Pine decline from a physiological perspective

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Personal perspective

- **How well is the root system is doing its job?**
  - acquiring water and mineral nutrients
  - storing energy
  - maintaining vertical support
- **Symptoms suggest the root system is not doing its job.**
- **The incidence of decline may worsen if resources become more limiting.**
- **Management can be used avoid predisposing conditions.**

Presentation outline

- **Decline characteristics linked to tree physiology.**
- **Key physiological mechanisms** that naturally allow southern pines to take advantage of, or tolerate a range of stand conditions.
- **Consequences of failed mechanisms** that can’t keep up with what is required of them, or simply fail altogether.
- **Data that justify investigating the role of physiology in pine decline.**

Decline characteristics linked to physiology

- **Brown, H.D.; McDowell, W.E. 1968.** Status of loblolly pine die-off on the Oakmulgee District, Talladega National Forest, Alabama—1968. USFS Southeastern Area S&PF Report 69-2-28.
- **Roth, E.R.; Peacher, P.H. 1971.** Alabama loblolly pine die-off evaluation. USFS Southeastern Area S&PF Report 72-2-9.
- **Miller, R.E. 1979.** Loblolly pine die-off status report. USFS Southeastern Area S&PF Report 79-2-8.

- Sparse, chlorotic crowns
- Poor diameter growth and possible mortality
- Large cone crops one year before mortality
- Lateral root deterioration and fine root mortality one year before crown symptoms
- Mature loblolly pine alone or mixed with shortleaf pine on sites that originally supported longleaf pine

Decline characteristics linked to physiology

- **Hess, N.J., Otrosina, W.J., Carter, E.A., Steinman, J.R., Jones, J.P., Eckhardt, L.G., Weber, A.M., Walkinshaw, C.H. 2002.** Assessment of loblolly pine decline in central Alabama. GTR-SRS-48.
- **Hess, N.J., Eckhardt, L.G., Menard, R.D., Goddard, A.J., Carter, E.A. 2005.** Assessment of loblolly pine decline on the Shoal Creek/Talladega Ranger Districts, Talladega National Forest, Alabama and Choccolocca State Forest. USFS FHP Report 2005-02-05.
- **Otrosina, W.J., Bannwart, D., Roncadori, R.W. 1999.** Root-infecting fungi associated with a decline of longleaf pine in the southeastern United States. Plant and Soil 217:145-150.
- **Eckhardt, L.G., Weber, A.M., Menard, R.D., Jones, J.P., Hess, N.J. 2007.** Insect-fungal complex associated with loblolly pine decline in central Alabama. Forest Science 53:84-92.

- Sparse, chlorotic crowns, poor diameter growth, deteriorating roots, mature loblolly pine on sites that originally supported longleaf pine

- Disturbed sites (i.e. soil erosion by past land use)
- Unthinned, overstocked stands
- Presence of root disease (*Phytophthora cinnamomi, Pythium* spp., *Heterobasidium annosum, Leptographium* spp.)
- Longleaf pine

Decline characteristics linked to physiology

- **Indicators of resource deficiencies**
  - Chlorotic crowns
    - nitrogen, magnesium, iron, zinc, or calcium deficiencies
  - Loblolly > longleaf pine, eroded sites
    - loblolly pine is more resource-demanding than longleaf pine
    - decline is most prevalent for loblolly pine planted “off-site, or on eroded sites

Decline characteristics linked to physiology

- **Indicators of inadequate carbon fixation or allocation**
  - Sparse crowns
    - Less leaf area and whole-crown carbon fixation
    - Less carbohydrate allocated to the root system
  - Poor diameter growth
    - Less carbohydrate allocated to stemwood
    - More allocated to the root system and defense chemicals
  - Lateral root deterioration, fine root mortality, root disease
    - Inadequate carbohydrate allocated to roots and ectomycorrhizae
    - Less carbohydrate allocated to defensive chemicals
  - Unthinned, overstocked stands
    - Light limitations to photosynthesis are possible
    - Self-pruning has reduced the live crown
    - Self-thinning is delayed after crown closure

