



Quantifying safe seed transfer distance and impacts of tree breeding on adaptation



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ABSTRACT

Tree seed zones that are too large can compromise forest plantation health and productivity due to maladaptation arising from some populations being transferred long distances, whereas tree seed zones that are too small can result in unwarranted seed collections or excessive numbers of breeding zones. There has been little discussion, however, regarding the development and use of transfer functions for quantifying critical (i.e., safe) seed transfer distance (CSTD) or how artificial selection might affect CSTD. Using data from a large, multi-site provenance test for Douglas-fir and Interior spruce containing both genetically selected and wildstand seed sources, we illustrate an approach to quantify CSTD using Euclidean climate transfer distance modeled with a half-normal transfer function. A wide range of CSTDs was calculated and most transfer functions showed that selected seed sources were considerably taller than wildstand seed sources when transferred short or medium climate distances. Contrarily, selected seed sources were shorter than wildstand seed sources when transferred long climate distances. CSTDs were shorter for Douglas-fir than for spruce, and shorter when calculated using height rather than survival as the transfer function response variable.

These findings suggest that (1) unfavorable changes in adaptation due to artificial selection will be observable only when seed is transferred considerably beyond the CSTD; (2) differences in adaptation between selected and wildstand seed classes may not warrant separate seed transfer guidelines for these seed classes; (3) British Columbia's Douglas-fir and Interior spruce breeding programs are generating significant height gain; (4) methods presented here produce logical transfer functions that can be used to calculate reliable site-specific CSTDs; (5) use of conservative (short) CSTDs may be advisable when tests are young; and (6) provenance tests should be located in disparate climates.

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1. Introduction

Seed transfer guidelines are fundamental to forestry operations, particularly in climatically complex environments. Guidelines that are too permissive can result in compromised health and productivity of planted forests (Zobel and Talbert, 1984); guidelines that are too stringent can lead to excessive wildstand seed collection efforts or unwarranted numbers of breeding and seed production programs, adding significant cost to forestry activities (Crowe and Parker, 2005). Unaccountably, seed zones for the same species in adjacent jurisdictions are sometimes assigned substantially different sizes (Howe et al., 2006), despite species in those jurisdictions having similar post-Pleistocene evolutionary histories (e.g., Washington state and British Columbia) (St. Clair et al., 2005).

Despite these observations, methods for quantifying the distance that populations can be safely transferred, which we call *critical seed transfer distance*¹ – CSTD – (Ukrainetz et al., 2011), have seen little change or discussion since 1990 (Stern, 1964; Campbell, 1974; Eriksson et al., 1980; Rehfeldt, 1982; Campbell, 1986; Park and Fowler, 1988; Raymond and Lindgren, 1990).

New approaches to seed zone delineation (Parker, 1996; O'Neill and Aitken, 2004; Crowe and Parker, 2005; St. Clair et al., 2005; Hamann et al., 2011), and new online seedlot selection systems (e.g., <https://glfc.cfsnet.nfis.org/mapserver/seedwhere/seedwhere-about.php?lang=e> and <http://sst.forestry.oregonstate.edu/>) (both

¹ To avoid being confused with the maximum regulatory distance seed may be transferred (seed transfer limit) or with the range of distances populations are moved in provenance tests (maximum seed transfer distance), we use the term *critical seed transfer distance* (CSTD) to refer to the distance, beyond which seed transfer is expected to result in tree performance that is below an acceptable threshold (Ukrainetz et al., 2011). In this report the threshold is defined as 90% of the height or survival expected of a local seed source.

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accessed March 20, 2014)), require CSTD to be estimated for each species. Similarly, interest in species distribution modeling techniques has exploded recently (Elith et al., 2006; Iverson and McKenzie, 2013), as they are intended to identify the future distribution of species' climatic niche where planting of populations of local species may expand to help maintain the adaptedness of planted forests as climates change (i.e., assisted migration). However, knowing where a species may be suitable in the future does not obviate the need to know which populations of a species will perform well in areas of potential new habitat: assisted migration only heightens the need for accurate information regarding CSTDs.

A further rationale for examining appropriate seed transfer distance concerns the potential that artificial selection for growth may alter cold hardiness or allocation of plant defence resources (Hannerz et al., 1999a,b; Yanchuk et al., 2008), thereby compromising growth or health of seedlings produced from selective breeding programs when they are transferred (Ledig, 1992). Impacts of artificial selection on adaptation traits may be most evident when trees are stressed, as may occur when they are transferred from their native climatic or edaphic environment or when climate changes. Previous research has shown that artificial selection for growth rate has not appreciably altered the genetic diversity of reforestation seed sources. For example, levels of expected and observed heterozygosities were found to be similar in seed orchard parents and wild stand trees in *Pinus nigra* using random amplified polymorphic DNA (Çengel et al., 2012), and in *Picea glauca* using isozymes (Stoehr and El-Kassaby, 1997). Similar results were obtained when quantitative traits of orchard progeny and wildstand seedlings were compared in a common garden test (Stoehr et al., 2005). While artificial selection for growth rate did not impact genetic diversity in these studies, the effects of artificial selection for growth rate on phenology and resource allocation may be revealed only when trees are stressed. Consequently, transfer functions – which relate population growth or health to population transfer distance in a common garden environment – may detect impacts on population performance not exposed by typical genetic diversity measures. Quantifying responses of seed transfer on selected and wildstand seed sources is therefore needed to ensure that seedlot selection systems appropriately constrain seed transfer so that forest health and productivity are not compromised by seedlot selection or tree breeding.

