



## 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

traits (i.e. growth potential, phenology, and morphology) has been extensively examined for the purposes of choosing suitable seed sources for afforestation or protection (Read, 1980, 1983; Van Haverbeke, 1986).

## 2. Materials and methods

### 2.1. Study sites

The study was conducted on trees in three-range wide ponderosa pine provenance trials in central North America near Alliance, Halsey, and Plattsmouth, Nebraska, USA (Fig. 1). The three plantations are located across a gradient of moisture and temperature conditions (Tables 1 and 2). Because these sites are within 100 km of latitude, photoperiod patterns are relative similar among sites.

#### 2.1.1. Site I: Alliance, Nebraska

The westernmost plantation is located 2 km west of Alliance in western Nebraska. The soil is a Keith loam that is characterized by deep, well-drained soil on loess-covered upland (USDA, 1981). Soil organic matter is about 0.82%.

#### 2.1.2. Site II: Halsey, Nebraska

The central plantation is located in the Nebraska Sandhills on the Nebraska National Forest, about 20 km from Halsey, Nebraska. The soil is a typical Ustipsamment (Valentine fine sand, hilly) (Sherfey et al., 1965) with a composition of 93% sand, 3% silt, and 4% clay. Soil organic matter is about 0.28%.

#### 2.1.3. Site III: Plattsmouth, Nebraska

The easternmost of the three study plantations is located on the University of Nebraska's Horning State Farm, less than 1 km from Plattsmouth, Nebraska. The soil is a silty clay loam soil derived from loess. Soil organic matter is about 0.96%.

### 2.2. Plant materials

The plantations were established as completely randomized block designs in 1968 with trees planted at a spacing of 2.5 m × 3 m. Seventy-nine populations were planted in four-tree linear plot at Alliance and Halsey and 50 populations were planted in 10-tree linear plots at Plattsmouth. Seeds were collected from 7 to 15 trees in each of 70 natural populations throughout the var. *scopulorum* range, east of the

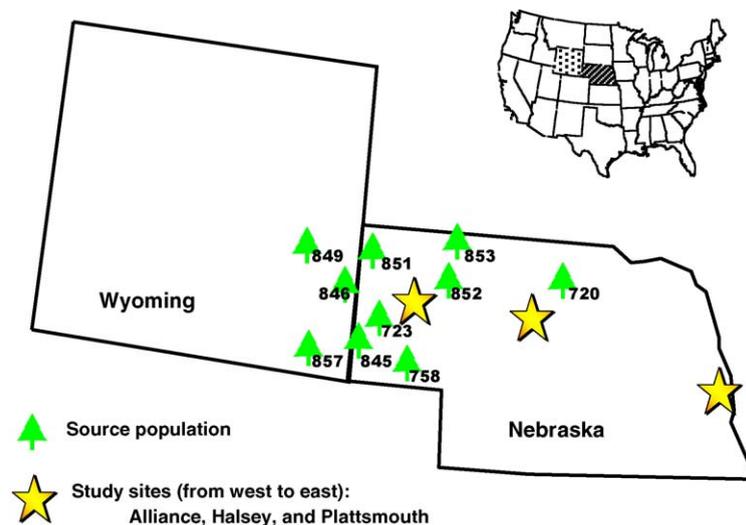


Fig. 1. A schematic map of 10 natural populations of *Pinus ponderosa* from Nebraska and Wyoming and three study sites in Nebraska, USA.

Table 1

Phytogeographic and climatic characteristics<sup>a</sup> of collected trees from 10 populations of ponderosa pine and study sites

