

## AMONG-PROVENANCE VARIABILITY OF GAS EXCHANGE AND GROWTH IN RESPONSE TO LONG-TERM ELEVATED CO<sub>2</sub> EXPOSURE

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**Abstract:** Genetic variability can have profound effects on the interpretation of results from elevated CO<sub>2</sub> studies, and future forest management decisions. Information on which varieties are best suited to future atmospheric conditions is needed to develop future forest management practices. A large-scale screening study of the effects of elevated CO<sub>2</sub> on 15 half-sibling sources of genetically superior ponderosa pine (*Pinus ponderosa* Dougl ex P. Laws.) is presented. These sources represent multiple elevations and latitudes throughout California. Among-provenance variability in the effects of elevated CO<sub>2</sub> on gas exchange and growth, and their correlation with geographic origin were investigated in ponderosa pine seedlings subjected to ambient or elevated CO<sub>2</sub> concentrations (525  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> and 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>) for more than two years in open-top chambers. Substantial among-provenance variability in growth response to elevated CO<sub>2</sub> was evident, with 8 sources demonstrating no significant growth response to elevated CO<sub>2</sub> while 7 sources responded positively. For all sources, elevated CO<sub>2</sub> increased photosynthesis (ranging from 19% increase at 525  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> to 49% increase at 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>). A modest correlation existed between geographic origin and above ground growth response to elevated CO<sub>2</sub>.

**Keywords:** Genetic variability, elevated CO<sub>2</sub>, climate change, pine, conifer, photosynthesis, growth.

### 1. Introduction

The projected rise in atmospheric CO<sub>2</sub> concentration and the consequential effects on climate will have profound effects upon terrestrial ecosystems (Cramer and Leemans, 1993; and Rind *et al.*, 1990). Globally, forest ecosystems represent the most persistent standing biomass of all terrestrial ecosystems and therefore play a significant role in the present and future global carbon (C) cycle. The importance of forests and their interactions with climate are considerable. Forests occupy 22 % of the earth's land area (excluding Polar Regions), and account for two-thirds of terrestrial photosynthetic C assimilation (Waring and Schlesinger, 1985). In addition to photosynthesis, forests contribute significantly to the hydrological cycle through evapotranspiration, and nutrient cycles that occur within the forest biosphere. The extent of the impact associated with elevated CO<sub>2</sub> concentration on future forest management practices, however, remains uncertain.

For tree species, a general trend has been reported of increased C assimilation that leads to increased growth of young trees. Increased growth is the result of biochemical and physiological adaptations that optimize C acquisition and allocation (Acock and Allen, 1985; Eamus and Jarvis, 1989). These growth responses vary widely between genera (Tolley and Strain, 1984), species within the same genera (Rogers *et al.*, 1994) and intraspecifically (Houpis *et al.*, 1995).

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Variability in the observed difference in the response to elevated  $\text{CO}_2$  will have substantial impact as land managers and plant breeders begin to focus attention on the use of forests as C sinks, on the desirability of establishing vast areas of new plantations, and on the development of new forest management practices in response to increasing  $\text{CO}_2$  (Kellison and Weir, 1987; Sedjo, 1989). Forest plantations can be used in mitigation strategies for the reduction of atmospheric  $\text{CO}_2$ . If atmospheric  $\text{CO}_2$  continues to rise, plantations can be designed to optimize the enhanced productive capacity associated with increasing  $\text{CO}_2$  concentrations. Since there are species and genotype specific responses to elevated  $\text{CO}_2$ , tree breeding can have a substantial impact on the performance of these plantations (Ceulemans *et al.*, 1996; Ceulemans *et al.*, 1995; Callaway *et al.*, 1994). In tree breeding, it is desirable to develop genotypes that can grow well in a wide range of environments (Weber *et al.*, 1996). Genotypic differences in performance are also important in the establishment of plantations used for existing forest practices and future  $\text{CO}_2$  sequestration strategies. This is due to the fact that genotypes must be well adapted to a wide range of  $\text{CO}_2$  concentrations, as they will be planted under current ambient conditions, and over the course of their rotation, experience significant increases in atmospheric  $\text{CO}_2$ .

