From Forest Nursery Notes, Winter 2008

© 54. Calcium uptake, partitioning, and sinuous growth in Douglas-fir seedlings.
Littke, K. and Zabowski, D. Forest Science 53(6):692-700. 2007.

Calcium Uptake, Partitioning, and Sinuous Growth in Douglas-Fir Seedlings

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Abstract: Sinuosity is a growth deformation affecting Douglas-fir *[Pseudotsuga menziesii* (Mirb.) Franco] and other conifers. Ca, an essential nutrient in tree growth and cell development, may be deficient in these stands and could be causing sinuous growth. An experiment was conducted to test whether low Ca availability causes sinuous growth in Douglas-fir seedlings. Douglas-fir 1 + 1 seedlings were grown in a greenhouse with high to low Ca availability. After 6 months of growth, the seedlings were measured for sinuosity and separated into new-needles, new-stem, old-needles, old-stem, and roots. High Ca fertilized seedlings had greater new-needle biomass and growth than low Ca fertilized seedlings. High Ca availability also led to higher Ca concentration and content, including higher foliar membrane-associated Ca, Ca-pectate, and Ca-oxalate than low Ca seedlings. Low Ca availability had no significant effect on sinuosity. Although high Ca availability did not alleviate sinuous growth in Douglas-fir seedlings, it did lead to higher growth, foliar biomass, and membrane-associated Ca. FOR. SCI. 53(6):692-700.

Keywords: Douglas-fir, calcium, sinuosity, 1 + 1 seedlings, greenhouse

AS AN ESSENTIAL TREE NUTRIENT, Ca is involved in secondary cell wall synthesis and lignification, cell wall stabilization, cation—anion balance, chemical and physical defense, and stress tolerance. Calcium concentrations in *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) foliage should be higher than 0.25% (Reuter et al. 1997). Foliage with a Ca concentration of 0.2% or less is defined as deficient. Severe Ca deficiencies can prevent normal bud growth (Davis 1949) or cause yellowing in younger foliage and needle abscission.

When Ca is sequestered in the needle, this form of Ca cannot be recycled for cell processes, which could lead to Ca deficiencies. When Ca is sent to a conifer needle it can be stored as membrane-associated Ca, Ca-pectate, or Ca-oxalate (Fink 1991; Schaberg et al. 2001; Borer et al. 2004). Membrane-associated Ca is used for normal cell processes and as part of a messaging pathway when environmental stresses occur (DeHayes et al. 1997). Membrane-associated Ca can be extracted from ground tissue with water, but acetic acid may also extract some membrane-associated Ca (Borer et al. 2004). Ca-pectate is stored in the middle lamella in growing tissue (McLaughlin and Wimmer 1999) and is extractable by acetic acid (Fink 1991). Conifers excrete oxalic acid into the apoplast to form Ca-oxalate especially because Ca binds P in the cell. This third form of Ca can only be dissolved by a strong acid such as hydrochloric acid and is therefore unavailable to the plant (Fink 1991). If a tree uses all of its membrane-associated Ca, it could become Ca deficient even though a nutrient analysis would show sufficient total amounts of Ca in the needles due to storage of Ca as Ca-oxalate (Schaberg et al. 2001).

Calcium deficiencies could cause stem growth deformities when other nutrition levels are adequate. A growth deformity known as sinuosity is plaguing second and third growth Douglas-fir stands in Washington and Oregon, especially near the coast. Sinuosity is described as the presence of crookedness within the internode of a leader (Spicer et al. 2000).

Sinuosity has been linked to fast-growing trees (Grob and Carlson 1994). Causes of crooked leaders in conifers have been investigated, but no one explanation has been found. Bent tap roots in *Pinus taeda L.* (loblolly pine) and *Pinus elliottii* Engelm. (slash pine) can cause sinuous growth (Gatch et al. 1999). Radiata pine can develop "speed wobbles" (otherwise known as Toorour syndrome) when grown on old pasture sites; high N availability was examined as a cause, but could not be linked to sinuosity (Carlyle et al. 1989). Deficiencies in nutrients such as B, Cu, and Zn have been examined as causes of sinuous growth in Australia (Turvey et al. 1992) and British Columbia (Carter et al. 1986), although none of these nutrients have been identified as a source of sinuous growth.

Sinuous growth deformities cause reaction wood to form on the concave part of the bend (Timell 1986). Reaction wood contains more lignin and less cellulose than normal wood. As a result, the presence of reaction wood decreases the value of commercial lumber (Middleton et al. 1989) and pulp and paper (Blair et al. 1974). Additionally, severe reaction wood can cause warping in kiln-dried lumber (Rune and Warensjo 2002). Therefore, sinuosity is an economic problem for Douglas-fir growers.

In this study we tested the hypotheses that Ca deficiency

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Acknowledgments: The authors thank the Weyerhaeuser Company for their support of this project. Also, the authors thank Bill Carlson and Will Littke for their leadership and assistance during this experiment. We also thank the following Weyerhaeuser Company employees for their help with this study: John Browning, Edgar Fuchs, Carol Larson, Anna Leon, Pam Nielsen, Patty Ward, Elaine Welty, and Kristi Wiegand.

Manuscript received March 6, 2007, accepted July 17, 2007