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Modeling temperature and light acclimation of photosynthetic capacity in seedlings and mature trees of *Pinus ponderosa*

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Abstract

A preliminary step to understand the impact of possible rise in temperature on carbon dynamics of forests is to examine the temperature elasticity of key processes involved in carbon fixation in forest trees. For seedling and mature ponderosa pines of three genotypes, we used a response-surface methodology and ANOVA to evaluate changes in maximum net photosynthesis ($A_{n\ \mathrm{max}}$), and its corresponding light ($L_{An\ max}$) and temperature ($T_{An\ max}$) to diurnal and seasonal changes in ambient temperature during summer and autumn. As seasonal ambient temperature decreased: (1) $A_{n\ max}$ did not change in seedlings or mature trees, (2) $L_{An\ max}$ did not change in mature trees, but it decreased for current-year foliage of seedlings from 964 to 872 μmol photons m^{-2} s^{-1}, and (3) $T_{An\ max}$ did not change in seedlings but it decreased in mature trees for both current- and one-year-old foliage, from 26.8 to 22.2, and 24.6 to 21.7 °C, respectively.

Keywords Light acclimation, temperature acclimation, Photosynthetic capacity, Ponderosa pine

Introduction

The global mean temperature in the next 100 years may increase by 1-4 °C [1]. Temperature is an important factor affecting plant biochemical and physiological processes. Plants have been evolved under warming and cooling periods. However, plants' ecological stability and reproductive success in their current habitat may depend on their potential to cope with projected increase in temperature. Photosynthesis is a key process that involves many temperature-dependent biochemical reactions [2].

Temperate forest plants experience diurnal and seasonal changes in temperature that may affect photosynthetic adaptation/acclimation to long- and short-term temperature fluctuations. In this study, we investigated maximum photosynthetic capacity ($A_{n\ \mathrm{max}}$) and its associated temperature ($T_{An\ max}$) and light ($L_{An\ max}$) levels as related to diurnal and seasonal changes in ambient temperature in ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws) in the field.

We examined current- and one-year-old foliage in both seedlings and mature trees of three ponderosa pine genotypes. These genotypes have been selected by the USDA Forest Service for future plantations in California, and differ in their phenotypic vigor. The unique aspects of this research are: 1) both mature trees and seedlings are used, 2) plants acclimated naturally to seasonal conditions in the field and then their photosynthetic response was measured under rapid changes in temperature and light levels (resembling rapid, diurnal changes), and 3) no previous study of this nature has caught our attention for the three important ponderosa pine genotypes we used.

Materials and Methods

Plant material consisted of mature clones of three ponderosa pine genotypes (USDA Forest Service designations 3087, 3088, 3399) and their related half-sib seedlings. The clonal trees were part of a grafted seed orchard growing at the USDA-Forest Service Chico Tree Improvement Center (CTIC) in Chico, California. Grafts of clones 3088, 3087, and 3399 displayed low, moderate, and high vigor, respectively, in terms of growth, foliage color, and foliage retention characteristics when growing at CTIC. We deliberately included this clonal variation to explore whether photosynthetic elasticity would be differentially expressed among genotypes differing in degree of local adaptation.

The clonal trees were produced from bud scion grafted onto three-year-old rootstocks. The grafts were planted at the CTIC in the mid to late 1970's. Although these grafts were 12- to 15-yr old at the time of the study, they expressed mature characteristics in terms of branch and needle morphology, and cone production. Half-sib seedlings of the three clones were grown from seed of the three clonal source trees. Seeds were sown in containers in the spring of 1989, and seedlings were grown in a greenhouse for one season, and then transplanted to the field in the spring of 1990.

