Root architecture alteration of narrow-leafed lupin and wheat in response to soil compaction

Ying Long Chen[a,b], Jairo Palta[c,d], Jonathan Clements[e], Bevan Buirchell[d], Kadambot HM Siddique[b], Zed Rengel[a,b]

[a]Soil Science and Plant Nutrition, School of Earth and Environment, The University of Western Australia (M087), 35 Stirling Highway, Crawley WA 6009, Australia

[b]The UWA Institute of Agriculture, The University of Western Australia (M082), 35 Stirling Highway, Crawley WA 6009, Australia

[c]CSIRO, Plant Industry, Private Bag No. 5, Wembley WA 6913, Australia

[d]School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia

[e]The Department of Agriculture and Food, Western Australia, 3 Baron-Hay Court, South Perth, WA 6151

Corresponding author: yinglong.chen@uwa.edu.au

ABSTRACT

Root system architecture influences nutrient and water uptake efficiency and thus plant growth and productivity. Root architecture traits conferring efficiency in capturing resources from soil are considered a key factor in crop breeding for enhanced water and nutrient uptake. Mechanical impedance such as soil compaction is common in the Western Australian wheatbelt, limiting root growth and crop productivity. The present study investigated root responses to subsoil compaction in two field trials at Wongan Hills (central wheatbelt) and Buntine (northern wheatbelt) in Western Australia. Substantial alteration to rooting patterns was observed in the commercial wheat cultivar Wyalkatchem and in narrow-leafed lupin (*Lupinus angustifolius*) grown in sandy soils where compaction is common. The root systems of narrow-leafed lupin plants were dominated by a short and thickened taproot (10–26 cm depth, 7–14 mm root-collar diameter) and horizontally distributed primary lateral roots when compared to previous observations of the same genotypes under non-compacted soil conditions. Genotypic variability in root architecture traits among four wild genotypes and four commercial cultivars (Mandelup, Merrit, Quilinock and Tanjil) of narrow-leafed lupin was demonstrated. Taproot length, total root length, root surface area, root

mass and root collar diameter were the most important root traits correlated to shoot yield (P<0.001). Deep ripping resulted in significantly improved rooting depth (up to 100 mm) and root distribution in wheat in the soil profile compared to non-ripped soil, where roots were restrained mainly in the top 0–30 cm layer. Root number, root length, root length density, root mass and grain yield of plants grown in deep-ripped soil were increased by 38, 36, 27, 24 and 19%, respectively, compared to those of non-ripped treatment. The data from this study form the basis for future research leading to selection and breeding for suitable root traits for soil constraints and provides information for alleviating management of compacted soil in deep sandy soils.

Key words: deep ripping; genotypic variability; narrow-leafed lupin (*Lupinus angustifolius*); root architecture traits; subsoil compaction; wheat (*Triticum aestivum*)

1. Introduction

Root system architecture influences nutrient and water uptake efficiency in crops. It is widely accepted that root architecture plays a vital role in crop growth and productivity. Root architecture traits efficient in capturing resources from soil are considered important in crop breeding for enhanced nutrient capture. Crops often show plasticity in their root architecture to varying soil environmental factors, including physical, chemical and biological properties of soil. Soil mechanical impedance, particularly soil compaction, is a major cause limiting root growth and development, thereby restricting capture of water and nutrients and eventually yield (Bengough *et al.* 2011; Unger and Kaspar 1994; Whalley *et al.* 2008).

The ability of soils to withstand compaction is related to soil properties (such as soil texture, organic matter content and clay mineral type) and moisture content (Hamza and Anderson 2005; Tekeste *et al.* 2008). Compaction influences soil strength, aeration and water flow, creating inter-related stresses which may act simultaneously to influence root growth and distribution. Soil compaction, a component of land degradation syndrome, is often caused by conventional agriculture (Batey 2009; Soane and Ouwerkerk 1994; Tracy *et al.* 2011). The intensification of cropping systems and the evolution of agricultural machinery may have contributed to the widespread increase in soil compaction (McGarry 2001; Tracy *et al.* 2011). Soil compaction can also develop naturally in duplex soils (about 20 cm of sand over clay) with high bulk densities as found in Western Australia (Gregory 2006).

In Western Australia, soil compaction, often associated with subsoil hardpans and acid soils (Tang et al. 2002), is recognized as one of the major subsoil constraints limiting crop root growth into the subsoil and thus compromising crop ability to take up water and nutrients. An estimated 13 million hectares (70%) of arable soils are moderately to highly susceptible to subsurface compaction in Western Australia (Greacen and Williams 1983, DAFWA 2006). In addition to compaction, hardpan can form as a result of natural soil packing and chemical cementation processes and these may occur throughout the soil profile. Furthermore, with increased depths of subsoil compaction, changes at depths below 40 cm are virtually permanent, and deep compaction causes persistent and possible permanent reductions in crop yield (Batey 2009; Håkansson and Reeder 1994).

To improve crop yield performance in compacted soils, two practical strategies may be considered: one is to select genotypes with beneficial root traits, and the other is to alleviate soil compaction by deep ripping. It is well understood that different crop species or different genotypes of the same species may differ in their response to various subsoil constraints, such as soil aluminium (Al) toxicity (Khabaz-Saberi *et al.* 2012, Tang *et al.* 2003). Acuña and Wade (2012) showed that wheat genotypes differ in adaptation to soil conditions, including

physical constraints.

High yields can also be achieved through the amelioration of compaction with deep ripping (Delroy and Bowden 1986), resulting in deep rooting and hence better access to subsoil water and nitrogen (Hall *et al.* 2010; Tennant and Hall 2001). Due to difficulties in examining root growth, the effect of deep ripping on root development down the profile is not well documented.

Western Australia is the world's largest producer of lupin, largely narrow-leafed lupin (*Lupinus angustifolius*). The typical root system of narrow-leafed lupin is taproot-dominant, which often is typified by a deep taproot with a number of short primary lateral roots (some wild genotypes also produce limited numbers of long lateral roots at depth) (Chen et al. 2011b, 2012). Our recent studies demonstrated that narrow-leafed lupin exhibited significant genotypic viability in root system architecture under various laboratory growth environments (Chen *et al.* 2011b, 2012, 2013a,b). However, there is considerably less information about the potential variability in root architecture among narrow-leafed lupin genotypes to tolerate soil compaction.

Crop performance and productivity grown in the compacted soil may be improved by (1) identifying and selecting crop genotypes with superior root architecture traits for better adaptations, and (2) ameliorating soil structure to alleviate soil-compaction stress on root growth. The aim of the present study was to exercise these two practical strategies to address a paucity of knowledge on a differential response of various genotypes to soil compaction as well as a role of deep ripping in distribution of roots down the profile. Two separate field experiments were conducted to (1) determine genotypic variability in root system architecture of narrow-leafed lupin genotypes in response to soil compaction and a hardpan at Wongan Hills, and (2) examine the rooting patterns of bread wheat grown in deep–ripped and non-ripped profiles in the sandplain region at Buntine. Narrow-leafed lupin and wheat were predominate crops at the Wongan Hills and Buntine sites in Western Australian wheatbelt with an increasing concern on soil compaction. Deep ripping has been managed at Buntine, while the paddock at the Wongan Hills site had never been deep ripped.

2. Materials and methods

2.1 Field trial 1 (narrow-leafed lupin)

Four wild and four commercial cultivars of narrow-leafed lupin (*L. angustifolius*) were used to determine the genotypic variability in root response to soil compaction. Four wild genotypes with contrasting root architecture were selected from a previous screening study using the semi-hydroponic phenotyping system (Chen *et al.* 2011a, 2012), and evaluated in

various growth media (Chen *et al.* 2011b). Among the selected four genotypes, #085 has the largest root system with longest taproot and highest number of lateral roots. Genotype #060 is the second largest genotype with the most lateral roots at depth. Genotype #044 has the smallest roots with moderate taproot length, and short, sparse lateral roots, and #084 is a small genotype with fine roots, short taproot and short lateral roots. Countries of origin of the four selected genotypes are Germany (#060), Greece (#044), Portugal (#084) and Spain (#085). Four local cultivars (with year of release) included in this field trial were Mandelup (2004), Merrit (1991), Quilinock (1999) and Tanjil (1998).

