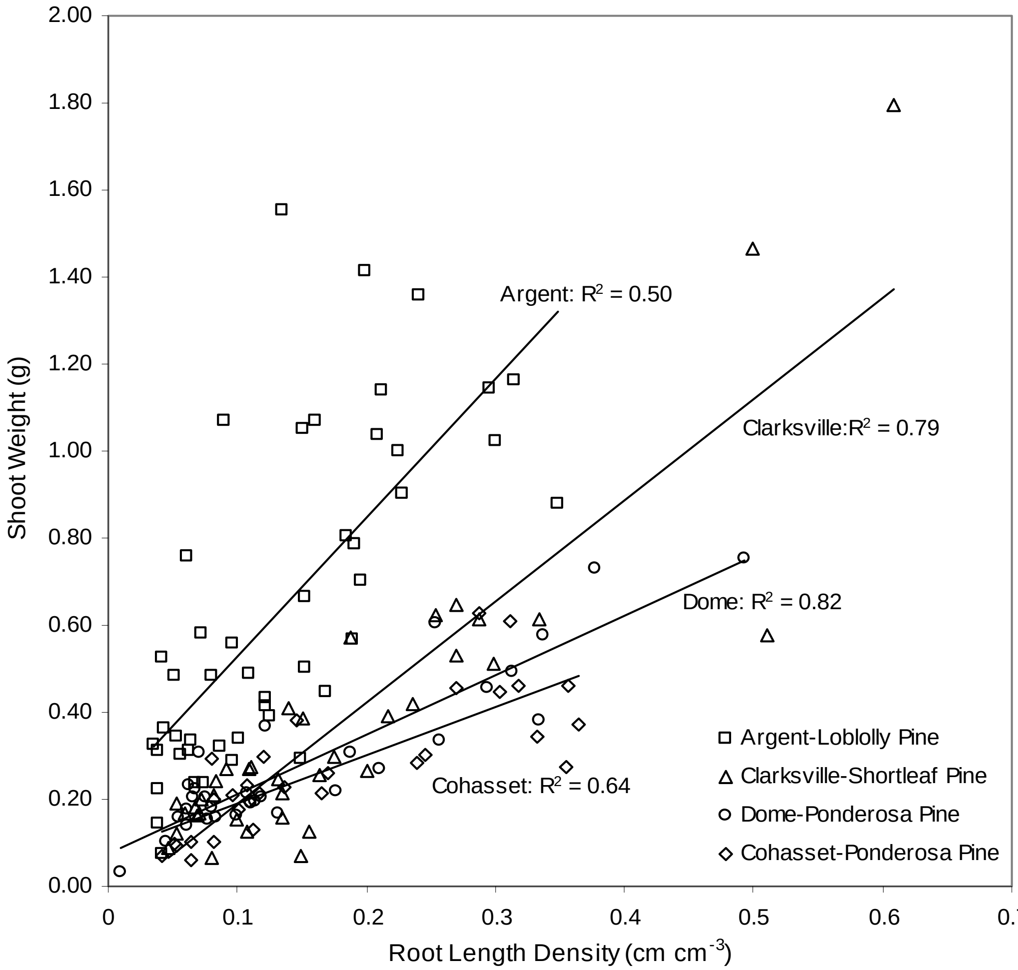

Figure V.5. Shoot weight as a function of root length density for loblolly and shortleaf pines growing on the Argent and Clarksville soils, respectively, and ponderosa pines growing on both the Dome and Cohasset soils.

1995). Shoot biomass of all pine species was significantly ($p = 0.01$) related to RLD (Fig. V.5). Fifty percent of loblolly pine shoot weight variation was explained by RLD and explained 64 and 82 % of ponderosa pine shoot weight growing on the Cohasset and Dome soils, respectively. The ratio of RLD to shoot mass was 1.10, 1.38, 2.32 and 3.15 for the ponderosa pines on Cohasset and Dome soils, short leaf pines and loblolly pines, respectively.

