of the widely occurring soil types. In natural landscape multiple soil problems such as salinity, high soil strength, poor soil aeration etc may occur simultaneously, therefore, future research are shouted by incorporating other soil limitations and various types of soil.

Acknowledgments

The senior author acknowledges the support from the University of Adelaide in the form of an International Postgraduate Student Scholarship as well as support from the Cooperative Research Centre for Future Farm Industries in the form of a supplementary scholarship and project support.

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CHAPTER 6

FIELD CORROBORATION OF LABORATORY TECHNIQUES TO PREDICT SUCCESSFUL ESTABLISHMENT OF TREES ON HOSTILE SOILS

The work contained in this chapter has been submitted as a research paper to the *Journal of Arid Environments*.

Azam G, Nuberg IK, Grant CD, Emms J, Murray RS (2013) Field corroboration of laboratory techniques to predict the successful establishment of trees on hostile soil in degraded landscapes. *Journal of Arid Environments* (Submitted, JAE13-171).

STATEMENT OF AUTHORSHIP

Field corroboration of laboratory techniques to predict the successful establishment of trees on hostile soil in degraded landscapes. ***Journal of Arid Environments*** **(submitted, JAE13-171).**

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Abstract

A field survey and a planting experiment were conducted following laboratory and glasshouse experiments that suggested that the success of revegetating harsh, semi-arid landscapes is strongly correlated to a species' ability to exert high root growth pressure or to maintain root elongation rates over extended periods (Azam et al, 2012; 2013a). The field survey was conducted near Monarto, South Australia, where soil physical properties were thought to vary in response to management history and where there were significant differences in establishment of direct-seeded trees. The planting experiment was conducted nearby where the planting method of several tree species was varied. We found that the larger seeded *Acacia* species were more successful than the smaller seeded *Eucalyptus* species when both were direct-seeded. Among the small-seeded species, transplanting of 90 day-old-seedlings was more successful than those of direct-seeded ones. Differences in success rates of various tree species and planting methods in the field were thought to be strongly reflected in the performance of the trees in the laboratory, which suggests land managers and revegetation agencies have greater chances to select superior tree species and planting methods to maximize success of revegetation efforts in semi-arid landscapes.

1. Introduction

Interest in revegetation of degraded landscapes (e.g., post-mined and abandoned agricultural farmland) in arid and semi-arid regions continues to grow due to numerous ecological, environmental and economic benefits (Anderson and Ostler, 2002; Caldwell et al., 2009; Lamb et al., 2005). This expansion of revegetation has been fostered by improvement of tree establishment and management practices (Caldwell et al., 2009; Cao et al., 2008; Gladstone and Ledig, 1990; Graham et al., 2009) – yet different tree planting methods remain either unreliable or too expensive (Azam et al., 2012). This is because there is a limited number of species with proven credentials and they encounter enormous challenges (e.g. hostile soils) during their establishment in degraded landscapes of low rainfall regions (FAO, 1989). However, there must be many more potential tree species due to the occurrence of diverse tree species in arid and semi-arid regions (Kozlowski, 1999), yet insufficient management information and inappropriate selection of revegetation methods effectively limits their use in revegetation of degraded landscapes (Barrett-Lennard, 2002; Commander et al., 2009).

In low rainfall environments, soil water status plays a major role in the success of tree establishment by its impacts on numerous ecological and biological processes (Newman et al., 2006). Low soil water available for plants and high soil strength are serious limiting factors for root exploration (Caldwell et al., 2009; Eavis, 1972; Masle, 2002). Therefore, successful tree establishment and subsequent survival in low rainfall environments depends on the ability of their roots to penetrate faster into deep soil layers and draw on subsoil resources until the next occurrence of rainfall (Bengough et al., 2011). This is possible by those tree species which can exert sufficient root growth pressure on surrounding soils and send their roots to deeper soil horizons before the top soil dries out (Bengough, 2012).

Azam et al. (2013a) showed that tree species which grow in the shallower soil of the elevated zone of a soil catena (e.g., *Eucalyptus leucoxylon* F.Muell) can exert significantly greater root growth pressure than those of other species which grow in deeper, wetter and lower areas of the same catena (e.g., *E. camaldulensis* Dehnh.). More importantly, they found root growth pressure of some tree species such as Acacia salicina Lindl. increases over time, which may allow them to tackle comparatively harder subsoil when they grow older. Furthermore, Azam et al. (2013b) showed the elongation ability of roots varied among tree species and was strongly correlated with the ability of roots to exert axial growth pressure for which large-seeded species were superior to those of small-seeded species when both groups were direct-seeded. They also found lateral roots of transplanted seedlings of small-seeded species elongated 2-5 times faster than the primary roots of seedlings that had been direct-seeded. These findings suggested that revegetation of degraded landscapes by direct-seeding can be more successful for large-seeded species than those of small-seeded ones, and that transplanting of small-seeded species can be more successful than direct seeding. These laboratory findings need to be tested in real field conditions, because development of tree communities in degraded landscapes is more complex due to the interactions between the inherent ecosystem and biophysical processes (Arnold et al., 2012; Zhang et al., 2005).

This study corroborates the findings of earlier studies conducted under controlled environmental conditions with field observations (Azam et al. 2013a; 2013b). The objectives of this study were (i) to survey and evaluate the performance of a number of direct-seeded tree species in terms of their seed to tree conversion rate, mortality rate and biomass production, and (ii) to evaluate the relative performance of a number of small-seeded tree species that were established by both direct-seeding and transplanting.

2. Materials and methods

This study had two parts: 1] a case study investigating a reforestation project which was established by direct seeding; 2] a planting experiment evaluating the relative performance of direct seeding and transplanting of tree seedlings under similar soil and environments.

2.1 Site descriptions

The case study was conducted on three paddocks on a single property in Rockleigh (latitude 34° 59' S, longitude 139°04’E), South Australia. One of the three paddocks at the Rockleigh site was cultivated for approximately 20 years to produce cereal crops (e.g. wheat and barley) while the remaining two paddocks were grazed by sheep for the same duration. The planting experiment was conducted in a section of the Monarto Zoo (latitude 35° 06' S, longitude 139°10' E), South Australia which had previously been cropped for approximately 20 years. Cultivated paddocks were mechanically tilled in each cropping cycle and every crop was fertilized using inorganic fertilizers under rainfed conditions. Grazed paddocks were never cultivated or fertilized (Table 1). All paddocks had soils with loamy sand textures, which were classified as Rudosols in the Australian Soil Classification (Isbell, 2002).The area falls within a semi-arid Mediterranean climate (winter-dominant rainfall) receiving a mean annual rainfall of 344 mm and an annual potential evaporation of 1,400-1,600 mm.

2.2 Tree establishment and management

At the Rockleigh case study site, two grazed paddocks were revegetated in August 2004 and the cultivated paddock was revegetated in August 2010. The revegetation experiment at the Monarto site commenced during August 2011. All the direct seeding operations at both sites were conducted by volunteers from the organization called ‘Trees For Life’, who used the same tree species and seeding rate at both sites (Table 2). Although seed viability was not tested, this was not thought to be a limiting factor as seeds were freshly collected from the same mother plants and were used at several different sites in South Australia successfully (Pers. Comm. Mr. David Hein, Direct Seeding Manager, Trees For Life, Adelaide, South Australia). Seeds were planted using a specialized seeder that first removed (scalped) the top 5 cm of soil in planting lines to minimize weed infestation and at the same time planted the seeds at 5-10 cm soil depth (based on seed sizes of the seeds). Ninety-day-old seedlings of the small-seeded species (Table 2) were transplanted, only at the Monarto site, in August 2011 immediately after the completion of the direct seeding operation. Seedlings were transplanted in the same line where seeds were sown. Thirty seedlings of each species were planted with a spacing of 3 m between plants (intra-line) and approximately 4 m between lines (inter-line). Transplanted seedlings were allowed to grow without any irrigation or tree guarding as were the direct-seeded trees.

2.3 Soil sampling and analyses

Soil sampling was conducted based on a Randomized Complete Block Design (RCBD). At the Rockleigh property, each of the two grazed paddocks was subdivided into three blocks while the cultivated paddock was subdivided into seven blocks based on the paddock size and land slope. Within each block a 10 m x 10 m area was selected to collect soil samples and to take field measurement of soil penetration resistance. Soils were collected in May 2011 from two types of micro-sites, i.e., on the direct seeding line (DSL) and between the direct seeding lines (BDSL). Three replications of intact soil cores were collected from each micro-site in a block using bulk density rings (diameter 5 cm; height 5 cm). Before the insertion of the bulk density ring, the top 5 cm of soil was scalped to avoid mixing of un-decomposed plant litter and organic top soil; so the intact core was from a depth of 5-10 cm from the surface. These intact cores were used to measure soil volumetric water content curves at different matric suctions by placing them on porous ceramic plates connected to either hanging columns of water or sealed in special pressure chambers (models 1500F1, 1600; manufactured by Soil Moisture Equipment Co., California). When determining the water retention curve at each matric suction, soil penetration resistance was also measured using an automated laboratory penetrometer (recessed shaft, cone-base diameter 2.38 mm, tip semi-angle 30°, model Lloyd LFPlus 1 kN, manufactured by C.S.C. Force Measurement, Inc., USA) progressing at a constant speed of 3 mm min−1. It was not possible to record the penetration resistance on the samples when the matric suction was greater than 50 m because the required forces exceeded the capacity of the available equipment (i.e. 5.5 MPa). Soil bulk density was measured using the intact core samples after the soil water retention and penetration resistance measurements were completed. Field penetration resistance was measured using an impact penetrometer at three points around the intact core sampling point at field moisture conditions. One small sample was collected from each intact core sampling point for the field moisture measurement. A composite bulk sample was collected from each micro-site in a block to measure soil pH and EC in saturated paste extracts (Janzen, 1993), total organic carbon (Walkley-Black method, Nelson and Sommers, 1982), total N (the Kjeldahl method, Bremner and Mulvaney, 1982), total P (digestion with nitric acid - perchloric acid, Olsen and Sommers, 1982) and total K (digestion with hydrofluoric acid - perchloric acid - nitric acid, Knudsen et al., 1982).

