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# MEASUREMENT OF TRANSPIRATION IN PINUS TAEDA L. AND LIQUIDAMBAR STYRACIFUA L. IN A CLOSED ENVIRONMENT GROWTH CHANGER USING TRITIATED WATER

by

Joan K. Czoch B.S. June 1972, Wilkes College

A Thesis Submitted to the Faculty of Old Dominion University in Partial Fulfillment of the Requirements for the Degree of

MASTER OF SCIENCE

BIOLOGY

OLD DOMINION UNIVERSITY August, 1975

Approved by:

Gerald F. Levy
Paul W. Kirk, Jr.

Daniel E. Schenshine (Director)

#### ABSTRACT

MEASUREMENT OF TRANSPIRATION IN Pinus taeda L.

AND Liquidambar styraciflua L. IN A CLOSED

ENVIRONMENT GROWTH CHAMBER USING TRITIATED WATER.

Joan Katherine Czoch Old Dominion University, 1975 Director: Dr. D. E. Sonenshine

Transpiration rates of loblolly pine (Pimus taeda L.) and sweetgum (Liquidambar styraciflua L.) were measured at two different water vapor pressure deficits (V.P.D.) in a controlled environment growth chamber using tritiated water as a tracer. The trees were maintained in a sealed plant bed containing a hydroponic nutrient solution. Samples of leaves, chamber air, spiked nutrient and control solutions were assayed for activity using liquid scintillation techniques. The transpiration rate of sweetgum (4.95 ml/hr/gm) was found to be 5 times greater than that of loblolly pine (1.03 ml/hr/gm) at the lower V.P.D. and 8 times greater at the higher V.P.D. (15.99 ml/hr/gm for sweetgum vs. 2.19 ml/hr/gm for pine). Transpiration in both species rose with increasing vapor pressure deficit although sweetgum increased its output by 3 times while pine only doubled its rate. Cyclical changes in transpiration rates were noted in both species; the sweetgum cycle peaked at 6 hour intervals and the pine cycle at 9 hour intervals.

## ACK NOWLEDGMENTS

The author would like to acknowledge certain people without whose kind cooperation and assistance this project would not have been possible: Dr.'s Paul W. Kirk, Gerald F. Levy, James F. Matta and Daniel E. Sonenshine for their time and guidance during the course of my research and the writing of this paper, Misses Mary Keith Garrett and Pat Gammon of the Dismal Swamp Mational Wildlife Refuge for their help in locating the sweetgum, Mr. Christopher Lambert of the Virginia Division of Forestry for donating 100 loblolly pine seedlings to the study, Edward Layton for his assistance in constructing the plant bed cover, and most of all, to my parents, for, although they did not understand my work, it was their support and encouragement which sustained me throughout my graduate career.

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### TNTRODUCTION

Many attempts have been made to obtain accurate measurements of transpiration rates. Some of the earliest laboratory techniques included: potometers, potted plant or gravimetric methods, closed container and cuvette methods (Salisbury and Ross, 1969). One of the first field studies was conducted by Thornthwaite (1951) who utilized the vapor method and evapotranspirometer. Other field measurements included the tent method, lysimeters and detached leaf method (Salisbury and Ross, 1969). Most laboratory and field methods attempt to utilize a plant out of its environment and, consequently, are subject to gross errors due to disturbance of the entire plant or one of its parts. The study of transpiration in trees has presented even greater difficulties and little research has been done on this subject. Musin (1969), Pautova (1971) and Penska (1971) utilized methods similar to those described above to measure transpiration in trees under field conditions. Ito (1970) was the first to use the controlled conditions of a plant growth chamber to study the effect of various environmental factors on transpiration rates using Pinus densiflora and P. thunbergii.

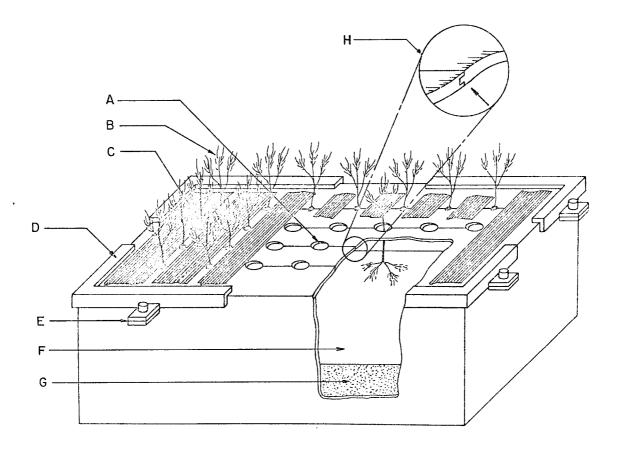
A significant advance in technique was made by Woods and O'Neal (1965) who used tritiated water as a tracer. These workers introduced it into the soil of a North Carolina forest tract and measured the amount of labelled water transpired by the trees and collected in polyethylene bags placed over the branches. Difficulties arose, however, when temperature increases in the collecting bags introduced errors by modifying the transpiration rates. Kline et al. (1970) further advanced the method by injecting tritiated water directly into the trunks of some tropical trees and measuring the activity levels in the leaf water. Kline et al.

