

## Chapter 8. General discussion and conclusions

### 8.1 Impact of Land-use on FRMD, root traits, C stocks and root litter mineralisation rates

#### 8.1.1 Land-use and profile distribution of FRMD and associated root traits

The large FRMD under improved pastures compared with native pastures and woodlands is consistent with earlier studies (Lodge & Murphy, 2006; Garten *et al.*, 2011; Dodd & Mackay, 2011). Such large FRMD as observed under improved pastures is a precursor to SOM build-up (Conant *et al.*, 2003; Garten *et al.*, 2011) and suggests that improved pastures on the Northern Tablelands of NSW could be more important in sequestering C than either native pastures or woodlands. Moreover, the typically large RTL, RLD, FRV and RSA under improved pastures tend to be associated with extensively branched root systems associated with efficient exploration of soil pore space for increased acquisition of water and nutrients (Fitter, 1987; 2002). Increased foraging efficiency for water and nutrients is important for large root biomass production (Hodge, 2004; Lodge & Murphy, 2006; Garten *et al.*, 2011) as a precursor to SOM build-up (Conant *et al.*, 2003; Garten *et al.*, 2011). It is also worth to note that RTL, FRV and RSA were larger under both improved pastures and native pasture compared with the woodlands. These root traits were positively correlated with large soil C stocks under the native pastures in the Southern Tablelands of NSW (Guo *et al.*, 2008a) and suggest that pastures could play a more important role in sequestering soil C than woodlands.

The typically small FRMD across the land-use  $\times$  site combinations imply that if roots are an important source of C in deeper soil layers (Dodd & Mackay, 2011), then other root sources other than FRMD may be responsible for inputting that C belowground. The results also highlight the need to physically translocate the  $> 80\%$  FRMD concentrated in the 0 – 0.1 m depth especially under the pastures to deeper layers. Among the strategies proposed (Dodd & Mackay, 2011) include: (i) introducing naturally deep-rooting grasses like *P. aquatica* under native pastures or increasing their proportion under improved pastures, (ii) breeding for deep-rooting species and (iii) deep placement of fertilisers (e.g. during subsoiling) as opposed to broadcasting on the surface as currently practiced by farmers on the Northern Tablelands of

NSW. However, under the current conditions on the Northern Tablelands of NSW, applicability of these strategies under the constraints in which farmers operate is likely to remain a challenge. The characterisation of FRMD and associated root morphological traits are explored at greater detail in chapter 2.0. In the following chapter, FRMD and the root morphological traits evaluated in chapter 2.0 are examined within the context of soil C and N stocks.

### ***8.1.2 Land-use, root traits and accumulation of C and N stocks with depth***

The large root and soil C and N stocks observed under improved pastures were consistent with the largest FRMD and associated root morphological traits observed under improved pastures. The results indicate that under improved pastures, the large FRMD and associated root morphological traits translated into large soil C stocks. These findings support earlier work (Conant, *et al.*, 2003) that build up of root biomass precedes accumulation of soil C. When averaged over depth and site, soil C stocks under the woodlands were significantly larger than under the native pastures, although the FRMD under the two land-uses was comparable. Probably, a larger fraction of C under the woodlands was in form of particulate organic matter (POM) that was not recorded as root biomass compared with the native pasture. As was observed in section 8.1.1, only the main effect of depth was strong on distribution of root and soil C and N stocks. About 89.4% of root C stock was in the 0 – 0.3 m depth where it could be vulnerable to losses via respiration (Baddeley & Watson, 2005) without practical steps towards translocating these C and N stocks to subsurface horizons potentially for better sequestration (Rasse *et al.*, 2005; Uselman *et al.*, 2007) (see section 8.1.1).