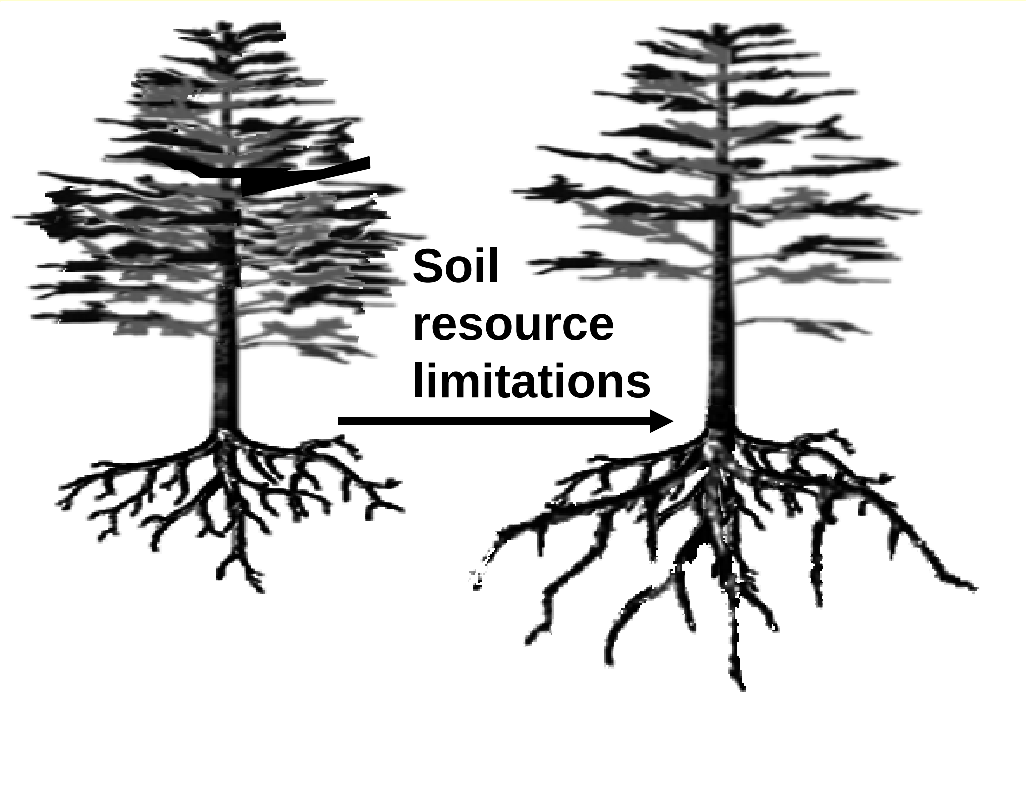
Key physiological mechanisms

- **Normally, southern pines avoid resource deficiencies**
  - Downward leaf area adjustment
  - C allocation shifts that favor root system growth
  - Internal recycling of mobile nutrients

Mixed hardwood and loblolly pine, age 15 years, North Carolina								
Pine stand information		**LAI (m^2/m^2)**		**RAI (m^2/m^2)**		**A_R:A_L**		
Enon clay loam	Lakeland sand	Loam	Sand	Loam	Sand	Loam	Sand	**Hacke et al. (2000) Oecologia 124: 495-505.**
1320 trees/ha at 20 yr	15 m^2/ha at 11 yr; 1260 trees /ha at 8 yr	**3.2-4.6**	**1.6-2.0**	**5.5**	**14.2**	**1.7**	**9.8**	
Longleaf pine, multi-aged, Georgia								
Mesic (sandy upland terrace with an argillic horizon)	Xeric (sandy upland ridge with no argillic horizon)	Mesic	Xeric	Mesic	Xeric	Mesic	Xeric	**Addington et al. (2006) Plant, Cell, and Environment 29: 535-545.**
10.7 m^2/ha; 230 trees/ha	2.7 m^2/ha; 54 trees/ha	**0.7-1.1**	**0.2-0.4**	**1.3**	**0.7**	**1.2**	**1.7**	

