Gas Exchange for Managed Ponderosa Pine Stands Positioned Along a Climatic Gradient

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INTRODUCTION

The "Garden of Eden" experiment was set up to determine how intensive silviculture affects sustainable productivity of ponderosa pine (*Pinus ponderosa* var. *ponderosa*) plantations (Powers and Ferrell, 1996). Plantation productivity is constrained (Powers and Reynolds, 2000) by both site potential (i.e., soils, climate) and by existing site conditions (e.g., inter- and intraspecific competition, age, density, genetics, herbivory, and disease). By managing these conditions to the maximum extent possible, it is possible to improve site potential.

In California, where ponderosa pine is the most widely planted tree, moisture availability and secondarily, nutrient availability, are the most common factors limiting seedling growth (Powers and Ferrell,

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[Haworth co-indexing entry note]: "Gas Exchange for Managed Ponderosa Pine Stands Positioned Along a Climatic Gradient." Reynolds, Philip E., and Robert F. Powers. Co-published simultaneously in *Journal of Sustainable Forestry* (Food Products Press, an imprint of The Haworth Press, Inc.) Vol. 10, No. 3/4, 2000, pp. 257-265; and: *Frontiers of Forest Biology: Proceedings of the 1998 Joint Meeting of the North American Forest Biology Workshop and the Western Forest Genetics Association* (ed: Alan K. Mitchell et al.) Food Products Press, an imprint of The Haworth Press, Inc., 2000, pp. 257-265. Single or multiple copies of this article are available for a fee from The Haworth Document Delivery Service [1-800-342-9678, 9:00 a.m. - 5:00 p.m. (EST). E-mail address: getinfo@haworthpressinc.com].

1996; Shainsky and Radosevich, 1986). In California's Mediterranean summer-dry climate, the growing season usually begins in early April as soils warm, and extends into July until soil drought dominates the site (Oliver et al., 1983). Woody shrubs, especially manzanita (*Arctostaphylos* sp. L.) and ceanothus (*Ceanothus* sp. L.) are generally regarded as pine's strongest competitors for soil moisture and nutrients. By managing these competitors, pine water potential can be increased, nutrient uptake improved, and growth increased on a variety of sites. McDonald and Fiddler (1990) observed that pines grown without competing shrubs had predawn water potentials 0.7 MPa higher than those surrounded by shrubs. Minimum potentials for pines growing with competing shrubs were reached by mid-morning during summer, but delayed until mid-afternoon for those grown without shrubs. Since pines close their stomates to conserve water when potentials drop below –1.2 MPa (Lopushinsky, 1969), usually just after sunrise during hot summer months, extending the period of higher water potential when stomates remain open is crucial to maximizing active periods of photosynthesis. In addition, photosynthetic rates are generally increased with greater N availability and uptake (Mitchell and Hinckley, 1993).

Whereas site conditions, and to some extent soils, can be managed, climate cannot. For droughty sites, periods of active photosynthesis during hot summer months may be greatly reduced compared with other sites with greater annual precipitation and more moderate temperatures. If however, annual precipitation is received mostly in the form of snow, the total number of days of active growth when photosynthesis is feasible may also be restricted. The present study was initiated to quantify climatic variability for pine sites positioned along an environmental gradient and to determine the affect of climatic variability on pine physiological response for managed and unmanaged ponderosa pine stands.

METHODS

This study is a component of the Garden of Eden Project, located throughout northern California, and has been reviewed in considerable detail elsewhere (Powers and Ferrell, 1996). The project was initiated in 1985 to study the effects of vegetation and insect control, fertilization, and combinations thereof on plantation development. For the project, a complete factorial design is being used at eight locations scattered throughout the Sierra, Cascade, and Coastal ranges of northern California. Each location consists of 24 contiguous, rectangular plots measuring 19.5 m × 21.9 m each. Three replications of the eight factorial treatment combinations per plantation were assigned in a completely randomized design. Treatments consisted of controls (C), fertilized (F) only, vegetation control (H) only, vegetation control + fertilized (HF), insecticides (I) only, fertilized + insecticides (FI), vegetation control + insecticides (HI), and vegetation control + fertilized + insecticides (HFI). Treatments were applied repeatedly (i.e., as needed for insecticides, annually for herbicides, and biennially using a ramp schedule for fertilizers) until crown closure (i.e., approximately 9 years). For purposes of this experiment, only the first four treatments (i.e., no insecticides) were used.