(1972) used this same technique in succeeding experiments in attempts to measure the transpiration rates in coniferous forests.

This study has integrated the rapid tritium tracer method with the controlled environment chamber approach to produce a measurement of transpiration which is fast, efficient and accurate. Transpiration was measured in four experiments using sweetgum (<u>Liquidambar styraciflua L.</u>) and loblolly pine (<u>Pinus taeda L.</u>), two tree species native to the Virginia coastal plain. Rates were determined utilizing tritiated water as a tracer at two different water vapor pressure deficits in a controlled environment growth chamber.

### MATERIALS AND METHODS

Sweetgum seedlings were removed from a fallow field on the outskirts of the Dismal Swamp, Suffolk, Virginia; the loblolly pine seedlings were obtained from the Virginia Division of Forestry. The trees were removed with the soil intact, placed in polyethylene trash cans and transported to the greenhouse where they were watered with tap water and allowed to adjust to transplant shock for one week. Subsequently, they were removed from the soil and taken to the laboratory in tap water where the roots were washed thoroughly. The trees were then replanted in a black, plexiglas plant bed containing acid-washed quartz sand and 6 liters of a standard mutrient solution (Newcomb et al. 1964). The bed was sealed with a slatted, tongue and groove, aluminum top; the seams were covered with aluminum duct tape and plasticine clay was positioned around the base of each tree to complete the seal (Fig. 1). The trees were allowed to remain in this condition until the following morning. At approximately 0900 hours of this morning, the plant bed was placed in a Sherer Model CEL 37-14® plant growth chamber and a 2 millicurie (mCi) spike of tritiated water was added to the nutrient solution. A control bed containing 6 liters of distilled water was placed next to the nutrient bed in the chamber. This bed was not covered and remained exposed to the atmosphere of the chamber. The door of the growth chamber was then sealed, using General Electric RTV® electrical adhesive and sealant. The collection period began at 1500 hours the same day for sweetgum and 1200 hours for pine and continued at 3 hour intervals for a period of 48 hours. Samples were made of leaves, mutrient solution, control bed water and chamber air. Approximately 7.2 cubic feet/minute of chamber FIGURE 1. Diagramatic representation of the plant bed: A) opening for insertion of small tree stem, B) young tree,
C) Aluminum duct tape to seal seams,
D) plexiglas supports to keep the top firmly in place, E) support clamps,
F) spiked hydroponic nutrient solution,
G) acid-washed sand, H) tongue-and-groove edge of slatted Aluminum top.



air was drawn out for a period of 8 minutes by a vacuum pump which led to a series of 3 Beckman Value Vials <sup>®</sup> in a dry ice and acetone bath.

All samples were duplicated and analyzed for activity using liquid scintillation techniques.

Aliquots of 0.5 mls of mutrient solution, control bed water and chamber atmospheric samples were mixed with 10 mls of Amersham-Searle PCS® cocktail. Leaf samples, (0.1 gm for sweetgum and 0.05 gm for pine), were ground, digested with 50 ul of cellulase solution and quick frozen to disrupt the cell walls. Subsequently, they were thawed and treated with 2 mls of Amersham-Searle NCS® tissue solubilizer and held at 45°C for at least 45 minutes to complete digestion. Sample preparation was completed with the addition of 10 mls of PCS®. Activity was measured with a Beckman LS 250® liquid scintillation detector using a wide window tritium isoset and programmed for 1% error. Each sample was counted 6 times to reduce errors from chemoluminescence and color quench.

Chamber conditions for the 1.84 V.P.D. experiment were 70°F and 90% RH while the 6.74 V.P.D. experiment utilized a temperature of 77°F and a relative humidity of 76%. The first conditions correspond to a typical June day for Norfolk, Virginia, the second, to a typical July day at this same location (U.S.N.O.A.S., 30 year average). In each instance, the plants were subjected to a constant illumination of about 1310 foot candles from both fluorescent and incandescent sources.

A 3 level nested analysis of variance was done to determine the difference between transpiration rates in the 2 species and the 2 sets of environmental conditions. A single a priori test was made which compared the species to one another. Transpiration rates were calculated for sweetgum and loblolly pine under the controlled conditions.

### RESULTS

Mutrient solutions exhibited decreased radioactivity with time in all cases (Fig. 2). Activity declined more rapidly during the sweetgum studies than during the pine studies in which tritium levels were approximately 3 times greater.

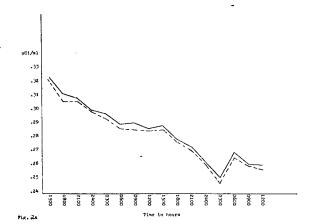
Control bed water increased in activity in all cases (Fig. 3). However, sweetgum controls increased more rapidly than pine controls.