There have been a few studies on the intraspecific variability in the  $\text{CO}_2$  response of tree species (e.g. *Populus* hybrids, Ceulemans *et al.*, 1996). Inter-population variation in *P. ponderosa*, (Callaway *et al.*, 1994; DeLucia *et al.*, 1994) and intra-population variation in the deciduous *Betula alleghaniensis* (Wayne and Bazzaz, 1995) have been examined. Thus, little information is known about intraspecific (among populations) tree growth response to elevated  $\text{CO}_2$ . In our study, we investigated among population (half-sib seed source) growth and gas exchange differences of a major commercial conifer species, *P. ponderosa*, to elevated  $\text{CO}_2$ , and whether the observed differences could be correlated to geographic origin. Understanding these underlying physiological and/or growth responses to elevated  $\text{CO}_2$ , and the extent of population variability is the first step in tree breeding.

## 2. Material and methods

### 2.1 PLANT MATERIAL AND GROWTH CONDITIONS

*Pinus ponderosa* seedlings from 15 half-sibling seed sources of different geographic origin (Table I) were grown at various atmospheric  $\text{CO}_2$  concentrations in standard outdoor open-top chambers (OTC, a cylindrical shaped outdoor chamber, 3 m diameter and 3 m height; Rogers *et al.*, 1983) at the Lawrence Livermore National Laboratory exposure facility (Livermore, California). The 15 sources represent among-population variability throughout California. The seedlings were grown from seed and in 3 L containers containing a soil medium consisting of 2 parts clay, 3 parts red lava rock, 1 part colma sand, and 3 parts bark. All seedlings were well-watered and fertilized using a one-half strength Hoagland's solution.

TABLE I

Geographic origin of ponderosa pine half-sib sources from California included in this study. Source identification number, and classification of breeding zone and seed zone are based on the US Forest Service, Region 5 Tree Improvement Program.

| Source | Elevation<br>(m) | Source Location of Origin |                  | USFS          |           |
|--------|------------------|---------------------------|------------------|---------------|-----------|
|        |                  | Latitude<br>(deg.)        | Longitude (deg.) | Breeding Zone | Seed Zone |
| 3088   | 1330             | 38.8                      | 120.4            | 3             | 526       |
| 3089   | 1800             | 38.8                      | 120.0            | 3             | 526       |
| 3287   | 1730             | 39.8                      | 120.6            | 2             | 523       |
| 3306   | 1570             | 34.8                      | 119.9            | 3             | 531       |
| 3363   | 1570             | 37.3                      | 119.3            | 3             | 532       |
| 3382   | 1770             | 39.4                      | 120.7            | 2             | 525       |
| 3435   | 1930             | 37.2                      | 119.3            | 4             | 533       |
| 3589   | 1870             | 35.6                      | 118.6            | 4             | 540       |
| 4266   | 1500             | 40.6                      | 121.4            | 7             | 732       |
| 4304   | 1500             | 40.3                      | 120.6            | 7             | 771       |
| 4315   | 1730             | 39.8                      | 120.6            | 7             | 732       |
| 4731   | 830              | 41.2                      | 121.4            | 5             | 521       |
| 11953  | 1170             | 40.7                      | 123.3            | 5             | 312       |
| 13005  | 1170             | 41.2                      | 121.5            | 7             | 742       |
| 17520  | 570              | 41.0                      | 122.4            | 5             | 521       |

## 2.2 CO<sub>2</sub> TREATMENTS

Seedlings of each source were exposed to three CO<sub>2</sub> exposure concentrations consisting of ambient (approximately 350  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>), 525  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> and 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>. The concentration of CO<sub>2</sub> in the OTCs was monitored using dedicated CO<sub>2</sub> analyzers (Horiba Model PIR-2000; all analyzers were zero and span checked daily and underwent a complete multipoint calibration every month). Chamber air was sampled twelve times per hour at canopy height, at the center of the chamber, for approximately one minute, and the values of CO<sub>2</sub> concentration were averaged over the one-minute sampling period. Over the entire length of the study, the chamber CO<sub>2</sub> concentrations were maintained 24 hr day<sup>-1</sup> within  $\pm 5\%$  of the treatment concentration. Exposure began in April 1993 and continued through to October 1995.

## 2.3 GROWTH MEASUREMENTS

Seedling growth during the 1995 growing season was evaluated based on height and diameter of the main stem measured in August 1995. Height was measured to the

nearest 0.5 cm using a tape measure. Diameter was measured to the nearest 0.1 mm at the cotyledon whorl using a vernier caliper. Measures of total height and diameter were used to estimate main stem volume ( $\pi * \text{radius}^2 * \text{height}$ ).

