Partitioning root and heterotrophic respiration from soil CO_2 efflux in two loblolly pine clones that differ in growth efficiency and carbon allocation

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Problem

- Belowground carbon allocation (BCA) supports root production and maintenance, rhizosphere food webs, mycorrhizal fungi, and provides the majority of soil detrital C. These complex and interrelated processes make BCA the most unpredictable component of the forest C cycle.
- Recent evidence suggest that photosynthetic supply can explain the majority of the seasonal variation in soil autotrophic (R_a, root and rhizosphere) and potentially, heterotrophic (R_h) respiration. Thus, BCA may vary in predictable ways with changes in growth, phenology, and resource availability (water, nutrients, atmospheric CO_2).
- We measured soil CO_2 efflux (S_f) in young (8-9 years-old) loblolly pine clones known to differ in growth efficiency and carbon allocation to determine how genotype and silviculture influence BCA. The root exclusion pipe method was used to partition S_f into R_a and R_h components.

Methods

Study site: The Cross Carbon Study is a long-term research project designed to quantify the relationship between resource availability, stand productivity, and carbon sequestration in clonal loblolly pine plantations.

The study is a 2 x 2 factorial combination of two clones (Arborgen: AA93 and AA32) and two logging residue treatments in a RCB design replicated three times (12 plots). Soil organic matter treatments consisted of no addition (-LR) and soil incorporation at planting of 25 Mg ha^{-1} comminuted logging debris (+LR, C:N≈700). Clones were planted in January 2005 (1280 TPH).

Clones represent a narrow crown (NC: AA93) and broad crown (BC: AA32) ideotype. Both clones have similar stem growth rates; however, the NC ideotype had less leaf biomass (15-20%) **(Figure 1)** and greater growth efficiency than the BC ideotype **(Figure 2)**. During the second year of growth, the BC clone had greater fine root length and turnover (Pritchard et al. 2010).

Figure 1

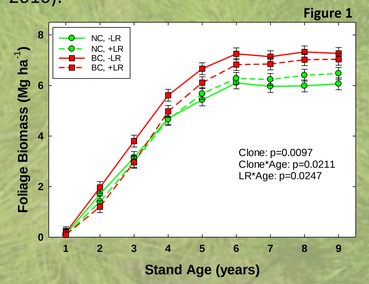
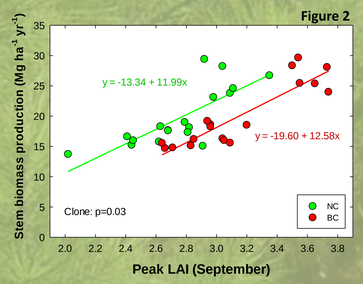


Figure 2



Partitioning Soil CO_2 efflux (S_f) into R_a and R_h

Soil CO_2 efflux was partitioned into R_a and R_h using root exclusion pipes (J. Seiler, *personal communication*). Three locations between trees were randomly selected in each plot. At each location, S_f was measured with a Licor 6400 in two positions 15 cm apart. After the initial S_f measurement, a 10.7cm diameter by 20cm pipe was driven into the ground in one of the two positions. The pipe severed roots thereby halting carbohydrate supply flow, creating a small root exclusion zone. S_f was measured periodically in the pipe until S_f had stabilized (85-100 days). This approach assumes: that as carbohydrate supply is depleted, $R_a \rightarrow 0$, little root death or decomposition has occurred, and S_f is primarily R_h. To capture the seasonal variation in R_a/S_f, root exclusion pipes were installed at six different times (March, July, October 2012 and March, June and October 2013).

Hypotheses

We hypothesized that:

H1 - because of greater leaf and potentially greater canopy photosynthesis, the BC clone would have greater S_f, R_a, R_h, and R_a/S_f than the NC clone,

H2 - R_a/S_f would vary seasonally with changes in aboveground growth, and

H3 - +LR treatments would increase R_h and MBC.