At the Monarto site, the experimental plot was subdivided into three blocks and three replications of intact cores were collected in November 2011 from DSL in each block at a depth of 5-10 cm using the same bulk density rings described above. All measurements were the same as described for the Rockleigh soils; three composite samples were collected from the whole area for various other measurements in the laboratory.

2.4 Plant sampling and measurements

Plant sampling was based on a RCBD where the same block used for soil sampling was selected to count plant density. The same sampling method was used to estimate biomass on standing trees, but only in grazed paddocks. At the Rockleigh site, the number of trees was counted in May 2011 for each identified species for all three paddocks. An additional count was made for the recently established paddock (cultivated) in August 2012 to estimate mortality rate for young plants. Plant biomass was estimated for the two grazed paddocks on 8-year old living trees (in August 2012) of the most successful species, i.e., *Acacia pycnantha* Benth., *A. argyrophylla* F.Muell. and *Eucalyptus leucoxylon*.

Table 1

Site and farm characteristics and description of tree establishment projects used at all the sites

Paddock and site	Cropping history	Land and soil types	Establishment method	Establishment month and year	Annual rainfall (mm)[a]
Cultivated, Rockleigh	Cropped; 1.6 ha; wheat and barley; 20+ years; fertigated (super phosphate; urea etc)	South facing; slope 4-10%; loamy sand; no rocks	Direct seeding	August, 2010	513
Grazed hill-top, Rockleigh	Sheep grazing; 0.8 ha; 20+ years	East facing; slope 3-6%; loamy sand, rocky (upper half)	Direct seeding	August, 2004	375
Grazed, hill-toe, Rockleigh	Sheep grazing; 0.6 ha; 20+ years	South facing; slope 12-14%; loamy sand, highly rocky	Direct seeding	August, 2004	375
Cultivated, Monarto	Cropped; 0.2 ha; wheat and barley; 20+ years; fertigated (super phosphate; urea etc)	Flat; loamy sand; no rocks	Direct seeding and transplanting	August, 2011	433

[a] *Mean annual rainfall 344 mm; mean annual potential evaporation 1,400-1,600 mm; mean annual actual evapotranspiration 400-500 mm (source: Bureau of Meteorology, Australia)*

Table 2

List of tree species, types of seeds, seeding rate and characteristics of transplanted seeding

Establishment method	Species	Seed and seeding types	Seeding or planting rate (per ha)
Direct seeding	*Acacia argyrophylla, A. calamifolia, A. menzellii, A. pycnantha*	Large seeds	~10,000
	Senna artemisioides, Dodonaea viscose, Allocasuarina verticillata	Medium seeds	~30,000
	Eucalyptus leucoxylon, E. fasciculosa, E. odorata, E. porosa, Melaleuca lanceolata	Small seeds	~30,000
Transplanting	*E. leucoxylon, E. kochii, E. loxophleba, E. platypus, M. lanceolata, M. uncinata*	Small seeds 90-d old seedling	~830

Seven trees of each of the major species were felled to establish species specific tree allometrics. Each tree was then subdivided into main trunk (pruned at 1.5 m height), branches (>1 cm diameter), twigs (<1 cm diameter) and leaves, and weighed. Dry biomass was measured on subsamples for each plant component and finally converted to total dry biomass for each plant. Equivalent tree diameter, assuming the tree trunk as a truncated cone, was calculated as:

$$D_e = \sqrt{\frac{D_t^2 + D_t D_b + D_b^2}{3}} \ ,$$

where D_e = equivalent diameter, D_t = diameter at 1.5 m height and D_b = diameter at the base (Zegada-Lizarazu et al., 2007). An allometric equation was derived by plotting total dry biomass against De. For the biomass estimation for the whole paddock, Dt and Db were measured on each standing tree in each of the 3 blocks (10 m x 10 m) in each paddock. For the *Acacia* species there were 30 or more trees (sum of the three blocks). For *E. leucoxylon*, there were less than 30 trees (sum of the three blocks), so we measured tree diameters from additional blocks (same size as mentioned above) until we had measurements from 30 trees.

At the Monarto site, the first tree count was made after three months of tree establishment, i.e., in November 2011, before the onset of summer. Another count was made in November 2012 to calculate the tree mortality rate for the different species and establishment methods.

2.5 Statistical analyses

Data on tree establishment rate, tree density and tree mortality for all paddocks were subjected to a one-way analyses of variance (ANOVA) using the statistical software package SPSS, version 11.5 (SPSS Inc., Chicago, IL, USA). For biomass estimation of older trees (in grazed paddocks only), allometric models were developed using MS Excel. Tree diameter and estimated tree biomass for the grazed paddocks were also subjected to a one-way ANOVA using SPSS as mentioned above. Data on a number of soil chemical and physical properties were also tested for a one-way ANOVA using SPSS. Soil water retention and soil penetration resistance data were fitted to the models of Groenevelt et al. (2004) and Grant et al. (2010) using the statistical software package MathCAD, version 14 (Mathsoft 2008).

3. Results

3.1 Seedling establishment, survival and tree growth

At the Rockleigh site, within the same paddock, there were significant ($P \leq 0.05$) differences in the seedling establishment rate from direct-seeding between the different species. Seedling establishment of *Acacia* species was significantly ($P \leq 0.05$) greater than *Eucalyptus* and other species (Table 3). There were also significant ($P \leq 0.05$) differences in the establishment rate of different paddocks especially for large-seeded species. The two grazed paddocks had 8-10 times greater establishment of *Acacia* and other species than that of the cultivated paddock. Overall, the cultivated paddock had significantly lower ($P \leq 0.05$) establishment than the grazed paddocks (Figure 1a). There was no significant ($P > 0.05$) difference in establishment between the two grazed paddocks (Table 3). At the Monarto site, seedling establishment was similar to those of the two grazed paddocks at the Rockleigh site (Table 3). As the seeding rate was much greater for the *Eucalyptus* species than it was for the large-seeded *Acacia* species (Table 2), the difference in tree densities of small and large-seeded species was much smaller than it was for the establishment rate. At the Rockleigh site, there was no significant ($P > 0.05$) difference in tree density for species of different seed sizes in the cultivated paddock. However, in both grazed paddocks, *Acacia* trees outnumbered the *Eucalyptus* trees (Table 3). In the grazed paddocks, there was also a considerable number of other woody species such as the shrub *Senna artemisioides* Randell. Overall, the cultivated paddock had significantly ($P \leq 0.05$) lower tree density compared to those of the grazed paddocks (Figure 1b). There was no significant ($P > 0.05$) difference in tree density for the two grazed paddocks (Figure 1b), especially for *Acacia* and other species (Table 3). At the Monarto site, tree density was significantly ($P \leq 0.05$) greater for *Acacia* compared to those of the *Eucalyptus* and other species (Table 3).

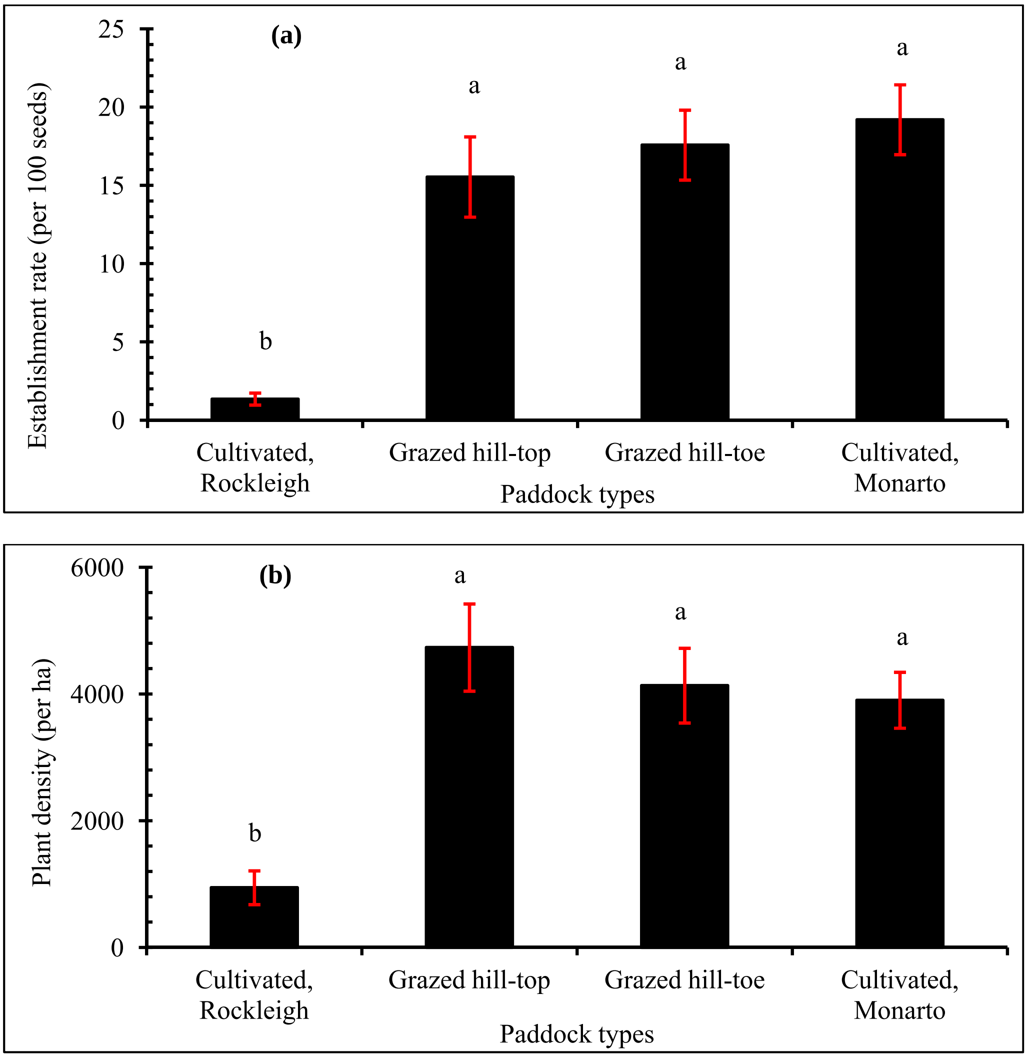

Fig. 1. Comparisons of (a) overall recruitment rate and (b) tree density of three paddocks at the Rockleigh site and one paddock at the Monarto site. Error bars represent standard error of the mean and bars accompanying same letter (within the group) are not significantly ($P \leq 0.05$) different from each other.