The eight sites were established between 1985 and 1988. Three of these sites, having widely varying characteristics, were chosen for this study. They included: (1) Whitmore (732 m, hot and dry, annual precipitation ~ 114 cm. yr^{-1}, snow rare, planted 1986), (2) Feather (1219 m, wet and warm, precipitation ~ 178 cm. yr^{-1}, snow occasional, planted 1988), and (3) Chester (1463 m, cool and dry, precipitation ~ 89 cm. yr^{-1}, snow normal for 5 or 6 months, planted 1987). All plantations occur on soils derived from volcanic material, and the Chester site is characterized by a high coarse cinder content. Soils at Whitmore are clays and those at Feather are loams. The Whitmore and Chester sites were brushfields that were cleared prior to planting. Feather was a natural stand of pine that was logged prior to planting. The highest estimated site index (base age 50 years) for all eight sites was 30 m at Feather. Whitmore ranked intermediate at 23 m and Chester was near the bottom at 20 m (i.e., lowest was 17 m).

Five pines spanning the range of heights were randomly selected and tagged at the centre of each of the twelve treatment plots at each location. Beginning in February 1995, stomatal conductance (G_s), transpiration (E), and net assimilation (NA) for tagged pines (upper crown, new foliage) and associated environmental parameters [photosynthetically-active radiation (PAR), air temperatures, and vapour pressure deficits (VPD)] were measured using a Li-Cor LI-6200 portable photosynthesis unit (Li-Cor Inc., Lincoln, NE). Subsequent measurements occurred in May, June, August, and December. Projected needle areas were determined with a Delta-T leaf area meter and corrected to actual surface areas using a ratio of 2.8 as recommended by Cannell (1982). Water use efficiencies (WUE) were calculated using the formulas (actual WUE = NA/E, Larcher 1980 and intrinsic WUE = NA/G_s, Farquhar and Richards, 1984). Mesophyll conductance was calculated using the formula: G_m = NA/CINT (Leverenz, 1981). Plant water potentials for shoots were measured with a model 3005 plant water status console (Soilmoisture Equipment Corp., Santa Barbara, CA).

To examine overall site differences, data for the four treatments were pooled prior to analysis. Possible differences in PAR for the three sites were evaluated using standard analysis of variance (ANOVA) procedures (Snedecor and Cochran, 1967). Site-related differences in air temperature were examined using analysis of covariance (ANCOVA) with PAR as a covariate. Site differences in plant water potential and VPD were studied using multiple analysis of variance (MANOVA) with air temperature and VPD as covariates for plant water potential and with air temperature and plant water potential as covariates for VPD. Gas exchange data, including G_s, E, NA, actual WUE, intrinsic WUE, and G_m were analyzed using MANOVA with PAR, air temperatures, plant water potential, and VPD as covariates. Treatment means were compared by Tukey's Test at 5% level of significance. Statistical analysis and graphics were performed using CSS Statistica (StatSoft, Tulsa, OK) versions 3.1 (DOS) and 5.1 (Windows).

RESULTS

PAR was highest at Chester in June (Table 1). Air temperatures tended to be highest at Whitmore, intermediate at Chester, and lowest at Feather throughout the measurement period (Table 1). At all sites, the lowest plant water potentials occurred in June and August, when Whitmore was significantly lower than the other two sites (Table 1). In May and December, the three sites differed, with the highest water potentials observed at Whitmore, and the lowest at Chester. Vapour pressure deficits were generally highest at Whitmore and Chester throughout the measurement period; VPD was lowest at Feather (Table 1).

Throughout most of the measurement period, G_s rates were higher or tended to be highest at Feather (Table 2). E and NA rates were higher at Feather in August when these parameters were lower at the

TABLE 1. Seasonal site differences for photosynthetically-active radiation (PAR), air temperatures, plant water potential, and vapour pressure deficits (VPD).