Key physiological mechanisms

<u>C allocation shift from shoot to root</u>



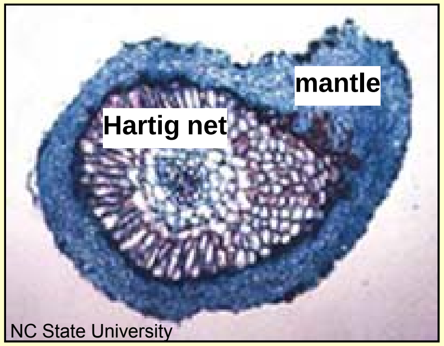
- **Downward leaf area adjustment**
  - conserves water
  - maintains cellular nutrition
- **C allocation shifts that favor the root system**
  - root system expansion
  - energy for ectomycorrhizal fungi
  - deep root growth
- **Internal recycling of mobile nutrients**
  - Example: N and Mg to enzymes and chlorophyll in young foliage
  - Example: K to stomatal guard cells

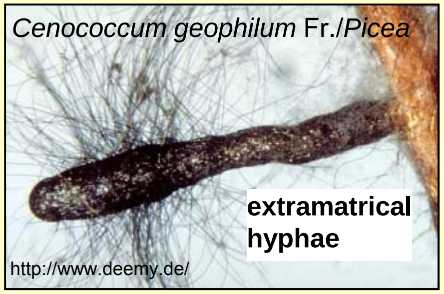
Key physiological mechanisms

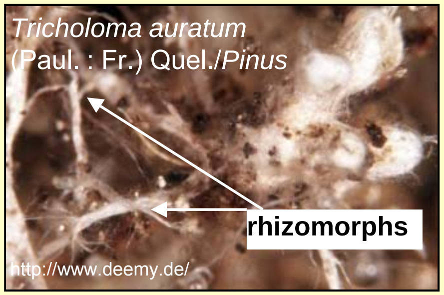
It is important to respect the energy needs of ectomycorrhizae.

- **Sims et al. (2007) Mycorrhiza 17: 299-309.**
  - Ergosterol analysis to quantify EM fungi
  - Hartig net, mantle, extramatrical hyphae, rhizomorphs, fruiting bodies
  - Closed-canopy longleaf pine, sandy soil
  - EM fungus production was **49 g / m^2 / yr**
  - **95%** was extramatrical hyphae and rhizomophs

- **Jones et al. (2003) Oecologia 134: 132-143.**
  - In-growth cores to assess fine root production
  - < 2 mm diameter pine roots and EM
  - 70-yr-old longleaf pine, sandy loam soil
  - Fine root production was **52 g / m^2 / yr**







EM extramatrical hyphae are a vital part of the root system.

Key physiological mechanisms

- **Downward leaf area adjustment**
  - conserves water
  - maintains cellular nutrition

- **C allocation shifts that favor the root system**
  - root system expansion
  - energy for ectomycorrhizal fungi
  - deep root growth
    - deep water supports fascicle physiology.
    - allows the hydraulic redistribution of water to shallow roots.
    - **Hacke et al. (2000) Oecologia 124: 495-505.**
      - Sand: ~190 cm rooting depth
      - Loam: ~20 cm rooting depth
      - Deep roots in sand supplied the water that was needed to avoid root xylem cavitation and maintain whole crown transpiration.

- **Internal recycling of mobile nutrients**
  - Example: N and Mg to enzymes and chlorophyll in young foliage
  - Example: K to stomatal guard cells

Key physiological mechanisms

- **Downward leaf area adjustment**
  - conserves water
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- **C allocation shifts that favor the root system**
  - root system expansion
  - energy for ectomycorrhizal fungi
  - deep root growth
- **Internal recycling of mobile nutrients**
  - Retranslocation before fascicle senescence
    - **Dalla-Tea and Jokela (1994) Forest Science 40: 650-662.**
      - Supplied 8 to 36% of the next year's aboveground demand for P.
  - Mobilization to supply tissues when a deficiency occurs
  - Mobilization to support a specific process
    - Example: K from older foliage to the stomatal guard cells of younger foliage to improve stomatal function during drought.