## 2.4 GAS-EXCHANGE MEASUREMENTS

Net photosynthesis ( $P_n$ ), stomatal conductance ( $g_s$ ), and leaf internal  $\text{CO}_2$  concentration ( $C_i$ ) were measured in August 1995, on current-year-old foliage using an open-loop photosynthesis system consisting of a portable infrared gas analyzer and microprocessor controller (model LI-6400, Licor Inc., Lincoln, NB). Values for  $P_n$ ,  $g_s$ , and  $C_i$  were calculated according to equations derived by von Caemmerer and Farquhar (1981). Gas exchange measurements were taken on a single fascicle, which was placed across the width of the LI-6400 cuvette. Gas exchange results are expressed on a total leaf surface area basis. Total leaf surface area was geometrically determined by measuring the radius and length of the needle inside the cuvette. All measurements were taken mid-morning (0900–1030) and light intensity (PAR) within the cuvette was maintained constant at  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  (saturating light intensity for *P. ponderosa*). Cuvette temperature was set at a leaf temperature of  $25^\circ\text{C}$ . The mean leaf temperature over all gas exchange measurements was  $25 \pm 0.1^\circ\text{C}$  (leaf temperature ranged from  $24.2$  to  $25.9^\circ\text{C}$ ). The mean leaf-air VPD over all gas exchange measurements was  $2.0 \pm 0.2 \text{ kPa}$  (leaf-air VPD ranged from  $1.8$  to  $2.2 \text{ kPa}$ ). All measurements were made at the treatment  $\text{CO}_2$  concentration.

## 2.5 EXPERIMENTAL DESIGN

The study was conducted using a split-plot design. The three levels of atmospheric  $\text{CO}_2$  concentration, the main plot factor, were randomly assigned to 18 OTCs to provide six replicates. Within each chamber, 15 sources of *P. ponderosa* were grown. Thus, source represented a sub-plot factor. Within each chamber, one seedling from each of the 15 sources of *P. ponderosa* was selected for measurement. The effects of  $\text{CO}_2$  concentration and source on gas exchange were determined using analysis of covariance (ANACOV) with leaf-to-air vapour pressure deficit and air temperature as covariates. Treatment and source effects on seedling size were evaluated by analysis of variance (ANOVA) using log-transformed dependent variables to stabilize variance. Significance of  $\text{CO}_2$  and  $\text{CO}_2$ -within-source effects was tested using either linear or quadratic orthogonal contrasts. Source differences were tested using the least significant difference (LSD) criterion if source effects were significant as indicated by ANOVA or ANACOV.

The relationship between geographic location of origin and physiological or growth performance was evaluated by means of regression. Each response variable was independently regressed on latitude, longitude and elevation. Interaction effects of location variables were not included due to high multicollinearity. Separate models were fitted for each  $\text{CO}_2$  treatment.

### 3. Results

#### 3.1 CO<sub>2</sub> EFFECTS

Net photosynthesis ( $P_n$ ) and intercellular CO<sub>2</sub> concentration ( $C_i$ ) were significantly influenced by CO<sub>2</sub> concentration ( $p=0.0033$  and  $p<0.0001$ , respectively). Averaged over all half-sib sources,  $P_n$  was increased by 19% and 49% at 525 and 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>, relative to 350  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> (Figure 1). Increased  $P_n$  was associated with increased  $C_i$  of 32% at 525  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> and 88% at 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> (Figure 1). In contrast, stomatal conductance ( $g_s$ ) did not change significantly with CO<sub>2</sub> concentration ( $p=0.434$ ) although mean  $g_s$  at 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> was almost 18 percent less than that at 350  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> (Figure 1).

#### 3.2 SOURCE EFFECTS

Among sources,  $P_n$  varied from 5.54  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in source 3589 to 6.91  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in source 4266, with the source effect being significant ( $p=0.0168$ , Figure 2). As with CO<sub>2</sub> response,  $g_s$  did not vary significantly among sources ( $p=0.216$ ). In contrast to the CO<sub>2</sub> response of  $P_n$ , significant source variation in  $C_i$  was not evident ( $p=0.291$ ).