Although the establishment rate and tree density of *Eucalyptus* species for the cultivated paddock were similar to that of the grazed paddock at the hill-top and greater than that of the grazed paddock at the hill-toe in 2011 (Table 3), tree density dropped significantly for the cultivated paddock at the Rockleigh site in 2012. This was due to the high mortality rate for *Eucalyptus* and *Acacia* species in the cultivated paddock (Figure 2a). After the summer of 2011-2012, the mortality rates were 78% and 20% for *Eucalyptus and Acacia* species respectively. Overall, 60% of the total young plants could not survive the harsh conditions in the cultivated paddock. There was no significant (P > 0.05) difference in mortality rates of different species at the Monarto site (Figure 2a).

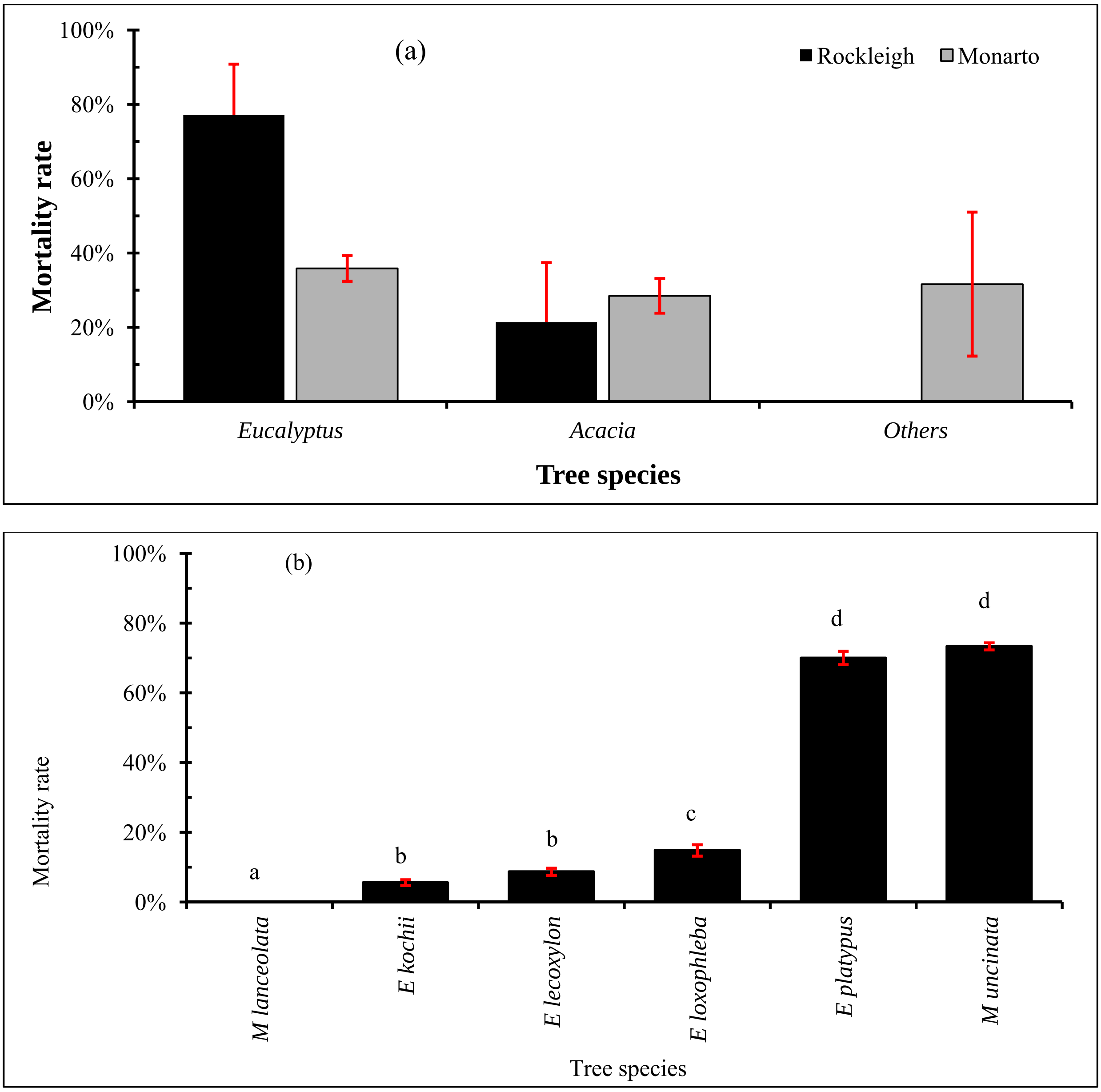

Fig. 2. Comparisons of mortality rate of (a) direct seeded seedlings and (b) transplanted seedlings during 2011-2012 summer. Error bars represent standard error of the mean of the variables and bars accompanying same letter (within the group) are not significantly ($P \leq 0.05$) different from each other.

The relative success rates of direct-seeded and transplanted seedlings were evaluated only at the Monarto site. Direct seeding of small-seeded species (Table 1) resulted in a poor establishment rate compared to the large-seeded species (Table 3). In addition, 36% of the *Eucalyptus* seedlings did not survive their first summer after germination (Figure 2a). By comparison, most of the transplanted seedlings of the *Eucalyptus* species had low mortality rates except for *E. platypus* Hook. (Figure 2b). More than 90% of the transplanted seedlings of *E. kochii* Maiden & Blakely and *E. leucoxylon* survived the harsh summer without any irrigation provided. For the transplanted species there was zero mortality of *Melaleuca lanceolata* Otto but > 75% mortality for *M. uncinata* R.Br. Direct seeding of *M. lanceolata* was a complete failure and *M. uncinata* was not included in direct seeding.

Dry biomass was estimated only for 8-year-old trees in the two grazed paddocks at the Rockleigh site. *Acacia pycnantha*, *A. argyrophylla* and *Eucalyptus leucoxylon* were the three most successful species. Both *Acacia* species produced larger biomass than *E. leucoxylon* where *A. pycnantha* produced the highest biomass especially for older trees of the same diameter (Figure 3a). There was no significant ($P > 0.05$) difference in equivalent tree diameter between the species and between the paddocks (Figure 3b). There was a significant ($P > 0.05$) difference in estimated biomass production of three species (Figure 3c). In both paddocks, *A. pycnantha* produced significantly ($P > 0.05$) greater estimated biomass than that of other two species.

3.2 Environmental variables

The annual rainfall was comparatively greater in all three establishment years (i.e., 2004, 2010 and 2011) compared to that of the mean annual rainfall for the area (345 mm) and there was no significant ($P > 0.05$) difference in the mean maximum temperature for the three direct seeding years except a hotter month of October in 2004 (Figure 4a, 4b). Year 2010 had the highest annual rainfall (513 mm) followed by the year 2011 (433 mm) and 2004 had the lowest annual rainfall. Although there was no significant difference in cumulative rainfall, the temporal distribution varied among the three direct seeding scenarios. In both 2010-2011 and 2011-2012, there were considerably higher amounts of rainfall after the germination of seeds (during the following summer) compared to that of 2004-2005 (Figure 4a). As the area experiences annual potential evaporation of about 1,400 mm, none of the rainfall regimes can satisfy the evapotranspirational demand. None of the tree establishment years experienced frosting after the direct seeding operations (Bureau of Meteorology, Australia). However, some of the direct seeding projects such as the one conducted in 2004-2005 had better success than those of the other two years - this probably indicates the relevance of other factors than those of environmental variables.

Table 3

Seedling recruitment rate and plant density for direct seeded paddocks in two sites. Mean values followed by ± standard error of the mean. Different letters superscripted to the standard errors indicate significant difference at $P \leq 0.05$

Site	Paddocks	Establishment rate (no. seedlings per 100 seeds)			Density (plants per ha)		
		Small seeds	Large seeds		Small seeds	Large seeds	
		Eucalyptus spp	*Acacia* spp	Others	*Eucalyptus* spp	*Acacia* spp	Others
Rockleigh	Cultivated	1.67 ± 0.71^{b}	4.29 ± 0.68^{a}	0.34 ± 0.01^{b}	500 ± 212^{ns}	429 ± 68^{ns}	100 ± 0^{ns}
	Grazed hill-top	2.11 ± 1.06^{b}	29.7 ± 2.7^{a}	3.78 ± 1.71^{b}	633 ± 318^{c}	2,967 ± 273^{a}	1,133 ± 296^{b}
	Grazed hill-toe	0.67 ± 0.19^{b}	30.0 ± 4.5^{a}	3.11 ± 0.45^{b}	200 ± 58^{b}	3,000 ± 458^{a}	933 ± 186^{b}
Monarto	Monarto Zoo	1.84 ± 0.54^{b}	29.3 ± 4.5^{a}	1.41 ± 0.14^{b}	555 ± 162^{b}	2,926 ± 450^{a}	422 ± 41^{b}