Consequences of disrupted stress avoidance

- **Downward leaf area adjustment**
  - Less whole-crown carbon fixation
  - Reduced fraction of carbon allocated to the root system

- **C allocation shifts in favor root system**
  - Inadequate root and EM growth that worsens soil resource limitations

- **Internal recycling of mobile nutrients**
  - Inefficient function of some processes in new tissues
    - stomatal control by guard cells (K)
    - chlorophyll synthesis (Mg, N)

These conditions could lower biochemical defenses and increase attractiveness to insect pests.

Consequences of disrupted stress avoidance

Hypothesis

- Failure of one or more resource stress avoidance mechanisms plays a critical role in pine decline.

- The failed stress avoidance mechanism(s) and the cause of this failure vary by location.

Justification

Sources of information

- **Longleaf pine nutrition at Fort Benning, GA**
  - Mary Anne Sword Sayer, Lori Eckhardt, and Emily Carter
- **Longleaf and slash pine nutrition and growth at Eglin Air Force Base, FL**
  - Sandy Pizzolato, Center for Environmental Management of Military Lands, Natural Resources Section—Forestry Element, Eglin Air Force Base, FL
- **US Forest Service, Southern Research Station, Pineville, LA**
  - Longleaf pine rooting and soil physical properties
    - Mary Anne Sword Sayer and Dave Haywood
  - Longleaf pine physiological responses to crown scorch
    - Mary Anne Sword Sayer and Dave Haywood

Justification- foliar nutrition

- **Fort Benning, GA**
  - Foliar nutrition of 3 dominant and healthy longleaf pine trees in each of 16 plots
  - Plot age fell into 4 ages classes: <10, 10-20, 20-40, and >40 yr
  - 9 PD-unlikely plots and 7 PD-likely plots by the loblolly pine decline risk map

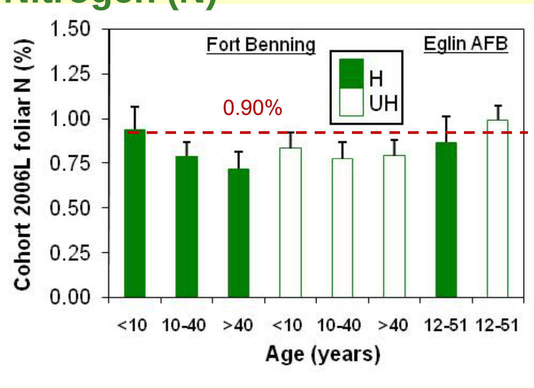
  Eckhardt and Menard (2008) For. Ecol. Manage. 255: 1735-1739

  - Sandy soils (Cowarts fine sandy loam, Ailey loamy sand, Troup fine sand)
  - July 2007, during the growing season
  - 2006L and 2007-1 and 2007-2 cohorts of foliage, small woody roots

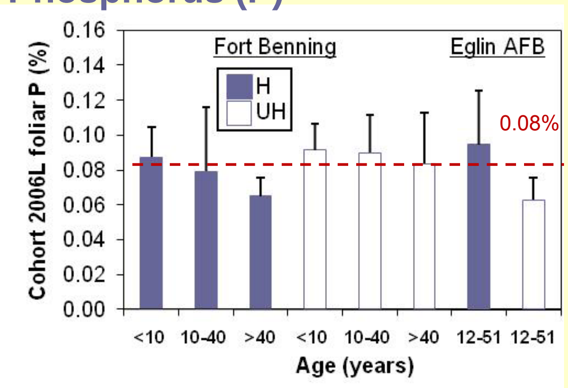
- **Eglin Air Force Base, FL**
  - Access to a data set containing foliar nutrition, soil fertility, and annual height growth for 24 stands (19 longleaf pine, 5 slash pine)
  - Stand age ranged between 12 and 51 years
  - Stands were labeled as normal or stunted based on height growth.
  - Sandy soils (Lakeland sand, Troup fine sand)
  - February 2006, dormant season
  - 2005L cohort of foliage