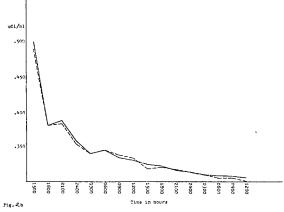
Air tritium levels fluctuated greatly in all studies (Fig. 4). In the 1.84 V.P.D. sweetgum experiment, air tritium concentrations exhibited a high initial value of 2.46 x 10<sup>-3</sup> uCi/ml which decreased almost 80% in the following 6 hours to 5 x 10<sup>-4</sup> uCi/ml. Subsequently, air activity generally leveled off and then began to exhibit a series of peaks at 6 hour intervals. A similar but more strongly defined 6 hour cycle of peaks appeared in the 6.74 V.P.D. sweetgum experiment after an initial erratic period (Fig. 5b). In both the 1.84 and the 6.74 V.P.D. pine studies, air tritium levels initially dropped and then increased throughout the remainder of the experiment (Fig. 5c-d). No evidence of a cycle was apparent.

Sweetgum leaves samples during the 1.84 V.P.D. study contained varying amounts of tritium (0 to .037 uCi/gm)(Fig. 5a). Leaves sampled during the 6.74 V.P.D. experiment contained tritium concentrations 3 times greater than those of the previous study (Fig. 5b). A cyclic pattern became noticeable toward the end of this study. A set of peaks and troughs with the same 6 hour pattern also appeared.

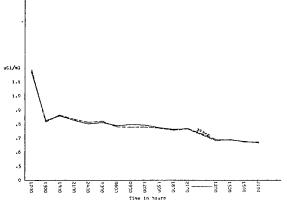
Pine needles in both 1.84 and 6.74 V.P.D. experiments revealed a 9 hour cycle of peaks (Fig. 5c-d). This cycle was not matched by air values. In both studies, tritium levels in the pine needles appeared

FIGURE 2. Tritium concentrations of the mutrient solution in uCi/ml in the: a) 1.84 V.P.D. sweetgum experiment, b) 6.74 V.P.D. sweetgum experiment, c) 1.84 V.P.D. pine experiment, d) 6.74 V.P.D. pine experiment.









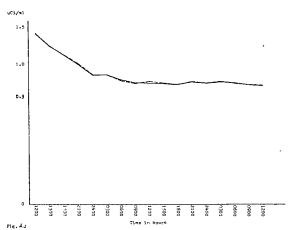


FIGURE 3. Activity of the control bed in uCi/ml in the: a) 1.84 V.P.D. sweetgum experiment, b) 6.74 V.P.D. sweetgum experiment, c) 1.84 V.P.D. pine experiment, d) 6.74 V.P.D. pine experiment.

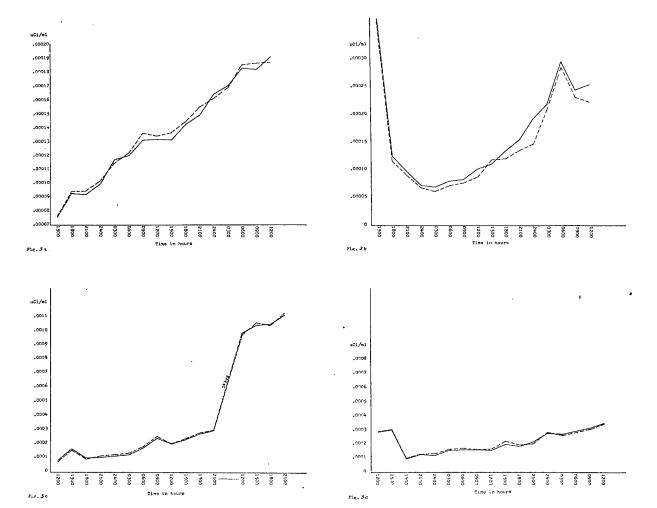
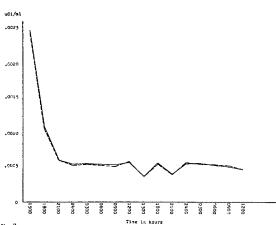
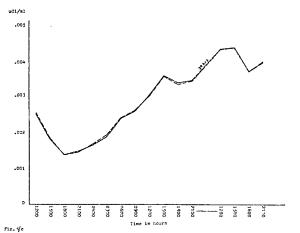


FIGURE 4. Atmospheric tritium concentrations in uCi/ml in the: a) 1.84 V.P.D. sweetgum experiment, b) 6.74 V.P.D. sweetgum experiment, c) 1.84 V.P.D. pine experiment, d) 6.74 V.P.D. pine experiment.