This work builds on previous reports that examine impacts of tree breeding on forest genetic resources (Stoehr and El-Kassaby, 1997; Stoehr et al., 2005). Capitalizing upon a large set of provenance field trials (110,000 trees at 29 test sites) containing both wildstand and selected populations for two widespread, ecologically and economically important tree species established in exceptionally diverse environments, we develop transfer functions from which we calculate CSTD at each site. We quantify responses of seed transfer on different seed classes (selected vs. wildstand) and species (Douglas-fir vs. Interior spruce), and examine how transfer function response variable and test environment affect estimates of CSTD. By relating CSTD to site climate, we generate a site-specific CSTD which we illustrate in a focal point seed transfer system (Parker, 1996). Finally, using height gain estimated from transfer functions for selected and wildstand seed classes, we are able to compare predicted and realized gains in height.

2. Materials and methods

2.1. Seed sources

Trees studied in this project were located in provenance tests that contained operational wildstand (non-tested) populations as well as seed orchard seedlots and families from tested parents of Douglas-fir (*Pseudotsuga menziesii* var. *glauca* and var. *menziesii* (Mirb.) Franco) and Interior spruce (*Picea glauca* (Moench) Voss,

P. engelmannii Parry ex Engelm. and their hybrids) breeding programs (Table 1). Wildstand populations were assigned to the wildstand seed class and orchard seedlots to the selected seed class. Parents possessing breeding values² > 10% were assigned to the selected seed class, as this is the approximate lower limit of parental breeding values in British Columbia (BC) seed orchards; these parents would be representative of parents currently contained in BC seed orchards. Open-pollinated families from mother-trees having breeding values < 10% and control-pollinated families having mid-parent breeding values < 10% were assigned to the wildstand seed class. Operational wildstand seedlots were comprised of seed collected from at least 10 open-pollinated parents located generally within 1 km (but occasionally up to 8 km) and 100 m elevation from a central collection point.

Douglas-fir seed sources were from 3 BC government research projects: (1) the Submaritime provenance trial (EP 1200) containing 43 open-pollinated wildstand populations sampled along continentality and elevation gradients from BC's Coast Range (Krakowski and Stoehr, 2011), 31 BC coast × BC coast and BC coast × BC interior full-sib families, and 34 BC interior open-pollinated families; (2) the Trinity Valley provenance trial (EP 710) containing 64 open-pollinated wildstand populations from throughout the species' range (Jaquish, 1990); and (3) the Nass-Skeena provenance trial (EP 976.02.20) containing 18 open-pollinated interior families, and 7 full-sib coast families, 52 open-pollinated interior families and 15 coast populations. ('Coast' refers to locations on the west side of the Coast Range divide.)

Spruce seed sources were from the Interior spruce climate change/genecology project (EP 670.71.12), and contained 91 open-pollinated Interior spruce wildstand seedlots from throughout western North America, and 35 BC, Alberta and Ontario seed orchard seedlots or seedlots created by bulking seed from 6 elite open-pollinated or full-sib families. (Henceforth, we use the term 'population' when referring collectively to the genetic entries examined in this study (seedlots, populations and families).

2.2. Sites, design and measurements

The 12 Douglas-fir provenance test sites and 17 Interior spruce provenance test sites used in this analysis sample a large portion of the northern part of the geographic and climatic range of these species in western North America (Fig. 1, Table 1). The 8 sub-maritime Douglas-fir field test sites were planted in 1996 in single-tree plots at 3 × 3 m spacing in each of 7 replications, except for the CLRS site, a farm-field setting where each population was planted four times per block at 0.75 × 0.75 m spacing in each of 7 blocks. Two systematic 50% thinnings in 2000 and 2009 reduced the total number of trees to 1056. The Trinity Valley test site was established in 1975 with each population planted in a 5-tree square plot at 3 × 3 m spacing in each of 3 replications. The 3 Nass-Skeena test sites were planted in 1988 in a split-plot design containing 4 randomized complete blocks. Main plots consisted of the 10 BC Douglas-fir seed zones with 10 family-subplots per zone. Each subplot was planted as a 10-tree row-plot at 2 × 2.5 m spacing. The 17 Interior spruce test sites were planted in 2005 in an alpha design (see Section 4.4) containing 16 incomplete blocks of 8 four-tree row plots at 1 × 2 m spacing in each of 8 replicates. (All test sites were planted with 1-year-old seedlings raised in standard conifer seedling nursery conditions.

Height and survival were assessed on the Douglas-fir trees at age-15 and on the Interior spruce trees at age-6. Measurement ages refer to years in the field.

² Breeding values in BC represent the % gain in wood volume expected at rotation, relative to the expected volume of a local, wildstand seedlot (Xie and Yanchuk, 2003).

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