All the root morphological traits investigated were weakly correlated with SOC and DOC stocks (see chapter 3). However, the  $R^2$  values in this study were close to or even better than those reported in related studies attempting to correlate soil C stocks and root morphological traits (Klumpp and Soussana, 2009). With the exception of RTL that was better correlated with SOC, all the other root morphological traits were better correlated with DOC. Most likely, the strength of the interrelationships investigated in this study would have been strengthened, had the changes in root traits with age, growing season and species composition that can potentially regulate C fluxes at the root-soil interface (Gartern *et al.*, 2011) been accounted for. For example, DOC is a dynamic C pool that is strongly associated root phenology and climatic

conditions (Uselman, 2006; Uselman *et al.*, 2007). Due to time constraints and the amount of work involved, this study could not account for changes in root traits with age.

### ***8.1.3 Decomposability of root litters under different land-uses and litter source***

Decomposability of root litters at 86 DAPI was comparable under all land-uses and there was also no evidence that subsurface root litters were less decomposable than surface root litters. Probably, root litter decomposability was controlled more by temperature and moisture in the chambers that were maintained constant throughout the incubation period rather than either by root litter quality or location of root litter in the soil profile. A combination of lower soil temperature and higher moisture content that we observed deeper than 0.1 m has been reported to suppress litter decomposability (Rasse *et al.*, 2005; Baker *et al.*, 2007) and might have been the reason for the lower turnover rates of subsurface root litters compared with surface root litters as observed by Baddeley and Watson (2005).

The decomposability of root litters needs to be investigated *in situ* to establish if the prevailing conditions rather than differences in root litter quality are the reason for the reported higher turnover rates of surface compared with subsurface root litters (Baddeley and Watson, 2005). Otherwise, in our study, when both surface and subsurface root litters were exposed to the same conditions, there were no significant differences in root litter decomposability, regardless of the land-use from which the root litters were collected. One important implication of this study is that model estimates of root litter turnover (Santantonio and Grace, 1987; Publicover and Vogt, 1993) and input of root litter C to soil (Pansu *et al.*, 2009) can be relied on as long as soil temperature and moisture content can be assumed to be constant, since the models estimates are based on the assumption that decomposability is constant. The second implication is that if prevailing field conditions are the responsible for the suppression of root litter decomposability in subsurface horizons, then the benefits of practices like subsoiling that expose naturally buried root litter to the surface would have to be weighed against the costs of increased decomposability of such root litters. This section is addressed to some detail in chapter 4.0.

## **8.2 Species effects on FRMD, root traits, C stocks and root litter decomposability**

### ***8.2.1 Species and profile distribution of FRMD and associated root traits***

The interactive effect of light and species on FRMD and associated fine root traits, fine root biomass C and N as well as soil C and N were not related to season of the year, implying that species responses were specific to intensity of shading. Although high light intensity (0% shading) increased fine root biomass and fine root C across all species, shading favoured accumulation of soil C under the C<sub>3</sub> species (Fig. 8.1). The positive effect of high sunlight intensity on FRMD is evidence that light regulates dry matter allocation to roots. This was not unexpected for the sun-adapted species: *A. richardsonii* and *C. ventricosa* because in such species, high light intensity has been shown to increase photosynthesis, stomatal conductance and consequently, dry matter allocation to roots (Poorter *et al.*, 2012). Down-regulation of these processes at low light intensity (Ballare *et al.*, 1991; Wahl *et al.*, 2001; Begna *et al.*, 2002; Poorter *et al.*, 2012) could explain the suppression of FRMD at 75% shading which was significant on the sun-adapted species. One of the strategies that sun-adapted species adopt to adapt to low sunlight intensity is increased allocation of photoassimilates to low-order root branches that are associated with reduction in root biomass because of their low tissue density (Ryser & Eek, 2000). This root fraction has however, been found to dominate root functions related to input of C to soil (Guo *et al.*, 2008b). If the goal is optimisation of FRMD, our results indicate that this is happening under the more open land-uses with minimum shading intensity like improved pastures and native pastures characterised by few scattered trees. In contrast *M. stipoides* did not seem to be particularly affected by the level of shading, although it also tended to have larger FRMD at 0% shading. This was not expected because high light intensity should suppress dry matter allocation to roots of shade-tolerant species when unshaded (Ryser & Eek, 2000).