Original number <sup>b</sup> or study site	Location	Geographic information			Climatic characteristics				Vegetation type (+associate tree species) <sup>c</sup>
		Latitude (N)	Longitude (W)	Elevation (m)	Extreme maximum temperature (°C)	Extreme minimum temperature (°C)	Annual mean temperature (°C)	Annual precipitation (mm)	
720	Ainsworth, Nebr.	42°42'	99°48'	701	44.4	−36.1	9.4	555	I (Juniperus)
723	Scottsbluff, Nebr.	41°48'	103°48'	1402	43.3	−44.4	9.2	371	II (Juniperus)
758	Potter, Nebr.	41°12'	103°12'	1372	43.3	−37.8	8.6	416	III
845	Harrisburg, Nebr.	41°30'	104°00'	1554	43.3	−44.4	8.6	435	II (Juniperus)
846	Ft. Laramie, Wyo.	42°12'	104°30'	1280	41.7	−44.4	8.7	304	II
849	Shawnee, Wyo.	42°48'	105°00'	1585	41.1	−41.7	9.3	300	II
851	Ft. Robinson, Nebr.	42°42'	103°30'	1280	41.7	−38.3	8.7	379	IV
852	Rushville, Nebr.	42°30'	102°30'	1158	42.2	−40.6	8.3	450	IV (Juniperus)
853	Whiteclay, Nebr.	42°54'	102°30'	1097	42.8	−41.7	8.3	450	IV (Juniperus)
857	Buford, Wyo.	41°12'	105°18'	2347	37.8	−38.9	7.6	338	II (Pinus flexilis)
Site 1	Alliance, Nebr.	42°06'	102°52'	1210	43.3	−41.1	9.0	405	IV (conifer spp.)
Site 2	Halsey, Nebr.	41°54'	100°19'	825	46.1	−37.2	8.3	591	I (mainly conifers)
Site 3	Plattsmouth, Nebr.	41°00'	95°54'	335	46.1	−33.9	10.3	1030	V (many tree spp.)

Seeds were collected from at least 10 individual trees within each population located at western Nebraska (Nebr.) and southeastern Wyoming (Wyo.), USA. Three study sites are located from the west to east of Nebr., USA.

<sup>a</sup> Information for 10 populations is from Read (1980). Information for three test sites is from Weather.com (August 2, 2004).

<sup>b</sup> Original numbers are the seedlot numbers from USDA Forest Service, Rocky Mountain Research Station.

<sup>c</sup> Information is from USDA (1981). I, mid and tall grass plant community; II, short and mid grass prairie; III, short grass prairie; IV, mixture of short, mid, and tall grasses; V, mid and tall grassland with a higher percentage of switchgrass plus some hardwood trees.

Table 2

Summary of annual, January, and July mean temperatures and total precipitation at three sites across Nebraska, USA from 1991 and 1996

Site	Year	Annual mean temperature (°C)	January mean temperature (°C)	July mean temperature (°C)	Annual precipitation (mm)
Alliance	1991	8.9	−6.4	22.5	324
	1992	8.6	−0.1	19.1	330
	1993	6.9	−6.2	19.7	492
	1994	9.0	−4.2	21.6	347
	1995	8.2	−5.5	22.2	510
	1996	7.6	−7.4	22.3	508
Halsey	1991	9.5	−7.4	23.5	446
	1992	8.7	−0.1	18.7	654
	1993	7.2	−9.4	20.8	687
	1994	8.7	−6.3	21.4	461
	1995	8.3	−4.1	22.7	705
	1996	6.8	−9.3	21.7	527
Plattsmouth	1991	10.9	−8.8	24.3	687
	1992	10.7	0.3	21.7	837
	1993	9.1	−7.0	24.0	1207
	1994	10.5	−7.7	22.9	663
	1995	10.3	−5.1	25.9	641
	1996	9.1	−7.4	23.0	702

Continental Divide, and 9 populations for var. *ponderosa* range, west of the Continental Divide. Sampled trees were at least 100 feet apart. Seeds from individual trees within a population were bulked into population seedlots, sown, grown, and studied from 1965 through 1968 at the USDA Forest Service Bessey Nursery near Halsey (Read, 1980). Results from 10 and 15 years old trees were also reported (Read, 1983; Van Haverbeke, 1986).

In the present study, five trees from each of 10 populations of var. *scopulorum* appearing at all three sites were randomly selected from three adjacent blocks. These populations from a narrow range of latitude in western Nebraska and eastern Wyoming were chosen to minimize the potential confounding of latitudinal and photoperiod effects with physiological traits (Fig. 1). More detailed geographic information, seed source climatic data, and some records of collected trees from these populations are presented in Table 1.

### 2.3. Experimental methods

Our experimental procedure consisted of measurements of leaf water potential, carbon isotope composition for leaves and cellulose from wood cores, and specific leaf area for trees on three sites. In addition, we measured tree height and diameter at breast height for these trees after they were selected in 1994. Population means in height at age 26 years were significantly correlated with population means at age 15 years ( $r = 0.91$ ,  $P < 0.0001$ ).