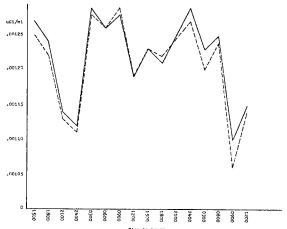


Fig. 45

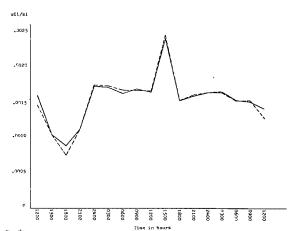
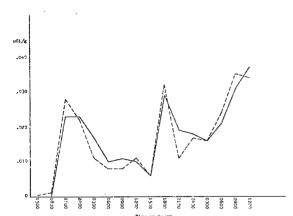
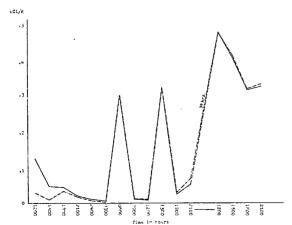


fig. 4a

- FIGURE 5. Leaf sample activity in uCi/gm from the:
  - a) 1.84 V.P.D. sweetgum experiment,
  - b) 6.74 V.P.D. sweetgum experiment,
  - c) 1.84 V.P.D. pine experiment, d) 6.74
  - V.P.D. pine experiment.



Pig. 5 a



Pig. 5 c

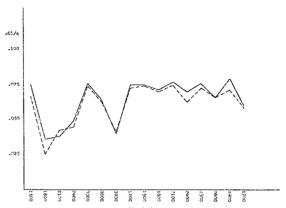
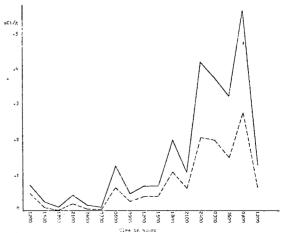


Fig. 5b Time in hou



F14.50

to reach their greatest concentrations every 9 hours. Two peaks occurred simultaneously in both pine experiments (at 1200 and 0600 hours).

A three level nested analysis of variance of these data showed that there was a highly significant difference between the two species at the 95% level as did an a priori test at the 90% level (Table 1). It also revealed a highly significant difference between the two sets of environmental conditions. The final F test showed that there was no significant difference in sample preparation at the 95% level.

Transpiration rates were calculated for each species under the controlled conditions (Table 2). It was found that the transpirational rate of sweetgum was 5 times greater than that of pine at the lower V.P.D. and 8 times greater at the higher V.P.D. Transpiration rates for both species increased at the higher V.P.D. In the sweetgum experiment, rates at the 6.74 V.P.D. were 3 times greater than that of the 1.84 V.P.D. while pine rates were twice as high at the 6.74 V.P.D.

It must be noted that the 1.84 V.P.D. pine experiment was not carried through the same length of time as the others even though there were 16 sampling values. After the initial 36 hours, the experiment was halted for a period of 39 hours and then resumed for an additional 12 hours.

#### DISCUSSION

Transpiration rates were found to vary between species; these rates were also found to increase in response to the greater environmental stress imposed upon them. Verification was provided when the data was subjected to a 3 level nested analysis of variance. The F test among major groups (species) indicated a difference in transpiration rates between the 2 species (P = 0.05, F = 45.245) as did an a priori test on the 90% level. A highly significant value was obtained which substantiated the idea of specificity of transpiration rates. Each species, depending upon its physiology, will transpire more or less than another under the same conditions. The F test among subgroups (V.P.D.s) confirmed the difference in transpiration values under the varying V.P.D.s. Both species responded to the greater stress of the 6.74 V.P.D. by increasing their transpiration rates as expected on the basis of their known autecology. In both cases, values for activity in control and leaf samples were consistently higher at the higher V.P.D. conditions.

Equally conclusive evidence for the difference in transpiration rates was obtained when rates were calculated for each species under the different V.P.D.s. Overall transpiration rates were calculated for the 48 hour testing period. It was found that the measured transpiration rate of sweetgum was 5 times greater at the lower V.P.D. than that of pine and 8 times greater at the higher V.P.D. Water taken up by the gum seedlings was quickly transpired and resulted in a high transpiration rate (4.95 ml/hr/gm at the 1.84 V.P.D. and 15.99 ml/hr/gm at the 6.74 V.P.D.). Water absorbed by the pine seedlings may have remained within the stomatal pits and resulted in an increase in radioactivity but not in the transpiration rate (1.03 ml/hr/gm at the 1.84 V.P.D. and 2.19

ml/hr/gm at the 6.74 V.P.D.). The data also revealed that both species transpired more heavily under the 6.74 V.P.D. than the 1.84 V.P.D.

These differences are in keeping with the individual species' morphology.

The stomata and guard cells of sweetgum are located on the surface of the leaf and so present little or no resistance to fluid evaporating to the surface. On the other hand, loblolly pine exhibits xeromorphic adaptions and their structures are so designed as to reduce water loss. Fluid taken up by the tree probably accumulates in the sunken stomatal pits with a small loss to the atmosphere and consequently, a lower transpiration rate.