Results

Figure 3

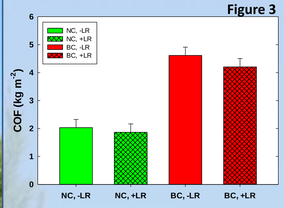


Figure 4

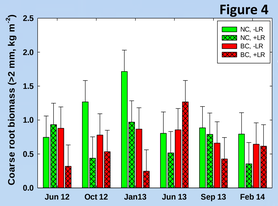


Figure 5

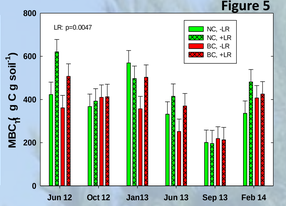
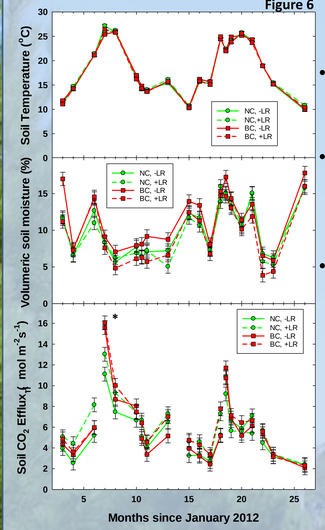


Figure 6



- **Figure 3**: Logging residue treatment (+LR) increased the quantity of coarse organic fragments (COF, >2mm). Still highly significant 8-9 years after treatment installation.
- **Figure 4**: There was less coarse root biomass (>2 mm) in +LR treatments (-LR: 0.91; +LR: 0.62 kg m^{-2}; se=0.11; p=0.019).
- **Figure 5**: Microbial biomass carbon (MBC) was 16% greater in +LR treatments (-LR: 353.0 µg C g $soil^{-1}$; +LR: 419.6 µg g $soil^{-1}$; p=0.005). There were no clone or clone by LR interactions for COF, root biomass, or MBC.
- **Figure 6:**
  - There were no clone or LR treatment effects on soil temperature or soil moisture.
  - Mean S_f in the +LR treatment (6.28±0.16) was 12% greater than in the –LR treatment (5.56±0.16) (p=0.04). The higher rates of S_f in +LR were similar to increase MBC.
  - There were no clone or clone x LR effects on S_f; however, there was a clone x season effect (p=0.003), where S_f was 17% greater in BC clone in July 2012 (*).

Partitioning S_f into R_a and R_h

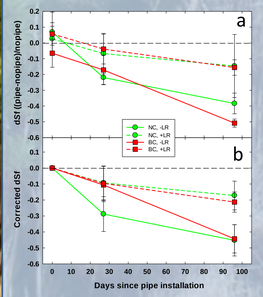


Figure 7: Autotrophic respiration (R_a) was estimated by calculating the difference in S_f between pipe (i.e. root exclusion) and no-pipe positions. For example, S_f was measured two times after pipe installation in July 2012. In panel a, S_f is expressed as the relative difference between pipe and no-pipe positions ($dS_f=(S_{f,pipe}-S_{f,no-pipe})/S_{f,no-pipe}$). In panel b, dS_f has been corrected for the initial difference between positions before pipe installation (Day 0). S_f was significantly reduced in root exclusion pipes (i.e. corrected $dS_f<0$, $p < 0.05$) 96 days after pipe installation. dS_f was greater in +LR than –LR treatments (p=0.03).

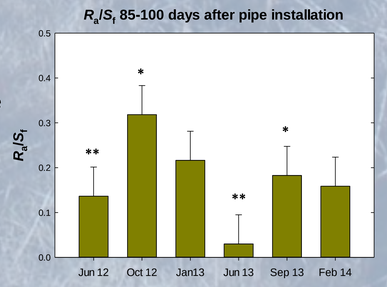


Figure 8: The ratio R_a/S_f averaged 0.21, but ranged from 0.03 (NS) to 0.32, depending on time of year. R_a was a larger component of S_f when pipes were installed during the summer (*) than in early spring (**). When all data were combined, there were no significant clone, LR, or treatment by time interaction effects on R_a/S_f.

Seasonal differences in BCA and root carbohydrate storage may have contributed to the observed pattern in dS_f. The small pipe effect in the spring is likely due to two factors: 1) trees preferentially allocate more carbon to stem and shoot growth during the early part of the growing season (Johnsen et al. 2006, Maier et al. 2010), thus there is little BCA at this time, and 2) roots have larger concentrations of starch in early spring than in the summer (Ludovici et al. 2002). This stored carbohydrate could sustain R_a in the root exclusion pipes.