Loblolly pines had the greatest proportion of above ground biomass compared to the other species. Loblolly pine shoots were generally twice the height and weight compared to the other two pine species; however, average RLD (0.13 cm cm^{-3}) and mass were slightly less than the other species. Although the models for the California soils varied, there was no difference between the mean shoot weight, height and RLD on the Cohasset and Dome sites (0.16 and 0.17 cm cm^{-3}, respectively). Root length density ranged from 0.01 to 0.49 cm cm^{-3} for the Dome-ponderosa combination and 0.04 to 0.37 cm cm^{-3} for the Cohasset-ponderosa combination. Compaction increased available water holding capacity of these soils.

DISCUSSION

For all four forest soil-tree species combinations, root growth decreased with compaction, and the magnitude of the effect was moderated by θ_v. Good growth occurred across a broader range of θ_v when the ρ_b was low. As density increased, θ_v at either the dry or wet end of the spectrum interacted with ρ_b to create poorly aerated and high soil strength conditions, thereby diminishing the range in which growth occurred. The general regression model describing RLD as a linear function of ρ_b and quadratic function of θ_v was significant and explained most of the variation in RLD. However, it is clear that root growth response was soil and species specific.

Although we can not differentiate the exact causes of root growth limitations, it appears that soil strength and poor aeration, and combinations thereof are the primary causes of growth decreases at high ρ_b. Eavis (1972), attempted to separate the effects of soil aeration, soil strength and moisture stress on pea seedling growth and found that, generally, soil strength affected root growth in the Ψ_w range of -0.01 to -0.1 MPa, and water stress was the main factor at Ψ_w greater than -0.35 MPa. Voorhees et al. (1975) found that between Ψ_w of -0.01 to -0.1 MPa, pea seedling root elongation was more sensitive to aeration when soil strength was low and that RLD increased with increasing strength. Our data generally agree with these findings. At the dry end of the water spectrum, when Ψ_w was between -0.01 and -1.5 MPa, all soils except Argent, had soil strengths >2.0 MPa. At low ρ_b, inadequate water and poor aeration were the most likely cause of growth reductions. Furthermore, poorly aerated soils can cause physiological imbalances that lead to nutrient deficiencies. Although we fertilized our seedlings throughout the experiment, many seedlings grown at the highest water/highest densities were chlorotic, suggesting N deficiencies. Nitrogen and other minerals were found to be deficient in shoots of Pinus contorta growing in compacted remolded soil cores (Conlin and ven den Driessche, 1996).

The four soils used in this study were formed from various parent materials and had different organic matter contents. Three of the soils had sandy loam textures (Dome, Cohasset and Argent), yet the combination of various soil physical properties caused each to respond differently to compaction. For example, soil strength values were as high as 3.5 MPa for the Cohasset soil at a ρ_b of 1.21 Mg m^{-3} and θ_v of approximately 0.14 cm^3 cm^{-3}. In contrast, the Argent soil never exceeded 2.0 MPa even at ρ_b as high as 1.61 Mg m^{-3} at a similar θ_v. These soil differences created water and air dynamics variations which subsequently affected seedling growth response.

The LLWR is being used as an indicator to assess soil physical quality for a range of agricultural and forest soils (da Silva and Kay, 1996;Tormena, et al., 1999; Betz, et al., 1998; Zou, et al., 2000). It can also be used to determine the amount of time that seasonal soil water conditions are ideal for growth. da Silva and Kay (1996) found a strong correlation between corn shoot growth and the percentage of time θ_v fell outside the LLWR. Kelting (1999) determined the percentage of time (Pin) that predicted daily θ_v were within the LLWR for a southeastern loblolly plantation but did not relate that directly to plant growth responses. We found significant differences for several growth responses of tree seedlings growing within the LLWR and those growing outside the range, but the results varied with parameter measured and species. Based on our results, we would suggest that the LLWR may not be applicable to species such as loblolly pine without modification. Nonetheless, the LLWR has good potential for evaluating soil quality, and in conjunction with species-specific growth models, can help determine potential productivity declines due to forest management impacts.