#### 2.3.1. Leaf water potential

We measured predawn ( $\Psi_{pd}$ ) and midday ( $\Psi_{md}$ ) leaf water potential with a pressure chamber (PMS Instrument Company, Corvallis, Oregon) on a single fascicle pulled from the detached branch on four times in 1995 (June, July, August, and September) and on three times in 1996 (June, July, and August).

#### 2.3.2. Carbon isotopic composition

In late fall of 1994, foliage samples were collected from each age class from 1993 to 1994 on each tagged tree. We sampled foliage from exposed branches from the top one-third of the live crown on the south side of each tree to make sure that leaf was well coupled to the atmosphere (Jarvis and McNaughton, 1986). The samples were oven-dried at 70 °C for at least two days

and finely ground to pass a 40-mesh screen. In addition, we also collected four wood cores from each tree at four directions (N, S, E, W) using a four mm increment bore (Mora, Sweden). The cores were air dried and smoothed with sandpaper to enhance ring boundary definition. For each core, we separated annual rings from a dry year (1991) and wet year (1993). The four samples from each annual ring were pooled into one sample representing that tree for a particular year. Because cellulose is not transferred between annual growth rings of trees (Tans et al., 1978), we extracted cellulose (overall mean = 70%, S.E. = 5%) for each pooled sample (Leavitt and Danzer, 1993). Stable carbon isotope ratios were calculated as  $\delta = R_{\text{sample}}/R_{\text{standard}} - 1$ , where  $R$  is the molar ratio of heavy to light isotope ( $^{13}\text{C}/^{12}\text{C}$ ), the standard for  $\text{CO}_2$  in both atmosphere and plant organic sample is  $\text{CO}_2$  from Pee Dee Belemnite limestone (Craig, 1957). Both foliage and cellulose samples were combusted in an automated elemental analyzer before passing into a mass spectrometer. Then, carbon isotope discrimination ( $\Delta$ ) was calculated as  $(\delta_{\text{air}} - \delta_{\text{sample}})/(1 + \delta_{\text{sample}})$  assuming that  $\delta^{13}\text{C}$  value in the air was  $-8\text{‰}$  (Farquhar et al., 1989). In the late fall of 1995 and 1996, the current-years' foliage and annual ring were sampled and processed as described previously.

#### 2.3.3. Nutrient analysis

Nitrogen concentration (%) was determined on foliage collected in July of 1995 following Kjeldahl method. Other macro- and some micronutrients were analyzed by the energy dispersive X-ray fluorescence technique (Knudsen et al., 1981).

#### 2.3.4. Leaf morphology

We measured specific leaf area for all trees at the three sites in 1995. Leaf area was measured with the LI-COR area meter. Specific Leaf Area (SLA) was calculated on projected leaf area divided by leaf dry weight. Needle length in 1996 was measured for those needles collected from the detached branch for leaf water potential measurement.

### 2.4. Statistical analysis

Repeated measures analysis of variance (ANOVA) under SAS GLM procedure (SAS Institute) was used

Table 3

Degrees of freedom (d.f.), mean squares (MS), and *F*-values (*F*) for repeated measures of analysis of variance for predawn ( $\Psi_{pd}$ ) and midday ( $\Psi_{md}$ ) water potential among 10 populations of ponderosa pine grown at three sites in 1995 and in 1996

Source of variation <sup>a</sup>	1995					1996						
	d.f.	$\Psi_{md}$ (MPa)		d.f.	$\Psi_{pd}$ (MPa)		d.f.	$\Psi_{md}$ (MPa)		d.f.	$\Psi_{pd}$ (MPa)	
		MS	<i>F</i>		MS	<i>F</i>		MS	<i>F</i>		MS	<i>F</i>
Between subjects												
Site (S)	2	7.5372	10.37*	2	2.8481	36.01***	2	9.4536	9.49*	2	1.8999	46.65***
Blk (site)	6	0.7269	3.11**	6	0.0791	9.00***	5	0.9959	21.16***	5	0.0407	4.78**
Population (P)	9	0.0343	0.43	9	0.0144	0.70	9	0.0919	1.85	9	0.0236	1.05
S × P	18	0.0714	0.90	18	0.0281	1.37	18	0.0503	1.01	18	0.0239	1.07
P × Blk (S)	54	0.0797	0.34	53	0.0205	2.33***	45	0.0496	1.05	45	0.0225	2.64***
Error (I)	185	0.2338		59	0.0088		60	0.0471		60	0.0085	
Within subjects												
Month (M)	3	6.0988	211.4***	3	0.0505	98.84***	2	1.3628	116.43***	2	0.0505	12.75***
M × S	6	4.5352	81.67***	6	0.3271	16.19***	4	0.7840	9.81**	4	0.3271	15.02***
M × Blk (S)	18	0.0555	1.92*	18	0.0218	8.69***	10	0.0800	6.83***	10	0.0218	5.50***
M × P	27	0.0285	1.10	27	0.0070	2.15**	18	0.0172	0.98	18	0.0070	0.94
M × S × P	54	0.0244	0.87	54	0.0065	2.17***	36	0.0192	1.09	36	0.0065	0.88
M × P × Blk (S)	162	0.0281	0.97	159	0.0075	0.87	90	0.0176	1.50*	90	0.0075	1.89***
Residual	555	0.0288		177	0.0040		120	0.0117		120	0.0040	