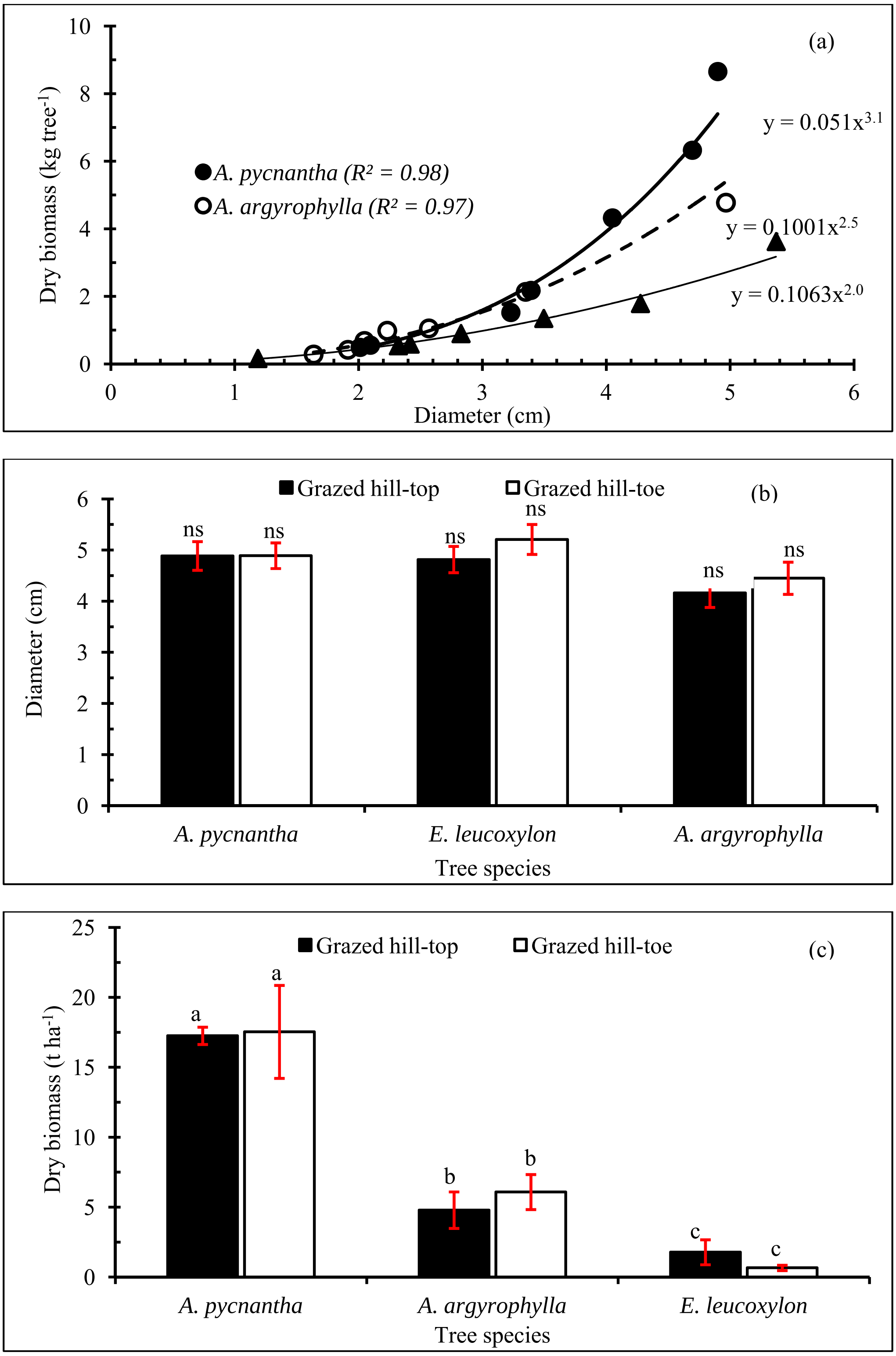

Fig. 3. Comparisons of (a) tree allometrics used to estimate dry biomass for whole paddock, (b) equivalent diameter of the sampled trees ($n \geq 30$), and (c) estimated dry biomass for whole paddock for three species after 8 years of establishment in two grazed paddocks at the Rockleigh site. Error bars represent standard error of the mean of the variables and bars accompanying same letter (within the group) are not significantly ($P \leq 0.05$) different from each other.

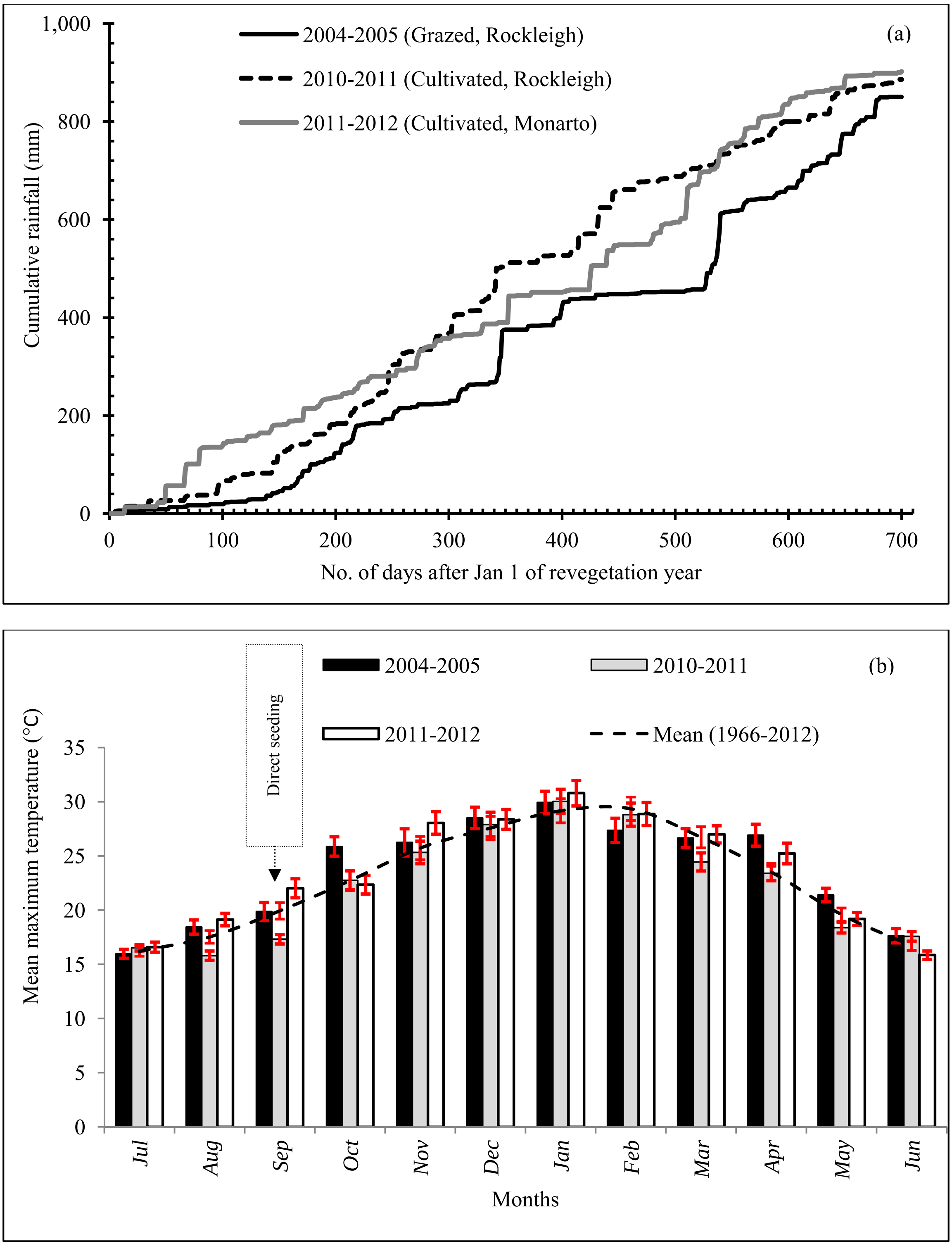

Fig. 4. Estimates of (a) cumulative rainfall for two consecutive years starting from January 1 of the direct seeding year, and (b) mean maximum temperature for three direct seeding years (source: Bureau of statistics, Australia).

3.3 Soil pH, EC and soil fertility

There was no significant (P > 0.05) difference between paddocks in any of the soil chemical properties when soil samples were taken from DSL (Table 4). Soil pH, measured in saturated paste extracts, were within a range of 6.04-6.23 which is suitable for most of the plant species. None of the soils was saline as the electrical conductivity values ranged between 0.34 and 0.49 dS m-1. There was no significant (P > 0.05) difference in total organic carbon (TOC) content and the values were within a range of 0.93-1.12 %. There was no difference in any of the major nutrients, i.e., N, P and K in the soil.

For the soil taken from BDSL, most of the chemical properties were insignificantly (P > 0.05) different for different paddocks. There was only a difference in N content where the grazed paddock at the toe of the hill had a significantly (P ≤ 0.05) higher N content compared to the cultivated paddock. Although both of the grazed paddocks had higher TOC content compared to the cultivated paddock, the difference was not statistically significant (P > 0.05). Soil from BDSL had higher TOC and N content compared to the soils from DSL.

3.4 Soil physical properties

Table 5 presents the results of some soil physical property analyses. There was no significant (P > 0.05) difference in soil particle size distribution, i.e., clay content. Soil from DSL of the two grazed paddocks had significantly (P ≤ 0.05) higher gravel content compared to that of the cultivated paddock at the Rockleigh site. Soil from BDSL of the grazed paddock at the top of the hill had significantly (P ≤ 0.05) higher gravel content than that of the other paddocks, which was a consequence of historical soil erosion. As expected soils from both micro-sites in the cultivated paddock were significantly (P ≤ 0.05) compacted, having higher bulk density, compared to those of the two grazed paddocks. There was a significant difference in bulk densities of the two grazed paddocks where the soil at the top of the hill was significantly less compacted than that at the toe of the hill (Table 5).

Table 4

Comparisons of selected soil chemical properties of three paddocks at the Rockleigh site and one paddock at the Monarto site. Mean values followed by ± standard error of the mean. Different letters superscripted to the standard errors indicate significant difference at $P \leq 0.05$

Micro-sites	Paddocks	pH	EC (dS m^{-1})	TOC (%)	Total N (mg kg^{-1})	Total P (mg kg^{-1})	Total K (mg kg^{-1})
DSL	Cultivated (n = 21)	6.22 ± 0.12^{ns}	0.49 ± 0.05^{ns}	0.93 ± 0.07^{ns}	762 ± 90^{ns}	247 ± 22^{ns}	291 ± 19^{ns}
	Grazed hill-top (n = 9)	6.04 ± 0.02^{ns}	0.38 ± 0.03^{ns}	1.04 ± 0.02^{ns}	989 ± 60^{ns}	303 ± 7^{ns}	267 ± 66^{ns}
	Grazed hill-toe (n = 9)	6.23 ± 0.09^{ns}	0.34 ± 0.03^{ns}	1.12 ± 0.21^{ns}	1076 ± 136^{ns}	296 ± 55^{ns}	241 ± 13^{ns}
	Monarto Zoo (n = 9)	7.06± 0.05^{ns}	1.08 ± 0.02^{ns}	0.91 ± 0.06^{ns}	842 ± 76^{ns}	224 ± 32^{ns}	301 ± 16^{ns}
BDSL	Cultivated (n = 21)	6.00 ± 0.13^{ns}	0.57 ± 0.12^{ns}	1.13 ± 0.07^{ns}	1020 ± 82^{b}	286 ± 20^{ns}	288 ± 19^{ns}
	Grazed hill-top (n = 9)	5.94 ± 0.08^{ns}	0.34 ± 0.05^{ns}	1.43 ± 0.17^{ns}	1270 ± 110^{ab}	306 ± 10^{ns}	271 ± 74^{ns}
	Grazed hill-toe (n = 9)	6.14 ± 0.18^{ns}	0.35 ± 0.01^{ns}	1.55 ± 0.20^{ns}	1498 ± 198^{a}	370 ± 33^{ns}	253 ± 6^{ns}

