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Plants on the move: Assisted migration of forest trees in the face of climate change

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ABSTRACT

Climate change is impacting distributions of both fauna and flora, including many crops. In order to ensure the health and vigor of the species we depend upon for food and fiber, assisted migration strategies may need to be implemented. This is especially true for long-lived forest trees. Multinomial logit regression was used to develop a Categorical Universal Response Function (CURF) to delineate deployment zones for loblolly pine (*Pinus taeda* L.) using 15-year measurements from the Western Gulf Forest Tree Improvement Program (WGFTIP) Geographic Seed Source Study (GSSS). The CURF uses performance categories for the response variable, and the model assigns the probabilities with which the performance for a given seed source will fall into these various categories. First and second powers of minimum temperature of the coldest month, summer precipitation, and variation measures of these two metrics at both the seed source site of origin and the test location were used as independent variables. Planted tree volume, accounting for both survival and growth, was used as the response variable. Model performance was good, with the AUC score ranging from 0.785 to 0.808, depending on (1) whether or not the variable interactions were included and (2) the variable selection criterion used (AIC or BIC). Resulting models were then applied to historic weather patterns to illustrate inferred deployment zones for three seed sources. The projected performance generally agreed with the current consensus on loblolly pine seed movement guidelines. The models developed here can be readily implemented in a Decision Support System as they (1) suggest sets of adapted loblolly pine families from which foresters can choose based on local knowledge, (2) can be easily expanded to include other variables, and (3) can be applied to outputs from projected climate scenarios to extrapolate into the future.

1. Introduction

Historical changes in climate have been linked to profound shifts in the distribution and abundance of species (Crowley and North, 1988; Mayhew et al., 2008), and projected future changes in climate (Boer et al., 2000; Giorgi and Lionello, 2008; Hsu and Chen, 2002; Karl and Trenberth, 2003) may cause population and species extinctions (Carpenter et al., 2008; Parmesan, 2006; Pounds et al., 1999; Raxworthy et al., 2008), changes in phenology and trophic interactions (Edwards and Richardson, 2004), range shifts (Parmesan and Yohe, 2003), migration events (Jackson and Sax, 2010; Thuiller et al., 2005), altered biotic stresses (Aitken et al., 2008), and maladaptations of species to local conditions (Savolainen et al., 2007; St Clair and Howe, 2007). Negative effects on commercial crops also have been projected (Deryng et al., 2014; Lobell et al., 2011), with concomitant socio-economic impacts (Lal et al., 2011). Effective management of commercial forests, in particular, will require long-term strategies to help mitigate the anticipated impacts of climate change (Millar et al., 2007), with a key component of such strategies taking the form of assisted migration, or the selection and deployment of seeds from trees that are best adapted to projected local conditions (Ledig and Kitzmiller, 1992; Millar et al., 2007; Ying and Yanchuk, 2006).

One of the most important forest tree species in the USA is loblolly pine (*Pinus taeda* L.), which is a major component of southeastern forest ecosystems (Baker and Balmer, 1983; Baker and Langdon, 1990). It is also the most commercially important forest tree species in the southern United States (Baker and Langdon, 1990) and has been a subject of intense cultivation. Its natural

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habitat stretches from warm-temperate and subtropical climates into the more continental conditions in the interior across the southeastern states, demonstrating the adaptation of the species to various ranges of temperature and rainfall. Recurring periods of drought that affected the area over the last millennium (Seager et al., 2009) have likely contributed to shaping these adaptations. However, cyclical variations in climate conditions have disturbed the species throughout its history, presumably since speciation about 7–13 million years ago (MYA; Willyard et al., 2007), with shifts during the Pleistocene being particularly important (Millar, 1993). As could be expected from both the paleoclimatic records and from the broad spectrum of habitat conditions, variation among local populations in response to differing environments has been observed, along with some degree of genotype-environment (GxE) interactions (McKeand et al., 1997; Roth et al., 2007), likely supporting adaptation to local selective pressures (Eckert et al., 2010; Schmidtling, 2001). Indeed, various seed sources perform differently on different planting sites (Schmidtling, 2001). Despite the correlation of gradation in climate conditions with geographic distance, large variation among families within provenances is also evident (Jayawickrama et al., 1998), further complicating the picture (see Table 1 for definition of terms).