Note: Significant levels for repeated measures are given as corrected probability.

<sup>a</sup> Blk, block effect; Blk (S), block within site effect.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

for predawn and midday xylem water potential, and carbon isotope discrimination in foliage and in cellulose (Potvin et al., 1990). We used the following model:

$$\begin{aligned}
 Y_{ijklm} = & \mu + S_i + B(S)_{ij} + P_k + PS_{ik} + PB(S)_{ijk} \\
 & + e_{ijkl} + M_m + MS_{im} + MB(S)_{ijm} + MP_{km} \\
 & + MPS_{ikm} + MPB(S)_{ijkm} + \varepsilon_{ijklm}
 \end{aligned}$$

where  $Y_{ijklm}$  is an observation of dependent variable in  $l$ th tree at  $i$ th site (S),  $j$ th block (B) within  $i$ th site,  $k$ th population (P), and  $m$ th month (M).  $\mu$  is the overall mean. S, B(S), P, PS, and PB(S), that represent source of variation between subjects, are effects of site, block within site, population, and interaction among them, respectively. Time effect (M) and other interactions (MS, MB(S), MP, MPS, and MPB(S)) are variation within subjects (Potvin et al., 1990). We used block within site as an error term for testing site effect, PB(S) for P and PS effects, MB(S) for MS effect, MPB(S) for MP and MPS effects,  $e$  for B(S) and PB(S), and  $\varepsilon$  for M, MB(S) and MPB(S). Height,

diameter at breast height (1.4 m), specific leaf area, needle length, and nutrient concentration were analyzed by analysis of variance with the first part of model mentioned earlier. The relationships between variables were determined by linear regression and correlation coefficients (Pearson's  $r$ ).

### 3. Results

#### 3.1. Leaf water potential

Predawn ( $\Psi_{pd}$ ) and midday ( $\Psi_{md}$ ) water potential differed significantly among sites, while population and population by environmental effects in  $\Psi_{pd}$  and  $\Psi_{md}$  were not significant in either year except for population by block within site interactions in  $\Psi_{pd}$  (Table 3; Fig. 2). Interactions between population × month and population × month × site were only significant in  $\Psi_{pd}$  at year 1995. Both  $\Psi_{pd}$  and  $\Psi_{md}$  varied among months, sites, and their interactions. Predawn  $\Psi_{pd}$  was highest and most stable at Halsey and most variable at Alliance in both years (Fig. 2).