The trial was established at the Department of Agriculture and Food Western Australia (DAFWA) research station at Wongan Hills, WA (30.54°S, 116.43°E). The soil type was gravelly sand over gravel, pH 6.0 (in $CaCl_2$) and the paddock had never been deep ripped. In 2011 the paddock was sown to clover-based pasture, and in 2012 it was sown to wheat. Soil preparation in May 2013 involved running over the ground with 18-cm knife points and the fertilizer applied was 80 kg/ha Big Phos Manganese (CSBP) = calcium dihydrogen phosphate and gypsum (P, S, Ca, Mn of 13, 6.8, 14, 5.22 % w/w). The soil had a compaction layer at 20–30 cm and hardpan below about 30 cm. At podding stage the averaging soil penetrometer resistance were about 3.4 (20–30 cm) and 7 MPa (below 30 cm).

The experiment used a randomized complete block design with five plots (2.5 $\times$ 4 m each 5 m apart). Each plot contained eight rows with one genotype per row randomly allocated. The trial was hand-sown at 2-cm depth. Narrow-leafed lupin was maintained as per standard practices for this crop in the area. The paddock has a recent history of being sown to lupins, and no additional rhizobial inoculant was applied.

Root systems were assessed at podding stage using the “shovelomics” technique (Trachsel *et al.* 2011) with a few genotypes still flowering. This method is to visually score root traits after the whole root system was excavated from soil. Plots #1, #3, and #5 were chosen for sampling. Two randomly-selected plants from each row were sampled and the data averaged at analysis. Shoots were separated from the roots and put into paper bags for assessing dry weights. The whole root system of each plant with attached bulk soil was excavated manually and placed in large polybags for transportation to the laboratory for measurements.

Root sample with bulk soil was first soaked in a large bucket with tap water and washed using running water. The root system and broken fine roots (<5%) were placed on a sieve (400 μm) and further washed free of soil. The root system was then laid on a flat tray with clean water and photographed using an overhead-fixed digital camera. Root collar diameter, taproot length and number of lateral roots with base diameter $\geq$1 mm, and number of root

nodules were measured manually for each plant. Lateral roots were then cut off from the taproot and scanned (broken fine roots included) in greyscale at 300 dpi using a desktop scanner (Epson Expression Scan 1680, Long Beach, United State). Images were analyzed using WinRHIZO software (v2009, Regent Instruments, Montreal, QC, Canada). The roots were partitioned into 11 diameter classes: <0.25, 0.25–0.4, 0.4–0.6, 0.6–0.8, 0.8–1.0, 1.0–1.2, 1.2–1.5, 1.5–2.0, 2.0–2.5, 2.5–3.0 and >3.0 mm. The debris removal filter was set to discount objects less than 0.1 cm^2 with a length/width ratio <5. Shoot and root tissues were dried in a fan-forced oven at 70 ^oC for 5 days and then weighed.

Data for total root length, root surface area, root volume, average root diameter (taproot excluded) and diameter class length (root length within a diameter class) were generated in WinRHIZO from root images. Relative diameter class length was the diameter class length divided by total root length for the genotype (yielding a proportion of root length to normalize disparity between plants of different sizes). Specific root length (root length per unit mass) was calculated as total root length divided by root dry mass. Lateral root density was used to evaluate number of lateral roots (base diameter ≥1 mm) per taproot length. Root dry mass and root volume were used to calculate root tissue density (mass per volume).

2.2 Field trial 2 (bread wheat)

A field experiment was conducted on a commercial grain-growing property near Buntine (29.99°S, 116.57°E) in Western Australia. The site was located in the northern wheatbelt of Western Australia, characterized as the sandplain soils that are subjected to a range of biophysical constraints such as subsurface acidity and compaction. The soil was deep yellow sand to at least 3.0 m with a small percentage of gravel found below 1.5 m. A compaction layer was at around 20–30 cm depth.

A randomized complete block design was established with eight plots (10 m wide × 20 m long). Two weeks before seeding, four plots were deep ripped to 30 cm while the other four were not ripped. A local wheat cultivar Wyalkatchem was used and seeds were sown in May at the break of season (after first rain). At sowing, the equivalent of 30 kg N/ha as urea, 75 kg P/ha as amended superphosphate (with Cu, Zn, Mo and S) and 55 kg K/ha as KCl was banded with the seed. A top-dressing application of N (40 kg/ha) as urea was made when plants were at the 3–4 leaf stage.

When crops were at 50% ear emergence (i.e. half of the plants in each plot having visible ears), a ditch 1.0 m wide × 1.5 m long × 1.5 m deep was dug 1.7 m from the edge of each plot. Sand from one of the internal walls of the ditch was removed with water using a pump, and the root system down to 1.0 m was uncovered. A transparent acrylic sheet 0.24 m wide × 1.0 m long was clamped to the wall and all visible roots were traced on the acrylic

sheet using a waterproof permanent pen. The transparent sheet with the mapped roots for each plot was divided into 10-cm sections starting at 0–10 cm, and photographed with the same digital camera (DMC-TZ20, Panasonic Co, Osaka, Japan) from the same position (distance and angle); the images were analyzed for root number and length using WinRHIZO software. Root length density was calculated as the root length in each section divided by the visual soil volume of the corresponding section. The visual soil volume (Hurd 1967; Hurd and Spratt 1975) of each section was calculated by multiplying the surface area of the section (24 $\times$ 10 cm) by the visual soil depth. The visual soil depth (0.5 cm) was the horizontal soil depth in which the roots were visible.

Aboveground biomass and grain yield were measured at final harvest by sampling a 1.0 m^2 quadrat in the centre plot to minimize edge effects. Plants in each quadrat were cut at the soil surface and the plant material separated into leaves, stems and spikes before being dried in a fan-forced oven at 70^{o}C for at least 48 h and then weighed. Spikes were counted and threshed by hand, and grain was redried and weighed. Harvest index (HI) was calculated as grain yield divided by total aboveground biomass at harvest $\times$ 100.

2.3 Data analyses

Root traits and biomass data from each experiment were analyzed separately for the main effects of genotype (lupin) or deep ripping (wheat) using the general linear model (GLM) multivariate analysis in the PASW Statistic 18 (IBM Corporation, New York, United States). When all parameters of each experiment were included in the GLM analysis, no serious departure from multivariate normality was found as indicated by the multivariate standard errors of skewness and kurtosis. For the lupin experiment, linear regression analysis was performed to determine the relationship between root traits. Lupin root traits with significant variation (P<0.05) were selected for (i) principal component analysis (PCA) to identify determinants of root architectural variability across genotypes (Jolliffe 2002), and (ii) hierarchical cluster analysis using furthest neighbour method to classify the relationship among genotypes.

3. Results

3.1 *Genotypic variability in narrow-leafed lupin roots (Field trial 1)*

3.1.1 Rooting patterns and variation in root trait

The root system of all tested narrow-leafed lupin genotypes was dominated by a short and strong taproot and a number of thickened primary lateral roots (i.e. first-order branches) (Fig. 1). The maximum depth that the taproot could grow was 26 cm measured from the root collar (Table 1), indicating a significant impact of mechanical impedance due to hardpan on

the growth and elongation of the taproot. The lateral roots grew mostly horizontally in the topsoil layer. Lateral roots originating from the vertical taproot exhibited wide angles up to 135 degrees (i.e. diverging upwards from the horizontal). Even after washing, larger lateral roots (usually ≥1 mm in base diameter) remained in their positions at the same angle from the taproot. All sampled plants had second-order lateral roots; only some plants also had short, dense third-order lateral roots largely on the end part of the second-order lateral roots. Root systems had effective and frequent nodulation with nodule numbers ranging from 20 to 120 per root system at the time of assessment (Table 1).

The extent of variation in the 10 measured root traits differed across all genotypes, with the coefficient of variation (CV) values ranging from 18.5 to 41.5 (Table 1). Nodule number, total root length, root mass and SRL had CV values ≥30. Analysis of variance showed significant differences in nodule number (P<0.001); lateral root number, total root length and root tissue density (all P<0.01); taproot length, root collar diameter and SRL (all P≤0.05). Root biomass displayed large variation (CV=32.6) across genotypes and significant differences among genotypes (P≤0.05) (Table 1).