Not only did shading influence dry matter allocation to roots but also the depth at which these species placed their FRMD. The effect of shading on profile distribution of FRMD was particularly evident within the 0 – 0.5 m depth. This is an important result because although light had for long been speculated to influence the depth at which plants grow roots (Feldmand, 1984), we could not find studies to back-up this claim.

The pattern in seasonal distribution of FRMD with depth was similar for *A. richardsonii* and *M. stipoides*, with up to 97% of FRMD under either species occurring in the 0 – 0.1 m depth by

early summer when the FRMD of the two species was at its peak. Maximisation of root growth in the surface horizons could have been a response to the warming of topsoil after winter. Such concentration of FRMD in topsoil depths is not good for C sequestration since the rate of turnover of that biomass is higher (Baddeley & Watson, 2005) and therefore, more vulnerable to losses to the atmosphere as CO<sub>2</sub>-C via decomposition (Jobbagy & Jackson, 2000).

### **8.2.2 Species, root traits and depth distribution of root or soil C and N stocks**

The between species differences in root and soil C and N stocks were due to differences in photosynthetic pathways and life histories of the species. Coincidentally, the C<sub>3</sub> species, *A. richardsonii* and *M. stipoides* were also winter species whereas *C. ventricosa* was a C<sub>4</sub> summer grass. The winter species persisted throughout the growing seasons whereas *C. ventricosa* senesced in winter; died in spring and re-sprouted in the following summer when FRMD of the winter grasses was peaking. Persistence enabled the C<sub>3</sub> species to fix more C and take up associated N, resulting in larger root C and N stocks compared with *C. ventricosa*. Our results indicate that persistence was associated with conservation of larger root C and N stocks whereas senescence and death were associated with larger soil C and N stocks. Root- or shoot-conserving species have been shown to convert their root or shoot C to SOM much more slowly than the non root or shoot conserving species (Personeni & Loiseau, 2004). The larger soil C and N stocks under *C. ventricosa* which had typically smaller root C and N stocks compared with the C<sub>3</sub> species point to more rapid conversion of the root C and N stocks of this species to SOM. This was also encountered by Conant *et al.* (2003) who observed that the more intensively grazed pastures with smaller root C had larger soil C stocks than the ungrazed ones with large root C stocks, which was attributed to more rapid conversion of root C to SOM.

The effect of shading on root and soil C and N stocks was both species-specific and also seasonal. High sunlight intensity and shade had opposing effects on root and soil C and N stocks. The larger root C and N stocks for all species at 0% compared with 75% shading were consistent with FRMD (section 8.1.1). These results highlight the positive role of sunlight in stimulating dry matter allocation to roots. It is not clear why there were larger soil C and N stocks at 75% shading compared with 0% shading that had larger root C and N stocks. We propose: (i) higher conversion of root C and N stocks to soil C and N stocks coupled by suppression of decomposition rates by the lower soil temperatures and higher soil moisture

observed at 75% than at 0% shading; (ii) higher conversion of root C and N stocks to soil C and N stocks but which was exceeded by losses via decomposition driven by the conducive soil temperature and soil moisture observed at 0% than at 75% shading;