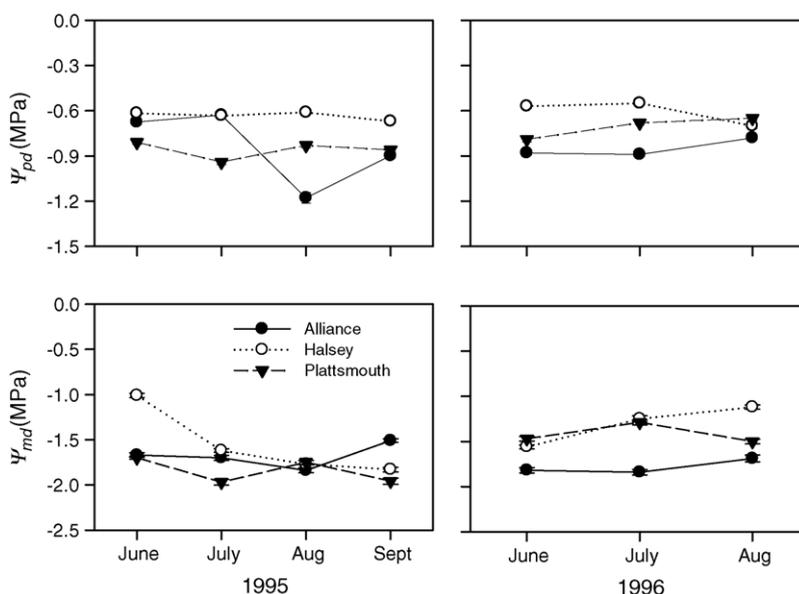


Fig. 2. Mean predawn and midday xylem water potential ( $\Psi$ ) for *Pinus ponderosa* grown at three study sites in Nebraska, USA in 1995 and 1996. Vertical bars represent mean of all measurement at that date. Where error bar is absent, it is smaller than symbol.

### 3.2. Carbon isotope discrimination

Populations did not vary ( $P > 0.279$ ) in either foliage or cellulose  $\Delta$ , while year, site, and year by site interactions were highly significant ( $P < 0.001$ ) (Table 4; Fig. 3). The interaction between population and site was only significant in cellulose  $\Delta$ . This interaction was mainly influenced by a population from Potter (#758), which changed  $\Delta$  rank at different sites.

Carbon isotope discrimination was about 2‰ higher in foliage than in cellulose at all sites. For those years when we measured both foliage and cellulose, correlations between  $\Delta_{\text{leaf}}$  and  $\Delta_{\text{cellulose}}$  were 0.71, 0.77, and 0.91 ( $P < 0.0001$ ,  $n = 150$ ) in 1993, 1995, and 1996, respectively (Fig. 4). Removing two outliers from the  $\Delta_{\text{cellulose}}$  data from Plattsmouth in 1993, improved the correlation to 0.83. Year-to-year correlations were also significant for foliage  $\Delta$  ( $0.75 \leq r \leq 0.94$ ,  $P < 0.0001$ ) and cellulose  $\Delta$  ( $0.62 \leq r \leq 0.86$ ,  $P < 0.0001$ ).

### 3.3. Population variation in growth, morphology, and foliar nitrogen concentration

In contrast to physiological traits, the populations varied significantly in height, diameter, specific leaf

Table 4

Degrees of freedom (d.f.), mean squares (MS), and  $F$ -values ( $F$ ) for repeated measures of analysis of variance for carbon isotope discrimination in foliage ( $\Delta_{\text{leaf}}$ ) and in cellulose ( $\Delta_{\text{cellulose}}$ ) among 10 populations of ponderosa pine grown at three sites

Source of variation	d.f.	$\Delta_{\text{leaf}}$ (‰)		$\Delta_{\text{cellulose}}$ (‰)	
		MS	$F$	MS	$F$
<b>Between subjects</b>					
Site (S)	2	381.32	159.28***	342.11	253.75***
Blk (site)	6	2.39	2.79*	1.35	1.01
Population (P)	9	1.84	1.26	1.04	0.54
P × S	18	1.66	1.14	4.38	2.28*
P × Blk (S)	54	1.46	1.70*	1.92	1.44
Error (I)	60	0.86		1.33	
<b>Within subjects</b>					
Year (Y)	3	36.16	236.41***	23.77	45.28***
Y × S	6	17.09	143.23***	7.86	8.04***
Y × Blk (S)	18	0.12	0.78	0.98	1.86*
Y × P	27	0.16	0.77	0.84	1.32
Y × S × P	54	0.20	0.98	1.11	1.76**
Y × P × Blk (S)	162	0.20	1.34*	0.63	1.20
Residual	180	0.15		0.52	

Note: Significant levels for repeated measures are given as corrected probability.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