Table 5

Comparisons of selected soil physical properties of three paddocks at the Rockleigh site and one paddock at the Monarto site. Mean values followed by ± standard error of the mean. Different letters superscripted to the standard errors indicate significant difference at $P \leq 0.05$

Micro-sites	Cropping types	Clay (%)	Gravel (%)	Uncorrected bulk density (g cm^{-3})	Corrected bulk density (g cm^{-3})
On the direct seeding lines	Cultivated (n = 21)	11.6 ± 1.0^{ns}	3.3 ± 1.2^{b}	1.55 ± 0.02^{a}	1.54 ± 0.02^{a}
	Grazed hill-top (n = 9)	9.1 ± 1.2^{ns}	18.0 ± 0.4^{a}	1.44 ± 0.01^{b}	1.27 ± 0.04^{c}
	Grazed hill-toe (n = 9)	9.0 ± 0.1^{ns}	12.1 ± 5.0^{a}	1.47 ± 0.01^{b}	1.43 ± 0.03^{b}
	Monarto Zoo	10.3 ± 1.8^{ns}	2.03 ± 1.02^{b}	1.62 ± 0.03^{a}	1.62 ± 0.03^{a}
Between the direct seeding lines	Cultivated (n = 21)	10.5 ± 1.0^{ns}	3.3 ± 1.1^{b}	1.53 ± 0.01^{a}	1.51 ± 0.02^{a}
	Grazed hill-top (n = 9)	10.0 ± 0.6^{ns}	18.0 ± 3.6^{a}	1.41 ± 0.02^{b}	1.26 ± 0.05^{b}
	Grazed hill-toe (n = 9)	11.3 ± 0.3^{ns}	4.3 ± 1.9^{b}	1.42 ± 0.04^{b}	1.39 ± 0.01^{c}

Figure 5a shows soil moisture status of the three paddocks on a hot summer day at the Rockleigh site. Soils from all paddocks were very dry, however, soil from BDSL in the grazed paddock hill-toe had significantly ($P \leq 0.05$) higher moisture content (Figure 5a) and lower penetration resistance compared to those of the other two paddocks (Figure 5b). Water retention curves were significantly different ($P \leq 0.05$) among the paddocks and micro-sites (Figures 6a, 6b). The cultivated paddock had significantly lower water content at the wet end. Soil from Monarto had lower water contents at all levels of matric suction than that of the Rockleigh soils (Figure 7), which reflected their higher sand contents.

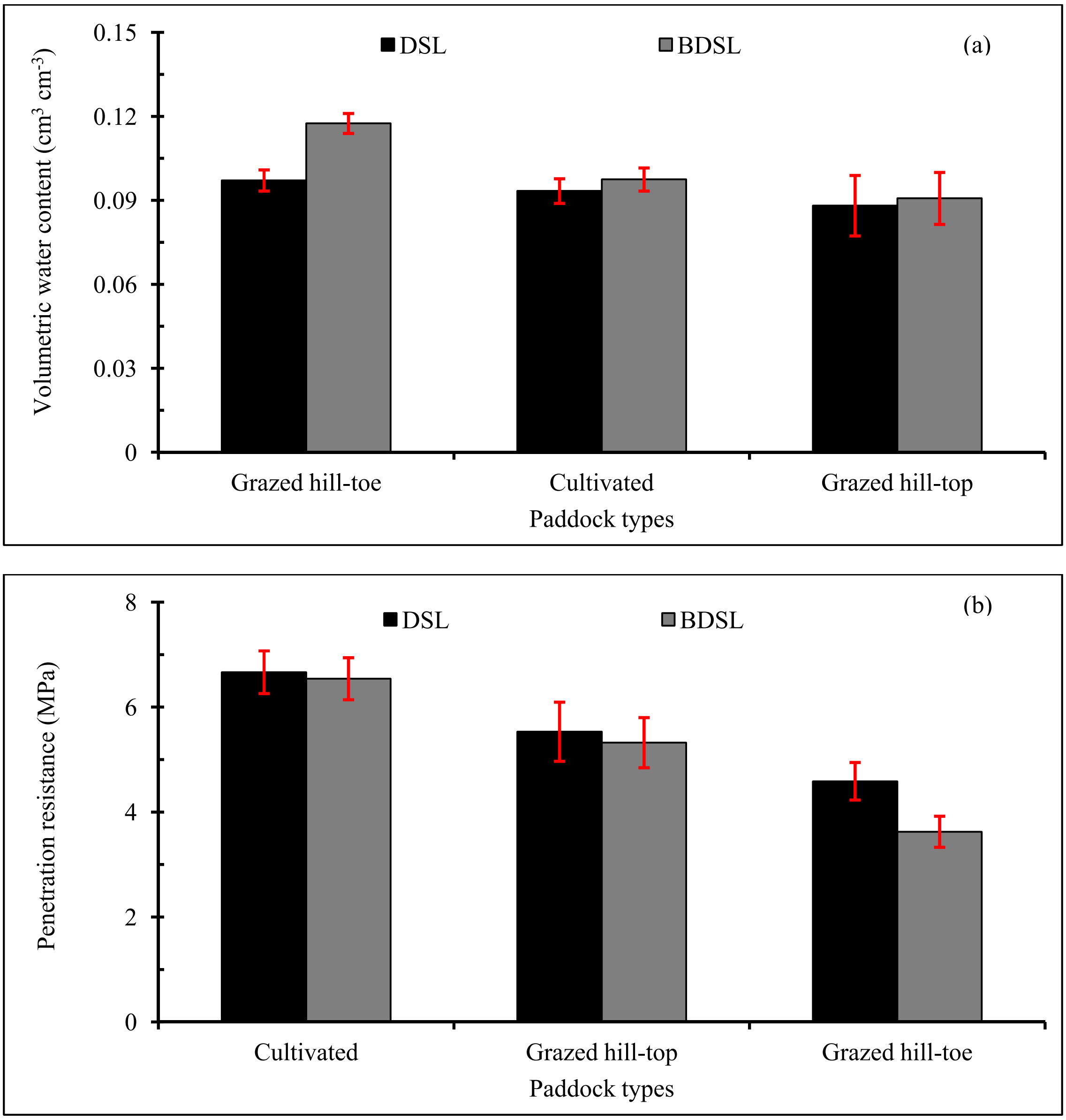

Fig. 5. Field measurements of (a) soil volumetric water content, and (b) penetration resistance of soils of three paddocks at the Rockleigh site. Soils were collected from two micro-site, i.e., on the direct seeding lines (DSL) and between the direct seeding lines (BDSL). Vertical bars represent standard error of the variables.

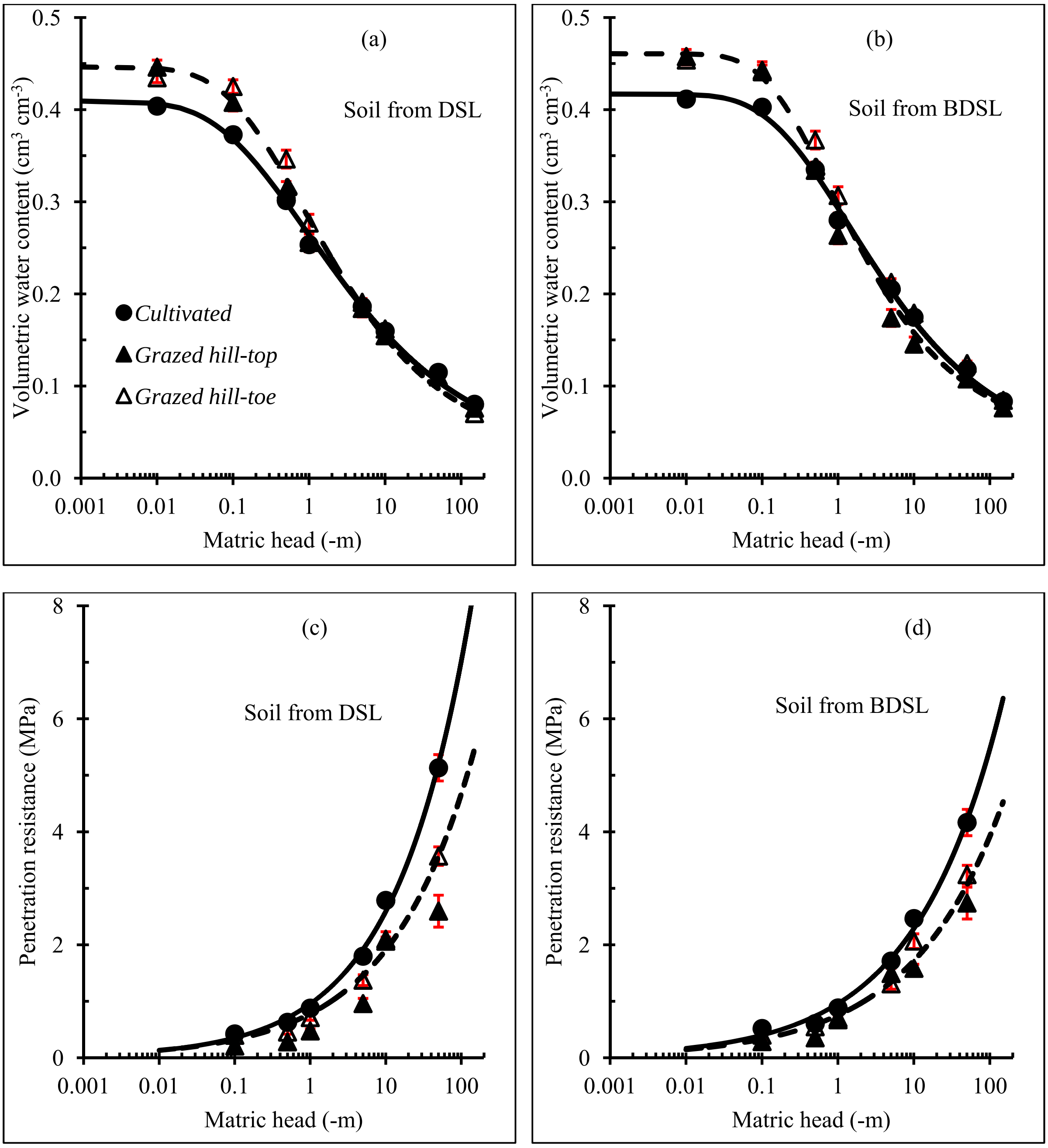

Fig. 6. Relationships between (a and b) matric head (-m) and volumetric water content (cm^3 cm^{-3}) and (c and d) matric head (m) and penetration resistance (MPa)for 5-10 cm top soil collected from two micro-sites of three paddocks at the Rockleigh sites. Vertical bars represent standard error of the variables. Scatter pots present the measured values of the variables while broken and broken line features present the modelled values of the variables of soils of the two grazed paddocks (averaged) and the cutivated paddock respecticely.