The CTIC is located in the Sacramento Valley at the base of the west slope of the Sierra Nevada (N 39.8º Latitude, W 121.9º Longitude; elevation 75 m), at the lower elevation limit of ponderosa pine habitat. The climate is Mediterranean with hot, dry summers and mild, wet winters. Mean temperature is greater and mean precipitation is lower at the CTIC site compared with the natural habitat of the parent trees. Soil is a Vina silt loam, alluvium, about 120-cm deep. Soil fertility was maintained by annual application of soil sulfur (220 kg ha^{-1}, pure elemental S), ammonium sulfate (1100 kg ha^{-1}, 24% S and 21% N), manganese sulfate (140 kg ha^{-1}, 50% Mn), and N:P:K (1200 kg ha^{-1}, 16:20:0). Plant material was watered biweekly from May to October. Competing herbaceous species and rodents were removed regularly. These cultural treatments minimized potential confounding effects of resource limitations with that of experimental treatments (temperature and light).

Six mature trees, two from each genotype, were planted in the field in a completely randomized manner. Therefore the experimental design for mature trees was a CRD with two mature trees per treatment. For seedlings, the field layout was a randomized complete block design (RCBD), in which the three genotypes were randomized within two sites (blocks) resulting in having two seedlings per treatment. We used three temperature and three light levels (explained below). The three temperature levels were sub-plots within each genotype, and the three light levels were sub-plots within each temperature level. Measurements for the two foliage ages and two seasons were analyzed separately.

Net photosynthesis (A_n) was measured on one replicate in the mornings and on the second replicate in the afternoons (between 0800 to 1900 h) in late August (period I) and mid November (period II). Midday mean (SE) temperatures in August and November were 37 (0.38) and 24 (0.27) °C, respectively.

A_n was measured under controlled temperature, light, vapor pressure deficit (VPD), and external CO_2 conditions using an infrared gas analyzer and data acquisition console (Li-6200, Licor, Inc., Lincoln, NE) interfaced with a 0.95-liter temperature-controlling cuvette (DDG-9920, Data Design Group, La Jolla, CA) and temperature controller (CN9111, Omega Engineering, Stamford, CT). Light was supplied by two 27-watt, Electronic Compact Warm Fluorescent Lamps (2700K Chromaticity, 82% Color Rendering Index, General Electric Co.). Ambient light was excluded. Within the cuvette, VPD was held at 1.5 ± 0.5 kPa using a dew point generator (Li-610, Licor, Inc., Lincoln, NE), and the CO_2 concentration was maintained at 340 ± 5 µmol mol^{-1}.

For each replicate, 8 to 12 needles were placed flat inside the temperature-controlling cuvette and exposed to a series of target temperatures that followed the diurnal progression of ambient temperature. The sequence of target temperatures was 18, 25, and 32 °C for the morning measurements, and 32, 25, and 18 °C for the afternoon measurements. The measurement protocol for a given sample consisted of achieving a target temperature followed by sequential measurements at light intensities of 250, 500, and 1000 µmol photons m^{-2} s^{-1}. With each change in temperature/light condition, the cuvette environment was allowed to equilibrate with respect to CO_2 concentration, VPD, and temperature. This equilibration was maintained for an additional 15 minutes and then A_n was measured and calculated per unit area and time.

In mature trees, A_n was measured on current- and one-year-old foliage in August and November. In seedlings, A_n was measured on both foliage ages in August, but not all seedlings/genotypes retained healthy one-year-old foliage in November, and thus, for seedlings seasonal comparisons would be made on current-year foliage only.

Response-surface regression analysis was performed on each set of photosynthetic responses to the nine combinations of three temperature-by-three light levels for each sample to derive estimates of maximum photosynthesis ($A_{n\ \mathrm{max}}$) and corresponding light ($L_{An\ max}$) and temperature ($T_{An\ max}$) values. This resulted in a total of 24 response surface models [3 genotypes × 2 plant forms (mature, seedling) × 2 diurnal measurements (morning, afternoon) × 2 seasonal measurements]. Response surface analysis was performed using the *RESREG* procedure of the *SAS System*. Detailed explanation of our response surface analysis is given elsewhere [3].

Analysis of variance was then performed on estimates of $A_{n\ \mathrm{max}}$, $L_{An\ max}$, and $T_{An\ max}$, which were obtained from the individual response surface models, to detect the main or interactive effects of genotype, plant form, diurnal, and seasonal differences.