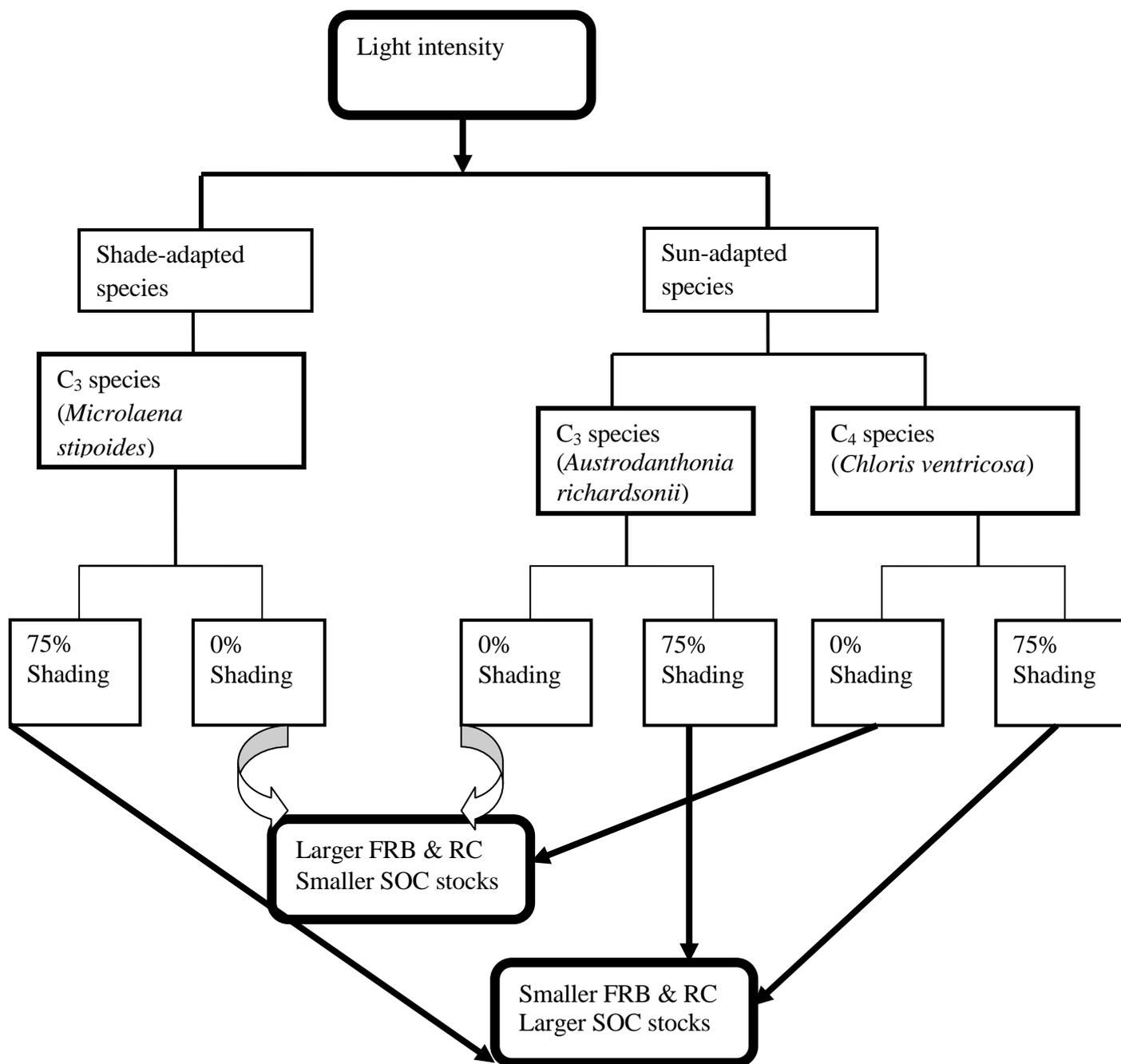


Fig. 8.1. Interactions between light intensity, species and root and soil C stocks

(iii) higher conservation of root C and N in biomass as opposed to conversion to soil C and N stocks at 0% shading. Further studies *in situ* are needed to establish the actual reasons for increased root C and N at 0% shading but larger soil C and N stocks at 75% shading.

All the species underwent similar changes in the distribution of root and soil C and N stocks with soil depth at 0% and 75% shading, suggesting that this was a response to shading and was not related to photosynthetic pathway or sun-/shade-adaptability of the species. This study provides evidence to what has long been postulated, that light might regulate the depth at which plants grow roots (Feldman, 1984). The larger soil C and N stocks at 75% shading compared with 0% shading contrasted with the larger root C and N stocks at 0% shading. This effect was also extended to deeper layers at least within the 0 – 0.5 m, implying that high sunlight intensity and shade had opposing effects on accumulation of root and soil C and N stocks down the soil profile. If the longevity of C increases with the depth at which it is located (Jobbagy & Jackson, 2000), our results indicate that C sequestration is increased by the presence of shade, although the reasons remain unclear.

