



Seeing the Forest through the Trees

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Physiological Effects of Organic Soil Consumption on Mature Longleaf Pines (*Pinus palustris*)

Joseph O'Brien¹, J. Kevin Hiers², Kathryn Mordecai¹ and Doria Gordon³

¹USDA Forest Service, Southern Research Station, Athens, Georgia, 30602, USA

²J.W. Jones Ecological Research Center, Newton, Georgia, 39870, USA

³The Nature Conservancy, Gainesville, Florida, 32601, USA

Introduction

Longleaf pine ecosystems depend on frequent fires to maintain both the overstory pines and a high diversity understory plant community. At one time these forests dominated the coastal plain of the southeastern US, but currently longleaf stands occupy less than 3% of their historical extent, usually as isolated fragments (Gilliam and Platt 2006). One consequence of this fragmentation has been the reduction of fire frequency with some stands remaining unburned for decades. A major effect of this reduction in fire frequency is the development of an organic soil horizon. In frequently burned stands, fire consumes litter and the mineral soil surface remains mostly exposed. In unburned stands, low litter decomposition rates, especially in xeric sites, result in the formation of a deep forest floor (Hendricks et al. 2002). Mature trees colonize a well developed O-horizon with numerous fine roots. These roots are lost after the organic soil is consumed by fire. Root consumption could cause both acute and chronic stress to a tree. Loss of fine roots could immediately lower nutrient and water uptake rates, reduce carbohydrate pools, and require resources to be allocated for root replacement and repair, perhaps at the expense of some other process. The impact of stored carbon losses and inhibited mineral nutrient uptake would also likely cause chronic effects such as reduced leaf area, changes in leaf nitrogen balance, lowered tissue repair rates, and inhibition of chemical defenses. As a first step to understanding the physiological consequences of fine root loss, we measured whole tree transpiration and chlorophyll concentrations in mature longleaf pines growing in an area with a well developed O-horizon exposed to varying degrees of duff consumption and crown scorch.

Methods

We conducted experimental burns in a stand of long unburned longleaf pine forest at Fort Gordon Military Base, Augusta, GA, USA. The site had not been burned in at least 50 years and had a well developed O-horizon, with an average depth of 16.1 cm (± 3.1 S.D.). Tree sampling was stratified by soil type (Arenic Frangiudults) and topography (ridge tops). Within the site, 20 trees with a DBH of approximately 35 cm and similar stature were chosen. The 20 selected trees had a mean DBH of 37.1 cm (± 2.7 S.D.) and a height of 19.6 m (± 2.4 S.D.). Initially, the plan was to experimentally manipulate fire damage, but on June 25, 2005 a wildfire passed through the study area three days

after the first root consumption treatments. No direct observations were made of the wildfire, but post fire measurements indicated that both forest floor consumption and crown scorch were highly variable and extensive. Two study trees escaped the fire, and the remaining 18 received varying degrees of scorch and root consumption. An additional three unburned trees were added to the study after the fire.

Following the fire, we measured the amount of duff consumed in a 4 m diameter circle centered on the tree bole. Consumption was estimated using both duff pins that were in place prior to the fire and by visual estimates. A linear correlation between visual estimates of consumption and the duff pins measurements showed the effectiveness of the visual estimates ($R^2=0.92$, $p<0.0001$). Percent crown scorch was estimated visually in 10% increments. One month prior to the fire, sap flow sensors were inserted into each tree. The wildfire destroyed the originals and replacements were deployed approximately one month following the fire. The first post-fire sap flux measurements occurred in mid-August 2005 after damaged crowns had reflushed new leaves. The outputs from the probes were averaged and transformed into sap flux estimates after Granier (1987). Chlorophyll content was measured in foliage samples collected immediately prior to the fire, then at 3 months following the fire. Post-fire chlorophyll content was standardized and presented as an index by subtracting the post-fire content from pre-fire content, then dividing by the pre-fire content. Consumption effects on sap flux were analyzed using random effects ANOVA and the chlorophyll content was analyzed using linear regression.