#### 3.3 CO<sub>2</sub> X SOURCE INTERACTION EFFECTS

Growth response to elevated CO<sub>2</sub> differed markedly among sources leading to significant CO<sub>2</sub> x source interaction effects on seedling height ( $p=0.0443$ ), diameter ( $p=0.0193$ ), and stem volume ( $p=0.0072$ ). Of the 15 sources studied, only 7 sources had a positive growth response to elevated CO<sub>2</sub>. Of the 7 sources that showed a positive response, 4 of these sources demonstrated a significant height response, 6 sources demonstrated a significant diameter response, and 7 sources demonstrated significant volume response to CO<sub>2</sub> concentration. No significant growth response was evident for 8 of the 15 sources. Of those sources having a significant response to elevated CO<sub>2</sub>, the height response tended to be at a maximum at 525  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> and decreased with a further increase to 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub> (Figure 3); diameter tended to increase linearly with increasing CO<sub>2</sub> concentration (Figure 3). Depending on the relative strength of diameter and height responses, the stem volume response was either linear (5 sources) or quadratic (2 sources; Figure 3).

#### 3.4 SOURCE PERFORMANCE IN RELATION TO GEOGRAPHIC ORIGIN

There was evidence for a geographic pattern in physiological performance that differed with CO<sub>2</sub> concentration. At 350 and 525  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>,  $P_n$  was not significantly influenced by elevation, latitude or longitude of source origin (Table II). However, at 700  $\mu\text{mol mol}^{-1}$  CO<sub>2</sub>,  $P_n$  increased with elevation and with latitude (Table II). Even with this significant response, geographic origin only accounted for 14% of the variation in observed  $P_n$  (Table II). There were no significant origin effects on  $g_s$  or  $C_i$ .

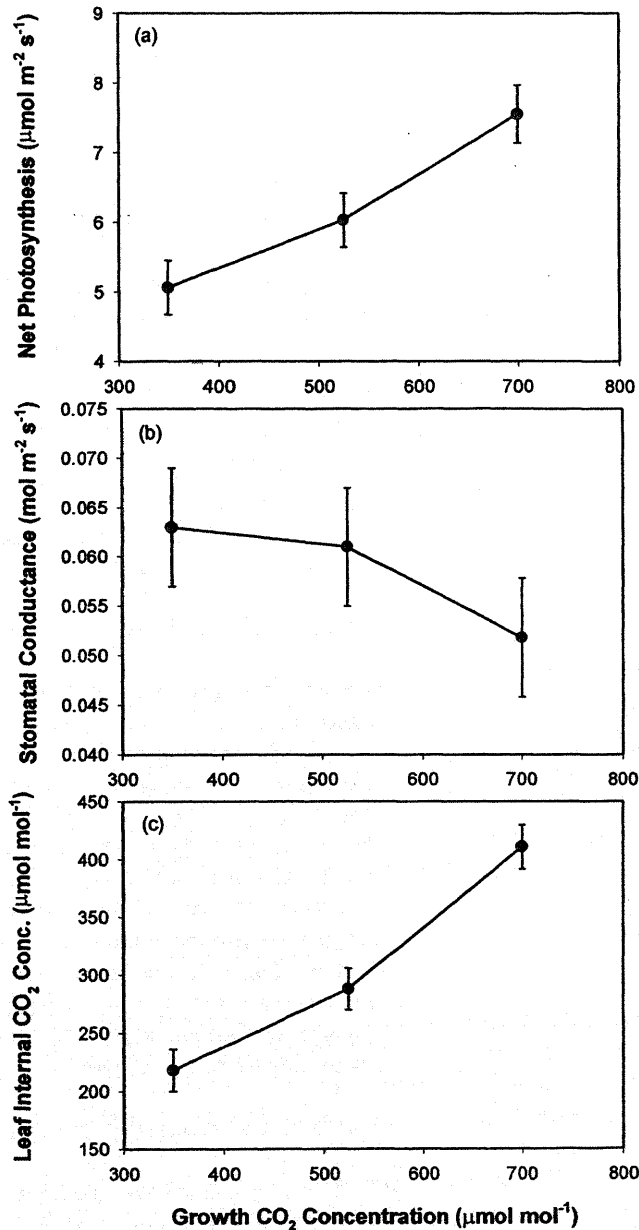


Fig. 1. Physiological responses of ponderosa pine seedlings to CO<sub>2</sub> concentration: a) net photosynthesis, b) stomatal conductance, and c) internal leaf CO<sub>2</sub> concentration. Values are means and standard errors of n=89-90 observations. Gas exchange measurements were made at saturating light conditions, ambient temperature, and growth CO<sub>2</sub> concentrations. Net photosynthesis and internal CO<sub>2</sub> concentration responses to CO<sub>2</sub> were linearly significant ( $p=0.001$  and  $p=0.0001$ , respectively) as determined by orthogonal contrasts.