A closer look at individual samples further supports these hypotheses. Mutrient solution values in all cases displayed a general decrease with time. This was a direct result of the uptake of nutrient solution by the transpiring trees. Since the experimental bed was thoroughly sealed, there was no other possible way in which the nutrient solution could have escaped but through transpiration. Since all the experiments were begun at approximately the same time with the same amount of nutrient solution and spike, the higher nutrient pine values correlate to a slower uptake. This may have had an indirect bearing on the pine transpiration rate.

The control solutions all gained activity throughout the experiments. In the 6.74 V.P.D. experiments, sweetgum values at the end of the collection period were 6 times higher than initial activity values while pine values were only 3 times higher. This suggests a higher air tritium concentration which resulted from the higher transpiration rate.

If sweetgum is comparable to red maple in biomass, 1 hectare of

this species in a mixed forest would yield 2300 1/hr at a 1.84 V.P.D. Under more severe environmental stress, it would transpire more than 7500 1/hr. This could be a significant factor in cloud and fog development. On the other hand, a similar population of pine in a mixed forest would transpire only 1800 1/hr at a 1.84 V.P.D. and 3800 1/hr under the greater stress. Where pine only doubled its rate, sweetgum more than tripled the volume of water lost, thus demonstrating the differing reactions of species to and upon their surrounding environment.

Another finding resulting from these experiments was the existence of transpiration cycles. These cycles proceeded regularly with no response to external factors, possible suggesting that they may be endogenous rhythms. Both air and leaf values support this idea.

Air activity was found to vary greatly from one sampling time to the next. In the sweetgum experiments, these values exhibited a 6 hour cycle beginning at 1200 hours in the 1.84 V.P.D. experiment and 0300 hours in the 6.74 V.P.D. experiment. The sharp peaks every 6 hours suggest a cyclical transpiration rate which reaches its maximum within this time period. Air values for pine did not exhibit any type of cycle. Air samples increased in activity with time in no apparent pattern.

Leaf samples taken during the 1.84 V.P.D. sweetgum experiment reveal varying amounts of tritium in no particular time sequence. They do not agree and cannot be compared with the values obtained during the 6.74 V.P.D. experiment which were 3 times higher. These latter values reflect the 6 hour cycle mentioned earlier in connection with air tritium concentrations. They are directly opposed to air values suggesting a time lag. When tritium concentrations are greatest in the leaves as

the result of a high transpiration rate, it may take some time for activity to build up in the air. By this time, the plants may experience a rest period and a subsequent decrease in transpiration while the air has reached its peak.

The opposite is true for pine. An increase in activity in pine needles does not reflect a higher transpiration rate but an accumulation of spiked water in the sunken stomatal pits. The pine also exhibited a cycle but with a different period. Activity in pine needles reached its maximum at 9 hour intervals in both experiments. However, this same cycle was not found in the chamber air, perhaps because the transpiration rate of pine was too low to saturate the air and produce the peaks.

It appears that the plants do transpire on a cyclical basis with certain periods during which they attain a maximum rate and others when they "rest". The erratic values first obtained could be the result of the trees' response to the shock of removal from soil to a sand culture environment and subsequent acclimation. After the initial trauma, latter results do point to the existence of a regular cycle. Gallagher and Daiber (1973) have reported endogenous photosynthetic rhythms in lower plants. The transpiration cycles demonstrated in loblolly pine and sweetgum could be the result of a similar process since guard cell photosynthesis effects stomatal regulation. The length of the cycles will vary from species to species depending upon the individual's physiology. These physiological and morphological differences are the principle reasons for the occurrence of specific transpiration rates and probably regulate the degree to which a tree may respond to changing environmental conditions.

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### APPENDIX I

Sequence of steps to determine transpiration rates using the tritium tracer method.

CPM - nutrient solution

CPM - actual nutrient solution

$$\frac{\text{CPM - actual}}{\text{efficiency of sample}} = \frac{X \text{ DPM}}{100\% \text{ efficiency}}$$

$$X = \text{DPM - sample}$$
(2)

$$\frac{DPM - sample}{.5 \text{ ml} - sample size} = DPM/ml$$
 (3)

$$\frac{DFM/ml - sample}{2.22 \times 10^{\circ} DFM/uCi} = uCi/ml - sample$$
 (4)

$$\frac{\text{DPM} - \text{sample}}{4.44 \times 10^9} \times 100\% = \% \text{ spike} - \text{sample}$$
 (5)

To obtain rates:

Obtain geometric mean of all values obtained in above manner (8)

geometric mean
original spike = ml (spiked water)/hr

ml (spiked water)/hr
% of dry leaf weight = ml(spiked water)/hr/gm (leaf tissue)

ml (spiked water)/hr/gm(leaf tissue)
% of spiked water x 100% total water =
% of spiked water

(11)

ml (actual water)/hr/gm (leaf tissue)

APPENDIX II

Activity of all samples collected during the 1.84 V.P.D. sweetgum experiment. The upper number represents the average of the first count, the lower number, the second.

