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Translocation of Carbon-14 in *Pinus ponderosa* Seedlings Subjected to Long-term Sulfur Dioxide and Water Stress

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ABSTRACT

The Rocky Mountain variety of ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm) was grown for two years in cylindrical plastic covered open-top chambers (3 m diameter by 3 m height) in an outdoor environment. Tree seedlings were subjected to three concentrations of SO_2 and three levels of water stress. The levels of SO_2 were annual hourly means of 0, 27, and 54 $nL \cdot L^{-1}$. The levels of water stress were based on soil water content, and were leaf water potentials of 0.1, 0.3 and 0.6 Mpa. After 10 months of treatment, seedlings were exposed to $^{14}CO_2$ to determine how stress altered the translocation of carbon. The effects of SO_2 and water stress were similar, with both reducing the total amount of available carbon translocated to roots. Unstressed seedlings exported more assimilate to roots and retained less assimilate in needle tissue as compared to any combination of SO_2 and water stress. When water stress was applied, there was no difference in the quantity of assimilate translocated to roots at any of the SO_2 levels. Therefore, the effects of SO_2 and water stress were not additive.

Key Words. SO_2, water stress, translocation, $^{14}CO_2$

INTRODUCTION

Since the start of the industrial revolution, air pollution has continually impacted vegetation. Due to the burning of fossil fuels and biomass, and smelting processes, global emissions of sulfur dioxide have risen steadily, surpassing natural sources (87 TgS and 60 TgS for anthropogenic and natural sources, respectively; Houghton et al. 1990). These emissions will not only influence climate change through the formation of aerosols, but will also have a direct effect on vegetation (Krupa 1997).

"Plant productivity is determined by a complex series of events leading from CO_2 fixation in the chloroplasts, formation of phloem-mobile and storage metabolites, and delivery of these to sink tissues. We are only just beginning to understand the extent of these complexities" (Madores and Lucas 1995). This partitioning of carbon determines plant health and vigor under nearly all conditions. The regulation of partitioning during times of stress imparts resilience to the plant, and subsequently leads to good or bad harvests. The damaging stresses of air pollution to vegetation are well-known, and nowhere is plant carbon allocation more important than in partitioning during times of stress.

Carbon translocation and stress have been studied over the last three decades for several groups of species including crops and natural grasses (Jones and Mansfield 1982a, Major et al. 1978, Shih et al. 1983), broad-leaved tree species (Dickson and Larson 1981, McLaughlin et al. 1979), and conifer species (McLaughlin et al. 1982, Schier 1970, Webb 1977). Amount of assimilate translocated in these studies varied widely, from as low as 0.1 to 5% translocated from labeled leaves/stems to nonlabeled leaves/stems (Jones and Mansfield 1982a) to as high as 45% (McLaughlin et al. 1979). However, the results from McLaughlin et al. (1979) may not reflect the actual assimilate translocated, since assimilate in the initially labeled branch was included. This assimilate remaining in the initially labeled leaf can be quite high. Based on measured respiration values and measured retention of assimilates, McLaughlin et al. (1979) estimated that the amount of $^{14}CO_2$ translocated from the labeled leaves ranged from 0% to 60%. So, it is unlikely that the 45% of assimilates found in all leaves was due to an appreciable amount in nonlabeled leaves.

Several studies have reported alterations in biomass and partitioning due to air pollutant injury (He et al. 1996, Heagle et al. 1979, Hogsett et al. 1985, Leininger et al. 1991, McBride et al. 1975, Norby and Kozlowski 1981, Vins and Mrkva 1973). Studies of pollutant effects on allocation patterns using $^{14}CO_2$ tracing are rare and for some pollutants, dated. For example, one of the most current studies of the effects of SO_2 on tree species was conducted 16 years ago by Jones and Mansfield (1982a) where they investigated the responses of translocation of $^{14}CO_2$ to SO_2 exposure in *Phleum pratense*. They showed assimilate translocated to roots to be reduced by SO_2, which could lead to a reduced root/shoot ratio. Thus, altered biomass allocation induced by SO_2 can at least in part, result from decreased transport to the root system.