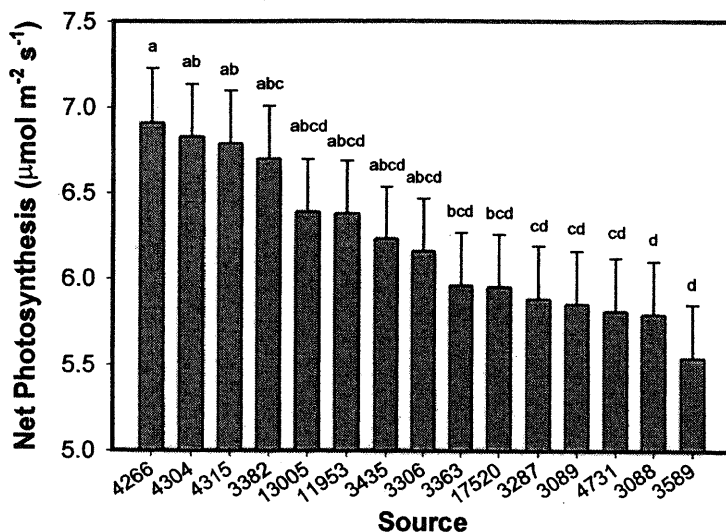


Fig. 2. Net photosynthesis by half-sib sources of ponderosa pine seedlings. Values are means and standard errors of  $n=17-18$  observations. Bars denoted by a common letter do not differ at the  $p=0.05$  level of significance as determined by the L.S.D. criterion. Overall source effect is significant at the  $p=0.017$  level.

In contrast to physiological performance, growth was more strongly and consistently influenced by source geographic origin. Seedling size tended to decrease with increasing elevation, latitude, and longitude. As illustrated for stem volume, geographic variables accounted for 32 to 35% of the observed variation in growth regardless of  $\text{CO}_2$  concentration (Table II). Under elevated  $\text{CO}_2$ , elevation and latitude were the strongest predictors of stem volume; at  $350 \mu\text{mol mol}^{-1} \text{CO}_2$ , longitude accounted for a substantial portion of observed variation in stem volume.

#### 4. Discussion

The substantial among-population variation in the growth response to elevated  $\text{CO}_2$  is consistent with earlier long-term studies with *P. ponderosa* (Houpis *et al.*, 1988; Betsche, 1994; Ceulemans *et al.*, 1996), although our data were measured over a greater number of sources and the extent of variability was greater. The variability in growth response to elevated  $\text{CO}_2$  cannot be attributed to geographic location as indicated by trends for increasing growth with decreasing latitude and elevation that were common to seedlings at all  $\text{CO}_2$  concentrations. Furthermore, those sources that did demonstrate a positive growth response included representatives of all USDA Forest Service breeding zones, covered the full range of latitudes included in the experiment and covered all but the lowest elevations included in the experiment (Table I and Figure 3).

In contrast to the growth response, seedlings from all sources demonstrated significantly increased photosynthesis and minor decreases in stomatal conductance at elevated  $\text{CO}_2$  concentrations. Geographic origin had little effect on gas exchange rates.

