

The ponderosa pine ecosystem and environmental stress: past, present and future

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In North America, ecosystems supporting ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) extend from the Black Hills of North Dakota west to the Pacific Ocean, north into Canada and south into Mexico (Figure 1). Conditions range from a moist, maritime Mediterranean climate (in the Klamath Mountains of northwestern California) to subalpine conditions (in the Rocky Mountains) to semi-arid woodlands (in the Southwest). Soils are commonly coarse textured and often nutrient deficient. In such cases, the presence of an understory of nitrogen-fixing shrubs can make an important contribution to site productivity.

Ponderosa pine is a thick-barked species that is tolerant of surface fires. Historically, light, periodic ground fires were common in ponderosa pine forests (Bork 1985) and resulted in the formation of park-like stands. Over the last century, however, the policy of protecting forests from wildfire has resulted in the development of a dense understory of suppressed pines and other conifers (McCune 1988), which has increased the

risk of conflagrations by allowing fuels to accumulate. As plant competition has increased, so have impacts associated with human activities. Large recreational demands are made on ponderosa pine forests, and fossil fuel use has enriched the atmosphere not only with CO₂, but with ozone and other pollutants.

In response to increases in these atmospheric trace gases, ponderosa pine ecosystems are probably experiencing changes in climatic conditions and atmospheric chemistry greater than any to which they have previously been exposed. As a consequence, empirical predictions of growth based on past management experience may no longer apply. In these circumstances, physiological ecology, which studies the underlying environmental interactions controlling biological processes, provides an avenue for assessing both the present status of ponderosa pine forests and the way in which their growth, distribution, and susceptibility to various stresses may be affected by future changes in management, climate and environmental chemistry.

Interest in the integrated physiological response of ponderosa pine to variation in climate, soil, atmospheric concentrations of CO₂ and ozone, and competing vegetation gave rise to a workshop “The Ponderosa Pine Ecosystem and Environmental Stress: Past, Present and Future,” which was held at Oregon State University in Corvallis on April 26, 1999. A collection of peer-reviewed papers from among those presented at the workshop appear in this issue of *Tree Physiology*. Here, we take the opportunity of considering these contributions in the context of long-term management concerns.

Andersen et al. (2001) present the results of an experiment with ponderosa pine seedlings growing with or without grass competition and with or without ozone stress. The study was conducted in open-top field chambers over a 3-year period. Grass competition reduced aboveground growth of pine seedlings, while increasing the relative growth of roots. The addition of ozone, however, altered the interactions with grass by affecting both the nitrogen and carbohydrate status of the pine seedlings. The study demonstrates the need to consider intraspecific competition for resources when assessing the response of trees to environmental change.

Grulke and Rezlaff (2001) report on a field study demonstrating that assimilation rates during summer drought are significantly lower and water stress is significantly greater in seedlings than in trees of all other age classes, whereas

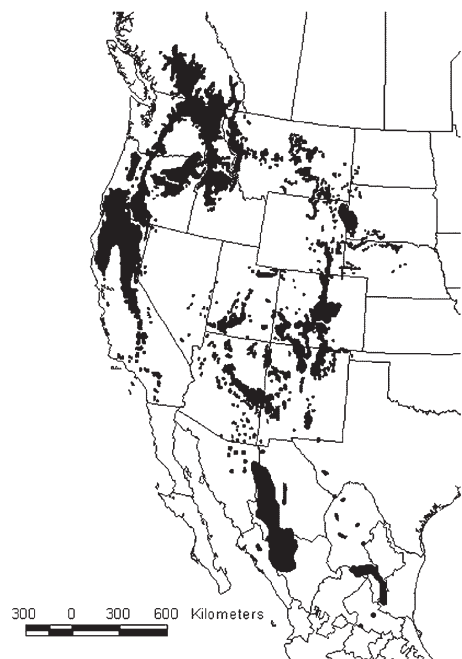


Figure 1. Ponderosa pine distribution in the western United States.

growth rates of seedlings are significantly lower, and carbon allocation patterns in seedlings and young trees differ substantially. The comparison demonstrates that it is inappropriate to draw inferences about mature trees from measurements on seedlings; but it also identifies common responses of trees of a broad range of age classes.

The paper by Michael Tausz et al. (2001) contrast the effects of ozone exposure and intense radiation characteristic of high elevations on leaf pigments and antioxidative protective compounds. These authors were able to distinguish biochemical responses to ozone from those attributed to intense radiation by making comparisons under ambient conditions and following overnight recovery. Their approach provides opportunities for comparisons across transects exposed differentially to pollutants.

Panek and Goldstein (2001) report on the response of ponderosa pine to irrigation during an extended drought. Their study confirmed that reduced stomatal conductance associated with drought decreases ozone uptake more than photosynthesis. The study demonstrates that to predict ozone damage, it is necessary to quantify not only the severity and duration of drought during the growing season but also interactions during the rest of the year that might affect stomatal conductance and the uptake of ozone and CO₂.

