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# Genetic and environmental control of Douglas-fir stem defects

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### ABSTRACT

We studied the genetic and environmental control of Douglas-fir (Pseudotsuga menziesii var. menziesii) stem defects across 22 breeding programs in western Oregon and Washington. Our goal was to understand the relationships between stem defects (forks and ramicorn branches) and growth. We tested the hypotheses that stem defects are associated with progeny test site productivity and distance to the coast, and then obtained robust estimates of genetic variances, heritabilities, and genetic correlations that can be used to design effective breeding programs. Stem defects were more frequent on high productivity sites and near the coast. Compared to the least productive site within each breeding program, the proportion of trees with stem defects was about twice as great on the most productive site. For example, the proportion of trees with ramicorn branches increased from 11% to 24%, and the proportion of trees with forks increased from 5% to 14%, between the shortest and tallest plantations. However, the relationships between stem defects and growth varied substantially within and among breeding programs ( $R^2 \leq 27\%$ ). Stem defects were also more frequent near the coast, but even harder to predict based on the locations of the plantations ( $R^2 \le 18\%$ ). Although stem defects are genetically variable, heritable, and have positive genetic correlations with growth, genetic variation and heritabilities for stem defects were low and highly variable. Nonetheless, stem defects can be reduced using direct backward selection, and are expected to increase only a small amount when genotypes are selected based on volume growth alone. The quantitative genetics of stem defects in Douglas-fir are generally consistent with what has been observed in other conifers. In general, focused breeding could be used to develop low-defect varieties, and these could be deployed to problematic sites. This approach might increase the value of reforestation programs overall, but it will be difficult to deploy low-defect varieties optimally because site productivity and distance to the coast are only weakly associated with stem defects. Although current multi-trait breeding approaches that consider growth and stem defects seem appropriate for most sites, controlled crosses between low-defect parents could be made in seed orchards, and the resulting seedlots could be deployed to sites that are known to be prone to defects (e.g., based on past data). Our results also suggest that (1) it might be possible to improve protocols and training for measuring stem defects, (2) breeders should monitor the among-site relationships between growth and stem defects in advanced generation breeding programs, and (3) low-defect genotypes should be identified and archived so they are available for future breeding.

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#### 1. Introduction

In Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*), stem defects are the second most important traits determining tree value (i.e., after volume growth). The two most important stem defects are forks and ramicorn branches. Forks consist of two or more branches that have assumed equal dominance after the terminal leader has been damaged or killed (Howe et al., 2006). Ramicorn branches are large, steep-angled branches (Helms, 1998) that occur

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when the terminal shoot temporarily loses apical dominance to a lateral branch (Schermann et al., 1997). Forks and ramicorn branches negatively impact tree value by decreasing the yield, grade, strength, and stability of lumber (Prescher and Ståhl, 1986; Schermann et al., 1997; Temel and Adams, 2000; Zobel, 1971). Additionally, transportation and processing are less efficient for trees with many stem defects (Shelbourne, 1969; Shelbourne, 1970; Temel and Adams, 2000). The Northwest Tree Improvement Cooperative (NWTIC) breeding program for coastal Douglas-fir has nearly 4 million field-tested trees, including more than 31,000 first-generation parents tested on 1016 progeny test sites (K. Jayawickrama, Personal communication.). Measurements made over the past 40 years by the NWTIC provide an excellent source of







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information for understanding the genetics of stem defects, and the environmental and genetic relationships between stem defects and growth.

Previous studies and observations suggested that stem defects are associated with site productivity. For example, the relationships between stem defects and growth were examined across 10 progeny test sites in the NWTIC Nehalem breeding program (Howe and Jayawickrama, 2002), a first-generation Douglas-fir program that was also included in this study. At age 11, correlations between growth and stem defects (i.e., the number of forks plus ramicorn branches) were surprisingly high. The number of stem defects was correlated with height (r = 0.95), dbh (r = 0.97) and stem volume (r = 0.99). Nonetheless, it was unclear whether the Nehalem program, was an unusual case, or broadly representative of the coastal Douglas-fir region. In contrast, in loblolly pine, Xiong et al. (2010) found no relationship between site quality and forking.

Other observations suggest that stem defects are more frequent near the coast. For example, high rates of stem defects have been observed in coastal plantations by many of the NWTIC members (S. Lipow, Personal communication). Although this could be directly related to the increased productivity of forests near the coast (Hudiburg et al., 2009; Latta et al., 2009), various factors may be involved. Coastal areas generally have more moderate temperatures, more summer precipitation, and more fertile soils than plantations further inland (Chmura et al., 2011; Coops et al., 2012; Landsberg and Sands, 2010; Wang et al., 2011). The less pronounced summer droughts and longer growing seasons near the coast could lead to more frequent second flushing and more stem defects (Howe et al., 2001).