Variable	Site	Feb.	May	Jun.	Aug.	Dec.
PAR ($\mu mol \cdot s^{-1} \cdot m^{-2}$)	Whitmore	788 a	675 b	1220 b	1288 a	429 b
	Feather	415 b	755 b	1250 b	1345 a	772 a
	Chester	–	899 a	1571 a	1325 a	718 a
Air temperature (°C)	Whitmore	11.97 b	20.54 a	28.21 a	29.48 a	17.59 a
	Feather	14.74 a	18.54 b	18.88 c	28.30 b	15.81 b
	Chester	–	18.15 b	24.16 b	29.20 b	13.59 c
Midday water potential (MPa)	Whitmore	–	−10.07 a	−15.95 b	−17.40 b	−8.70 a
	Feather	–	−10.70 b	−14.55 a	−15.89 a	−11.75 b
	Chester	–	−11.44 c	−14.81 a	−15.74 a	−15.15 c
Vapour pressure deficit (kPa)	Whitmore	9.87 a	14.49 b	26.95 a	32.95 a	8.55 b
	Feather	9.49 b	12.13 c	16.96 c	26.10 b	8.34 b
	Chester	–	15.32 a	23.27 b	33.93 a	10.22 a

Mean values are for all treatments. Monthly values followed by the same letter are not significantly different at the 5% level according to Tukey's Test.

Whitmore and Chester (i.e., droughtier) sites (Table 2). Seasonally, maximum NA rates were observed at Whitmore and Chester in June when the highest E rates for these sites were observed and when E rates at these sites were higher than at Feather. Overall, NA rates at Whitmore were highest during winter, spring and early summer months. Actual WUE was highest at Feather during late spring through August and higher at Feather than at Chester in May, June, and August, and higher at Feather than at Whitmore in June (Table 2). In February, actual WUE and NA were higher at Whitmore than at Feather. By contrast, intrinsic WUE tended to be highest at Whitmore and at Chester for most measurement dates and was higher at Whitmore than at Feather in February and higher at Chester than at Feather in May (Table 2). G_m was generally lowest for Whitmore, except in May, and tended to be highest and similar for the Feather and Chester sites (Table 2).

DISCUSSION

Environmental parameters and related physiological responses varied significantly between sites and seasonally. PAR tended to be some-

TABLE 2. Seasonal site differences for stomatal conductance (G_S), transpiration (E), net assimilation (NA), actual water use efficiency (WUE = NA/E), intrinsic water use efficiency (WUE = NA/G_S), and mesophyll conductance (G_m = NA/CINT).

Variable	Site	Feb.	May	Jun.	Aug.	Dec.
G_s ($mol \cdot m^{-2} \cdot s^{-1}$)	Whitmore	0.072 a	0.095 a	0.051 a	0.035 b	0.114 a
	Feather	0.069 a	0.105 a	0.058 a	0.059 a	0.114 a
	Chester	-	0.068 b	0.052 a	0.036 b	0.057 b
E ($mmol \cdot m^{-2} \cdot s^{-1}$)	Whitmore	0.49 a	0.90 a	1.46 a	1.15 c	0.87 a
	Feather	0.50 a	0.85 a	1.03 b	1.70 a	0.94 a
	Chester	-	0.86 a	1.40 a	1.38 b	0.66 b
NA ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	Whitmore	4.10 a	3.88 a	4.42 a	2.83 b	3.51 a
	Feather	2.60 b	3.76 a	4.44 a	4.45 a	3.54 a
	Chester	-	3.04 b	4.55 a	3.06 b	2.61 b
WUE = NA/E ($\mu mol\ CO_2 \cdot mmol^{-1}\ H_2O$)	Whitmore	9.43 a	4.36 ab	3.11 b	2.53 ab	4.04 a
	Feather	5.61 b	4.53 a	4.34 a	2.78 a	3.98 a
	Chester	-	3.67 b	3.34 b	2.22 b	4.11 a
WUE = NA/G_s ($\mu mol\ CO_2 \cdot mmol^{-1}\ H_2O$)	Whitmore	66.22 a	42.30 ab	90.17 a	88.46 a	33.50 b
	Feather	40.70 b	37.90 b	81.10 a	77.74 a	38.09 ab
	Chester	-	47.03 a	88.80 a	87.45 a	47.56 a
G_m = NA/CINT ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	Whitmore	11.36 a	10.90 b	14.52 b	10.41 b	6.96 b
	Feather	7.68 b	12.93 a	18.32 a	14.04 a	9.45 a
	Chester	-	10.42 b	18.21 a	12.70 a	8.30 ab