Other work has emphasized the importance of seasonal patterns in the flow and partitioning of assimilate (McLaughlin et al. 1979, Schier 1970, Webb 1977). White pine showed an increase in needle retention of photosynthate (McLaughlin et al. 1982). McLaughlin et al. (1982) concluded that decline of white pine in East Tennessee was attributable to stress brought on by oxidant injury. An increase in needle senescence was noted. Reduced carbon storage capacity was observed in the fall with a resulting shortage in carbon for new foliage formation in the spring. New needle growth was more self-reliant for its carbon supply and was shorter, which resulted in lower gross photosynthetic production and a higher retention of photosynthate.

With increasing concerns about the implications of climate change, there is a need to investigate the impacts of SO_2 in relation to its interactions with environmental parame-

ters, such as water availability, that may change under future climate scenarios. No studies to date have shown how water stress and SO_2 may interact and influence translocation patterns in conifers. Thus, one purpose of our study of SO_2 and water stress was to determine whether *Pinus ponderosa* would show a reduced storage capacity that would result in a carbon shortage the following spring. This long-term study would further show if a specific tissue organ was being preferentially affected by SO_2. Finally, this study would assess the possible interaction between water stress and SO_2 on the translocation of carbon.

MATERIALS AND METHODS

Plant Material

Seedlings of the Rocky Mountain variety of *Pinus ponderosa* var. *scopulorum* Engelm were obtained from the Colorado State Nursery in Fort Collins, Co. The seedlings were 2-year-old container stock with roots in 5 x 5-cm plugs. The seed source was the San Isabel National Forest near the town of Rye, Co. (38% latitude, 105% longitude).

The seedlings were transplanted into in 15-cm aluminum foil covered plastic pots. The potting mix contained equal parts of clay (Cohasset Series), redwood compost, Monterey #4 sand, and perlite (Jenkinson 1980).

Sulfur Dioxide Exposure

The seedlings were grown throughout the experiment in open-top chambers (Heagle et al. 1973, Rogers et al. 1983) at Lawrence Livermore National Laboratory. The air entering the open-top chambers was carbon-filtered prior to addition of SO_2.

A sampling line was centrally located in each chamber to monitor the level of SO_2. Chambers were monitored with a data acquisition system and TECO SO_2 analyzers (TECO, Hopkinton, Mass.) to maintain levels of SO_2 of 0 $nL \bullet L^{-1}$, 27 $nL \bullet L^{-1}$, and 54 $nL \bullet L^{-1}$ annual hourly means. These hourly mean concentrations are similar to those used by Pell et al. (1988). The high SO_2 treatment (annual hourly mean of 54 $nL \bullet L^{-1}$) represented a worse case scenario in the western United States for exposures near metal smelters (Hogsett et al. 1989, Leininger et al. 1991) and represent peak concentrations for moderately polluted areas (Krupa 1997). Data collection was continuous during hours of fumigation with updates every 15 minutes over the entire 26-month experiment. This resulted in SO_2 concentrations being controlled at ±10% of the desired levels. The Teflon sampling tubes were heated and insulated to prevent condensation.

Water Stress Treatments

Three levels of water stress were implemented concurrently with SO_2 exposure. Leaf water potential was not continually determined since this would have led to excessive tissue destruction. Instead, leaf water potential was determined periodically to establish the level of water stress induced by predetermined levels of water loss from the pot and plant. Seedlings grown under no water stress were maintained by watering after a loss of 30 g $H_2O \bullet L$ $soil^{-1}$ (leaf water potential of 0.1 MPa). Seedlings grown under low water stress were watered after a loss of 70 g $H_2O \bullet L$ $soil^{-1}$ (leaf water potential of 0.3 Mpa) and those grown under high water stress at a loss of 110 g $H_2O \bullet L$ $soil^{-1}$ (leaf water potential of 0.6 MPa). It was found that, due to the homogeneous potting medium used, as well as

the large amount of soil compared to seedling size, there was little variation among plants in the amount of the water drawdown within a particular water treatment level.