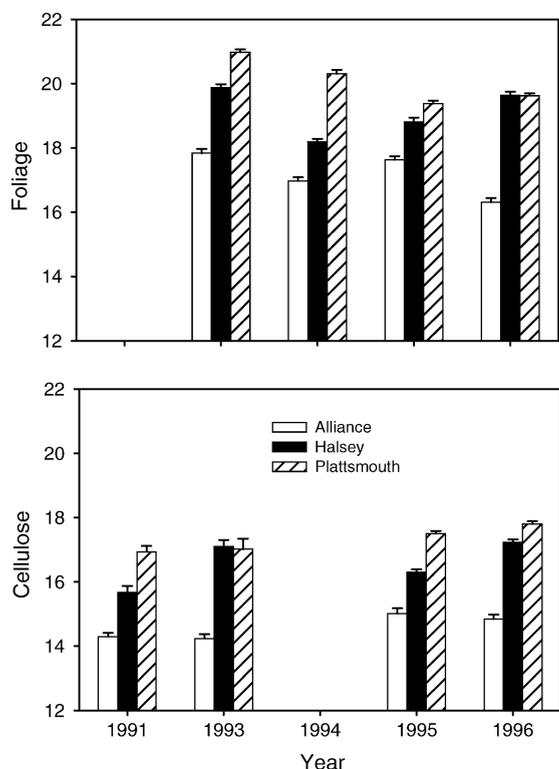


Fig. 3. Means (+1S.E.) of carbon isotope discrimination ( $\Delta$ ) on 1993–1996 foliage and cellulose from wood cores of 1991, 1993, and 1995–1996 in 10 populations of *Pinus ponderosa* mature trees grown at Alliance, Halsey, and Plattsmouth, Nebraska, USA.

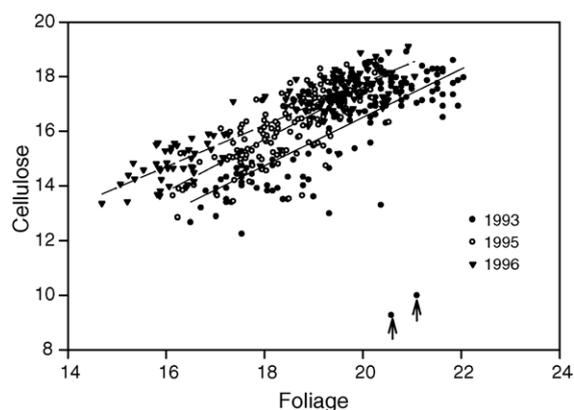


Fig. 4. Relationships in carbon isotope discrimination ( $\Delta$ ) between foliage and cellulose in *Pinus ponderosa* mature trees grown at three study sites in Nebraska, USA in 1993, 1995, and 1996.

area, and needle length (Table 5). Site effects were significant for all but SLA and the only significant interaction in SLA was between site and population. In general, mean height, diameter, and needle length of the plantations increased from west to east (Fig. 5). However, this trend was not reflected in specific leaf area. Neither population nor site by population variation in foliar nitrogen concentration was significant. The site effect on foliar N was only significant at  $P = 0.088$ . Trees at Alliance and Plattsmouth had slightly higher nitrogen concentration than trees at Halsey (mean  $\pm$  1S.E.:  $1.50 \pm 0.02\%$  for both Alliance and Plattsmouth,  $1.41 \pm 0.02\%$  for Halsey).

Table 5

Degrees of freedom (d.f.), mean squares (MS), and  $F$ -values ( $F$ ) for height (HT) and diameter at breast height (DBH, at 1.4 m) in 1994, specific leaf area (SLA) in 1995, needle length (LL) in 1996, and foliar nitrogen concentration ( $N$ ) in 1995 among 10 populations of ponderosa pine grown at three sites across Nebraska

Source of variation <sup>a</sup>	d.f.	HT (m)		DBH (cm)		SLA (cm <sup>2</sup> /g)		LL (cm)		N (%)	
		MS	$F$	MS	$F$	MS	$F$	MS	$F$	MS	$F$
Site (S)	2	427.29	1420.00***	713.27	74.00***	23.22	1.95	338.92	214.00***	0.1182	3.37
Blk (site)	6	0.30	0.47	9.60	0.70	11.89	1.17	1.59	0.54	0.0317	1.46
Population (P)	9	7.31	6.12***	56.96	3.85***	20.41	3.35**	18.32	5.81**	0.0215	0.99
S $\times$ P	18	0.88	0.74	12.28	0.83	13.63	2.24*	4.28	1.36	0.0240	1.10
P $\times$ Blk (S)	54	1.19	1.92	14.80	0.39	6.10	0.60	3.15	1.08	0.0218	1.00
Error	60	0.62		13.76		10.12		2.92		0.0217	

<sup>a</sup> Blk, block effect and Blk (S), block within site effect.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.001$ .