3.1.2 Genotypic variation in root traits

The eight narrow-leafed lupin genotypes differed in the size and depth of their root systems. The wild genotype #085 had the largest root system with total root length around 900 cm, followed by #060 (750 cm) and cv. Mandelup (660 cm) (Fig. 2). Wild genotypes #044 and #084 and cvs. Tanjil and Merrit had similar total root lengths (around 550 cm), whereas cv. Quilinock had the shortest total root length (290 cm). Variation in taproot length followed a similar trend as total root length, with the longest taproot in wild genotype #085 (23 cm) and shortest taproots in #084 (11 cm) and cv. Quilinock (12 cm) (Fig. 2). The number of primary lateral roots with base diameter ≥1 mm ranged from 8 to 15 per root system and differed significantly among narrow-leafed lupin genotypes (P=0.010, Table 1). Genotypes #060 and #085 had more primary lateral roots for both diameter categories (≥1 mm or <1 mm) than other genotypes, whereas #084 had the least (data not shown). Cultivar Merrit had longer primary lateral roots when compared to other genotypes. Third-order lateral roots were commonly found in wild genotypes. Genotype #084 was the only one with fourth-order lateral roots (data not shown).

Specific root length (SRL) differed significantly among genotypes (Fig. 3). Genotypes with a large proportion of fine roots often had high SRL values, such as genotype #044. Cultivar Quilinock had the lowest SRL value. These phenomena mirrored changes in average root diameter, and were reversely related to root tissue density (Fig. 3).

There was significant variation in root collar diameter ranging from 7 to 14 mm ($P \leq 0.05$, Table 1). The thickest roots were found in genotype #085 and cv. Tanjil (14 mm). Genotype #044 and cv. Quilinock had the thinnest root collar (7 mm) (data not shown).

There was no significant difference in average root diameter among genotypes (Table 1). About 48% of lateral roots were ≥1 mm in diameter including 12% ≥2 mm (Fig. 4). Of the 11 diameter classes, the highest proportion of roots (20–30%) was in the 0.25–0.4 mm diameter class for all genotypes, as shown by the relative DCL in Figure 4. Among all the genotypes, #044 had the highest proportion of roots in the relatively small diameter classes (up to 1 mm) and the least at the thicker end, indicating prevalence of fine roots. Cultivars Quilinock and Mandelup had a relatively greater proportion of thick roots than the other genotypes. Nodules were found on the root system of all sampled plants, but the number varied among genotypes (Table 1). Genotype #085 had the most nodules, followed by #084, #060 and Mandelup. Quilinock had the least number of nodules.

The eight genotypes varied substantially in both root and shoot biomass accumulation (Table 1, Fig. 5). Root dry mass was higher in the large-rooted genotypes, i.e. #085 and Mandelup, whereas the small-rooted #044 had the lowest root dry mass. Genotypes #085, Mandelup, Tanjil and #060 had more shoot biomass than the other genotypes.

3.1.3 Variance determinants among root traits

Seven of the ten root traits with probability values greater than 0.05 (Table 1) were selected to determine variance among parameters using PCA. The first two principal components were determined (eigenvalues >1) capturing 79.3% of the overall variance across the eight tested genotypes (Table 2). The first component representing 46.3% of the variability accounted primarily for five major root traits, and component two comprised 32.9% of total variability based on specific root length and root tissue density.

3.1.4 Correlation between root traits and shoot mass

There was a large variation in shoot biomass (CV=44.4) across genotypes and there were significant differences among the eight genotypes ($P<0.001$) (Table 1). Pearson's correlation analyses demonstrated relationship between each individual root trait and shoot mass (Table 3). Shoot mass was highly correlated with taproot length, root collar diameter, total root length, root surface area and root mass (all $P<0.001$), and lateral root number ($P<0.01$), and weakly correlated with nodule number ($P<0.05$) (Table 3). However, there was no significant correlation between shoot mass and root diameter, specific root length, lateral root density and root tissue density at $P<0.05$ level. Therefore, five root traits, i.e. taproot length, root collar diameter, total root length, root surface area and root mass, were the most important root traits contributing to shoot yield.

290 Pearson's correlation analyses also uncovered correlation among root traits (Table 3). The
291 number of nodules were strongly correlated with total root length (P<0.001) and root surface
292 area (P<0.01). The number of lateral roots with base diameter greater than 1 mm were
293 highly associated with taproot length, total root length and root surface area (all P<0.01), but
294 were weakly associated with root collar diameter and root mass. Taproot length was highly
295 correlated with total root length and root surface area but negatively correlated with lateral
296 root density (P<0.01). There was a strong correlation between specific root length and root
297 tissue density (P<0.001), and average root diameter (P<0.01). Correlation analysis showed
298 a non-significant relationship between root collar diameter and average root diameter
299 (P=0.25). *3.1.5 Genotype classification*

300 The same set of root traits as for PCA was subjected to hierarchical cluster analysis to
301 determine the relationship among the tested genotypes. The analysis generated two major
302 clades separating #085 (Clade I) from the other seven genotypes (Clade II) as shown in the
303 dendrogram (Fig. 6). Clade II was further divided into three groups when a rescaled distance
304 of 5 was considered. The eight genotypes clustered into four groups containing 1 (Group 1
305 and 2), 2 (Group 3) or 4 (Group 4) genotype(s). Group 1 (#085) represented the largest, and
306 Group 2 (cv. Quilinock) the smallest genotypes in terms of total root length. Mandelup and
307 #060 had medium-sized root systems (Group 3), and the remaining four genotypes with
308 small-sized root systems were grouped together (Group 4). The appropriateness of the
309 classification of the eight genotypes is generally supported by observations on major root
310 traits, including total root length and taproot depth (Fig. 2), and root dry weight (Fig. 5).

311 3.2 Wheat root responses to deep ripping (*Field trial 2*)

312 *3.2.1 Root morphology*

313 Root morphology of the wheat cultivar was mapped when half of the crops of each plot
314 had the visual ears (50% ear emergence). Deep ripping substantially increased root growth
315 in the deeper soil profile compared to the non-ripped treatment that produced shorter (not
316 beyond 80 cm depth) and fewer roots sparsely distributed between 30 and 80 cm depth (Fig.
317 7). In addition, roots in the top 30 cm of the soil profile showed different root structure and
318 distribution between the two treatments.

319 *3.2.2 Root number*

320 There was significant variation in the number of roots per unit area between deep ripping
321 and non-ripped treatments and among different soil layers (Fig. 8). Deep ripping contributed
322 to increased number of roots (by 38%) compared to the non-ripped treatment (Table 4). The
323 root system in both deep ripping and non-ripped treatments had a similar trend in growth
324 dynamics down the soil profile. The number of roots increased from the top 10 cm of the soil

325 profile and peaked at 10–20 cm depth (with about 400 roots/m^2 in the deep ripping
326 compared with 500 roots/m^2 in the non-ripped treatment) and then declined with depth.
327 Wheat grown in the deep ripping treatment had deeper roots (many roots down to 100 cm)
328 compared to 80-cm depth (a few roots) in the non-ripped treatment. Deep ripping stimulated
329 root growth in each 10-cm layer, except for the top 20 cm of the soil profile where more roots
330 were present in the non-ripped treatment. In the deep ripping treatment, there was about
331 twice as many roots at 70–80 cm depth as in the soil layers immediately above or below.

332 *3.2.3 Root length*

333 Changes in root length per unit area (Fig. 9) and in root number (Fig. 8) were similar.
334 Wheat had significantly longer (36%) root length in the deep ripping than the non-ripped
335 treatment (Table 4). This was also evidenced through the root length distribution down the
336 soil profile; compared to non-ripped treatment, deep ripping resulted in greater root length
337 across all layers of the soil profile except in the 10–20 cm layer (Fig. 9). Wheat had roots
338 down to 100 cm (deeper measurements were not made) in the deep ripping treatment, and
339 only up to 80-cm depth in the non-ripped treatment. These results indicate that wheat plants
340 grown in non-ripped soil modified their root system by proliferating more roots in the 10-20
341 cm layer where soil compaction was not a problem and significantly reducing root growth in
342 compacted soil.