To assure complete and uniform drainage, metal-support grids were placed under pots. In addition, rain covers were placed above chambers so that all added water was controlled.

Translocation Analysis

In November, after 11 months of SO_2 fumigation and water stress, seedlings from each of the nine treatment combinations were selected to determine the effects of stress on the translocation of photosynthetically fixed ^{14}C. Each seedling was placed in a translocation device to receive a pulse of ^{14}C as $^{14}CO_2$ (Figure 1). The method for exposing tissue to $^{14}CO_2$ and tracing the isotope through the plant over the course of one week was similar to McLaughlin et al. (1982). A preliminary experiment had shown that in *P. ponderosa* a daylight exposure of 5 minutes ensured that sufficient ^{14}C would reach the roots. This preliminary study revealed the importance of a sampling scheme that considered age class, needle location, and tissue type. We also found that the effect of needle location within an age class could be accounted for by sampling tissue at set intervals along the stem.

The exposures to $^{14}CO_2$ were made during mid-day, with ambient light levels when uptake would be highest. The translocation chamber was completely filled with $^{14}CO_2$ using a 2 $L \bullet min^{-1}$ flow rate over a 5-minute period. This flushed the entire chamber volume every 5 minute.

The translocation device was first opened, the internal fan was turned on, and the seedling placed into the device so all of the foliage was enclosed. The seedling was secured to the bottom plastic bag of the translocation device by using a rubber gasket to form a collar around the base of the seedling and then securing the bag to the gasket with a cable tie. After closing the device, the seedling was exposed to $^{14}CO_2$ gas for 5 min at 2 $L \bullet min^{-1}$ and then removed immediately.

Seven days after exposure, all plants were harvested, separated by tissue type, and analyzed for ^{14}C. Needle tissue was sampled from each age class by removing a fascicle every 5 cm along the stem. This technique increased the accuracy of determining total $^{14}CO_2$ uptake. After the tissue was collected, it was ground and separated into three subsamples. Subsamples were then wrapped in ashless filter paper and combusted in a Packard B306 Tri-Carb Sample Oxidizer (Packard Instruments, IL). The ^{14}C from the combusted subsample was captured in a Carbosorb E solution and mixed with a standard fluor (Permafluor E; Packard Instruments, IL). The resulting solution was then placed in a Packard Tri-Carb 4530 Liquid Scintillation Counter (Packard Instruments, IL) and counts per minute (CPM) of ^{14}C were obtained. Before and after every 25 samples, a ^{14}C standard and background blanks were run through the entire combustion and counting process. This enabled us to determine the counting efficiency of our processes, and convert CPM into disintegration per minute (DPM), and finally converted into Becquerels (Bq). Houpis (1989) provides a detailed description of the entire process.

The amount of ^{14}C translocated to a particular tissue type was calculated from the following equation:

$$Bq_t = (Bq / wt) * W ,$$

where

Bq_t = Bq found in a tissue type (needles and stems by age class, and buds and roots),
wt = weight of the subsample , and
W = total weight of the tissue type.

Experimental Design

This study was part of a larger study that lasted more than two years and was a completely randomized 3 x 3 factorial design. The larger study had two main factors, SO_2 and water stress. Three levels of each factor were studied; annual hourly means of 0 (no SO_2), 27, and 54 $nL \bullet L^{-1}$ SO_2; and no, low, and high water stress. Three seedlings (replicates) were randomly taken from each of the nine treatments. An ANOVA was used to determine differences in biomass and translocated ^{14}C in each of the tissue types (needles, stems, buds, and roots). Needle and stem tissue were also analyzed by age class using a three-factor ANOVA (with SO_2, water stress, and age class as factors).