Aspects of conifer shoot development and physiology could account for positive associations between productivity and stem defects. In particular, second flushing often contributes to stem growth (Adams and Bastien, 1994; Walters and Soos, 1961), but is also associated with an increased frequency of ramicorn branches in Douglas-fir and other conifers (Adams and Bastien, 1994: Hannerz et al., 1999: Howe et al., 2001: Schermann et al., 1997). Second flushing is the leader extension that occurs after the initial flush of leader growth has stopped and a temporary bud has been formed. Causes of second flushing include defoliation, weed control, extended photoperiods, and rain following a period of drought (Cline and Harrington, 2007). Sometimes, loss of apical dominance leads to second flushing in the lateral branches, but not in the leader, and this can result in ramicorn branches (Cline et al., 2009). The loss of apical dominance can be a result of decapitation or defoliation of the leader (Cline and Harrington, 2007). Furthermore, the second flush of growth is more susceptible to damage from late season droughts or early fall frosts (Anekonda et al., 2000; Howe et al., 2001), which can also lead to stem defects (Ningre and Colin, 2007). Finally, late season moisture and high nutrition (e.g., nitrogen fertilization) enhance second flushing (Cline et al., 2009; Hopmans et al., 1995; Stovall et al., 2011), Despite these relationships, other factors also cause stem defects, including animal browsing, insect damage, and late spring frosts (Bergquist et al., 2003; Kohmann, 2006; Ningre and Colin, 2007).

Our overall goal was to use information from operational breeding programs across Oregon and Washington to understand the environmental and genetic relationships between stem defects and growth. Specifically, we tested the hypotheses that (1) fastgrowing progeny test sites have more stem defects and (2) stem defects are more frequent near the coast. We then obtained robust estimates of genetic variances, heritabilities, and genetic correlations. Together, this information can be used to design breeding programs for Douglas-fir and other conifers that balance the genetic and phenotypic tradeoffs between stem defects and growth.

#### 2. Material and methods

#### 2.1. Plant materials

We used materials from 22 NWTIC open-pollinated first-generation breeding programs, each of which consists of a breeding zone, parent trees, and progeny tests. Parent trees were selected from natural stands within breeding zones, which are geographic areas for which individual breeding populations were developed. These parent trees were generally greater than 20 years old, with good crown development, growth, stem form and seed production. Because of the large number of parents tested in each program (mean = 267), they were grouped into sets of 30 to 47 parents each to facilitate field testing. The progeny from the earliest programs were grown in outdoor nurseries, but greenhouses were later used to grow containerized seedlings (Silen and Wheat, 1979). In some cases, two groups of progeny test sites were planted in different years because not all progeny for a single program could be grown at the same time. In other cases, two groups of families were planted in different years (i.e., at all progeny test sites). Progeny tests were planted using either the reps-in-sets or sets-in-reps experimental design (described in Magalska, 2011), and tree spacing ranged from 1.7 m  $\times$  1.7 m (5.5'  $\times$  5.5') to 3.1 m  $\times$  3.1 m  $(10' \times 10')$ . Although site preparation ranged from "no action" to scarification, burning, and herbicide treatment: the management regime was consistent within each progeny test site. The number of progeny test sites varied by program, ranging from 3 to 20 (mean = 8.5), and each family within a program was planted on an average of 6 sites. All progeny tests were planted in Oregon and Washington west of the Cascade crest. All sowings took place between 1969 and 1992, and all plantings took place between 1971 and 1993.

#### 2.2. Measured and derived variables

All measurements took place between 1983 and 2004 when the trees were 9 to 18 years old. Stem defects and growth traits were measured concurrently. Forking (FRK) and ramicorn branching (RAM) were scored as the number of whorls above breast height that had one or more forks or ramicorn branches. According to the NWTIC measurement protocol, forked trees are those with two or more stems "having equal stem diameters." In contrast, trees with ramicorn branches have one main stem and one or more "steeply-angled branches." For most analyses, we used the number of whorls with stem defects (i.e., number of whorls tree<sup>-1</sup> year<sup>-1</sup>) to enhance our ability to detect small differences among families and sites. However, we also conducted some analyses using the number of trees with stem defects (i.e., a binary variable) to judge the practical significance of our results. Diameter at breast height (DBH, millimeters) and height (HT, centimeters) were also measured. Tree volumes (VOL) were calculated according to Bruce and DeMars (1974), except for trees shorter than 183 cm (6'). For these trees, volumes were estimated as the volume of a cone. Basal diameter of the cone was derived from DBH and HT. Average annual stem defects and average annual growth were calculated by dividing the trait value by the measurement age. If transformations were necessary in later analyses, we replaced all zeros with positive values prior to transformation. These replacement values were equal to half the smallest positive value in the data set.

#### 2.3. Statistical analyses

For genetic analyses, all progeny test sites within a program are typically used in a single combined analysis. However, this was not a good approach for obtaining unbiased estimates of site means Download English Version:

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