343 *3.2.4 Root density*

344 Deep ripping significantly improved root length density (RLD) of wheat crops (by 27%)
345 compared with the non-ripped treatment (Table 4). Except in the top 10–20 cm of the soil
346 profile, wheat had higher root densities in soil layers when grown in the deep ripping
347 compared with the non-ripped treatment (Fig. 10). In the non-ripped treatment, RLD was
348 zero below the 80-cm layer. These findings are supported by other traits such as root
349 number (Fig. 8) and root length (Fig. 9).

350 *3.2.5 Root mass and grain yield*

351 Wheat had 24% more root biomass in the deep ripping than the non-ripped treatment
352 (Table 4). Compared to the non-ripped treatment, grain yield of wheat grown in the deep
353 ripping increased by 19% and the harvest index decreased by 4.2%.

354

355 4. Discussion

356 4.1. Crop root architecture alteration as adaption to soil compaction

The present study observed substantial alterations to root system architecture in narrow-leafed lupin and wheat grown in compacted soils at two field sites (Figs. 1, 7), indicating a capacity of these crops to adapt to soil compaction. Deep ripping significantly improved wheat root growth resulting in increased root length, depth and density. Genotypes of narrow-leafed lupin showed a variable capacity to grow roots in compacted soil. Interestingly, wild genotypes of narrow-leafed lupin grown in the field showed some of the similar rooting characteristics (such as long primary lateral roots in #085 and #060, fine lateral roots in #044 and third-order lateral roots in #084) as previously observed in various controlled environments (e.g. Chen *et al.* 2011b, 2012, 2013a), confirming the heritable nature of these traits.

Narrow-leafed lupin genotypes produced shorter and thicker taproots and increased diameter of both taproot and primary lateral roots due to subsoil compaction with formation of hardpan beneath 30 cm at Wongan Hills. Soil compaction significantly reduced taproot growth by up to four times (Table 1; Figs. 1, 2, 4), whereas root diameter significantly increased when compared with narrow-leafed lupin grown in a nutrient solution (Chen *et al.* 2011a, 2012) and in non-compacted soil (Bishop *et al.* 1986; Chen *et al.* 2011b, 2013a,b; Clements *et al.* 1993). Soil compaction also forced lateral roots to alter their direction of growth. Primary lateral roots of narrow-leafed lupin became stronger and longer and often grew horizontally or slightly upwards, with wide angles to the taproot (Fig. 1). It is likely that these lateral roots took in part the function of the taproot in capturing water and nutrients from the topsoil when subsoil compaction prevented both the taproot and lateral roots from growing deeper.

Altering root system architecture is an important strategy for crop adaptation to soil conditions. Genotype #085 had deeper taproot in compacted soil among the eight genotypes (Fig. 2). Root architecture traits such as taproot conferring improved root penetration may overcome external (soil) pressures resisting root elongation as discussed in Bengough *et al.* (2011). Narrow-leafed lupin genotypes differ in genetic variability in root traits may provide useful information for selecting genotypes with potential root traits for adapting hard soil, which is often associated with water deficit (Yusuf Ali *et al.* 2005). Richter *et al.* (2009) observed that mechanical stress elicited generation of lateral root in *Arabidopsis thaliana*. However, the present study showed no evidence of the restriction soil compaction on the number of lateral roots in various genotypes. A separate glasshouse experiment found that mechanical damage in the taproot of narrow-leafed lupin resulted in a significant increase in lateral root branching (Chen *et al.* unpublished). Physical bending of roots has been found to stimulate the formation of a lateral root on the convex side of the curve, enabling roots to maneuvre around obstacles (Tracy *et al.* 2011). This mechanism may be useful for avoiding

localized areas of acute soil compaction. Expanded root cortical cells (Clark and Barraclough 1999; Croser *et al.* 2000; Dexter 2004) and the presence of additional cell layers (De Kroon and Visser 2003; Materechera *et al.* 1991; Tracy *et al.* 2011) induced by the presence of mechanical impedance could explain thickened roots observed in lupin genotypes grown in compacted soil (Figs. 1, 4).

4.2 *Root trait variability in compacted soils*

The hierarchical cluster analysis based on seven important root architecture traits separated the eight narrow-leafed lupin genotypes into four groups (Fig. 6), indicating differential variability in root traits among genotypes. Indeed, genotypic variation in crop root systems has been documented extensively (e.g. reviewed in Nibau *et al.* 2008; Gregory 2006). The wild genotypes generally performed well in case of subsoil compaction, and one wild genotype (#085) surpassed the performance of the four commercial cultivars regarding root length and root biomass (Figs. 2, 5). In case of narrow-leafed lupin germplasm, variability and plasticity in various root traits has been identified in a core collection under a range of growing conditions (Chen *et al.* 2011b, 2012, 2013a,b). Pearson's correlation analyses demonstrated a number of root traits (such as taproot length, root collar diameter, total root length, root surface area and root mass, all $P<0.001$; Table 3) were highly correlated to shoot mass. Given that root trait variability influences efficiency of water and nutrient acquisition from soil and thus shoot yield, particularly under progressively receding soil moisture conditions (Kashiwagi *et al.* 2005; Rengel and Damon 2008; Rose *et al.* 2009), it is anticipated that the variability and plasticity in the root traits of narrow-leafed lupin reported here may be associated with differences in the acquisition of water and nutrients. Genotypes with the capacity to develop deeper and well-branched lateral roots are considered advantageous in adapting to subsoil compaction in relation to capturing water from subsoil reserves.

The capacity of crop root systems to grow into the subsoil is particularly important in areas where topsoils often dry out after flowering, forcing crops, eg. narrow-leaf lupin (Palta *el al.* 2004) and wheat (eg. Kobata *et al*. 1992), to rely on water in potentially compacted subsoil to complete grain filling and produce yield. Different crops and different genotypes of the same species may vary in their capacity to penetrate compacted soil (Iijima *et al.* 2003; Tracy *et al.* 2011). Due to variation in the severity of soil compaction at the two field sites used in the present study, there was no intention to compare root penetration capacity of wheat and narrow-leafed lupin.

4.3 *Deep ripping promoted wheat root growth in compacted soil*

Deep ripping of compacted soil alleviates plant stress induced by mechanical impedance and benefits root growth and distribution, which may be attributed to reduced soil strength, increased aeration and improved hydraulic conductivity (Tracy *et al.* 2011). In the present study, deep ripping (to 30-cm depth) had a significant impact on wheat root growth and distribution in a deep sandy soil prone to subsoil compaction. Similarly, increased wheat growth and grain yield after deep ripping has been reported in northeast Victoria (Ellington 1986) and the south coast of Western Australia (Hall *et al.* 2010; Sharma and Anderson 2014). Delroy and Bowden (1986) observed an improved rate of wheat root extension and consequently more efficient use of fertilizer nitrogen early in the season following deep ripping.

4.4 Conclusions

Soil compaction changed the rooting patterns of narrow-leafed lupin and wheat, thereby reducing root growth deeper in the soil profile. Deep ripping improved wheat root growth and distribution down the profile. Genotypic variability in root architecture traits among narrow-leafed lupin genotypes was demonstrated, and is important for further progress in selection and breeding programs for lupin varieties with root traits conferring adaptation to subsoil compaction and other subsoil constraints.

Acknowledgements

This work was supported by the Australian Research Council (DP130104825). We thank Stephen Milroy for allowing measurements in his experimental plots at Buntine; Kate Hoorweg, Bruce Thorpe, Cliff Staples and the lupin breeding technical team (DAFWA) for trial sowing, maintenance and assistance in field sampling; and Zhaoyong Shi for assisting in root collection at Wongan Hills.

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541

Table 1

Descriptive statistics and analysis of variation for root traits and shoot biomass of eight *L. angustifolius* genotypes grown in a field trial at Wongan Hills, Western Australia.