The number of samples required in each of the studies was determined by both a power test and logistic considerations. If differences existed, then Newman-Keuls Pairwise Comparisons were used (Neter and Wasserman 1985). For all comparisons, a $p<0.1$ (selected a priori) was used to determine significance. In all figures, mean values having the same lower case letter are not significantly different, as determined by Newman-Keuls Pairwise Comparisons.

RESULTS

Sulfur dioxide did not significantly affect the percentage of Bq found in any of the age classes of needles, or in any of the older age classes of stems. However, the buds and the youngest stem tissue had a significantly higher percentage of translocated carbon at 54 $nL \bullet L^{-1}$ SO_2. In contrast, the control treatment had significantly more carbon translocated to root tissue. Perhaps the most important finding (Figure 2) was that seedlings in the control treatment (no SO_2) had less carbon allocated to the top of the plant, with more carbon exported to roots, than did the seedlings in the treatments with SO_2.

Although the water stress effect was not entirely similar to that for SO_2, some of the trends in the allocation of translocated carbon were comparable. These included less carbon in the leaf tissue of the control seedlings, little or no difference among older age classes of stems, and the control seedlings having the greatest amount of carbon translocated to roots (Figure 3). However, the relative amount of translocated carbon found in the upper stem classes of control plants (no SO_2) was the opposite of that found in seedlings receiving SO_2. In the case of water stress, significantly more carbon was found in the youngest stem age classes of the seedlings in the control treatment than was found in seedlings in the high water stress treatment. Comparison of seedlings with and without water stress suggested that the increase in carbon translocated to roots and to the 0-year-old age class of stems (i.e., stem tissue associated with current age class of needles) was offset by a small increase in carbon translocated to the other tissue types at high water stress. A significantly higher quantity of carbon was found in the 0-year-old age class of

needles (i.e., current age class of needles) in the low water stress treatment (Figure 3), which was due to a significant interaction with SO_2.

The SO_2 x water stress interaction significantly affected the quantity of carbon translocated to the 0-year-old age class of needles, the 0- and 1-year-old age class of stems, and the roots (Figures 4a-c). The interactions for the 0-year-old age class of stems indicate that as SO_2 level increased, the amount of translocated carbon found in the 0-year-old age class of stems in the no water stress treatment increased compared to other water stress treatments. Another notable trend was that control seedlings (no SO_2 and no water-stress) had the lowest translocation to 0- year-old age class of needles compared to all other treatments. Also, the seedlings in the no SO_2 and no water stress treatment had the greatest amount of labeled carbon found in their roots. Levels of translocated carbon from all other treatment combinations were not significantly different. This indicates that, when comparing any stress combination, the control group exported significantly more carbon from the 0-year-old needles to the roots. Once the plants experienced stress, there was a significant decrease in carbon moving to roots.

DISCUSSION

It is well known that climate interacts with air pollution, and together they determine the plant's response to air pollution (Tingey and Olszyk 1985). Due to the influence of water availability on stomatal conductance, it would be expected that water stress would affect a plant's uptake of SO_2 through the stomates. In addition, SO_2 will influence the distribution of assimilate (Murray 1985, Gould and Mansfield 1988, and Murray and Wilson 1990). Our study demonstrated that the effects of SO_2 and water stress were similar to previous studies, with our results showing a reduction in assimilate translocation to roots. The SO_2 effect resulted in a higher retention of assimilates in needle tissue. This supports conclusions for *Pseudotsuga menziesii* (Leininger et al. 1991), *Phleum pratense* (Jones and Mansfield 1982a, 1982b, and Mansfield and Jones 1985) and *Pinus strobus* (McLaughlin et al. 1982). However, the difference in the amount of assimilate found in root tissue due to water stress was the result of higher retention of assimilate in stem tissue.