Time (EST)	Nutrient	Control	Air	Leaves
hours	uCi/ml	uCi/ml	uCi/ml	uCi/ml
1500	•324	7.55 x 10 <sup>-5</sup>	2.46 x 10 <sup>-3</sup>	0
	•322	7.63 x 10 <sup>-5</sup>	2.45 x 10 <sup>-3</sup>	.0003
1800	.312 .307	9.33 x 10 <sup>-5</sup> 9.40 x 10 <sup>-5</sup>	$1.09 \times 10^{-3}$ $1.08 \times 10^{-3}$	0.001
2100	.309	$9.18 \times 10^{-5}$	$6.10 \times 10^{-4}$	.023
	.307	$9.41 \times 10^{-5}$	$6.12 \times 10^{-4}$	.028
2400	.300	9.95 x 10 <sup>-5</sup>	5.43 x 10 <sup>-4</sup>	.023
	.299	1.02 x 10 <sup>-4</sup>	5.38 x 10 <sup>-4</sup>	.022
0300	.298	1.17 x 10 <sup>-4</sup>	5.56 x 10 <sup>-4</sup>	.017
	.294	1.14 x 10 <sup>-4</sup>	5.52 x 10 <sup>-4</sup>	.011
0600	.290	1.20 x 10-4	5.36 x 10 <sup>-4</sup>	.010
	.287	1.21 x 10-4	5.29 x 10 <sup>-4</sup>	.008
0900	•291	1.31 x 10 <sup>-4</sup>	5.31 x 10 <sup>-4</sup>	.011
	•286	1.37 x 10 <sup>-4</sup>	5.16 x 10 <sup>-4</sup>	.008
1200	.287	1.32 x 10 <sup>-4</sup>	5.77 x 10 <sup>-4</sup>	.010
	.285	1.34 x 10 <sup>-4</sup>	5.79 x 10 <sup>-4</sup>	.011
1500	.289	1.32 x 10-4	3.74 x 10 <sup>-4</sup>	.006
	.286	1.37 x 10-4	3.74 x 10 <sup>-4</sup>	.006
1800	•279	1.43 x 10 <sup>-4</sup>	5.70 x 10 <sup>-4</sup>	.029
	•277	1.44 x 10 <sup>-4</sup>	5.68 x 10 <sup>-4</sup>	.032
2100	.274	1.49 x 10 <sup>-4</sup>	4.05 x 10 <sup>-4</sup>	.019
	.271	1.55 x 10 <sup>-4</sup>	4.02 x 10 <sup>-4</sup>	.011
2400	.263	1.64 x 10 <sup>-4</sup>	5.72 x 10 <sup>-4</sup>	.018
	.261	1.62 x 10 <sup>-4</sup>	5.74 x 10 <sup>-4</sup>	.017
0300	.251	1.70 x 10 <sup>-4</sup>	5.66 x 10 <sup>-4</sup>	.016
	.248	1.68 x 10 <sup>-4</sup>	5.50 x 10 <sup>-4</sup>	.016
0600	.269	1.83 x 10 <sup>-4</sup>	5.22 x 10 <sup>-4</sup>	.021
	.265	1.85 x 10 <sup>-4</sup>	5.30 x 10 <sup>-4</sup>	.024

0900	.262	1.82 x 10	5.08 x 10	.031
	.260	1.86 x 10	5.14 x 10	.035
1200	.261	1.91 x 10	4.76 x 10	.037
	.257	1.87 x 10	4.76 x 10	.034

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APPENDIX III

Activity of all samples collected during the 6.74 V.P.D. sweetgum

experiment. The upper number represents the average of the first count, the lower number, the second.