Mean values are for all treatments. Monthly values followed by the same letter are not significantly different at the 5% level according to Tukey's Test.

what higher at Chester in June, probably because of high elevation and due to increasing midday solar angle early in the summer. Air temperatures varied with elevation, tending to be highest throughout the year at the lowest elevation Whitmore site. Although slightly higher in elevation, the Chester site tended to be warmer in June than Feather, probably because of less precipitation and lower humidity (unpublished data). Hot droughty conditions at Whitmore during late summer produced the lowest water potentials and highest vapour pressure deficits for the three sites. Early winter and spring rains, accompanied by cooler temperatures, resulted in higher water potentials, lower VPD, and generally higher NA at the Whitmore site. This seasonal shift clearly suggests that most gains in net productivity at low elevation sites probably occur during winter, spring and early summer months.

Vapour pressure deficits tend to increase as temperatures climb seasonally or diurnally and as water stress increases. High VPD and low plant water potential combine to reduce gas exchange rates. In this study, VPD was highest in August at the two droughty sites, Whitmore and Chester. Harrington et al. (1995) also observed that VPD was highest at drier sites. Very low precipitation at Chester, coupled with greater soil drainage (i.e., high cinder content), likely produced droughty conditions equal to those at Whitmore.

G_s, E, NA, actual WUE, and G_m were generally highest at Feather where precipitation was greatest. Concurrently, pine growth and foliar nutrient concentrations were also greatest at this site (Powers and Reynolds, 2000; Powers and Ferrell, 1996). These findings are consistent with those reported by others that gas exchange tends to increase as plant water stress is elevated or as availability of water increases (Jiang et al., 1995; Lieffers et al., 1993). In addition, Harrington et al. (1995) also observed that actual WUE was lower at drier, low-elevation sites, and decreased as VPD increased with decreasing elevation. By contrast, intrinsic WUE was highest for the two droughty sites, Whitmore and Chester. Lajtha and Getz (1993), studying NA and intrinsic WUE in pinyon pine-juniper communities along an elevation gradient, also observed that both species had higher WUE at the lowest, and presumably driest, sites. Combined, these two methods for calculating WUE show that ponderosa pine lowers G_s on droughty sites and increases G_s and E on sites where water is plentiful. Plantations on sites such as Feather, therefore, offer the best option for maximizing sustained productivity.

In this study, G_m tended to be similar for the two higher altitude sites, but higher at Feather. At Feather, foliar nutrient concentrations were highest, presumably because of greater uptake due to greater water availability. Water potential data for Chester in June and August suggests that water potentials were similar to Feather, and higher than those at Whitmore. Greater foliar N concentrations at Feather resulting from greater water availability, vegetation control, and fertilization could have contributed to this response (Powers and Reynolds, 2000; Powers and Ferrell, 1996). In studies involving fertilization or release from competing vegetation, it has generally been observed that G_s, E, NA, and G_m may all increase in response to higher foliar N (Lieffers et al., 1993; Mitchell and Hinckley, 1993). However, nutrient influences appear to be primarily on G_m rather than G_s.

CONCLUSIONS

The following apply for measurements made in 1995 (i.e., plantation ages, 8 yrs at Feather, 9 yrs at Chester, 10 yrs at Whitmore). Average crown closure occurred during yr 9 (Powers and Ferrell 1996). In 1995, crown closure had occurred at Whitmore and Feather, but not at Chester.