Knowledge of past climate at the point of origin for a seed source, coupled with contemporary weather conditions experienced by common-garden progeny tests, can be used to model responses of seed from different sources under various climate scenarios. This concept was used to develop the Universal Response Function (URF) for lodgepole pine (*Pinus contorta* Dougl. ex Loud.) which links genetic effects shaped by past climate (evolutionary adaptations) with environmental impacts of present climate (Wang et al., 2010). The method was successful in the case of Pacific Northwest populations of lodgepole pine (model $R^2 = 0.81$ for height). When applied to loblolly pine from the Western Gulf Forest Tree Improvement Program – Geographic Seed Source Study (GSSS), as described below, this technique was instrumental in confirming the importance of minimum temperatures for optimizing seed movement guidelines on the north to south (N–S) transect which supported the previous work by Schmidtling (1994), and identifying precipitation and variation in precipitation as major limiting factors on the west to east (W–E) transect. Direct adaptation of this concept, however, had rather limited explanatory power (Byram et al., 2013), as a substantial amount of variation remained unexplained. It was especially evident in the case of planted tree volume, a variable that accounted for both growth and survival. Other likely sources of the unexplained variation were local growing conditions not accounted for by the model (e.g. soil type, site preparation, drainage, and/or competition), and genetic variation among families within populations. Additional differences between the Western Gulf and the Pacific Northwest studies lie in the land form, past and present climate conditions, management practices, and the recent migratory and evolutionary history of the two pine species. Alternative approaches based on mixed-effects modeling were implemented for Douglas-fir (*Pseudotsuga menziesii*), a conifer also native to the Pacific Northwest (Isaac-Renton et al., 2014; Leites et al., 2012).

Although least-squares linear regression and multiple regression are among the most commonly used analytical techniques in forest science to estimate tree growth parameters, such as height and DBH (Wang et al., 2010; Yao et al., 2012), there are also other regression methods applicable to forest management problems. An alternative to the URF with the potential to offset a portion of the local variation unaccounted for by the URF model is the multinomial logit regression, a generalized linear model approach. In this study we identified the influential climate variables and forecasted the probable timber yield categories under variable climate conditions across the loblolly pine range for seed sources from the Western Gulf region of the USA using multinomial logit regression. It should be noted that these forecasts are supported by progeny test data within the Western Gulf region of the USA, but are extrapolations to the rest of the southeast, illustrating the potential to predict performance in novel climates. It should also be emphasized that the models were developed for seed sources representing only the Western Gulf region and there were no comparisons to other widely planted loblolly pine seed sources. In a broader sense, the case of loblolly pine deployment is a representative scenario of plant assisted migration, and therefore the method presented here can be readily generalized to other species and questions.

2. Materials and methods

2.1. Source of data

The Western Gulf Forest Tree Improvement Program – Geographic Seed Source Study (GSSS) was initiated between 1974 and 1978 in two series, each with plantings established in two different years. The 15-year measurements used in this study were based on data from 66 progeny test sites, 40 in Series I and 26 in Series II, scattered across the states of Arkansas (AR), Louisiana (LA), Mississippi (MS), Oklahoma (OK) and Texas (TX) (approximate locations shown in Fig. 1a). Families included in Series I represented provenances from Arkansas, Louisiana, Oklahoma and Texas generally following an N–S transect. Families in Series II represented a W–E transect, with families originating from Texas and Mississippi (approximate locations shown in Fig. 1b). Generally, five open-pollinated families were randomly selected as seed-parents to represent each provenance in the WGFTIP first-generation breeding population. For the purposes of this study, the approximate latitude and longitude of origin for each of the seed-parents were used in lieu of provenance designations. Progeny tests were generally established as six randomized complete blocks with linear plots of four trees in each plot (24 trees per family per location). The estimates of individual tree volumes were averaged by family plot for all planted trees and therefore accounted for survival (volume = 0 for dead trees).

Table 1
Definitions and disambiguation of terms.

Term	Definition
Family	A group of individual trees that descend directly from a common ancestor. Individuals from an open-pollinated family share the maternal parent, whereas their pollen donors may vary
Population	A collection of genetically similar individuals that can freely interbreed and occupy the same area
Progeny test	Assessment of the genetic value of a given tree through evaluation of its offspring. For direct comparison, selected trees may be tested under the same conditions (common garden tests)
Provenance	A geographic area in the species native range inhabited by genetically similar individuals
Seed source	The origin of the material from which the seed was collected. This may be from a provenance, a population, or a family, depending on context