Figure 9

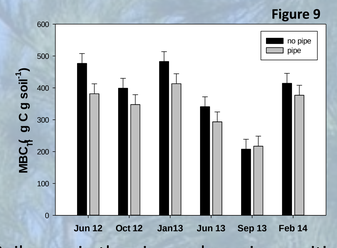
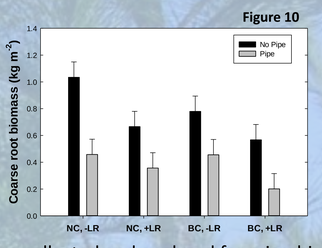


Figure 10



- Soil cores in the pipe and no-pipe positions were collected and analyzed for microbial biomass carbon (MBC, chloroform fumigation method) and root biomass.
- **Figure 7:** Mean MBC was reduced 13% in the pipes compared to no-pipe (pipe: 338.3, no-pipe: 386.8 µg C g $soil^{-1}$; se=13.9; p=0.006).
- **Figure 8:** Root exclusion pipes reduced live root biomass by 52%. Mean live root biomass was (no-pipe: 0.76; pipe:0.37; se=0.06; p<0.0001).

Heterotrophic respiration (R_h)

Figure 11

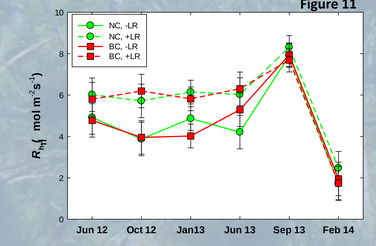


Figure 12

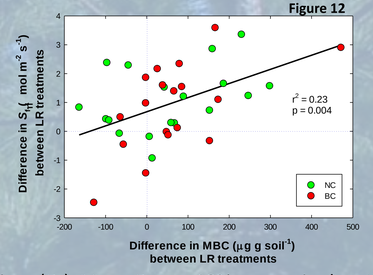


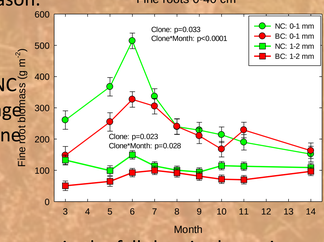
Figure 11: Soil CO_2 efflux measured in pipes (R_h). Mean R_h was 19% greater in the +LR (5.12±0.16) than in the –LR (4.15±0.16) treatment (p<0.0001). There were no significant clone or clone x LR effects.

Figure 12: The difference in S_f between +LR and –LR treatments was correlated to the treatment difference in MBC.

Conclusions

H1 - Clone effects on S_f were minor. There was a clone x season effect on S_f, where S_f tended to be greater in the BC clone during the summer. This clone x season effect was also observed by Tyree (2008) during the third growing season.

- There were no clone effects on R_a or R_h. This may have been due to greater fine root biomass in the NC treatment. In contrast to measurements made at age 2 (Pritchard et al. 2010), the NC clone had greater fine root biomass at age 9 **(Figure 13)**.



H2 – R_a/S_f average 21% , but varied seasonally being greater in the fall than in the spring. However,

- Seasonal variation in in BCA and root carbohydrate content likely contributed to variation in R_a/S_f. For example, we may have underestimated R_a/S_f in the spring when root carbohydrate content is high (we are currently processing roots for carbohydrate content).
- Root exclusion pipes significantly reduced live root biomass, thus there could have been increased R_h from root decomposition.
- Because of these uncertainties, the root exclusion pipe method, used by itself, is unlikely to produce robust estimates of R_a/S_f and R_h.

H3 - +LR treatments increased S_f , MBC, and R_h. These effects were still evident 8-9 years after planting. Increased soil carbon in the +LR treatments are expected to persist for 20+ years (Maier et al. 2012).

References: Johnsen et al. 2006. *Plant, Cell and Environment* 30, 128-134; **Ludovici et al.** 2002. *Forest Ecology and Management* 159: 261-270; **Maier et al.** 2012. *New Phytologist* 185:502-513; **Maier et al.** 2012. *Forest Science* 58: 430-445; **Pritchard et al.** 2010. *Tree Physiology* 30: 1299-1310; **Tyree et al.** 2014. *Soil Biology and Biochemistry* 69: 93-100.