There was no significant difference in penetration resistance at matric suctions at or below 5 m (Figures 6c, 6d). At matric suctions >5 m, soil from DSL in cultivated paddock at the Rockleigh site had significantly ($P \leq 0.05$) greater penetration resistance than those of the other two paddocks (Figure 6c). The difference continued to become larger with increasing soil matric suctions. At matric suction 50 m, the cultivated paddock at the Rockleigh site had nearly 1.5-2.0 times greater penetration resistance than those of the other paddocks. At a specific soil matric potential, soils from DSL had comparatively greater penetration resistance (Figure 6c) than the soils from BDSL (Figure 6d). Soil from the Monarto site had comparative low penetration resistance and values were quite similar to those of soils from the two grazed paddocks at the Rockleigh site (Figure 7).

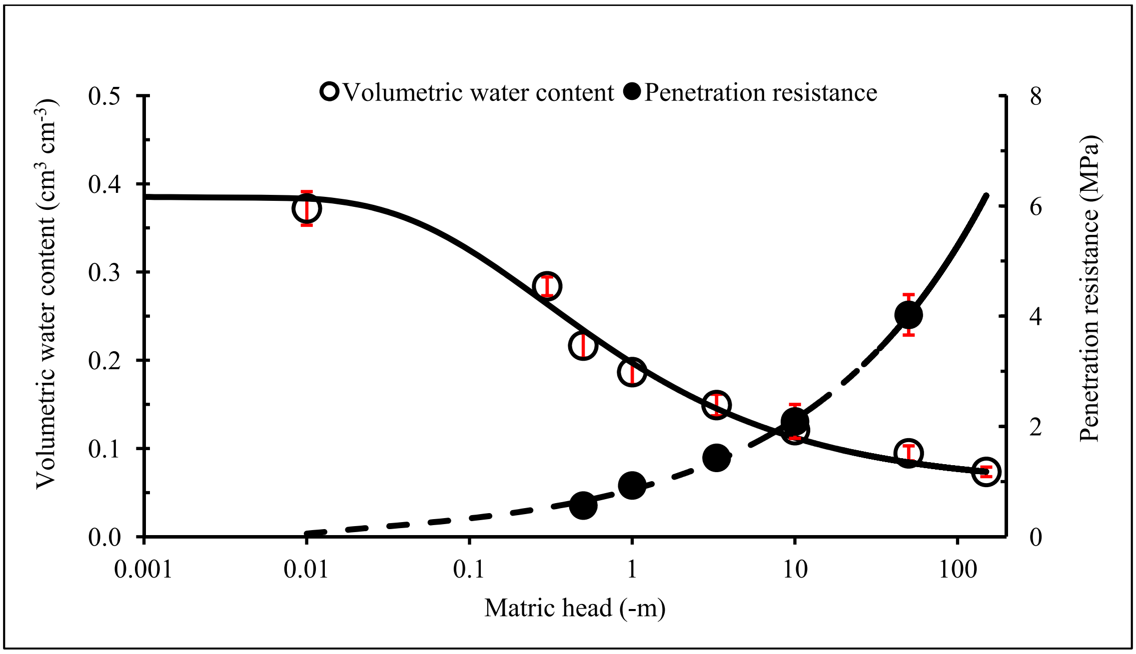

Fig. 7. Relationships between matric head (-m), volumetric water content (cm^3 cm^{-3}) and penetration resistance (MPa) for 5-10 cm top soil collected from direct seeding lines at the Monarto site. Vertical bars represent standard error of the variables. Scatter pots present the measured values and line features present the modelled values of respective variables.

4. Discussion

4.1 Root growth pressure to select species for direct seeding

Within a specific paddock, there was a higher seedling establishment rate and consequently higher tree density of direct-seeded *Acacia* species compared to those of direct-seeded *Eucalyptus* and other species (Table 3). The mortality rate of young plants of large-seeded *Acacia* species was also significantly smaller than that of *Eucalyptus* species, especially at the

Rockleigh site (Figure 2a). The general explanation for these differences could be the general effects of seed sizes – as literature suggests that large seeds of *Acacia* species contain greater food reserves which promote faster and more successful germination (Doust et al., 2006; Knight et al., 1998) and they also provide young plants with greater tolerance to extreme environmental conditions (López et al., 2000). However, the higher establishment rate, lower mortality and thus higher tree density of *Acacia* species is due to the superior ability of the roots of this species to elongate faster into the deep soil layers than those of the *Eucalyptus* and other species (Azam et al., 2013b). Particularly in strong dry soil, which is a very typical scenario in a low rainfall environment (FAO 1989), root elongation is strongly correlated with the ability of young plants to produce primary roots just thick enough to exert sufficient and increasing growth pressure over time (Bengough, 2012; Azam et at., 2013a). Consequently the plant species that can exert sufficient root growth pressures will send their roots quickly into deep soil horizons and enable them to take up more water (Eastham et al., 1990). Therefore, after successful germination, the ability of the roots of young plants to exert sufficient root growth pressures on sourrounding soils plays a vital role for the success of direct seeding (Bengough, 2012).

Finally, production of greater biomass by 8-year old *Acacia* trees, compared to those of *Eucalyptus* trees (Figure 3a), may also be related to the effect of seed size resulting large differences in early establishment and growth rate (Doust et al., 2006). Large-seeded acacias are also able to generate greater root growth pressure (Azam et al., 2013a) which enhances root penetration (Azam et al. 2013b) to explore a greater proportion of water and nutrients in hostile soils (Eastham et al., 1990).

4.2 Root growth pressure to select revegetation methods

Previously why direct seeding of small-seeded species resulted in poor recruitment rates across the paddocks at all sites (Table 3, <2% for *Eucalyptus* compared to ~30% for *Acacia*) was discussed (see *subsection 4.1*). At the Monarto planting experiment, there was a very high mortality rate of young plants of direct-seeded *Eucalyptus* species (Figure 2a) compared to those of transplanted seedlings of *Eucalyptus* species except for *E. platypus* (Figure 2b). This is clearly due to the fact that lateral roots of transplanted *E. leucoxylon, E. kochii* and *E. loxophleba* can exert sufficient growth pressures (Azam et al., 2013a) and consequently can elongate faster into strong subsoils relative to those of primary roots of direct-seeded plants of the same species (Azam et al., 2013b).

However, the ability to exert greater root growth pressure may not always make tree species successful – some species have other limitations that restrict their use. For example, *E. platypus* can exert reasonably high root growth pressure (Azam et al., 2013a) but this species produces a shallow root system which restricts them from taking up water from the deeper soil horizons (Burgess et al., 2001). For this reason the mortality rate of transplanted *E. platypus* was higher than those of other *Eucalyptus* species (Figure 2b). The survival rate may also be related to the relative sensitivity of a particular species to drought conditions – in this study, there was a significantly higher mortality rate of transplanted *M. uncinata* compared to *M. lanceolata* (see Figure 2b). The zero mortality rate of *M. lanceolata* may be related to their ability to synthesize greater concentrations of proline in the tissue systems which helps them tolerate drought conditions better than *M. uncinata* (Naidu et al., 1987).

4.3 Soils that need to be managed before revegetation

There was a significant difference in the establishment rate and tree density in different paddocks, especially for direct-seeded *Acacia* (Table 3). *Acacias* were highly successful in the two grazed paddocks at Rockleigh and in the cultivated paddock at Monarto compared to those in the cultivated paddock at Rockleigh (Figures 1a, 1b) and those reported elsewhere (see Knight et al. 1998; Woodall, 2010). The exceptionally poor performance of direct seeding with the large-seeded *Acacia* in the cultivated paddock at the Rockleigh site relative to that in the other paddocks can thus be related to soil conditions, because there was no difference in tree species, seed quality and environmental variables during the two establishment years.

Soils from DSL of different paddocks had no significant difference in soil pH, EC and other chemical properties (Table 4). This is due to the removal of top soils during direct seeding operations which left only subsoil. The relatively short time period since this operation meant the chemical properties of the exposed subsoil barely changed over time (Beatty and Corey, 1962). There was only a difference in N content of soils from BDSL of different paddocks (Table 4) where the two grazed paddocks had significantly ($P \leq 0.05$) higher N content compared to the cultivated paddocks. This suggests that the roots of some of the *Acacia* and/or legume pasture species probably fixed aerial N (Schulze et al., 1991). Although the differences in soil chemical properties among the different paddocks were not substantial, the relatively lower EC and higher TOC, N and P in the grazed paddocks may have contributed to the better establishment of trees in these paddocks – but these soil properties certainly do not explain such large difference (see Table 3) in the performance of direct seeding of any species in any paddocks (Hall, 1999).