Justification- foliar nutrition

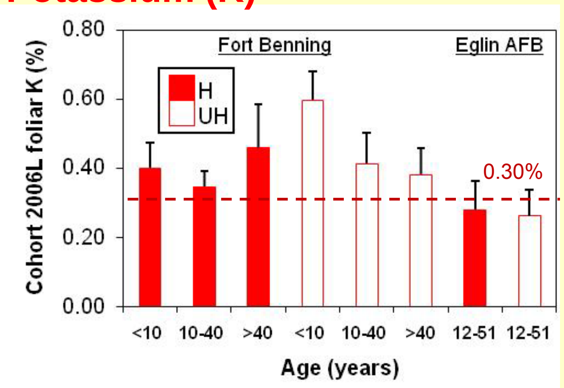
Nitrogen (N)



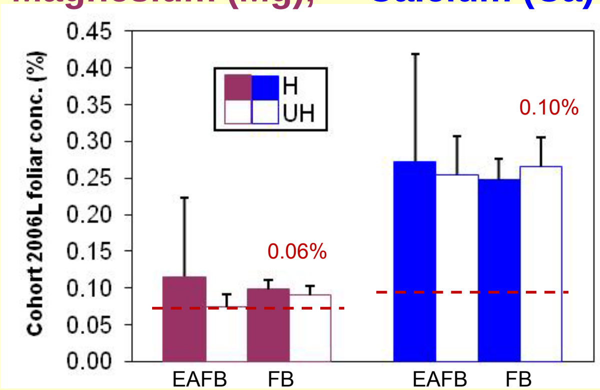
Phosphorus (P)



Potassium (K)



Magnesium (Mg), Calcium (Ca)



Results

- H/UH category did not affect nutrition at either location.
- Foliar nutrition was similar at both locations.
- Nutrition was sufficient at both locations based on recommendations for longleaf pine **(Dickens et al. (2003) Better Crops 87: 12-15).**
- Foliar Ca was high at both locations.

Justification- foliar nutrition

Results

- H/UH category did not affect nutrition at either location.
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- Foliar Ca was high at both locations.

Interpretation

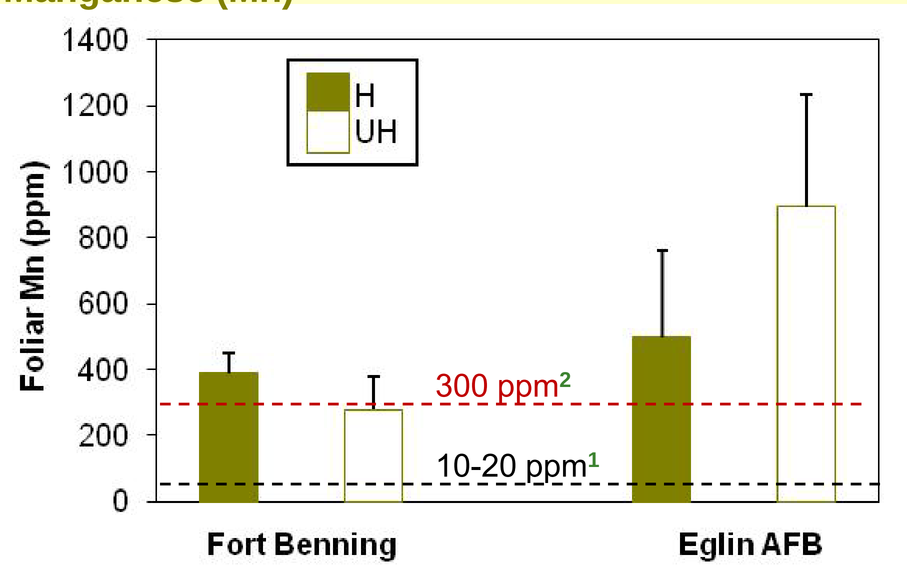
- Trees at both locations have adapted to nutrient-poor and droughty conditions.
  - Downward adjustment of leaf area
  - C allocation shift in favor root system
  - Internal recycling of mobile nutrients
- Elevated foliar Ca may occur naturally at these locations.
- Trees at both locations may need elevated foliar Ca to adapt to site conditions.