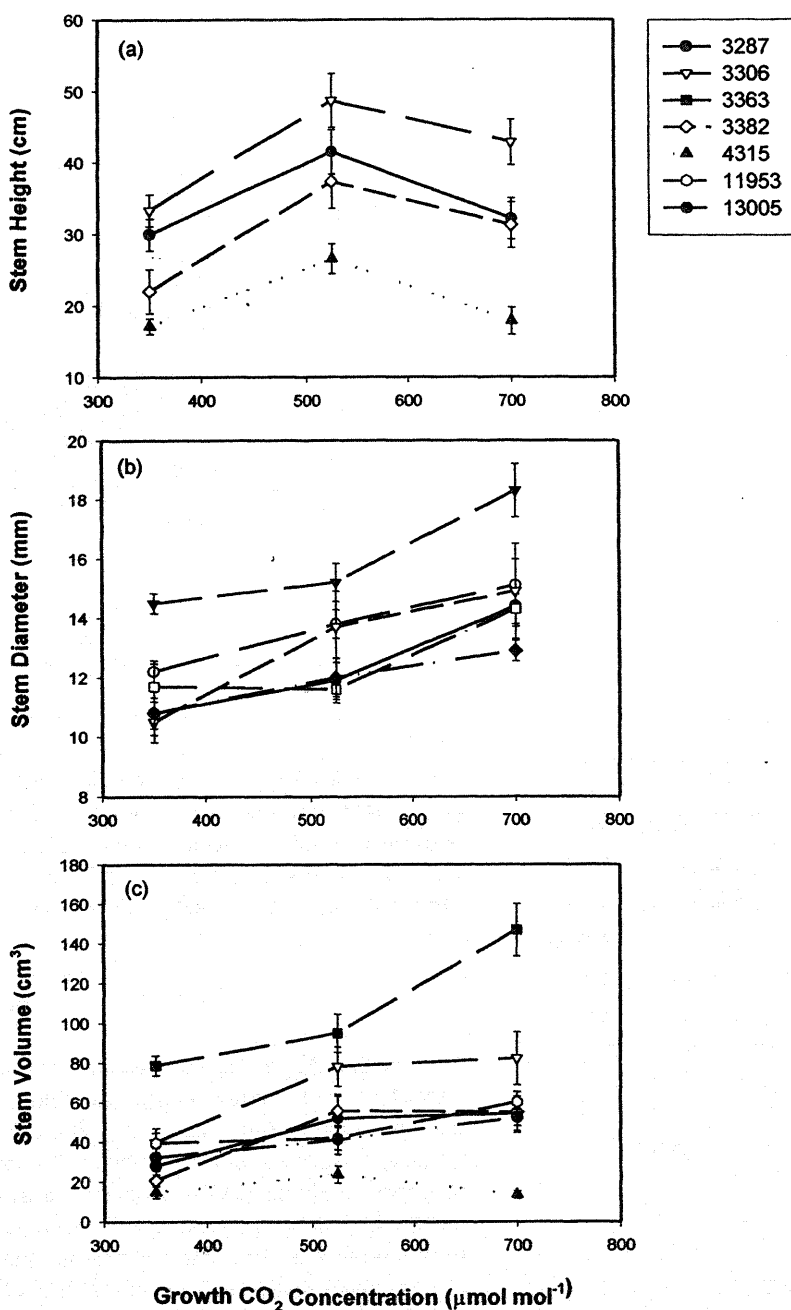


Fig. 3. Growth response to CO<sub>2</sub> concentration by half-sib ponderosa pine sources demonstrating significant a) stem height, b) stem diameter, or c) stem volume response. Values are means and standard errors of  $n=5-6$  observations. Stem height responses were significantly quadratic and stem diameter response were significantly linear as determined by orthogonal contrasts at the  $p=0.05$  level of significance. Stem value responses were either linear (sources 3287, 3306, 3363, 11953, 13005) or quadratic (sources 3382, 4315).

TABLE II.

Regressions of net photosynthesis and stem volume on geographic location of origin for 350, 525 and 700  $\mu\text{mol mol}^{-1}$   $\text{CO}_2$  treatments. Values are parameter coefficients (coeff.) and the probability that coefficients differ from zero (Prob.> $H_0$ ). Estimates of model fit include overall model significance (p), coefficient of determination ( $R^2$ ), and standard error of estimation ( $S_{y-x}$ ).