- The three sites differed significantly climatically. The Whitmore (lowest elevation) and Chester (highest elevation) sites were droughtiest while the Feather (high elevation) site was wettest. Temperatures were highest at Whitmore and lowest at Feather. In early summer, radiation intensity was greatest at Chester
- Because of these climatic differences the three sites differed in their seasonal phenology. Most net productivity occurred during winter, spring, and early summer at Whitmore when temperatures were cooler and rainfall frequent. At Chester, net productivity was restricted to May through December because of snow cover the balance of the year, with maximum net assimilation in June. At Feather, climatic conditions were generally favourable for net productivity year-round, with maximum net assimilation in August.
- Because of favourable year-round climate at Feather, G_S, E, NA, and actual WUE were highest at this site. Concurrently, growth and foliar nutrient concentrations were highest at this site.
- Because of summer droughty conditions, intrinsic WUE was highest at the Whitmore and Chester sites.
- The two methods of calculating WUE show that ponderosa pine lowers G_S on droughty sites and increases G_S and E on sites where water is plentiful.
- We conclude that plantations on sites such as Feather, therefore, offer the best option for maximizing sustained productivity.

REFERENCES

Cannell, M.C.R. 1982. World forest biomass and primary production data. Academic Press, London.

Farquhar, G.D. and R.A. Richards. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Aust. J. Plant Physiol. 11: 539-552.

Harrington, R.A., J.A. Fownes, F.C. Meinzer and P.G. Scowcroft. 1995. Forest growth along a rainfall gradient in Hawaii: *Acacia koa* stand structure, productivity, foliar nutrients, and water-and nutrient-use efficiencies. Oecologia 102: 277-284.

Jiang, Y., S.E. MacDonald and J.J. Swiazek. 1995. Effects of cold storage and water stress on water relations and gas exchange of white spruce (*Picea glauca*) seedlings. Tree Physiol. 15:267-273.

Lajtha, K. and J. Getz. 1993. Photosynthesis and water-use in pinyon-juniper communities along an elevation gradient in northern New Mexico. Oecologia 94: 95-101.

Leverenz, J.W. 1981. Photosynthesis and transpiration in large forest-grown Douglas fir diurnal variation. Can. J. Bot. 59: 349-356.

Lieffers, V.J., A.G. Mugasha and S.E. MacDonald. 1993. Ecophysiology of shade needles of *Picea glauca* saplings in relation to removal of competing hardwoods and degree of prior shading. Tree Physiol. 12: 271-280.

Lopushinsky, W. 1969. Stomatal control in conifer seedlings in response to leaf moisture stress. Bot. Gaz. 134: 258-263.

McDonald, P.M. and G.O. Fiddler. 1990. Ponderosa pine seedlings and competing vegetation: Ecology, growth, and cost. USDA Forest Service Research Paper, PSW-199.

Mitchell, A.K. and T.M. Hinckley. 1993. Effects of foliar nitrogen concentration on photosynthesis and water use efficiency in Douglas fir. Tree Physiol. 12: 403-410.

Oliver, W.W., R.F. Powers and J.N. Fiske. 1983. Pacific ponderosa pine. Pp. 48-52. In: Silvicultural systems for the major forest types of the United States. R.M. Burns (ed.). Agric. Handb. 445, USDA Forest Service, Washington, DC.

Powers, R.F. and P.E. Reynolds. 2000. Intensive management of ponderosa pine plantations: ensuring sustainable productivity in the 21st century. J. Sustainable For. 10(3/4):249-255.

Powers, R.F. and G.T. Ferrell. 1996. Moisture, nutrient, and insect constraints on plantation growth: the "Garden of Eden" experiment. New Zealand J. For. Sci. 26: 126-144.

Shainsky, L.J. and S.R. Radosevich. 1986. Growth and water relations of *Pinus ponderosa* seedlings in competitive regimes with *Arctostaphylos patula* seedlings. J. Appl. Ecol. 23: 957-966.

Snedecor, G.W. and W.G. Cochran. 1967. Statistical methods. The Iowa State University Press, Ames, Iowa.