Significant differences were observed in a number of soil physical properties of different paddocks (Table 5). Soils from the cultivated paddocks were more compacted than those of the two grazed paddocks which are consistent with the long-term impact of conventional tillage operations in the cultivated paddocks (Bennie and Botha, 1986). In consequence, the total porosity and water holding capacity of the soil were reduced greatly (Hamza and Anderson, 2005). This explains the lower volumetric water content of the cultivated paddocks at low matric suctions (Figure 6a, 6b). Another important observation was the significant difference in soil strength, i.e. penetration resistance of soils of different paddocks (Figures 5b, 6c, 6d). This can be explained by the differences in both compaction and soil water status of soil (Eavis, 1972). High soil strength from either compaction or water status can severely restrict tree root elongation (Zou et al., 2001). Although the ability to maintain root elongation varies among the tree species, in extremely hard soil (i.e. soil penetration resistance 5 MPa or more), root elongation of even the best performing species slows down by 80-90% (Azam et al., 2013b). The extremely high soil penetration resistance of the cultivated paddock at the Rockleigh site (both in the field and laboratory measurements), thus may be responsible for the poor success rate of revegetation by direct seeding compared to that in the other paddocks. There may have been other soil physical conditions (e.g. availability of continuous macropores) that enhanced plant establishment in the grazed paddocks by providing pathways for root penetration (Bengough 2012). This is consistent with the fact that the grazed paddocks had greater density of macropores than those of the cultivated paddocks (Chan and Mead, 1989). However, soil with such significant physical limitations as found in the cultivated paddock at Rockleigh can be managed by deep ripping to reduce soil penetration resistance and to increase root penetration deeper into the soil (Bennie and Botha, 1986).

5. Conclusions

Direct seeding was mostly successful for large-seeded *Acacia* species. This characteristic of large-seeded species appears to be related to their ability to exert greater and increasing root growth pressures over time and elongating their roots faster in hard soils than those of small direct-seeded species. This probably allowed large-seeded species to draw on the deeper soil resources and to survive in drier conditions. Small-seeded *Eucalyptus* species, on the other hand, lack such ability and they consequently are less successful than those of the large-seeded species. However, when small-seeded species were transplanted they were more successful than those of direct-seeded ones of the same species. This was again probably due to the superior ability of the lateral roots of transplanted seedlings to exert greater root growth pressure and to send their roots faster into deeper soil layers than those of direct-seeded ones. These findings corroborate the laboratory findings of Azam et al. (2013a; 2013b) and reconfirm that the ability to exert high root growth pressure can be used as a screening tool for selecting superior species for revegetating degraded, strong and dry soils in arid and semi-arid environments. However, this may not always be an effective tool if a soil possesses extreme physical limitations or if the plant species are limited in their rooting habit (e.g. shallow root systems) or the species are not able to cope with drought conditions typical of semi-arid environments. Soil with extreme physical conditions may need to be managed before any revegetation project is employed.

Acknowledgment

The senior author acknowledges the support from the University of Adelaide in the form of an International Postgraduate Student Scholarship and the Future Farm Industries Cooperative Research Centre for supplementary support.

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CHAPTER 7

SUMMARY, CONCLUSIONS AND FUTURE RESEARCH

Summary and conclusions

Woody perennials are widely recognized for their importance in revegetating arid and semi-arid landscapes; they can generate numerous ecological, environmental and economic benefits (Lamb et al. 2005; Caldwell et al. 2009; Donohue et al. 2009). Where rainfall is limiting, however, they are difficult to establish especially when they are planted directly from seeds rather than transplanted from nurseries. A review of the literature (Chapter 2, published by Azam et al. 2012 in *Plant and Soil*) revealed that edaphic factors have been largely ignored in efforts to establish woody perennials, and further that cultural techniques which may be successful in higher rainfall regions are often unsuccessful in more arid zones where environmental conditions are less forgiving. Apart from the limited supply of water in arid and semi-arid regions (which leads to greater salt retention in the root zone), high soil strength and poor subsoil aeration appeared to be the most limiting edaphic factors for plant establishment. The detailed effects of high soil strength and poor soil aeration on the growth of young woody perennials, however, are poorly understood compared with crop plants such as peas or barley. The literature suggested woody species share some important physiological traits to domestic crops (e.g. they exert a similar magnitude of axial root growth pressures compared with eucalypts and peas).

In relation to how plant roots cope with soils of high strength, it was postulated that the roots of woody species exert higher growth pressures on the soil and explore the soil more efficiently than crop plants and thus produce extensive (and deep) root systems, which can access water and nutrients when the surface dries out. Variation in the genetic pool among woody perennials was assumed to be responsible for this adaptive strategy but there was little solid evidence to support it. On this basis, I evaluated the maximum root growth pressures that several single- and multi-stemmed, small- and large-seeded woody perennials could exert and compared these to those of an annual crop (Chapter 3, published by Azam et al. 2013a in *Plant and Soil*). There was sufficient variation shown among the woody species in this study to speculate on links between high or low root growth pressures and the presence or absence of hard soils in the locations where each species occurred in the natural landscape. There was also strong evidence showing that even though the maximum root growth pressures generated by woody perennials were not hugely different from those of crop plants, they tended to increase over time (10 days) whereas those for the domestic plant did not change during this period. This suggests that woody plants continue to grow in hard soils while domestic plants tend to suffer. The extent to which this phenomenon occurs widely among woody species is unknown and warrants further investigation.

The differences in maximum root growth pressures among the woody species in Chapter 3 implied that similar variation should be exhibited by these plants when grown in hard soils in the absence of natural cracks and biopores. I therefore planted a selection of young seedlings in soils compacted to varying degrees and monitored the characteristics of their primary and lateral roots over time. This trial (Chapter 4, Azam et al. 2013b, accepted for publication in *Soil Research*, No.SR13-201) revealed that the diameter of the primary roots of the large-seeded woody perennials increased more consistently, and had greater ability to maintain the rate of root elongation, with increasing compaction than that of a reference crop plant. At all levels of soil compaction the primary roots of a large-seeded woody perennial were thicker and they elongated faster than those of the primary roots of small-seeded ones. Further, the study demonstrated that the ability of the primary and the lateral roots of the small-seeded species to penetrate strong soil varied with the methods of establishment. For example, the lateral roots of the transplanted seedlings elongated faster than those of their primary roots. By calculating the soil penetration resistance at which the rate of root elongation was halved relative to its maximum rate, $SR_{0.5}$, I was able to quantify the relative sensitivity of different plant species to compaction. For example, the roots of all the woody perennials generally had greater $SR_{0.5}$ values than those of the domestic plant. There was also significant variation in the $SR_{0.5}$ among the woody plants, and the primary roots of direct-seeded woody perennial seedlings had smaller $SR_{0.5}$ values than those of the lateral roots of their transplanted seedlings. Finally, the mean rate of root elongation was expressed relative to its maximum value (in the least compacted soil) to produce relative root elongation rates, L_R/L_{Rmax}, which were correlated with the mean maximum root growth pressures for several different woody species. The positive correlation suggested the natural habitat of different species might be related to the varying ability of their roots to exert high pressures on the soil. For example, *Eucalyptus leucoxylon* was found to exert greater mean root growth pressures than other species, and this species is generally found to dominate, when co-exist with other species such as *E. camaldulensis*, in dry (and hard) soils at higher altitudes; this is presumably because the ability of *E. leucoxylon* to overcome inherently high strength enables it to produce deep root systems that endure dry periods. By contrast, woody perennials that exerted low root growth pressures (e.g. *E. camaldulensis*) tend to occur in wet, marshy soils where their roots seldom encounter high soil strength.

In relation to how woody species cope with poorly aerated soils (which commonly occur with compacted, high strength subsoils), it was postulated woody perennials exhibit a wide range of sensitivity to waterlogging such that no single critical aeration status (e.g. volumetric soil air content of $\varepsilon_{air} = 0.1$ m^3 air per m^3 soil, from the literature) exists for all species in the way it does for most crop plants. For this study I used four woody perennials (chosen from previous studies above) plus a reference crop, barley (*Hordium vulgare* L.) to evaluate their relative tolerance to a range of soil aeration states (Chapter 5, Azam et al. 2013c, accepted for publication in *Soil Research*, No.SR13-219). This study revealed that the young seedlings of one eucalypt species (i.e. *E. camaldulensis*) were highly tolerant to waterlogging while others were highly sensitive (e.g. *E. kochii*). It also revealed that *H. vulgare* and *Acacia salicina* had moderate tolerance to waterlogging yet higher water use efficiencies than any of the eucalypts. Among the sensitive species, there was no single universal value of ε_{air} that was critical to plant performance; some species displayed a negative response to any reduction in $\varepsilon_{air} < 0.20$ m^{3}m^{-3}, while others were negatively impacted only when $\varepsilon_{air} < 0.15$ m^{3}m^{-3}. These differences can be justified by the species specific response of woody species to ε_{air}. Furthermore there was no single plant growth response common to all species: for some, poor soil aeration caused a reduction in shoot or root growth, while for others the response was seen only in terms of water use efficiency. The range in complexity and intensity of response by different woody perennials suggests there is plenty of scope to find better response measurements to poor soil aeration. The applicability of these findings needs validation under real field conditions, because the establishment and development of plant communities in degraded landscapes is more complex than can be imitated in laboratory and glasshouse studies.

To evaluate the applicability of my laboratory work to the real world, a plantation survey plus a planting experiment were conducted under semi-arid field conditions in South Australia (Chapter 6, Azam et al. 2013c, submitted to *Journal of Arid Environments*, No.JAE13-171). The survey revealed that large-seeded woody perennials (*Acacia* spp.) established more successfully than the small-seeded ones (i.e. *Eucalyptus* spp.) when planted from seed ('direct seeding'). My field-planting experiment revealed that transplanted seedlings of small-seeded species were more successful than the direct-seeded ones. The differences among the various tree species and planting methods in the field corroborated the findings from my laboratory studies, which suggest there are direct applications of the work for land managers and revegetation agencies attempting to select superior woody perennials and planting methods for revegetation efforts in arid and semi-arid regions.

In summary, five novel advances in root growth studies for woody perennials are presented in this thesis:

1. Measurement of the maximum primary and lateral root growth pressures for several woody tree species used to revegetate arid and semi-arid landscapes. Aside from presenting new data, this work also demonstrates that root growth pressures of primary roots of some species of woody perennials continue to increase over time, whereas those for domestic crops do not.
2. Measurement of the elongation rates for primary (direct-seeded) and lateral (transplanted) roots of woody species growing in hard soil, and presentation of the soil resistance at which their growth rates are reduced by 50%.
3. Presentation of a direct relationship between the maximum root growth pressure that a species can exert, and their corresponding rate of root elongation in hard soil. This relationship has been postulated in the past but never demonstrated before.
4. Evaluation of the response of different woody species to waterlogging and the finding that there are neither a single critical volumetric soil air content nor a single type of plant response to restricted soil aeration that applies to all woody species.
5. Field evaluation of the importance of root growth pressures for different species and different seedling ages for successful establishment of woody perennials in degraded soils.