Compaction and low and high θ_v explained the least RLD variation for the Clarksville-shortleaf pine, compared to the other soil-species combinations. Root and shoot growth variability was high, particularly for those seedlings grown at θ_v between field capacity and wilting point. Shoot weight and height decreased from the lowest to the highest ρ_b level by 25 and 33 %, respectively; however, the means were not significantly different due to the high variability. Shortleaf pine is a species that is found across a broad range of sites due to its tolerance for a wide range in soil conditions, however it does best on soils with silt loam and fine sandy loam textures (Lawson, 1992). Our soil, also a silt loam, had a wide LLWR allowing for less limited growth of this adaptable species across a wider range of water contents.

The Argent-loblolly combination, of the four soils we tested, appears to be the least affected by compaction and poor aeration. Increasing density decreased growth; however, the θ_v had much less influence on loblolly pine RLD. Overall growth was least limited due to a combination of Argent soil properties and species adaptations. The Argent soil, a fine sandy loam, had relatively low soil strengths, even at high ρ_b. We attribute this to the nature of the rounded, fine sand particles we observed and the clay mineralogy causing low shear strength. Low friction of these rounded, uniform particles, combined with the clay fraction's ability to hold water, allowed the roots to move more easily through the soil. Furthermore, loblolly pines are adapted to poorly aerated soils and can tolerate occasional flooding with root anatomy changes that allow O_2 to diffuse from the stem to the roots (Schultz, 1997). These changes include development of aerenchyma cells and intercellular spaces and formation of lenticels around the root collar (Mc Kevlin et al., 1987; Topa and McCleod, 1986).

Ponderosa pine growth decreased with increasing ρ_b on the Dome soil and was affected by inadequate aeration porosity when ρ_b were above 1.42 Mg m^{-3} and θ_v above 0.30 cm^3 cm^{-3}. The seedlings in these pots were much smaller and were chlorotic for most of the growth period. This soil and species are from a Mediterranean climate with little rainfall and rapidly draining soil, however, and inadequate soil aeration would seldom be a problem. The very dry conditions normally encountered, and subsequent increases in soil strength, could be detrimental to growth. Soil strengths for this soil were greater than 2.0 MPa when ρ_b was above 1.3 Mg m^{-3} and θ_v below 0.18 cm^3 cm^{-3}. Gomez et al. (2002) found enhanced ponderosa pine volume growth due to compaction on a similar sandy loam soil. On their site, ρ_b increased from 1.13 to 1.33 Mg m^{-3} in the top 30 cm and the resulting porosity change effectively increased available water by up to 10% on this typically droughty site. The non-compacted and compacted densities they found are comparable to the densities we created in our soil columns; however, we did not find the same growth increases with compaction. We attempted to maintain our soils at consistent θ_v and so the benefit of increased available water holding capacity was not evident. We believe the Dome soil we tested would have this same potential in a field situation. We found significant, albeit small, increases in available water for this soil. If compaction increased growth, we might expect a quadratic function describing growth as a function of ρ_b, rather than the linear response we achieved. However, we don't believe that a quadratic density response would be as strong as that for θ_v.

The Cohasset soil had a planar growth response to θ_v and ρ_b. Inadequate water and soil strength appeared to be the prime factors causing poor growth and high seedling mortality for this soil. Fifty percent of the trees that died were from the two lowest water levels. The Cohasset soil drained quickly. We were not able to maintain near-saturated conditions over time that could lead to poor aeration. Aeration porosity was less than 10% when ρ_b exceeded 1.13 Mg m^{-3}; however, none of the seedlings growing at 1.13 Mg m^{-3} were at θ_v that would cause aeration to be limiting. It was difficult to maintain high θ_v because infiltration and drainage was rapid at the lower ρ_b, and also fairly rapid at high ρ_b. Of the seedlings growing under the wettest conditions, we did not observe any hypoxic characteristics such as the chlorosis noted on the Dome-ponderosa pine seedlings. Aeration limitations due to low macroporosity from compaction may not occur for soils that are rarely saturated (Aust et al., 1998).