A detailed process model is used by Williams et al. (2001) to define both diurnal and seasonal variation in ponderosa pine stomatal conductance, taking into account interactions between atmospheric demand, soil water availability, and the total resistance to water flow between soil and leaf. Model predictions are compared with direct measurements of water vapor and CO₂ exchange measured at an old-growth pine site using the eddy covariance technique. This detailed analysis explains how the trees maintained a relatively constant transpiration rate during drought, through deep rooting, whereas a reduction in stomatal conductance with increased evaporative demand caused a proportional reduction in photosynthesis. A complete ecosystem analysis for water and carbon provides a valuable complement to the micrometeorological approach by separating physiologically related processes associated with trees (photosynthesis, transpiration, autotrophic respiration) from others (surface evaporation from plant surfaces, litter and soil, and heterotrophic respiration).

Because of concern over CO₂-induced global warming, forests may in the future be managed, at least in part, for CO₂ sequestration. Carbon sequestration by forests is strongly dependent on rates of respiration as well as of photosynthesis. As a contribution to understanding forest respiration and its control, Xu et al. (2001) estimated total ecosystem respiration in a ponderosa pine plantation by scaling up from sample measurements to the ecosystem based on model relationships that take account of microclimate and vegetation characteristics. Over the 5-month study, 67% of total ecosystem respiration was attributable to soil-surface CO₂ efflux. Of the remainder, 10% was attributable to stem and branch respiration and 23% to foliage respiration. Shrub leaves contributed about 24% to total foliage respiration. Root respiration accounted for 47% of soil-surface CO₂ efflux. A linear regression model based on soil and air temperatures explained about 91% of the variation

in total ecosystem respiration.

The paper by Law et al. (2001) compares CO₂ and water vapor exchange measured by the eddy covariance and other techniques during the summer at a young pine plantation in the Sierra Mountains of California and at an older forest situated in a rain shadow on the eastern flank of the Cascade Mountains in central Oregon. Although the young plantation received three times as much precipitation annually than the old forest, water stress was much more severe in the young plantation than at the old forest because of greater daily water use associated with a higher total canopy leaf area. Simulations of photosynthesis at both sites showed that milder temperatures and ample water availability outside of the summer season in the Sierras more than offset the disadvantage of carrying a higher leaf area through the summer drought.

From the contents of these papers and discussions at the workshop, it is clear that the influences of climate, pollutants and developmental stage on ponderosa pine systems are important and the effects on the uptake, transport and utilization of carbon dioxide, nutrients and water are not easily distinguishable. There are opportunities and challenges for both clarifying underlying processes and expanding the scope of analyses to include possible shifts in competition, climate and atmospheric chemistry across the entire ponderosa pine range. To meet these challenges will require a multi-disciplinary approach that includes measurements at various scales, modeling of processes in response to environment, and spatial and temporal integration of information to address atmospheric circulation, ozone and nitrogen deposition patterns, and responses to climate change.

References

- Andersen, C.P., W.E. Hogsett, M. Plocher, K. Rodecap and E.H. Lee. 2001. Blue wild-rye grass competition increases the effect of ozone on ponderosa pine seedlings. *Tree Physiol.* 21:317–325.
- Bork, J.L. 1985. Fire history in three vegetation types on the east side of the Oregon Cascades. Ph.D. Diss., Oregon State Univ., Corvallis (Diss. Abstr. 84-25990), 128 p.
- Gruelke, N.E. and W.A. Retzlaff. 2001. Changes in physiological attributes of ponderosa pine from seedling to mature tree. *Tree Physiol.* 21:273–284.
- Law, B.E., A.H. Goldstein, P.M. Anthoni, M.H. Unsworth, J.A. Panek, M.R. Bauer, J.M. Fracheboud and N. Hultman. 2001. Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. *Tree Physiol.* 21:297–306.
- McCune, B. 1988. Ecological diversity in North American pines. *Am. J. Bot.* 75:353–368.
- Panek, J.A. and A.H. Goldstein. 2001. Response of stomatal conductance to drought in ponderosa pine: implications for carbon and ozone uptake. *Tree Physiol.* 21:335–342.
- Tausz, M., A. Bytnerowicz, M.J. Arbaugh, A. Wonisch and D. Grill. 2001. Multivariate patterns of biochemical responses of *Pinus ponderosa* trees at field plots in the San Bernardino Mountains, southern California. *Tree Physiol.* 21:327–334.
- Williams, M., B.E. Law, P.M. Anthoni and M. Unsworth. 2001. Use of a simulation model and ecosystem flux data to examine carbon–water interactions in ponderosa pine. *Tree Physiol.* 21:285–296.
- Xu, M., T.A. DeBiase, Y. Qi, A. Goldstein and Z. Liu. 2001. Ecosystem respiration in a young ponderosa pine plantation in the Sierra Nevada Mountains, California. *Tree Physiol.* 21:307–316