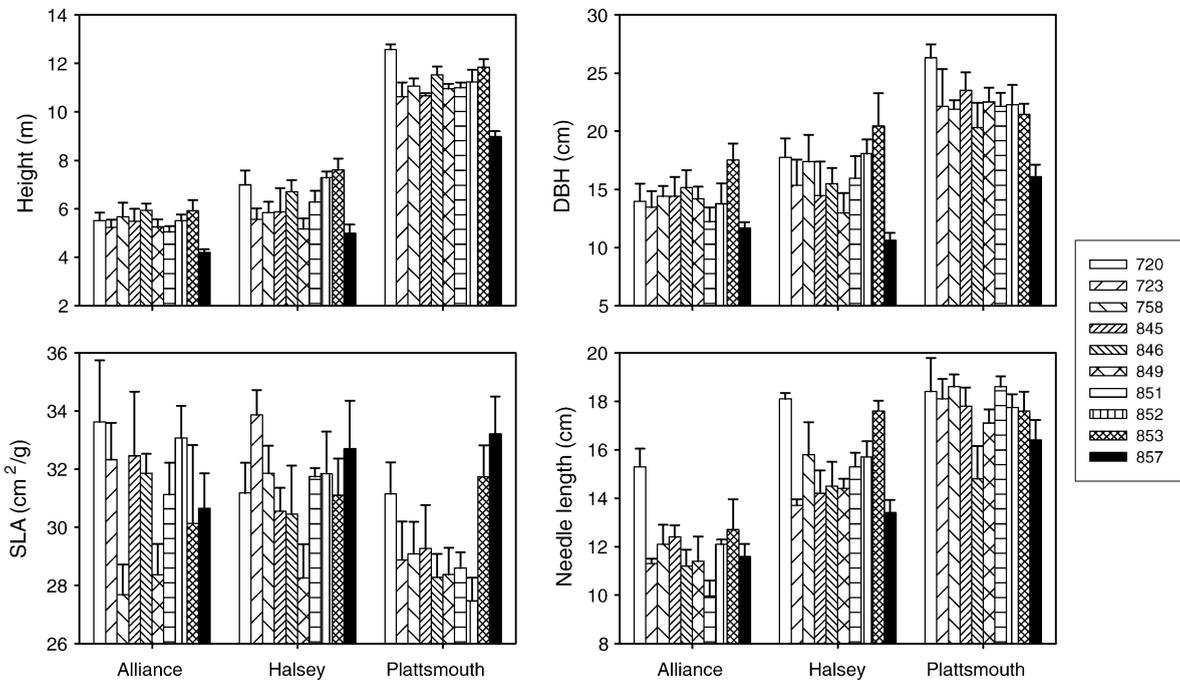


Fig. 5. Means (+S.E.) of height and diameter at 1.4 m height (DBH) in 1994, specific leaf area (SLA) in 1995, and needle length in 1996 in 10 populations of *Pinus ponderosa* mature trees grown at three sites in Nebraska, USA.

#### 4. Discussion

The results indicate that all variables responded to varied environmental conditions at different common gardens (Tables 3–5). From Alliance in the west to Plattsmouth in the east, both temperature and precipitation increase (Tables 1 and 2). Growth of the trees responded to this environmental gradient as expected: the trees grew tallest at Plattsmouth and least at Alliance (Fig. 5). The height and DBH growth were strongly correlated with the previous measurements at age 10 and 15 years (Read, 1983; Van Haverbeke, 1986). Because Halsey and Alliance are geographically closer and weather is similar, the amount of tree growth at Halsey was more similar to Alliance than to Plattsmouth.

The site difference in growth was obviously caused by environmental variation. Yet, the environment affects growth by influencing plants' morphological and physiological processes (Kramer, 1983). Morphologically, needle length followed the patterns of height and diameter growth across this environmental gradient; the trees at the wettest site (Plattsmouth)

have longer needles (Fig. 5) and more total leaf area (pers. obs.) than the trees at other, more xeric, sites. Specific leaf area, however, did not differ among sites, indicating that carbon investment per a given leaf area was not different across sites. Consequently, the trees have the potential to assimilate more carbon in the eastern sites than the trees in the west. Physiologically, the trend of isotope discrimination followed similar pattern as the growth: Plattsmouth > Halsey > Alliance. However, tree  $\Delta$  in Halsey is more close to  $\Delta$  in Plattsmouth than to  $\Delta$  in Alliance. This might reflect to the possible high stomatal conductance with less water stress demonstrated by higher predawn and midday water potential for trees at Halsey (Fig. 2). Yet, photosynthetic capacity would be lower than trees at Alliance due to the lower foliar nitrogen concentration in trees at Halsey (Field and Mooney, 1986). As a result, water use efficiency would be lower or carbon isotope discrimination would be higher.