A discontinuity in RLD of ponderosa pines growing on Cohasset soil was evident above a ρ_b of 1.0 Mg m^{-3}. Root growth decreased dramatically at the higher ρ_b. This is interesting given that we would generally consider this to be a low or even ideal ρ_b. However, for this soil, this density was very compacted. Forest soils such as Cohasset, with high organic matter contents, high porosities and andic properties, may be very compact even at "low" densities (Howard et al., 1981; Gomez et al., 2002). The decrease in root growth also coincided with a sharp increase in soil strength. Soil strength was less than 0.5 MPa below a ρ_b of 1.0 Mg m^{-3}, and above 1.5 MPa for ρ_b above 1.13 Mg m^{-3}, except at the very highest θ_v. Although ρ_b of this soil were generally low, even the smallest increase in ρ_b had a large effect on root growth. In contrast, Gomez et al. (2002) found no stem volume differences for 5-year old ponderosa pines growing on compacted Cohasset soil. They reported field ρ_b and growth measures from the same LTSP site from which we collected our loose Cohasset soil. The compacted field density they measured, 0.95 Mg m^{-3}, falls below the threshold ρ_b at which we found large soil strength increases. Compared with a clay and sandy loam soil, the loam Cohasset soil had the greatest increases in soil strength due to compaction, a finding similar to our strength results on compacted soil columns. Based on the LLWR we determined for this soil and data collected periodically from May to September by Gomez et al. (2002), the Cohasset LTSP site was within the LLWR during this period. Although we show that growth reductions due to poor aeration or high strength are possible for this soil, if moderate θ_v contents are present during most of the growing season, these factors will have little affect on growth.

Our models are the first step in the process of determining the root growth opportunity of these soils. The model should be adjusted to include seasonal water content variations in conjunction with seasonal rooting patterns and the proportion of time that ideal water contents for growth are present. Furthermore spatial heterogeneity of field ρ_b and subsequent rooting patterns will affect the ability of the model to predict productivity losses due to compaction. We used soil from the top 30 cm of the profile, which is the depth at which most roots are found and where compaction is often the greatest (Kozlowski, 1999). However, rooting is not restricted to the top 30 cm of soil, and roots will preferentially utilize any channels created by old roots or soil biota, thus reducing effects of compaction. Nambiar and Sands (1992) found that roots proliferated in perforations simulating natural soil channels of subsoil compacted zones, mitigating the effects of compaction on tree growth. Determining the percent of time soil moisture is adequate and the percent of roots utilizing root channels versus bulk soil matrix would help improve applicability of our models for assessing management impacts on root growth opportunity.

CONCLUSIONS

In general, trees grown on soils with lower densities have better ability to grow well across a broader range of soil moisture conditions. Soil strength and aeration limited growth, but the effect was not consistent across all soil-species combinations. The generalized RLD model generally worked, but the modifications needed to achieve the best fit show that response is both soil and species specific. We created LLWR and RLD models based on sieved, hand compacted surface soils. The uniformity of soil conditions and controlled watering in this greenhouse experiment allowed us to interpret soil physical property effects on growth. However, the final value of these models depends on their ability to predict growth response under field conditions. Using and testing these models with field compaction soil property changes, tree growth responses and seasonal water conditions is the next step. Combining this information with other models such as the LLWR will enhance our ability to determine overall potential loss of productivity due to compaction. Furthermore, we need to set guidelines for productivity loss that match with species and soil to determine best management for a site.