| Regression Models                                            |                            |                     |                            |                     |                            |                     |
|--------------------------------------------------------------|----------------------------|---------------------|----------------------------|---------------------|----------------------------|---------------------|
| Net Photosynthesis ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) |                            |                     |                            |                     |                            |                     |
| CO <sub>2</sub> Treatment                                    |                            |                     |                            |                     |                            |                     |
|                                                              | 350 $\mu\text{mol m}^{-3}$ |                     | 525 $\mu\text{mol m}^{-3}$ |                     | 700 $\mu\text{mol m}^{-3}$ |                     |
| Source                                                       | Coeff.                     | Prob>H <sub>0</sub> | Coeff.                     | Prob>H <sub>0</sub> | Coeff.                     | Prob>H <sub>0</sub> |
| Intercept                                                    | 13.74                      | 0.682               | -26.14                     | 0.564               | -42.08                     | 0.275               |
| Elevation                                                    | 0.00013                    | 0.580               | 0.00024                    | 0.440               | 0.00068                    | 0.011               |
| Latitude                                                     | 0.155                      | 0.286               | -0.075                     | 0.704               | 0.360                      | 0.033               |
| Longitude                                                    | -0.129                     | 0.672               | 0.279                      | 0.498               | 0.274                      | 0.433               |
| Model Fit                                                    |                            |                     |                            |                     |                            |                     |
| Model Signif.                                                |                            |                     |                            |                     |                            |                     |
| R <sup>2</sup>                                               | p=0.615<br>0.021           |                     | p=0.883<br>0.008           |                     | p=0.0012<br>0.138          |                     |
| S <sub>y-x</sub>                                             | 1.561                      |                     | 2.116                      |                     | 1.794                      |                     |
| Stem Volume (cm <sup>3</sup> )                               |                            |                     |                            |                     |                            |                     |
| CO <sub>2</sub> Treatment                                    |                            |                     |                            |                     |                            |                     |
|                                                              | 350 $\mu\text{mol m}^{-3}$ |                     | 525 $\mu\text{mol m}^{-3}$ |                     | 700 $\mu\text{mol m}^{-3}$ |                     |
| Source                                                       | Coeff.                     | Prob>H <sub>0</sub> | Coeff.                     | Prob>H <sub>0</sub> | Coeff.                     | Prob>H <sub>0</sub> |
| Intercept                                                    | 39.53                      | 0.0006              | 25.58                      | 0.022               | 25.17                      | 0.043               |
| Elevation                                                    | -0.00044                   | 0.0001              | -0.00035                   | 0.0001              | -0.00037                   | 0.0001              |
| Latitude                                                     | -0.092                     | 0.057               | -0.163                     | 0.001               | -0.221                     | 0.0001              |
| Longitude                                                    | -0.251                     | 0.014               | -0.114                     | 0.255               | -0.091                     | 0.415               |
| Model Fit                                                    |                            |                     |                            |                     |                            |                     |
| Model Signif.                                                |                            |                     |                            |                     |                            |                     |
| R <sup>2</sup>                                               | p=0.0001<br>0.326          |                     | p=0.0001<br>0.319          |                     | p=0.0001<br>0.355          |                     |
| S <sub>y-x</sub>                                             | 0.517                      |                     | 0.515                      |                     | 0.573                      |                     |

with the exception of increasing photosynthesis with increasing elevation of origin when grown at 700  $\mu\text{mol mol}^{-1}$   $\text{CO}_2$ . At this point we speculate that in sources from higher elevations, stomatal regulation and water-use efficiencies may not be well-adapted to the high evaporative demand at the low-elevation experimental site. Conversely, low-elevation sources may be more adapted to high evaporative demand, and therefore may have evolved more conservative gas-exchange characteristics. Since all seedlings were given an adequate water supply, less conservative stomatal regulation

by high elevation sources may lead to increased assimilation rates compared to low elevation sources. Grulke *et al.* (1993) demonstrated photosynthetic acclimation, while others have recently demonstrated that ponderosa pine of desert and montane origins have distinctly different water-relations, C assimilation, and C allocation characteristics that result in intraspecific differences in productivity (DeLucia *et al.*, 1988; Callaway *et al.*, 1994; Carey *et al.*, 1997; Carey *et al.*, 1998).

Together, the observed growth and photosynthesis responses suggest that with elevated CO<sub>2</sub>, increased C acquisition rates are possible throughout the California ponderosa pine genome. However, increased C acquisition will inconsistently translate to increased growth due to intraspecific variation in allocation of C to structural and transient sinks. Furthermore, intraspecific variation in allocation patterns may be associated with variation in the metabolic regulation of assimilate translocation (Pushnik *et al.*, 1998). Thus, in order to capitalize on future growth potential associated with elevated CO<sub>2</sub>, genotypic differences must be considered.

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