Variable	Unit	Minimum	Maximum	Mean	CV	*P*
Nodule number	/plant	20	120	67	**41.5**	0.000 ***
Lateral root (LR) number	/plant	8	15	11.4	20.2	0.010 **
Taproot length	cm/plant	10	26	16	29.3	0.038 *
Root collar diameter	mm	7	14	11.6	19.1	0.049 *
Total root length	cm/plant	223	994	592	**31.6**	0.004 **
Root surface area	cm^2/plant	125	339	246	24.1	0.135 *ns*
Average LR diameter	mm	0.90	1.90	1.23	18.9	0.112 *ns*
Specific root length	m/g	0.97	3.48	1.75	**34.8**	0.011 *
Lateral root density	/m	50	93	74	18.5	0.602 *ns*
Root tissue density	mg/cm	0.83	2.76	1.80	28.6	0.004 **
Root mass	g/plant	1.63	5.98	3.56	**32.6**	0.012 *
Shoot mass	g/plant	23	133	73	**44.4**	0.000 ***

Parameters with CV (coefficient of variation, %) values greater than 30% appear in bold type. Lateral root number = number of lateral roots with their base diameter greater than 1 mm. Average LR diameter = average lateral root diameter (taproot excluded). Specific root length (SRL) = total root length per unit of root biomass. Lateral root density = number of lateral roots (base diameter greater than 1 mm) per taproot length. Root tissue density = root mass per unit root volume. Probability values (*P*) were based upon a GLM multivariate analysis of eight genotypes. *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$; *ns*, not significant

552 **Table 2**
553 Principal component analysis of seven selected root traits of eight *L. angustifolius* genotypes
554 grown in a field trial at Wongan Hills, Western Australia, showing variable loading scores and
555 the proportion of variation of each principal component.
556

Root trait	Component 1	Component 2
Total root length	**0.77**	**0.61**
Root dry mass	**0.93**	–0.14
Specific root length	–0.35	**0.90**
Root tissue density	0.43	**–0.81**
Nodule number	**0.58**	**0.56**
Lateral root number	**0.72**	0.26
Root collar diameter	**0.79**	–0.23
Eigenvalue	3.24	2.31
Variability (%)	46.3	32.9
Cumulative variability (%)	46.3	79.3

557 Root traits with $P \leq 0.05$ (see Table 1) were included in the principal component analysis, and only eigenvalues
558 greater than 1 that are considered significant are presented (Tabachnik and Fidell 1996). Rotation converged in
559 seven iterations using Varimax with Kaiser Normalization method. Variable loading scores >0.50 for each
560 component appear in bold.
561

562 **Table 3**

563 Pearson's correlation matrix for 10 root traits and shoot mass of eight *L. angustifolius*
564 genotypes grown in a field trial at Wongan Hills, Western Australia.

565

	ND#	LR#	TRL	RCD	RL	RA	RD	SRL	LRD	RTD	RM
LR#	0.276										
TRL	0.524*	0.712**									
RCD	0.229	0.542*	0.549*								
RL	0.780***	0.673**	0.738**	0.405							
RA	0.632**	0.653**	0.743**	0.635**	0.776***						
RD	–0.098	0.058	0.060	0.304	–0.236	0.248					
SRL	0.244	0.019	0.065	–0.451	0.283	–0.178	–0.676**				
LRD	–0.453	–0.024	–0.697**	–0.204	–0.439	–0.388	0.128	–0.188			
RTD	–0.108	0.066	0.026	0.382	–0.142	0.222	0.845***	–0.854***	0.182		
RM	0.483	0.531*	0.577*	0.662**	0.668**	0.869***	0.323	–0.462	–0.250	0.534*	
SM	0.536*	0.731**	0.771***	0.741***	0.740***	0.787***	0.029	–0.143	–0.334	0.174	0.785***

566 Traits included in Pearson's correlation analysis are: Nodule number (ND#), Lateral root number (LR#), Taproot length (TRL),
567 Root collar diameter (RCD), Total root length (RL), Root surface area (RA), Average LR diameter (RD), Specific root length
568 (SRL), Lateral root density (LRD), Root tissue density (RTD), Root mass (RM), and Shoot mass (SM). Correlation is significant
569 at the 0.05 (*), 0.01 (**) or 0.001 (***) level.

570

Table 4

Root and grain parameters of wheat cultivar Wyalkatchem grown in the treatments with non-ripped and deep ripping to 30 cm at Buntine, Western Australia. Total root number, root length and root length density (RLD) in the top 100 cm of the soil profile were assessed by root mapping when crops were at 50% ear emergence (i.e. half of the plants in each plot having visible ears). Increments (%) of deep ripping over non-ripped treatments were also given for each parameter. LSD = Least significant difference.

Soil management	Root trait				Grain yield	
	Number ($/m^2$)	Length (m/m^2)	RLD (cm/cm^3)	Root mass (g/m^2)	Grain yield (g/m^2)	Harvest index (%)
Non-ripped	1401	22	0.88	447.8	215.2	0.48
Deep ripping	1936	29.9	1.12	553.5	256.1	0.46
Increased due to deep ripping (%)	38.2	35.9	27.3	23.6	19.0	–4.2
LSD ($P \leq 0.05$)	52	95.1	0.09	89.6	18.9	0.04

582 **Figure captions**

583 **Fig. 1.** Typical root system of *L. angustifolius* plant excavated in a compacted soil at Wongan
584 Hills, Western Australia (a), and in a non-compacted soil from a glasshouse trial (b). Lateral
585 roots were washed free from soil and repositioned at photographing. The root structure was
586 altered to adapt to soil mechanical impedance, which made the taproot (TR) shortened and
587 thick. The primary lateral roots (PLR) often grew horizontally within 0–20 cm topsoil.
588 Second-order lateral roots (2^{nd}LR) and third-order lateral roots (3^{rd}LR). Nodules (ND) on
589 lateral roots colonized by indigenous nitrogen-fixing bacteria (Bar=5 cm).
590
591 **Fig. 2.** Total root length (bars) and taproot depth (diamond symbols) of eight *L. angustifolius*
592 genotypes grown at Wongan Hills, Western Australia. Data were means (n=3) with ±
593 standard errors. For each trait, data with the same letter (capitals for total root length, and
594 lower cases for taproot depth) are not significantly different (P<0.05).
595
596 **Fig. 3.** Specific root length (m/g, bars) and root tissue density (mg/cm, diamond symbols) of
597 eight *L. angustifolius* genotypes grown in a field trial at Wongan Hills, Western Australia.
598 Data were means (n=3) ± standard errors. For each trait, data with the same letter (capitals for
599 specific root length, and lower cases for root tissue density) are not significantly different
600 (P<0.05).
601
602 **Fig. 4.** Distribution of root length in diameter classes among eight *L. angustifolius* genotypes
603 (a, wild genotypes; b, cultivars) from a field trial at Wongan Hills, Western Australia. Data
604 were means ± standard errors (n=3).
605
606 **Fig. 5.** Dry weight of shoots (bars) and roots (diamond dots) of eight *L. angustifolius*
607 genotypes from a field trial at Wongan Hills, Western Australia. Data were means (n=3) ±
608 standard errors. For each trait, data with the same letter (capitals for shoot dry weight, and
609 lower case for root dry weight) are not significantly different (P<0.05).
610
611 **Fig. 6.** Dendrogram of hierarchical cluster analysis using furthest neighbour method showing
612 clustering patterns of eight *L. angustifolius* genotypes from a field trial at Wongan Hills,
613 Western Australia. Seven selected root traits (P≤0.05) (see Table 2) were used in the analysis,
614 generating two major separations (Clades I and II) of the eight genotypes. Clade II was
615 further divided into four groups as indicated by the dashed line, i.e. Group 1 (#085), Group 2

(cv. Quilinock), Group 3 (cv. Mandelup and #060), and Group 4 (cvs. Merrit and Tanjil, #044 and #084).

Fig. 7. Variation in root morphology of wheat cultivar Wyalkatchem grown in soils treated with deep ripping or non-ripped at Buntine, Western Australia. Horizontal bars represent LSD.

Fig. 8. Variation in root number per unit area down the profile of wheat cultivar Wyalkatchem grown in soils treated with deep ripping or non-ripped at Buntine, Western Australia. Horizontal bars represent LSD.

Fig. 9. Variation in root length per unit area down the profile of wheat cultivar Wyalkatchem grown in soils treated with deep ripping (dark bars) or non-ripped (light bars) at Buntine, Western Australia. Horizontal bars represent LSD.

Fig. 10. Variation in root length density down the profile of wheat cultivar Wyalkatchem grown in soils treated with deep ripping (filled symbols) or non-ripped (open symbols) at Buntine, Western Australia. Horizontal bars represent LSD.