When plants accumulate biomass through carbon fixation from the atmosphere, water must be transpired through stomata on the leaf. In a drier environment, therefore, conserving water is an essential strategy for

plants to survive, grow, and reproduce (Fischer and Turner, 1978). One mechanism by which plants can reduce water use is by smaller leaves to reduce the transpiring leaf surface (Givnish, 1987). To do so, plants reduce total carbon fixation. Another potential adaptation is to increase water-use efficiency so that plants maximize the carbon fixation given available water (Cohen, 1970; Cowan, 1986). The results of the present study support former hypothesis; trees in the western sites have shorter needles compared to trees in the more mesic eastern site.

Population variation in ponderosa pine has been studied in common-gardens for selecting suitable seed sources for reforestation for many years. Significant variation was often found for growth, morphological, and phenological traits among populations (Conkle and Critchfield, 1988; Read, 1980, 1983; Rehfeldt, 1993 and references in his series of studies; Van Haverbeke, 1986). This variation has been interpreted as adaptive variation in response to environmental selectivity (Van Haverbeke, 1986). Similar to these previous studies, we found significant population differentiation in growth and morphology. However, we did not observe significant variation among populations in physiological traits. Lack of genetic variation in physiology was also found in several studies for this species. For example, Zhang et al. (1996) found that both growth (i.e., aboveground dry weight and height) and specific leaf area were significant among 26 diverse populations from New Mexico to British Columbia, whereas no difference was detected in gas exchange (i.e., net photosynthesis and stomatal conductance) and carbon isotope discrimination (Zhang and Marshall, 1995). Similar results were also found in a drought tolerance study including nine populations (Cregg, 1994). The patterns in ponderosa pine differ from that in other sympatric conifer species in the Rocky Mountains, *Pseudotsuga menziesii* and *Larix occidentalis*, within which population variation in gas exchange and carbon isotope discrimination has been detected (Zhang et al., 1993; Zhang and Marshall, 1994). It appears that adaptive modes of physiological responses to environmental heterogeneity are different among species.

Lack of population variation in physiological traits may also indicate population plastic convergence when these populations grow in a stressful environ-

ment (Levin, 1988). Because these populations were from the xeric habitats, selection pressures are strongest for survival and reproduction. It is physiological adjustment that enables species to achieve these priorities. Because neither population by site interaction nor population by time interaction was significant in intrinsic gas exchange measurements and in water potential (Table 3), all populations perhaps shared convergent norm of reaction in these variables (but see, Sultan, 1995). In contrast, a long-term measure of water-use efficiency by carbon isotope discrimination showed significant variation for either interactions between population and environment (e.g., site, block, etc.) or between population and time. Therefore, populations respond differently to different environments and times for carbon isotope discrimination. For example, when growing at Halsey, a population from Potter, Nebraska (#758) discriminated more against  $^{13}\text{C}$  at most times compared to other populations. Yet at other sites,  $\Delta$  of this population was either the intermediate or the lowest comparing to other populations. These results indicate a broader range of adjustment for this individual population to the variable environments.

Although the population by site interaction was non-significant for height and DBH (Table 5), the four populations (#845, #846, #849, and #857) from far west showed a unique pattern compared to other populations. Their height and diameter were the same at Alliance as at Halsey, or slightly shorter (Fig. 5). This is in contrast to the general trend that the trees were larger moving from west to east. Moreover, trees from population in Bufford, Wyoming (#857) were the smallest at all sites; its rank among population means did not change across sites. Apparently, this “Central Rocky Mountain” population clustered by Read (1983) and Van Haverbeke (1986) did not perform well when growing at these sites. Even though physiological characteristics showed a plastic adjustment in this population, the environmental change by moving it far from local habitat exceeded the capability of physiological adjustment.

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