Results and Discussion

We acknowledge the limitations of having three light and three temperature levels for the construction of the response surface models, as well as having two replications per each of the six light-by-temperature treatment combinations for seedlings or mature trees. However, such limitations were unavoidable due to scarcity of desired plant material. Time was also a limiting factor considering the amount of time needed to complete each photosynthetic measurement after equilibration to the six light-by-temperature treatment combinations.

All 24 response surface models demonstrated excellent fits as indicated by the *residual plots* (not shown) and $R^2 > 0.99$. All models had well-defined, stationary points of $A_{n\ \mathrm{max}}$. No significant three- or two-way interactive effects, genotype, or diurnal main effect were detected for any of the three responses ($A_{n\ \mathrm{max}}$, $L_{An\ max}$, $T_{An\ max}$) examined. Both seedlings and mature trees maintained similar $A_{n\ \mathrm{max}}$ in August and November (Table 1). In mature trees, $L_{An\ max}$ did not change significantly from August to November, but $T_{An\ max}$ decreased from 26.8 to 22.2 °C ($P < 0.01$) in current-year foliage, and from 24.6 to 21.7 °C ($P < 0.07$) in one-year-old foliage.

These results suggest that the photosynthetic capacity of experimental plants during active shoot growth was maintained under cool and short days in November, and that the optimal temperature for photosynthesis shifted in the direction of seasonal changes in the mean ambient temperature. Similar photosynthetic acclimation to temperature has been demonstrated in loblolly pine (*Pinus taeda* L.) seedlings grown under controlled environment [4] and in Scots pine (*Pinus sylvestris* L.) seedlings grown in open-top chambers [5].

In current-year foliage of seedlings $L_{An\ max}$ decreased significantly ($P < .03$) from 964 to 872 µmol photon $m^{-2}\ s^{-1}$, but it did not change in mature trees (Table 1).

Table 1: Mean (standard error) of maximum photosynthesis ($A_{n\ \mathrm{max}}$) and its corresponding temperature ($T_{an\ \mathrm{max}}$) and light ($L_{an\ \mathrm{max}}$) values for ponderosa pine seedlings and mature trees. Main-effect means are shown because of non-significant three- and two-way interactive effects of diurnal, seasonal, and genotype. Temperature: °C, light and $A_{n\ \mathrm{max}}$: µmol $m^{-2}\ s^{-1}$. Sample size is 2.

Plant	Foliage	Component	Mean (SE)		P
			August	November	
Seedling	current-year	$A_{n\ \mathrm{max}}$	7.87 (.5)	6.94 (.5)	0.24
		$L_{An\ \mathrm{max}}$	964 (25)	872 (25)	0.03
		$T_{An\ \mathrm{max}}$	26 (1)	24 (1)	0.16
Mature tree	current-year	$A_{n\ \mathrm{max}}$	7.59 (.5)	6.82 (.5)	0.48
		$L_{An\ \mathrm{max}}$	953 (23)	944 (23)	0.78
		$T_{An\ \mathrm{max}}$	26.8 (.8)	22.2 (.8)	0.01
	1-year-old	$A_{n\ \mathrm{max}}$	4.79 (.4)	5.49 (.4)	0.22
		$L_{An\ \mathrm{max}}$	929 (24)	875 (24)	0.14
		$T_{An\ \mathrm{max}}$	24.6 (1)	21.7 (1)	0.07

$L_{An\ max}$ of current-year foliage of seedlings decreased significantly from August to November, from 964 to 872 µmol photon $m^{-2}\ s^{-1}$. This decrease may be due to seedlings' adaptation to changes in understory conditions as light availability decreases with shortening day length.

Although seedlings were grown in the open in this study, it seems that they did not acclimate to higher light availability in the open and responded to the site of their long-term adaptation under canopy with low light.

Mature ponderosa pines, occupying co-dominant and dominant canopy positions, may not experience a wide range of seasonal light limitations but they may be exposed to a wider temperature range compared with seedlings, which are evolved under canopy with greater insulation from light fluctuations and subsequent effects on soil and above-soil temperature levels. If so, seasonal adjustment of $T_{An\ max}$ may be more important to mature tree fitness than seasonal adjustment of $L_{An\ max}$.