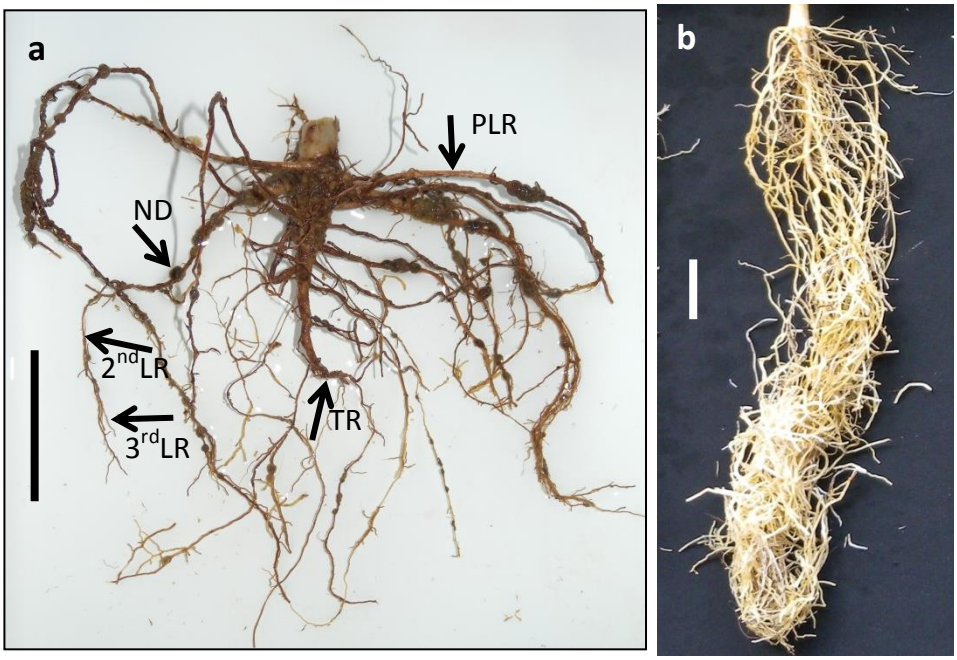

Fig. 1

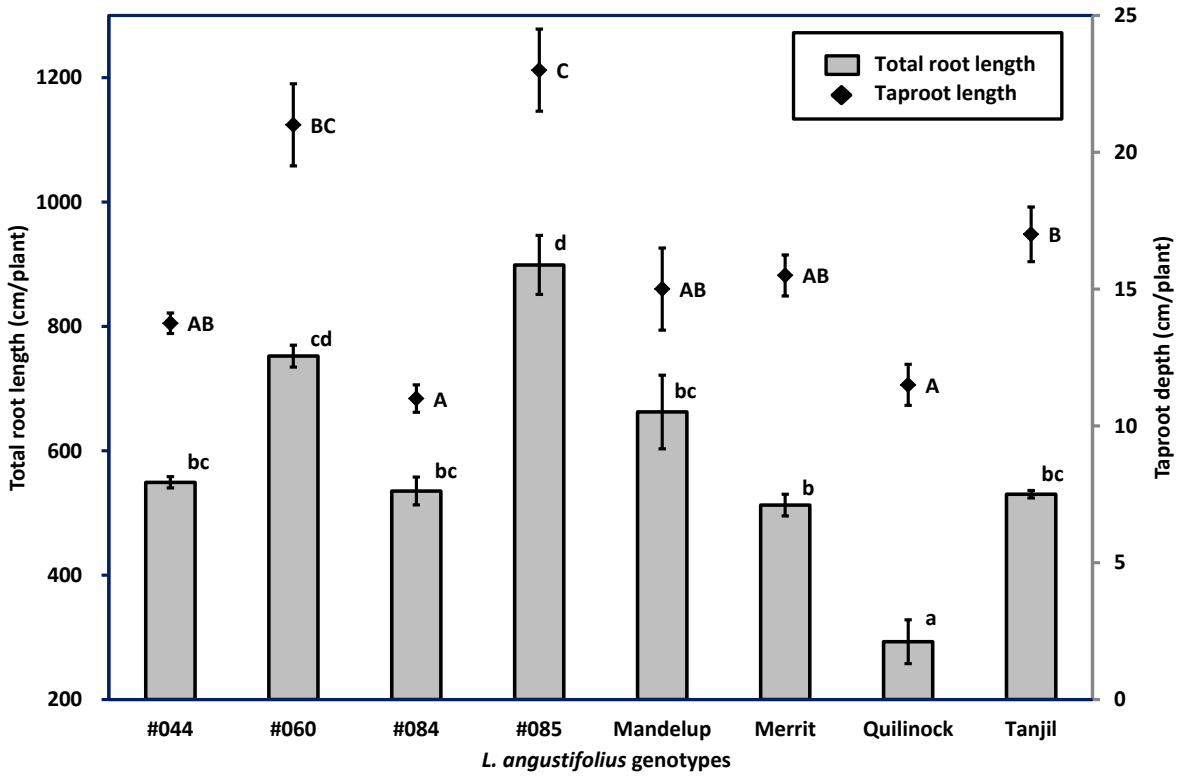
Total root length
Taproot length
Total root length (cm/plant)
Taproot depth (cm/plant)
1200
1000
800
600
400
200
25
20
15
10
5
0
AB
BC
C
cd
A
d
AB
AB
B
bc
bc
bc
bc
b
A
a
#044
#060
#084
#085
Mandelup
Merrit
Quilinock
Tanjil
L. angustifolius genotypes

Fig. 2

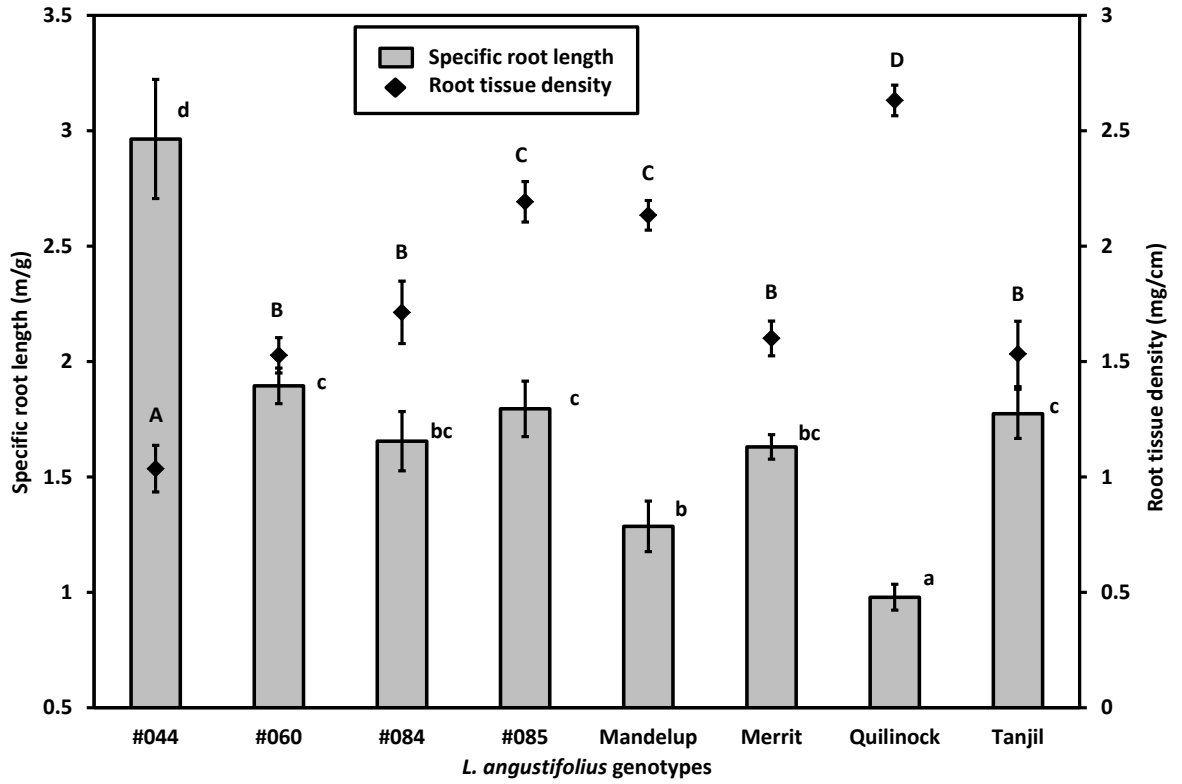
Specific root length
Root tissue density
Specific root length (m/g)
Root tissue density (mg/cm)
3.5
3
2.5
2
1.5
1
0.5
3
2.5
2
1.5
1
0.5
0
d
A
B
c
B
bc
C
c
C
b
D
a
B
bc
B
c
#044
#060
#084
#085
Mandelup
Merrit
Quilinock
Tanjil
L. angustifolius genotypes