Results and Discussion

All fire damaged study trees had at least 20% O-horizon consumption (mean = 50.2, ± 35.6 S.D.). Scorch rates averaged 10% (± 19.2 S.D.), though 11 of the 18 trees with O-horizon consumption had undamaged crowns. Mean sap flux rates did not vary among the study trees prior to the fire ($F_{1,19}=0.653$, $p=0.861$). Sap flux rates were estimated simultaneously in all 20 trees for a total of nine days post-fire. The mean daily sap flux over the nine day period was $0.488 \text{ kg dm}^{-1} \text{ hr}^{-1}$ (± 0.35 S.D.). The results of the random effects ANOVA indicated that only O-horizon consumption had a significant impact on mean post-fire sap flux rates and there was no interaction (Table 1).

Table 1. Results of the random effects ANOVA. The multiple R^2 for the model was 0.44 ($p=0.001$).

| | SS | D.F. | MS | F | p |
|---------------------|------|------|-------|-------|---------|
| Intercept | 3.77 | 1 | 3.767 | 47.67 | >0.0001 |
| Scorch | 0.01 | 1 | 0.007 | 0.09 | 0.77 |
| Consumption | 1.08 | 1 | 1.078 | 13.65 | 0.001 |
| Scorch* Consumption | 0.05 | 1 | 0.050 | 0.63 | 0.436 |
| Error | 1.50 | 19 | 0.079 | | |

Sap flux was negatively correlated with consumption as indicated by the beta coefficient of -0.70 ($t=-3.69$, $p=0.002$). Figure 1 displays the results of a linear regression showing the negative relationship between amount of crown scorch and standardized chlorophyll content (beta= -0.81, $R^2=0.60$, $p=0.009$).

Summary and Conclusions

Post-duff fire damage in longleaf pines seems to cause a cascade of chronic stressors with mortality often occurring several months after the fire. However, the loss of fine

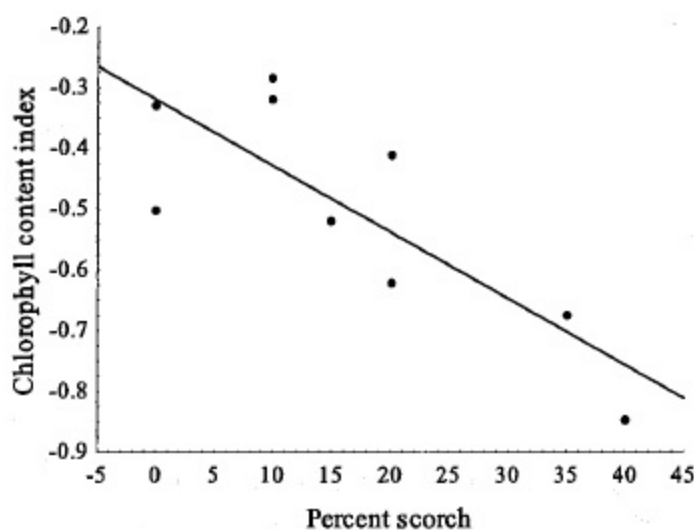


Figure 1. Linear regression of chlorophyll content and crown scorch. All trees had at least 20% duff consumption. It appears that resource limitation may have lead to a reduction in the ability to adequately provision new leaves with chlorophyll.

roots after O-horizon consumption can also create acute stress due to the reduction in water uptake and transpiration rates. Recent research suggests that longleaf pines maintain a constant allocation ratio between roots and aboveground tissue (Hendricks et al. 2006). Observations of study trees post-fire suggest that leaf area did decrease following O-horizon consumption. This decrease in photosynthetic capacity coupled with the loss of stored carbohydrates appears to be catastrophic to the trees; three of the 16 study trees with root consumption died within one year of the study and two more appeared near death with sparse crowns. The immediate loss in the ability to supply leaves with water could lead to chronic carbon limitations through a compensatory reduction in leaf area. Crown scorch is an additional acute stressor that may or may not occur simultaneously with root consumption. Since mineral nutrients are required to replace scorched leaves, root loss has the potential to further limit photosynthetic capacity. The loss of stored carbon and diminished photosynthetic capacity could lead to a cascade of indirect effects such as inhibited chemical defenses and reduced overall vigor. It appears that the inhibition of herbivore defenses might be critical as all three dead study trees succumbed to insect attack. These results suggest that the lowering of water and nutrient uptake rates might be the ultimate cause of mortality after duff fire.

Literature Cited

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