Previous research on the same plant material indicated genotype differences in mid-day photosynthesis for both mature trees and seedlings when averaged across measurements made from February to October [6]. In the current study, however, no genotype difference in the maximum photosynthesis is detected regardless of the seasonal change in the ambient temperature. This may be explained by a genotype-by-midday temperature interaction, as suggested elsewhere [6], because mid-day measurements under ambient temperature do not reflect potential maximum photosynthesis.

Although our current results do not indicate genotype differences in photosynthetic capacity, the fact that genotype 3088 retained one cohort of foliage, as opposed to genotypes 3087 and 3399 that retained two cohorts, suggests that at the CTIC, clone 3088 is farther displaced from its optimal environment than the other two genotypes. The retention of fewer foliage cohorts may indicate shifts in biomass allocation as a result of environmental stress. Alterations of biomass allocation have been reported for ponderosa pine growing under contrasting mountain and desert thermal regimes [7].

Based on the result that mature ponderosa pines can sustain maximum photosynthesis under almost 4.5 °C change in optimum temperature, it may be concluded that predicted increases in mean temperature between 1 and 4 °C would not have a serious effect on ponderosa pine photosynthetic capacity.

Additionally, our result may be valid under current range of temperature and may not hold under an elevated range of temperature due to global warming. Moreover, the effects of global warming should be considered in broader physiological and ecological terms. The effects of elevated range of temperature on biomass allocation [8] and respiration [9] must be considered with respect to the carbon budget at individual tree [4] and broader scales. Interspecific differences in photosynthetic performance and competitive ability are expressed at the ecosystem levels, affecting species composition [10]. Under a most optimistic scenario of no major direct effect of a 2-4 °C increase in mean temperature on ponderosa pine in monoculture, increased temperature may differentially affect the competitive ability of components of ponderosa pine ecosystems and result in unpredicted outcomes. Furthermore, having two replications limited the power of our analysis.

References

1. United Nations' Intergovernmental Panel on Climate Change: http://www.grida.no/publications/vg/climate/page/3076.aspx.
2. Long S. P. and Woodward FI. eds. (1988) Plants and temperature. Symposia of the Society for Experimental Biol., 42.
3. Momen B., Anderson P. D., and Helms J. A. (2001) Application of response surface methodology and ANOVA to detect pollution effects on photosynthetic response under varying temperature and light regimes. Forest Ecol. Mgmt. 152, 331-337.
4. Teskey R. O., and Will R. E. (1999) Acclimation of loblolly pine (*Pinus taeda*) seedlings to high temperatures. Tree Physiol. 19, 519-525.
5. Kellomäki S., and Wang K. (1996) Photosynthetic response to needle water potentials in Scots pine after a four-year exposure to elevated CO_2 and temperature. Tree Physiol. 16, 765-772.
6. Anderson P.D., Houpis J.L.J., Helms J.A., and Momen B. (1997) Seasonal variation of gas-exchange and pigmentation in branches of three grafted clones of mature ponderosa pine exposed to ozone and acidic rain. Environ. Pollut. 97, 253-263.
7. Carey E. V., DeLucia E. H., and Ball J. T. 1996) Stem maintenance and construction respiration in *Pinus ponderosa* grown in different concentrations of atmospheric CO_2. Tree Physiol. 16, 125-130.
8. Callaway R. M., DeLucia E. H., and Schlesinger W. H. (1994) Biomass allocation of mountain and desert ponderosa pine: an analog for response to climate change. Ecology. 75, 1474-1481.
9. Bassow S. L., and Bazzaz F. A. (1998) How environmental conditions affect canopy leaf-level photosynthesis in four deciduous tree species. Ecology. 79, 2660-2675.
10. Stroch M., Vrabl D., Podolinska J., Kalina J., Urban O., and Spunda V. (2010) Acclimation of Norway spruce photosynthetic apparatus to the combined effect of high irradiance and temperature. J. Plant Physiol. 167, 597–605.