



## Growth and physiological responses to varied environments among populations of *Pinus ponderosa*

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### Abstract

We investigated population responses in physiology, morphology, and growth of mature *Pinus ponderosa* trees to an environmental gradient across Nebraska, USA. Ten populations from western Nebraska and eastern Wyoming were grown in three 26-year-old provenance tests from the warmest and wettest site in the east (Plattsmouth) to the intermediate site in the middle (Halsey) to the coldest and driest site in the west (Alliance). We measured leaf morphology and water potential in 1995 and 1996, carbon isotope discrimination from foliage in 1993 to 1996 and from tree-ring cellulose for 1991, 1993, 1995, and 1996, and height and diameter at breast height (dbh) in 1994. We found that populations responded significantly to the environmental gradient in all traits. Trees grew significantly larger at the eastern site than at the other locations. The trend in height and dbh growth was Plattsmouth > Halsey > Alliance. Variation among the locations in needle length and carbon isotope discrimination in both foliage and cellulose followed the same pattern as growth. However, variation in xylem water potential differed from the trend in tree growth. Trees in Halsey had higher leaf water potential than trees at other sites. Populations differed significantly in morphological characteristics (i.e. specific leaf area and leaf length,  $F > 3.3$ ,  $P < 0.01$ ) and growth (i.e. height and dbh,  $F > 3.8$ ,  $P < 0.001$ ), whereas differences in physiological traits (i.e. leaf water potential, carbon isotope composition, and foliar nitrogen,  $F < 1.9$ ,  $P > 0.05$ ) were lacking among populations. We conclude that physiological plasticity is the primary mechanism that allows *P. ponderosa* to grow in various environments. Population differentiations in growth and morphology are the results of a long-term response of these populations to natural selection in their original habitat.

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## 1. Introduction

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) grows across a large and diverse geographic range of North America, from southern Canada to Mexico and from the Plains States of Nebraska and Oklahoma to the Pacific Coast (Little, 1971). Populations vary significantly in responses to these contrasting environments (Conkle and Critchfield, 1988; Read, 1980; Rehfeldt, 1990, 1993). For example, using cluster analysis on 13 traits including 3-year-seedling growth and phenological and seed characteristics, Read (1980) delineated 80 populations of ponderosa pine (var. *scopulorum* Engelm.) into seven geographic zones, all which differ in ecological conditions. Rehfeldt (1990) found that at least 40% of population variation in growth potential, leaf morphology, leaf phenology, and cold hardiness in 4-year-old seedlings could be explained by the elevation and geographic origin of the seed. Monson and Grant (1989) found that two families of ponderosa pine crosses differed significantly in photosynthetic gas exchange. Seedlings from a cross between two coastal parents showed higher rates of photosynthesis and transpiration but lower water-use efficiency than seedlings from coastal and interior parents cross, suggesting interior populations are better adapted to water limited conditions. Population differentiation requires selection, migration, mutation, and genetic drift, either alone or in combination (Lerner, 1954; Levins, 1968). Therefore, these evolutionary processes provide the primary mechanisms for adjusting to environmental heterogeneity.

Ponderosa pine may also adjust physiologically to environmental variability through physiological plasticity (Bradshaw, 1965). Variation in physiology and needle morphology of 23-year-old mature ponderosa pine trees grown in eastern Nebraska was subtle among diverse populations from eastside of Rocky Mountains (Cregg, 1993; Cregg et al., 2000). In a glasshouse seedling study, 27 open-pollinated families representing 9 geographically origins differed in survival and growth under an imposed drought, but not needle gas exchange (Cregg, 1993). Furthermore, net photosynthesis, stomatal conductance, and stable carbon isotope discrimination were not different among seedlings from 25 populations across the ponderosa pine distribution range (Zhang and Marshall, 1995). All of these studies suggest variation in photosynthetic gas exchange

among populations is subtle or non-significant in this species. Lack of population differentiation in physiological characteristics in a common garden indicates that this species has an extremely high plasticity of photosynthetic gas exchange in response to different environments (Zhang and Marshall, 1995). Therefore, physiological plasticity can be regarded as secondary mechanisms allowing plants for adjusting to heterogeneity.

Moreover, because environmental heterogeneity occurs in space and time, ponderosa pine, as a long-lived sessile and broadly dispersed organism, not only requires population variation in response of spatial variability, but also needs plasticity to deal with temporal variability at a local and spatial variability when they are moved in an exotic habitat. In this study, we measured stable carbon isotope discrimination and other physiological traits in ponderosa pine trees from 10 populations grown on three 26-year-old plantations along an environmental gradient. We address the following questions. (1) Do populations differ in carbon isotope discrimination, leaf water potential, and other leaf characteristics? (2) Does planting site affect these variables? (3) Is there an effect of interaction between population and planting site? (4) How do these trees respond differently to their environments?

Because of the relationship between carbon isotope discrimination and plant water use efficiency (O'Leary, 1981; Farquhar et al., 1982), we focused our investigation on understanding population variation in isotope discrimination and needle morphology. Carbon isotope composition is closely related to water use efficiency in plants including ponderosa pine (Zhang and Marshall, 1995; Zhang et al., 1996, 1997; Zhang and Cregg, 1996; Cregg et al., 2000; Olivas-Garcia et al., 2000). In the western Great Plains, water availability during the growing season is often low because evaporation exceeds rainfall (Dunne and Leopold, 1978). For trees to grow in the region, they must adapt to water stress. Therefore, water acts as a selective force to shape acclimation of individual and populations to this specific environment. *P. ponderosa* is one of few conifer species not only occurring naturally in the mid-western plains but also growing successfully as windbreaks and shelterbelts in the region (Little, 1971; Read, 1958). Population variation in numerous

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