Time (EST)	Nutrient	Control	Air	Leaves
	uCi/ml	uCi/ml	uCi/ml	uCi/ml
1500	.500	1.56 x 10 <sup>-3</sup>	1.27 x 10 <sup>-3</sup>	.075
	.490	1.53 x 10 <sup>-3</sup>	1.25 x 10 <sup>-3</sup>	.067
1800	•380	$1.25 \times 10^{-4}$	$1.24 \times 10^{-3}$	.036
	•380	$1.14 \times 10^{-4}$	$1.22 \times 10^{-3}$	.025
2100	.388	9.64 $\times 10^{-5}$	$1.14 \times 10^{-3}$	.038
	.384	8.84 $\times 10^{-5}$	$1.13 \times 10^{-3}$	.043
2400	•358	$7.00 \times 10^{-5}$	1.12 x 10 <sup>-3</sup>	.049
	•354	$6.66 \times 10^{-5}$	1.11 x 10 <sup>-3</sup>	.045
0300	.340	6.67 x 10 <sup>-5</sup>	1.29 x 10 <sup>-3</sup>	.076
	.340	6.20 x 10 <sup>-5</sup>	1.28 x 10 <sup>-3</sup>	.074
0600	• 346	8.02 x 10 <sup>-5</sup>	1.26 x 10 <sup>-3</sup>	.064
	• 346	7.20 x 10 <sup>-5</sup>	1.26 x 10 <sup>-3</sup>	.063
0900	•334	8.60 x 10 <sup>-5</sup>	$1.28 \times 10^{-3}$	.040
	•338	7.60 x 10 <sup>-5</sup>	$1.29 \times 10^{-3}$	.041
1200	•330	1.20 x 10 <sup>-4</sup>	$1.19 \times 10^{-3}$	.075
	•333	8.75 x 10 <sup>-5</sup>	$1.19 \times 10^{-3}$	.073
1500	.324	1.19 x 10 <sup>-4</sup>	$1.23 \times 10^{-3}$	.075
	.318	1.21 x 10 <sup>-4</sup>	$1.23 \times 10^{-3}$	.074
1800	.322	1.34 x 10 <sup>-4</sup>	$1.21 \times 10^{-3}$	.072
	.321	1.28 x 10 <sup>-4</sup>	$1.22 \times 10^{-3}$	.070
2100	.317	1.51 x 10 <sup>-4</sup>	$1.25 \times 10^{-3}$	.077
	.318	1.39 x 10 <sup>-4</sup>	$1.23 \times 10^{-3}$	.075
2400	•314	1.89 x 10 <sup>-4</sup>	$1.29 \times 10^{-3}$	.070
	•314	1.44 x 10 <sup>-4</sup>	$1.27 \times 10^{-3}$	.063
0300	.310	2.16 x 10 <sup>-4</sup>	1.23 x 10 <sup>-3</sup>	.076
	.310	2.09 x 10 <sup>-4</sup>	1.20 x 10 <sup>-3</sup>	.073
0600	.308	2.92 x 10 <sup>-4</sup>	$1.25 \times 10^{-3}$	.066
	.306	2.81 x 10 <sup>-4</sup>	$1.24 \times 10^{-3}$	.066

0900	.308	2.42 x 10 <sup>-4</sup>	1.10 x 10 <sup>-3</sup>	.079
	.306	2.29 x 10 <sup>-4</sup>	1.06 x 10 <sup>-3</sup>	.072
1200	•306	$2.52 \times 10^{-4}$	1.15 x 10 <sup>-3</sup>	.060
	•300	$2.40 \times 10^{-4}$	1.14 x 10 <sup>-3</sup>	.058

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APPENDIX IV

Activity of all samples collected during the 1.84 V.P.D. pine experiment. The upper number represents the average of the first count, the lower number, the second.

1.07 1.08	8.27 x 10 <sup>-5</sup>		
	7.49 x 10 <sup>-5</sup>	$2.57 \times 10^{-3}$ $2.60 \times 10^{-3}$	.128 .031
.723	1.61 x 10 <sup>-4</sup>	$1.84 \times 10^{-3}$	.049
.718	1.58 x 10 <sup>-4</sup>	$1.85 \times 10^{-3}$	.014
•754	1.04 x 10 <sup>-4</sup>	$1.40 \times 10^{-3}$	.041
•757	.977 x 10 <sup>-4</sup>	$1.40 \times 10^{-3}$	.034
.729	1.07 x 10 <sup>-4</sup>	$1.55 \times 10^{-3}$	.021
.732	1.15 x 10 <sup>-4</sup>	$1.53 \times 10^{-3}$	.018
.704	1.20 x 10 <sup>-4</sup>	$1.67 \times 10^{-3}$	.012
.708	1.24 x 10 <sup>-4</sup>	$1.70 \times 10^{-3}$	.009
.710	1.27 x 10 <sup>-4</sup>	1.93 x 10 <sup>-3</sup>	.007
.715	1.37 x 10 <sup>-4</sup>	1.98 x 10 <sup>-3</sup>	.003
.685	1.73 x 10 <sup>-4</sup>	$2.43 \times 10^{-3}$	.305
.681	1.76 x 10 <sup>-4</sup>	$2.44 \times 10^{-3}$	.303
.692	2.49 x 10 <sup>-4</sup>	$2.64 \times 10^{-3}$	.012
.678	2.56 x 10 <sup>-4</sup>	$2.66 \times 10^{-3}$	.013
.684	$2.07 \times 10^{-4}$	$3.12 \times 10^{-3}$	.007
.679	$2.07 \times 10^{-4}$	$3.07 \times 10^{-3}$	.010
.674	2.36 x 10 <sup>-4</sup>	$3.66 \times 10^{-3}$	•324
.672	2.41 x 10 <sup>-4</sup>	$3.65 \times 10^{-3}$	•322
.659	2.76 x 10 <sup>-4</sup>	3.44 x 10 <sup>-3</sup>	.028
.655	2.83 x 10 <sup>-4</sup>	3.40 x 10 <sup>-3</sup>	.032
.666	3.00 x 10 <sup>-4</sup>	3.52 x 10 <sup>-3</sup>	.054
.666	3.02 x 10 <sup>-4</sup>	3.50 x 10 <sup>-3</sup>	.071
	.718 .754 .757 .729 .732 .704 .708 .710 .715 .685 .681 .692 .678 .684 .679 .674 .672 .659 .655 .666	.718	.718