### ***8.2.3 Decomposability of root litters of different Species and litter source***

There was no significant effect of species, root litter type (surface vs subsurface) or soil quality on Cumulative CO<sub>2</sub>-C emissions from root litters at 99 DAPI. These results were not expected because of the significant differences in root litter C:N ratios across species and between root litter types. Subsurface root litters with typically wider C:N ratios were as decomposable as surface root litters with narrower C:N ratios when exposed to the same temperature and soil moisture conditions. Under similar conditions, no significant effect of soil quality on cumulative CO<sub>2</sub>-C effluxes from the root litters at 89 DAPI was detected. The results of this study indicate that C:N ratio was not an important driver of root litter decomposition rates as reported in earlier studies (Silver and Miya, 2001). Most likely, root litter decomposability was driven more by a combination of soil temperature and moisture content that were maintained constant during the incubation. It is also possible that the low rates of decomposition masked the effect of C:N ratio on decomposition rates so that soil temperature and soil moisture appeared to dominate.

Comparable cumulative CO<sub>2</sub>-C effluxes from root litters at 89 DAPI between species implies that reasons other than higher decomposability of the root litters were responsible for the larger SOC and SON stocks under *C. ventricosa* which had typically smaller root C and N stocks when compared with *A. richardsonii* and *M. stipoides*. Probably, (1) conversion of root biomass into POM that was measured as soil C rather than as root C may have been higher under *C. ventricosa* compared with the C<sub>3</sub> species. This is particularly so, given that this particular species first had to die before re-sprouting; (2) temperature and moisture that were not varied in this study might have overshadowed potential differences in root litter decomposability that would have been detected under field conditions; and (3) exudation as a process through which roots input C to soil (Jones *et al.*, 2009) might have been higher under *C. ventricosa* compared with *A. richardsonii* and *M. stipoides*.

Physical fractionation soil C under the different species, *in situ* incubation experiments and quantification C inputs into the soil by living roots e.g. via exudation (Jones *et al.*, 2009) or other insoluble C compounds like mucilage (Iijima *et al.*, 2003) may shed light on the actual reasons for the larger soil C stocks under *C. ventricosa*.

### 8.3 References

- Baddeley, J.A. & Watson, C.A. (2005) Influence of root diameter, tree age, soil depth and season on fine root survivorship in *Prunus avium*. *Plant and Soil*, 276, 15 – 22.
- Ballare CL, Scopel AL, Sanchez RA. 1991. Photocontrol of stem elongation in plant neighbourhoods: effects of photon fluence rate under natural conditions of radiation. *Plant, Cell and Environment* 14: 57 – 65.
- Baker JM, Ochsner TE, Venterea RT, Griffis TJ (2007) Tillage and soil carbon sequestration – what do we really know? *Agriculture, Ecosystems and Environment* 118, 1 – 5.
- Begna SH, Dwyer LM, Cloutier D, Assemat L, DiTomamaso A, Zhou X, Prithiviraj B, Smith DL. 2002. Decoupling of light intensity effects on the growth and development of C<sub>3</sub> and C<sub>4</sub> weed species through sucrose supplementation. *Journal of Experimental Botany* 53(376): 1935–1940.

Conant RT, Six J, Paustian K (2003) Land-use effects on soil carbon fractions in the south-eastern USA. I. Management-intensive versus extensive grazing. *Biology and Fertility of Soils* 38, 386-392.

Dodd, M. B., Mackay, A. D., 2011. Effects of contrasting soil fertility on root mass, root growth, root decomposition and soil carbon under a New Zealand perennial ryegrass/white clover pasture. *Plant and Soil* 349(1-2), 291–302.