Justification- foliar nutrition

- Elevated foliar Ca may occur naturally at these locations.
  - The root system surface absorbing area is high.
  - Ca moves from the root to the foliage in the transpiration stream.
  - Foliar Ca is immobile and therefore, it accumulates.

- Trees at both locations may need elevated foliar Ca to adapt to site conditions.
  - Foliar Mn was very high at both locations.
  - Trees have Mn tolerance mechanisms but they require Ca.

Manganese (Mn)

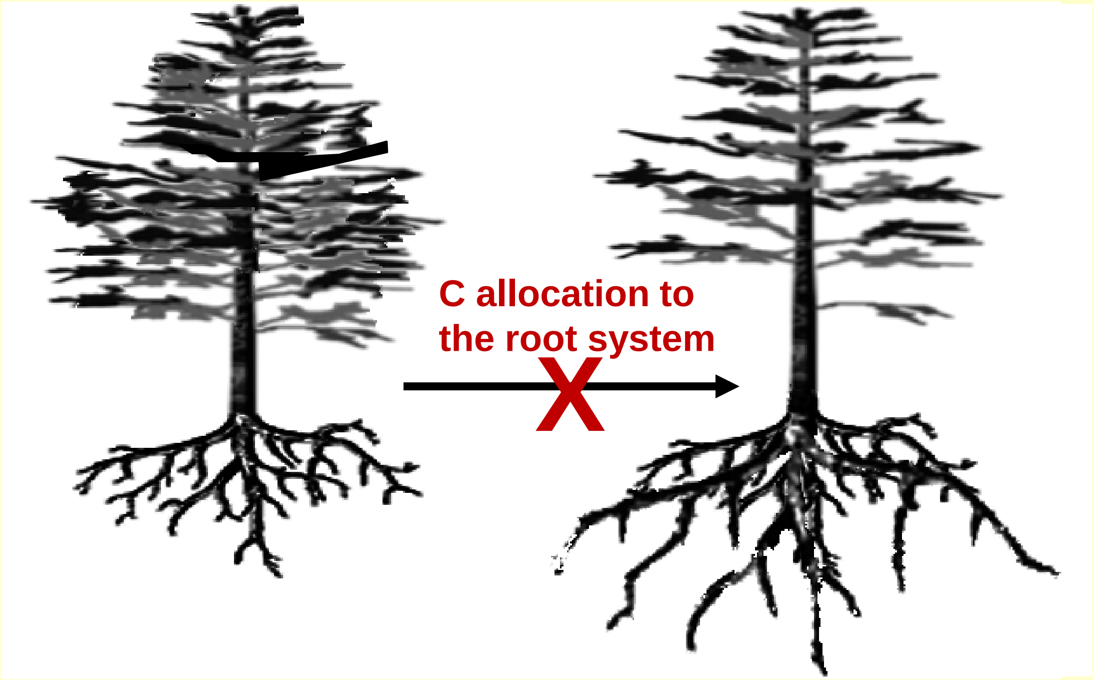


[1] **Marschner (1995) *Mineral Nutrition of Higher Plants*. 889 p.**

[2] **Van Lear and Smith (1990) Plant and Soil 36: 331-347.**

Justification- foliar nutrition

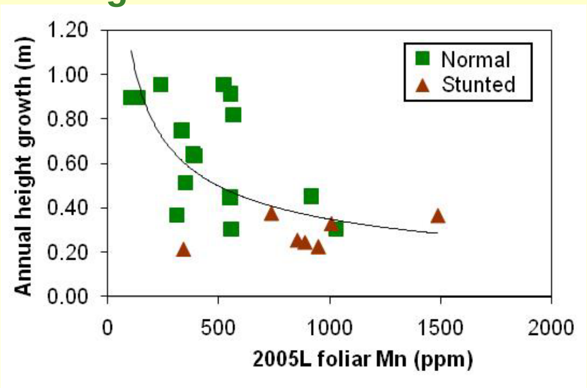
- Why worry about elevated foliar Mn?
  - Mn competes with Mg in biochemical reactions.
  - Mn interferes with Ca transport.
  - Mn accelerates the activity of polyphenoloxidase.