Fig. 3

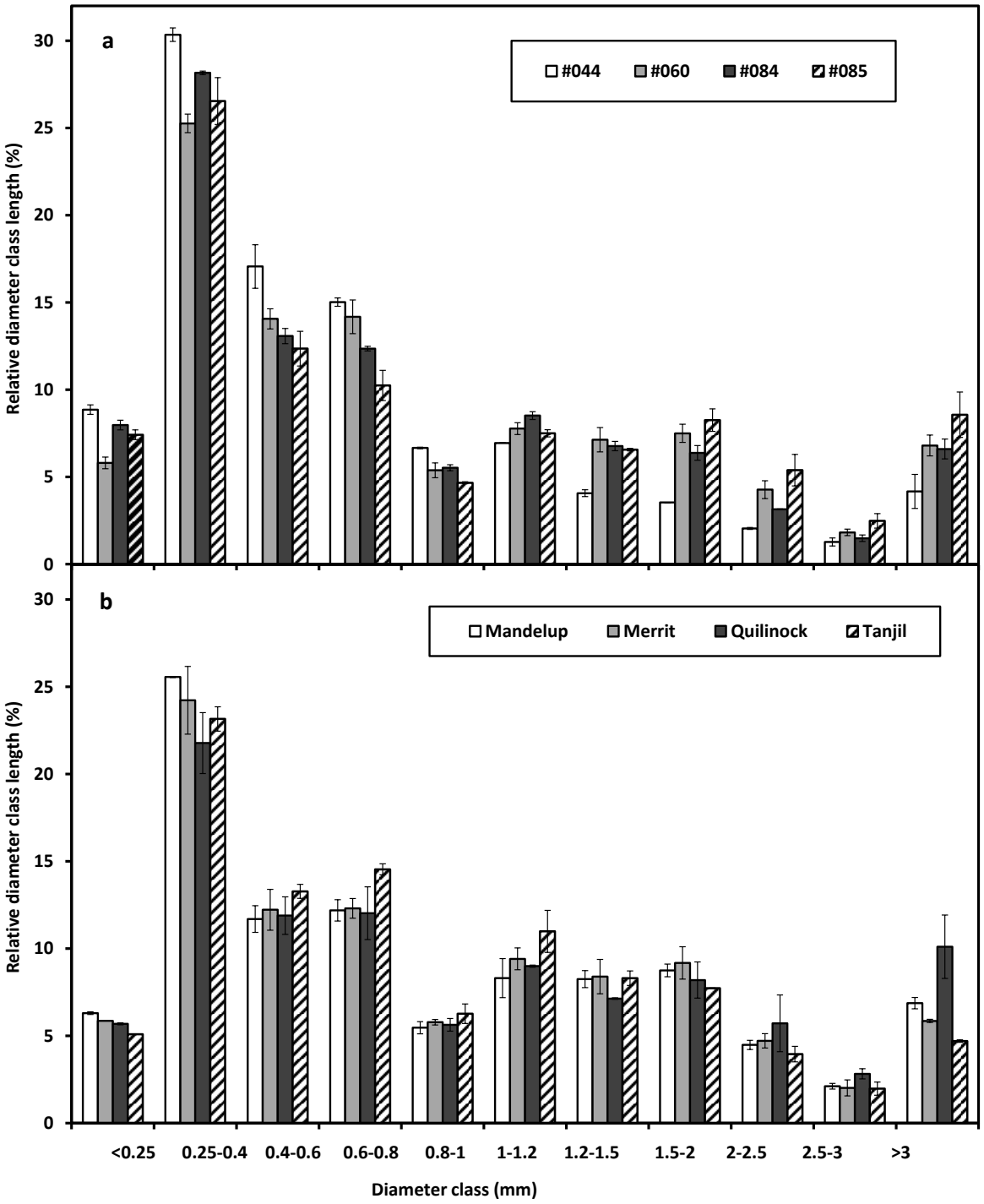
a
#044
#060
#084
#085
Relative diameter class length (%)
b
Mandelup
Merrit
Quilinock
Tanjil
Relative diameter class length (%)
<0.25
0.25-0.4
0.4-0.6
0.6-0.8
0.8-1
1-1.2
1.2-1.5
1.5-2
2-2.5
2.5-3
>3
Diameter class (mm)

Fig. 4

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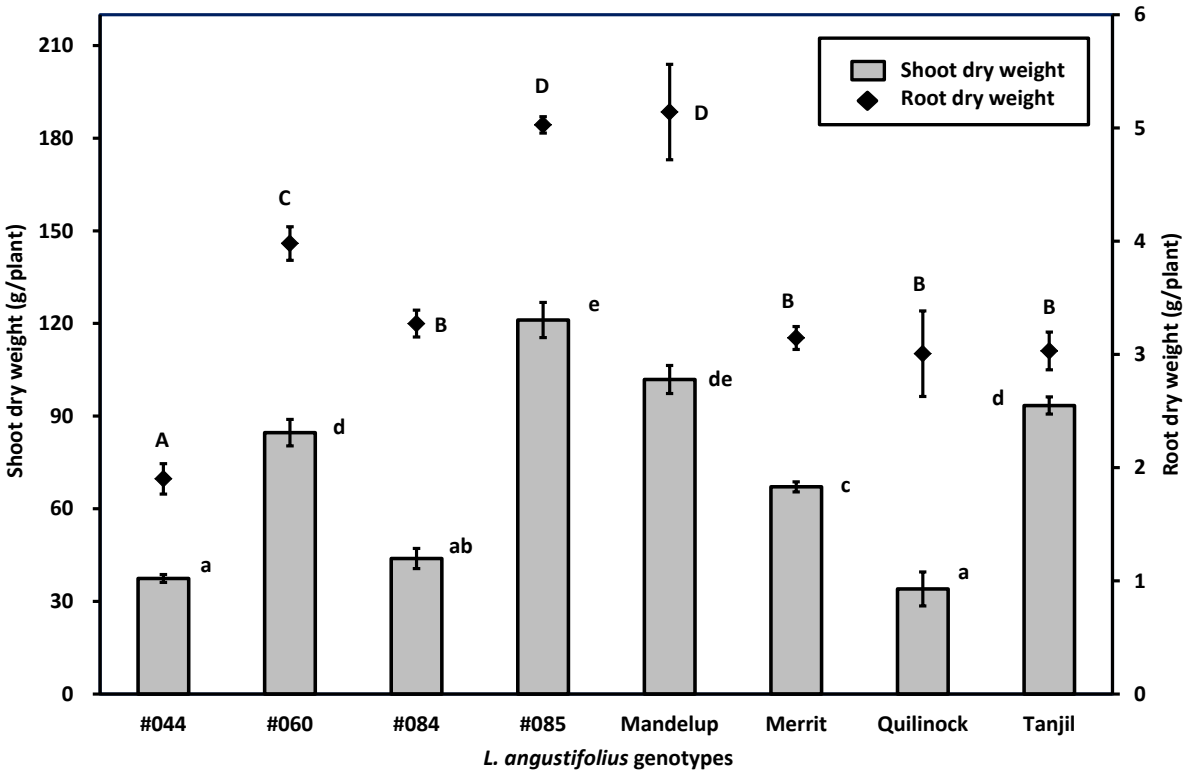