Feldman LJ. 1984. Regulation of root development. *Annual Reviews in Plant Physiology* 35:223–242.

Fitter, A.H. (1987) An architectural approach to the comparative ecology of plant root systems. *The New Phytologist*, 106(suppl.), 66 – 77.

Fitter, A.H. (2002) Characteristics and functions of root systems. *Plant roots, the hidden half* (eds Y. Waisel, E. Eshel & U. Kafkafi), pp. 15 – 32. Dekker, New York, USA.

Garten CT, Brice DJ, Castro HF, Graham RL, Mayes MA, Philips JR, Post III WM, Schadt CW, Wullschlegel SD, Tyler DD, Jardine PM, Jastraw JD, Matamala R, Miller RM, Moran KK, Vugteveen TW, Izaurrealde RC, Thomson AM, West TO, Amonette JE, Bailey VL, MettingFB, Smith JL (2011) Response of “Almo” switchgrass tissue chemistry and biomass to N fertilisation in west Tennessee, USA. *Agriculture, Ecosystems and Environment* 140, 289 – 297.

Guo LB, Cowie AL, Montagu KD *et al.* (2008a) Carbon and nitrogen stocks in a native pasture and adjacent 16-year-old *Pinus radiata* D. Don plantation in Australia. *Agriculture Ecosystems & Environment* 124 (3-4), 205-218.

Guo D, Li H, Mitchell RJ, Han W, Hendricks JJ, Fahey TJ, Hendrick RL (2008b) Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. *New Phytologist*, 177 443–456.

Hodge, H. (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytologist*, 162, 9–24.

Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* 10(2), 423 – 436.

Jones DL, Nguyen C, Finlay RD (2009) Carbon flow in the rhizosphere: carbon trading at the soil–root interface. *Plant and Soil*, 321, 5–33.

Klumpp K, Soussana J-F (2009) Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect trait approach. *Global Change Biology* 15(12), 2921-2934.

Lodge GM, Murphy SR (2006) Root depth of native and sown perennial grass-based pastures, North-West Slopes, New South Wales. I. Estimates from cores and effects of grazing treatments. *Australian Journal of Experimental Agriculture* 46, 337 – 345.

Pansu, M., Martineau, Y., Saugier, B., 2009. A modeling method to quantify in situ the input of carbon from roots and the resulting C turnover in soil. *Plant and Soil* 317, 103 – 120.

Personeni, E., Loiseau, P., 2004. How does the nature of living roots affect the residence time of carbon in the root litter continuum? *Plant and Soil* 267, 129–141.

Poorter H, Jiklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* 193: 30–50.

Publicover, D. A., Vogt, K. A., 1993. A comparison of methods for estimating forest fine-root production with respect to sources of error. *Canadian Journal of Forest Research-Revue* 23(6), 1179–1186.

Rasse DP, Rumpel C, Dignac MF (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil*, 269, 341 356.

Ryser P, Eek L (2000) Consequences of phenotypic plasticity vs inter-specific differences in leaf and root traits for acquisition of aboveground and belowground resources. *American Journal of Botany* 87, 402 – 411.

Santantonio, D., Grace, J. C., 1987. Estimating fine-root production and turnover from biomass and decomposition data - a compartment flow model. *Canadian Journal of Forest Research-Revue* 17(8), 900–908.

Silver, W. L., Miya, R. K., 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129, 407–419.

Uselman SM (2006) Production and fate of soluble organic carbon, nitrogen, and phosphorus during forest ecosystem development: root versus leaf litter. *PhD dissertation University of Nevada, Reno (Dissertation Abstract 3222985)*.

Uelman SM, Qualls RG, Lilienfein J (2007) Contribution of Root vs. Leaf Litter to Dissolved Organic Carbon Leaching through Soil. *Soil Science Society of America Journal* 71(5), 1555-1563.

Wahl S, Ryser P, Edwards PJ. 2001. Phenotypic plasticity of root anatomy in response to light intensity and nutrient supply. *Annals of Botany* 88: 1071–1078.