Justification- foliar nutrition

Eglin Air Force Base

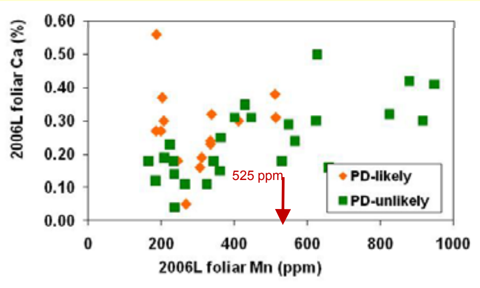
Relationship between height growth and foliar Mn

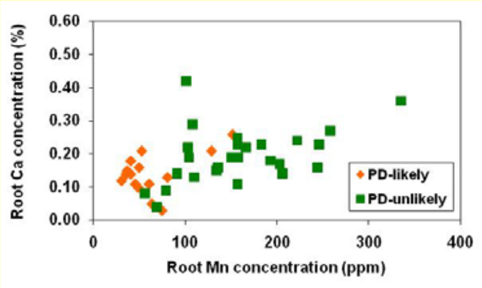


- Annual height growth declined as foliar Mn increased.
- Stunted stands had higher foliar Mn concentrations.

Fort Benning

Relationship between Ca and Mn in foliage and small roots





- Ca increased as Mn increased in foliage and small woody roots.
- The PD-likely trees had a smaller range of tissue Mn compared to the PD-unlikely trees.
- The trees on the PD-likely plots may have no longer appeared “dominant and healthy” when foliar Mn increased above 525 ppm.

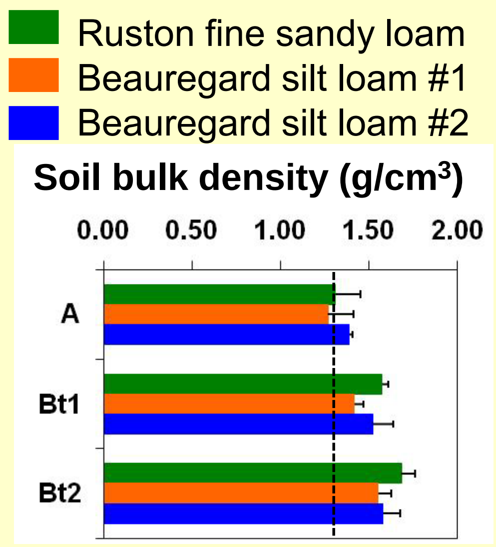
Justification- soil limitations to root growth

- Circumstances that may disrupt resource stress avoidance
  - Elevated foliar Mn and/or inadequate foliar Ca
  - **Soil limitations to root growth**
  - Leaf area re-establishment after crown scorch

Root-limiting characteristics of silt loam soils in LA

- High bulk density
- Low porosity
- Water deficit
- High soil strength

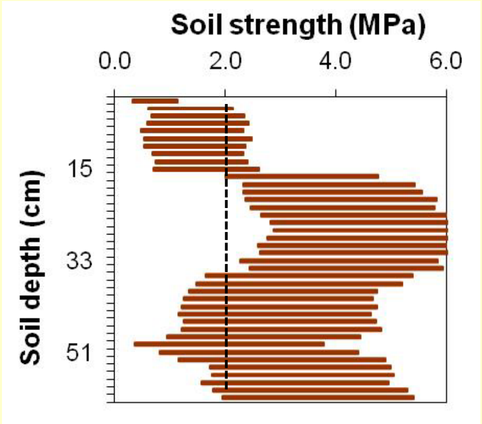
Kisatchie NF, LA



Root limitation at > 1.4 g/cm^3

Western LA

Guyton and Beauregard silt loams



Root limitation at > 2.0 MPa

Justification- soil limitations to root growth

- These soil limitations are overcome by cracks and old root channels.
- How do management activities that manipulate understory vegetation affect the size, amount, and distribution of these conduits?
- Do these conduits have a role in root system expansion and deep root growth during drought?