Future research

1. The maximum root growth pressures presented in this study were for a relatively limited number of woody perennials and they showed that there is considerable variation among species. This inter-species variation needs to be evaluated more carefully to eliminate other factors such as seed quality, cloning and provenance. If these factors are shown to have minimal impact, then a wider range of woody species needs to be examined to understand the full scope of variation in root growth pressures that are possible. The possibility of finding ‘super’ species capable of exerting significantly higher pressures than other species could identify ‘pioneer’ candidates for revegetating degraded landscapes. These could be co-planted with other species that exert lower pressures but have other features that would speed up the process of revegetation.

2. Knowledge of this sort can be extended to native and domestic species in higher rainfall zones to help them cope better with strong soils, which will become increasingly important if climate change predictions bring lower rainfall to agriculturally important regions. Of particular interest in this regard is the agricultural crop, *Hordium vulgare,* which was included for comparison in the aeration study. Barley has potential to grow under a wide range of soil water conditions such as those encountered in very dry or very wet soils, so knowledge about the ability of different barley cultivars to cope with hard and/or anaerobic subsoils may be crucial for selecting species that will cope with the vagaries of climate change.
3. Although the apparatus used to measure root growth pressures was relatively simple and inexpensive, it requires considerable technical skill to operate and not suitable for large scale use. To bring to fruition the scale of measurements suggested above, an even simpler apparatus needs to be built to facilitate multiple sample handling – a task suitable for someone skilled in cutting-edge technology for both plant propagation and computer science.
4. Although my laboratory and glasshouse work was largely corroborated in the field, most of it applied to relatively young species (days to months old) so may have limited applicability to older plants in the field. A longer term study is therefore required to evaluate the effects of soil conditions from young plants on long term establishment and survival across several years where variable rainfall and temperature are brought to bear. A good start in this regard would be to set up larger soil columns in the laboratory and glasshouse in parallel with similar field work. Clearly this would need to include a wider range of typical soils from arid and semi-arid regions, for which the effects of compaction and soil water/aeration status is evaluated in the field and in the laboratory.
5. The root growth experiments in this study involved harvesting, washing, and scanning roots to determine their mass, size, length and growth rates. These procedures are both invasive and laborious, and the results must be extrapolated to reality. Non-invasive methods such as *in situ* CT-Scanning need to be applied to the study of woody perennials to better understand the growth and architecture of their plant roots.
6. In the planting experiment in the field, the observations on woody perennial establishment were made for only two consecutive summers due to the time-bound nature of this research project. Such study should be carried out for longer period of time for better understanding of the long-term performance of different woody perennials in the field.

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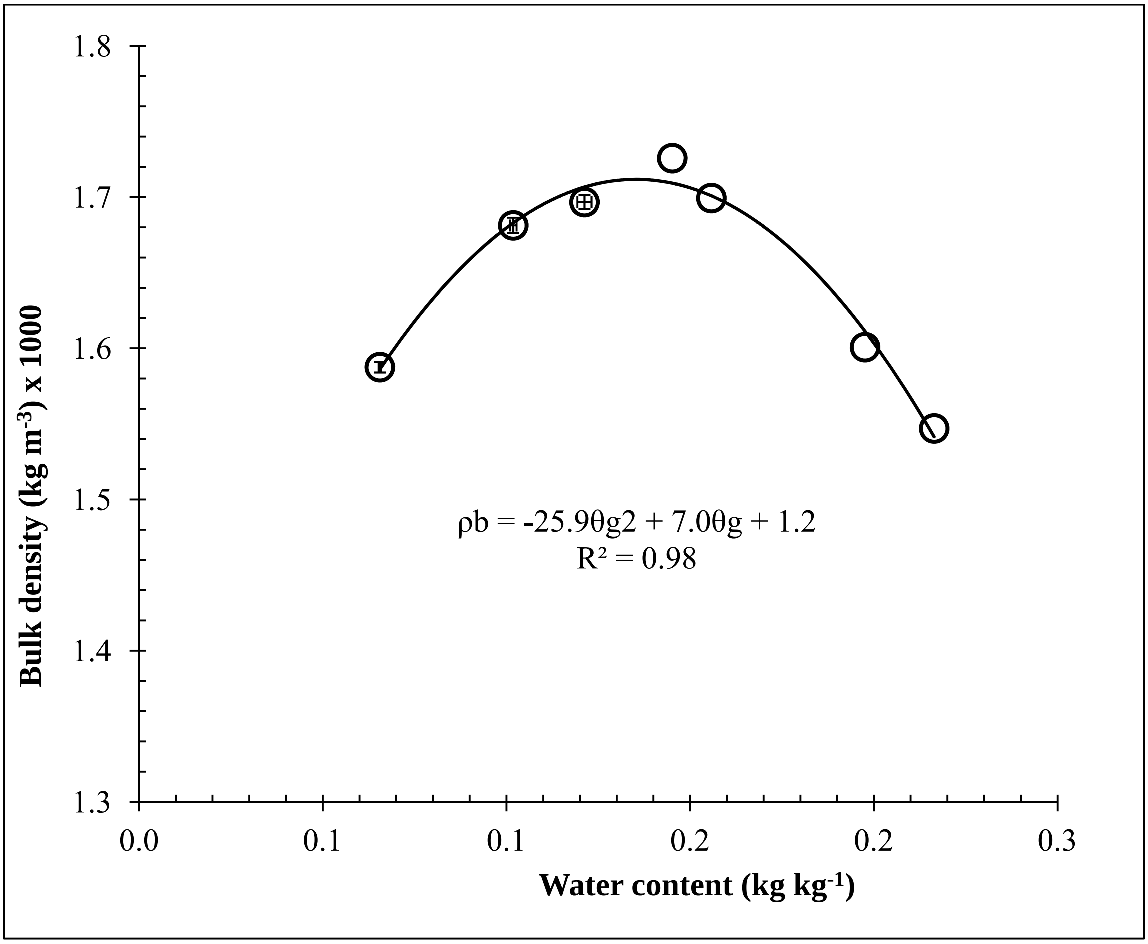
APPENDICES

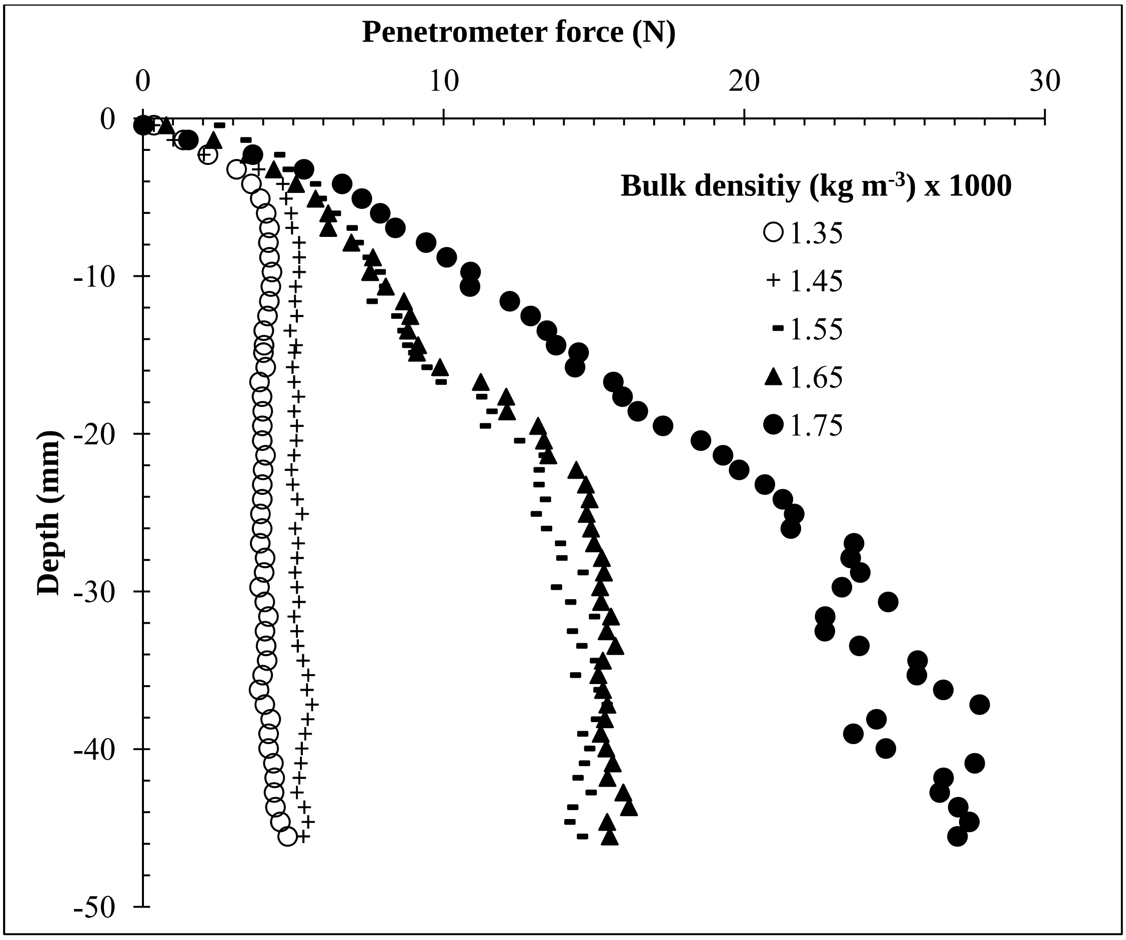
Appendix 1

Relationship between bulk density and gravimetric water content of a sandy loam soil compacted in a standard Proctor Test. Horizontal and vertical bars represent standard error of the mean of the respected parameters.



Appendix 2

An example of cone-penetrometer force (N) as a function of depth (mm) into packed soil (matric head = 3.3 m) for the five different levels of soil compaction. Key indicates the mean dry bulk density for each curve.



Appendix 3

Mean saturated hydraulic conductivity (m s^{-1}) as a function of soil compaction (kg m^{-3}). Error bars represent one standard error of the mean variable.