In our study, seedlings not stressed due to ample water and no SO_2 exposure exported more assimilate to roots at the expense of assimilate retention within needle tissue. All other combinations of SO_2 and water stress resulted in a significant reduction in translocation to roots. These findings are supported by reports that SO_2 not only reduces the production of assimilates (Strand 1995), but also inhibits their transport (Fialho and Bucker 1996, Gould and Mansfield 1988, McLaughlin et al. 1982, Murray and Wilson 1990, Noyes 1980) and sulfate transport (Herschbach et al. 1995). Reduced transport resulted in a decreased translocation to the root system and increased retention in leaves (Gould and Mansfield 1988 with *Triticum aestivum*, Jones and Mansfield 1982a with *Phleum pratense*, Lorenc-Plucinska 1986 with *Pinus sylvestris*). This pattern of increased retention of assimilates in needle tissue due to SO_2 stress is most likely a function of an increased need of assimilates for repair and maintenance in the damaged tissue (Wilson 1995, Wulff and Karenlampi 1996), detoxification mechanisms (Saraswathi and Madhava Rao 1995, Slovik 1996), or chemical defense mechanisms (Julkunen-Tiitto et al. 1995). Increased foliar retention means less assimilates translocated to roots, which

can reduce stored carbon available for growth in the following year. Thus, the observed suppression of growth by SO_2 (Houpis 1989) could be attributed to reduced photosynthesis, an increase in assimilates needed for repair and maintenance, and less carbon storage (Fialho and Baker 1996).

The interaction between increasing water stress and SO_2 is especially important since both stresses are common, and water stress may increase under certain future climate change scenarios (Pastor and Post 1988). Once water stress was applied, there was no significant difference in assimilates translocated to roots at any of the SO_2 levels. Jones and Mansfield (1982a) showed that increasing SO_2 concentration resulted in a significant reduction in the amount of assimilate translocated to roots. They hypothesized that SO_2 could exacerbate the effect of water stress. However, our results do not confirm this hypothesis because the plants subjected to both levels of water stress showed no alteration in their pattern of translocation to roots when exposed to SO_2. Thus, as suggested by Wilson (1995), exacerbation of water stress effects by SO_2 would not be expected, and plants growing in present or future drier habitats are less likely to exhibit SO_2- induced changes in allocation patterns as would be expected in more mesic habitats.

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Figure 1. Diagram of translocation device: Top view (1a) and Side view (1b).

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Figure 2. Percent of Bq found seven days after the initial pulse of $^{14}CO_2$ in the various tissue types for seedlings grown under increasing SO_2 concentrations. (LFx = leaf tissue, BDS = bud tissue, STx = stem tissue, RTS = root tissue; where x indicates the age (years) of the tissue.) Letters indicate statistical groupings for those tissue types that have significant difference, and statistical comparisons are made only within a particular tissue type as determined by the multiple comparison tests.

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Figure 3. Percent of Bq found seven days after the initial pulse of $^{14}CO_2$ in the various tissue types for seedlings grown under increasing water stress. (LFx = leaf tissue, BDS = bud tissue, STx = stem tissue, RTS = root tissue; where x indicates the age (years) of the tissue.) Letters indicate statistical groupings for those tissue types that have significant difference, and statistical comparisons are made only within a particular tissue type as determined by the multiple comparison tests.

Figure 3 is not available in this on-line version. Please contact library or author for hard-copy of this figure.

Figure 4. Percent of Bq found seven days after the initial pulse of $^{14}CO_2$ in the various tissue types for seedlings grown under increasing water stress; at 0 $nL \bullet L^{-1}$ SO_2 (4a), 27 $nL \bullet L^{-1}$ SO_2 (4b), and 54 $nL \bullet L^{-1}$ SO_2 (4c). (LFx = leaf tissue, BDS = bud tissue, STx = stem tissue, RTS = root tissue; where x indicates the age (years) of the tissue.) Pairwise comparisons for each tissue type were made between each of the nine treatments Letters indicate statistical groupings for those tissue types that have significant difference, and statistical comparisons are made only within a particular tissue type as determined by the multiple comparison tests.

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