Old root channels-
dead roots become conduits for root elongation.

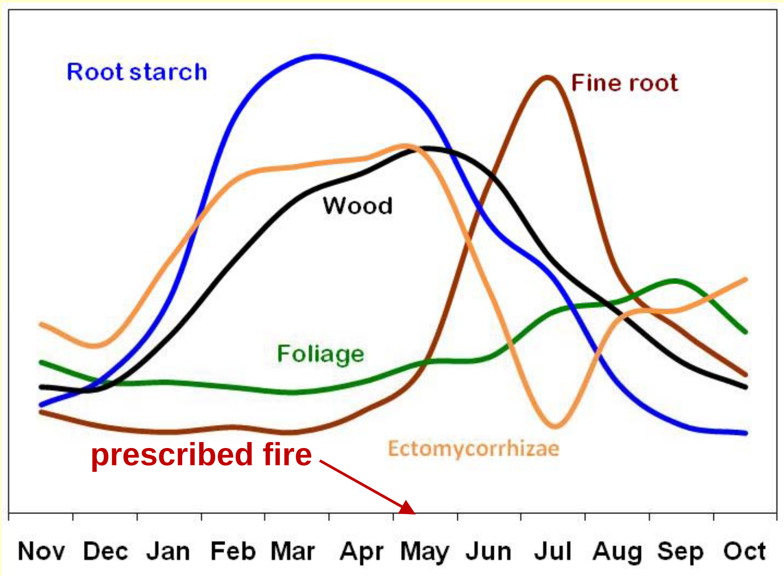
Justification- leaf area re-establishment

- Circumstances that may disrupt resource stress avoidance
  - Elevated foliar Mn and/or inadequate foliar Ca
  - Soil limitations to root growth
  - **Inability to re-establish leaf area after crown scorch**

- Leaf area re-establishment was completed by four months after crown scorch.
- Leaf area re-establishment was correlated with the availability and mobilization of root starch.
- There was no negative effect of crown scorch on stemwood growth, or fine root biomass.

Justification- leaf area re-establishment

Seasonality of growth and storage processes for pines in central LA



- Prescribed fire was applied in May.
  - Starch had accumulated in woody roots.
  - Small window of time before the fine root demand for energy would increase.
  - Larger window of time before the EM demand for energy would increase.

- Insuring leaf area re-establishment may be difficult.
  - Fascicle growth may already be slow.
  - Root starch may not be a plentiful energy source for fascicle growth (Sep.-Nov.).
  - In some years, water deficit could decrease the amount of current photosynthate available for new fascicle growth.

Pine decline from a physiological perspective

Summary

- Some symptoms of pine decline suggest that natural resource stress avoidance mechanisms have been disrupted.
- Disruptions may be due to an inadequate supply of energy to the root system, and/or poor root system function.
- Possible causes of inadequate root energy include:
  - Downward adjustments in leaf area that can no longer meet the root system energy requirement.
  - Elevated foliar Mn or a Mn:Ca imbalance that interferes with fascicle physiology.
  - Inability to re-establish leaf area after scorch.
- Possible causes of poor root system function include:
  - Inadequate root energy.
  - Soil limitations to root growth.

- How much leaf area is needed to sustain the expansive root systems of southern pine forests?
- Is there a point at which leaf area cannot meet the energy requirement of the expanding the root system?
- Can management activities preserve the leaf area-producing potential of a tree?
- Are the insect and disease problems of pine decline reduced by preserving leaf area?
- Is there an indicator of root system carbohydrate sufficiency that correlates to pine decline symptoms?

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