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667 Fig. 5
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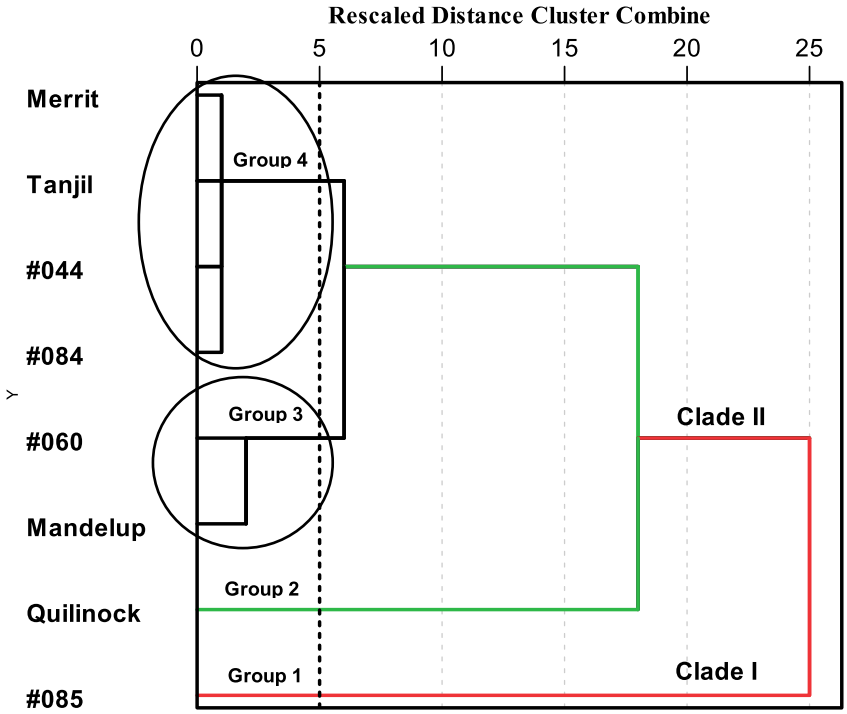

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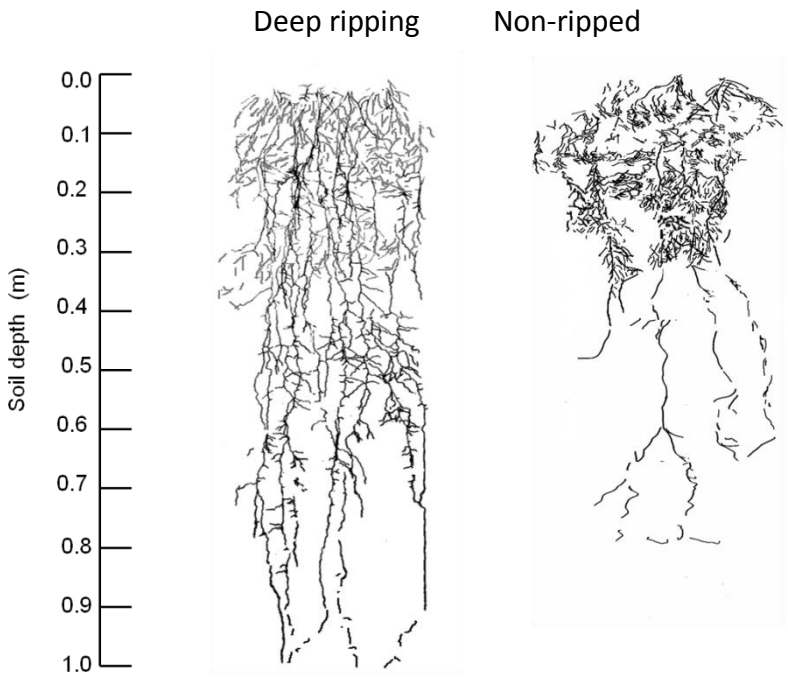

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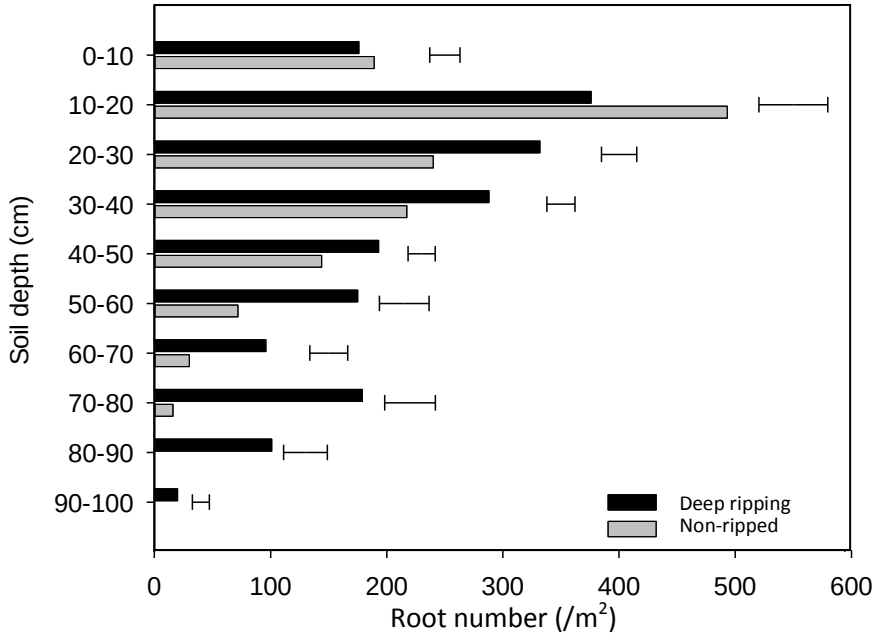

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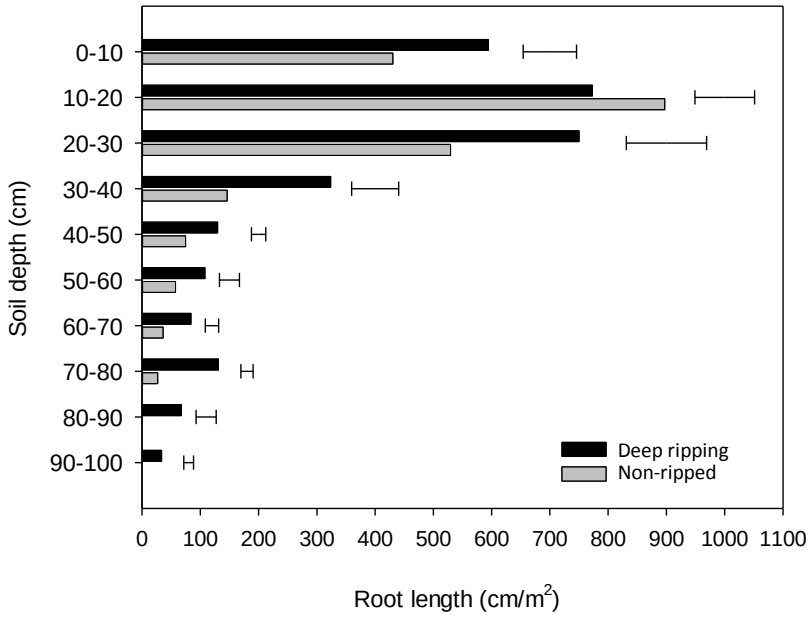

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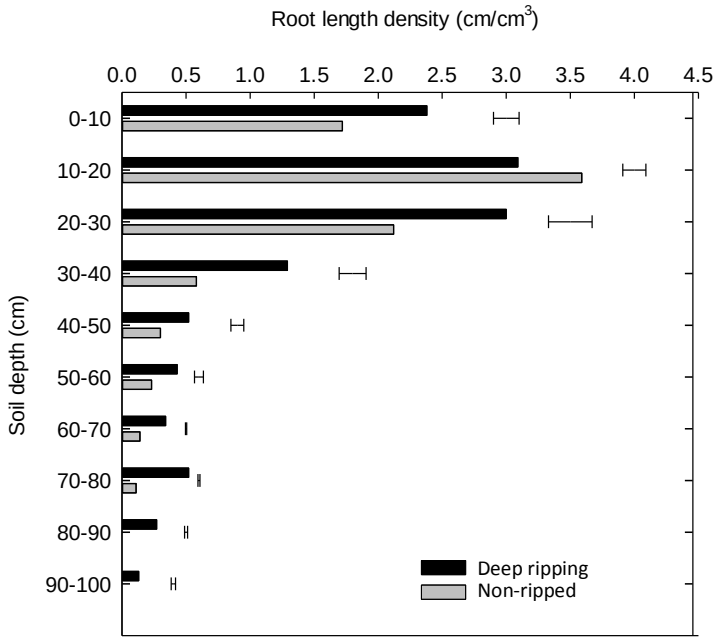

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701 Fig. 10
702