Short-term photosynthesis, root exudate, and fine root growth responses to fertilization and drought in clonal *Pinus taeda*

Jeremy P. Stovall  
Thomas R. Fox  
John R. Seiler

October 9, 2008  
SSSA Annual Mtg

My presentation is entitled short-term photosynthesis, root exudate, and fine root growth responses to fertilization and drought in clonal loblolly pine. I’d like to acknowledge my co-authors, Tom Fox and John Seiler, and my funding source, the NSF center for advanced forest systems.
We know we can manipulate 2 fundamental properties that influence growth 1) genetics, the ability of a plant to acquire and use resources and 2) the environment, or the availability of resources. However, these do not directly influence growth, but instead affect physiological processes, which in turn influence growth. Increase in leaf area well-established as long-term mechanism of growth response to fertilization. But leaf area is not a physiological process. Trees must DO something to get more leaves. This talk only deals w/ short term, i.e. PHYSIOLOGICALLY, HOW DO THEY GET MORE LEAF AREA, which leads to stem volume growth?

In this instance we are controlling genetics by deploying clones, and are altering resource availability with fertilization. The processes I’ll be investigating are photosynthesis and below-ground C allocation as mechanisms for allocating more C to increased leaf area.
In several years of clonal work we’ve observed a number of different clone-specific physiological growth strategies. In case one we see increased photosynthetic rates and increased growth rates. These clones fix more carbon through photosynthesis, which is allocated to new leaf area. In case 4 we see no photosynthetic response or growth response, another intuitive case. However, for clonal strategies 2 and 3, photosynthetic rates and growth rates indicate that something else is clearly going on. Our hypothesis is that in cases 2 and 4, changes in belowground C allocation account for differences in growth response to fertilization. This explains both case 2, where the additional carbon fixed is shunted belowground, and no above-ground growth response is observed, and case 3, where photosynthetic rates do not increase, but decreased C allocation belowground increase C available for more needle growth.
The experiment was replicated 5 times in large 2 story growth chambers at VT. In order to assess changes in belowground C allocation and apply effective treatments, we used a coarse, nutrient deficient quartz sand with no organic matter present. This allows us to control our fertilizer treatments and allows us to make the assumption that all organic matter in our system is derived from the trees in each pot. In order to test our hypothesis, we designed a 2x2x2 factorial experiment, with 2 levels of fertilization, 2 levels of irrigation, and 2 different clones. The clones were selected based on different crown ideotypes.
The one on the right is what we are calling a sawtimber ideotype, and is straight with small branches, and is an efficient grower that puts on lots of stem volume with a small canopy. The one on the left is what we are calling a biomass ideotype. It is branchy and bushy, and has a relatively large canopy, but is a fast grower as well.
Measurements

• Stem Volume: basal diameter, height
• Photosynthesis: LICOR LI-6400
• Root Exudates: XAD-7 Resin Capsules
  – In situ 21 days
  – In recurring rhizosphere near taproot
  – DI extract
    • Total Organic Carbon (TOC)
    • Anthrone Reactive Carbon (ARC)

Basically what’s written in slide
For the sawtimber ideotype it appears that the treatments are effecting growth exactly as we would expect: greater resource availability treatments have greater slopes. While you see that there was some disparity in the initial volumes of the trees randomly assigned to each treatment, it appears that the irrigated trees have increased their growth rate and are about to increase volume over the controls. The fert and fert irrigate treatments show higher slopes, and greater volume growth. The trend in the biomass ideotype is somewhat less extreme, but we do see a separation of the fert and fert irrigate treatments from the irrigate and control treatments. The main point here is that fertilization is improving growth rates, but its efficacy varies between these two clones.
Light saturated specific photosynthetic rates appear to be generally declining with time. From the significant effects shown at the right we can discern in the graph that the irrigated treatment appears to be showing increased rates in the sawtimber clone, but not in the biomass clone. It does not appear that fertilization is responsible for increasing photosynthetic rates in these two clone, with the exception of the most recent data from the biomass clone. Here senescence of the 2-year needles is already occurring, and retranslocation of the N from those needles to the rest of the canopy may be explaining this increase in the fert treatments. While we have not seen an increase in photosynthetic rates, in this system we do have frequent low-intensity changes to resource availability as we fertilize 2x per week rather than a single, large change as we see in the field with operational fertilization. We may then be less likely to pick up fert effect found in literature. But, the overall point from this data appears to be that fertilization is not increasing photosynthetic rates in these two clones.
Now, to move belowground. For TOC analyses of the DI extract, we observed no significant time interactions, so I’ve collapsed the data across all sample dates, as shown here. While none of the main effects or 2-way interactions are significant we do have a significant 3-way interaction between clone fert and irrigation. The graph on the next slide shows the exact same data as this figure, but in a different way to better examine this 3-way interaction.
The color coding is the same as the previous graph, with controls in yellow, fert in light green, irrigate in light blue, and fert-irrigate in dark green. In this figure our treatments occupy 3 dimensional space with the 2 clones differentiated on this axis, high and low fert treatments on this axis, and high and low irrigation treatments on this axis. The size of the spheres is proportional to the independent variable, root exudate TOC. Note that this larger blue sphere is in the foreground, and corresponds to the low fert-high irrigation sawtimber clone. We observe a number of interesting trends on this graph.

1. At low irrigation root exudation is insensitive to fertilization in the sawtimber clone.
2. The biomass clone, however, reduces exudation with fertilization at low irrigation.
3. This is the same trend we observe for the sawtimber clone at high irrigation.
   1. In these two instances this fits with our theoretical model, where fertilization reduces C allocation to root exudation, allowing that C to be allocated elsewhere in the tree, such as to new leaf area.
4. However, at high irrigation the biomass clone shows an increase in root exudation.
   1. This shows the exact opposite trend we would expect. One possible cause is that exudation per root length has decreased, but overall root length has increased as these trees show a volume response to fertilization, but our data is not sufficient to support this hypothesis.

So overall it appears that root exudation in response to fertilization depends on both genetics and water availability, but that in some instances, root exudation did decrease for both our clones in response to fertilization.
This slide shows the time trend between clones for anthrone reactive carbon in root exudate extracts. Anthrone reactive carbon consists of more labile and bacterially and fungally accessible low molecular weight organic acids and sugars. We observed significant clonal and time effects for ARC with repeated measures, although individual date ANOVAs showed only the last sample period having a statistically significant difference between the clones. You can see on this graph that the biomass ideotype is exuding more ARC during all time periods except days 63 to 84.

This is consistent with our theoretical model, since the biomass ideotype has showed less stem volume growth overall than the sawtimber ideotype, which is not allocating as much ARC to root exudates.
So, to summarize our results:
Both the sawtimber ideotype with sufficient available water and the biomass ideotype with some drought stress exhibit reduced belowground C allocation to root exudates in response to fertilization. This is consistent with our hypothesis for clonal strategy 3.

These preliminary results, coupled with the growing acreage being planted in clones, indicates that it may be important to consider clone specific physiological process when assessing fertilizer recommendations and carbon sequestration potential. In the context of papers presented 2 days ago, specific clones may alter N mineralization rates differently, and behave differently under elevated CO2 with climate change.
Thank you for listening, and I'll take any questions you may have.