1200	.588 .584	9.83 x 10 <sup>-4</sup> 9.76 x 10 <sup>-4</sup>	$4.40 \times 10^{-3}$ $4.40 \times 10^{-3}$	.483 .482
1500	•585	$1.04 \times 10^{-3}$	$4.45 \times 10^{-3}$	.409
	•586	$1.06 \times 10^{-3}$	$4.45 \times 10^{-3}$	.415
1800	•577	$1.05 \times 10^{-3}$	$3.77 \times 10^{-3}$	.319
	•576	$1.04 \times 10^{-3}$	$3.76 \times 10^{-3}$	.321
2100	•573	1.12 x 10 <sup>-3</sup>	4.04 x 10 <sup>-3</sup>	•327
	•576	1.13 x 10 <sup>-3</sup>	4.02 x 10 <sup>-3</sup>	•335

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Activity of all samples collected during the 6.74 V.P.D. pine experiment. The upper number represents the average of the first count, the

lower number, the second.

APPENDIX V

Time (EST)	Nutrient	<b>C</b> ontrol	Air	Leaves
hours	uCi/ml	uCi/ml	uCi/ml	uCi/ml
1500	1.26	3.12 x 10 <sup>-4</sup>	1.05 x 10 <sup>-3</sup>	.028
	1.25	3.13 x 10 <sup>-4</sup>	1.05 x 10 <sup>-3</sup>	.016
1800	1.13 1.12	.996 x 10 <sup>-4</sup> 1.02 x 10 <sup>-4</sup>	.890 x 10 <sup>-3</sup>	.009 .006
2100	.987	1.31 x 10 <sup>-4</sup>	1.13 x 10 <sup>-3</sup>	.043
	.983	1.31 x 10 <sup>-4</sup>	1.13 x 10 <sup>-3</sup>	.040
2400	.832	1.26 x 10 <sup>-4</sup>	1.73 x 10 <sup>-3</sup>	.017
	.836	1.34 x 10 <sup>-4</sup>	1.73 x 10 <sup>-3</sup>	.013
0300	.840	1.63 x 10 <sup>-4</sup>	$1.71 \times 10^{-3}$	.009
	.842	1.64 x 10 <sup>-4</sup>	$1.73 \times 10^{-3}$	.012
0600	.775	1.65 x 10 <sup>-4</sup>	$1.63 \times 10^{-3}$	.127
	.778	1.71 x 10 <sup>-4</sup>	$1.68 \times 10^{-3}$	.138
0900	.727	1.58 x 10 <sup>-4</sup>	$1.69 \times 10^{-3}$	.054
	.721	1.59 x 10 <sup>-4</sup>	$1.68 \times 10^{-3}$	.054
1200	•733	1.60 x 10 <sup>-4</sup>	1.66 x 10 <sup>-3</sup>	.072
	•741	1.65 x 10 <sup>-4</sup>	1.67 x 10 <sup>-3</sup>	.078
1500	.720	2.02 x 10 <sup>-4</sup>	1.60 x 10 <sup>-3</sup>	.076
	.724	2.25 x 10 <sup>-4</sup>	1.60 x 10 <sup>-3</sup>	.080
1800	•711	1.88 x 10 <sup>-4</sup>	1.53 x 10 <sup>-3</sup>	.201
	•714	1.96 x 10 <sup>-4</sup>	1.53 x 10 <sup>-3</sup>	.216
2100	•739	2.16 x 10 <sup>-4</sup>	1.59 x 10 <sup>-3</sup>	.113
	•745	2.09 x 10 <sup>-4</sup>	1.60 x 10 <sup>-3</sup>	.120
2400	.727	2.81 x 10 <sup>-4</sup>	1.63 x 10 <sup>-3</sup>	.420
	.726	2.86 x 10 <sup>-4</sup>	1.63 x 10 <sup>-3</sup>	.416
0300	.744	2.86 x 10 <sup>-4</sup>	1.64 x 10 <sup>-3</sup>	•374
	.745	2.65 x 10 <sup>-4</sup>	1.63 x 10 <sup>-3</sup>	•400
0600	.732	7.19 x 10 <sup>-4</sup>	$1.53 \times 10^{-3}$	•321
	.727	7.07 x 10 <sup>-4</sup>	$1.52 \times 10^{-3}$	•306

0900	.705	$3.15 \times 10^{-4}$	1.51 x 10 <sup>-3</sup>	•568
	.704	$3.10 \times 10^{-4}$	1.52 x 10 <sup>-3</sup>	•554
1200	.690	$3.53 \times 10^{-4}$	1.39 x 10 <sup>-3</sup>	.132
	.692	$3.49 \times 10^{-4}$	1.37 x 10 <sup>-3</sup>	.132