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SCHOOL OF SCIENCES AND HEALTH PROFESSIONS
OLD DOMINION UNIVERSITY
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MEASUREMENT OF TRANSPIRATION IN PINUS TAEDA L. AND LIQUIDAMBAR STYRACIFLUA L. IN AN ENVIRONMENTAL CHAMBER USING TRITIATED WATER

By

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and

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Technical Report

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Co-Investigator

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ABSTRACT

Transpiration rates of loblolly pine (*Pinus taeda* L.) and sweetgum (*Liquidambar styraciflua* L.) were measured at two different atmospheric 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 into which labeled water (spike) was introduced. Samples of leaves, chamber air, spiked nutrient solution and control water were assayed for ratio-activity using liquid scintillation techniques to determine transpiration rates. The transpiration rate of sweetgum in ml./hr./gm. (4.95) was found to be 5 times greater than that of loblolly pine (1.03) at 1.84 V.P.D. and 8 times greater at 6.74 V.P.D. (15.99 for sweetgum vs. 2.19 for pine). Transpiration (based on measurements of leaf radioactivity) in both species rose with increasing deficit; however 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 required a 6 hour interval whereas the pine cycle required a 9 hour interval.

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INTRODUCTION

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 attempted to utilize a plant out of its environment and, consequently, were subject to errors of interpretation 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), Pautove (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. Following the introduction of ^3H_2O into the soil of a North Carolina forest tract, water transpired by the trees was collected in polyethylene bags placed over the branches. Labeled water content was used to determine transpiration rates. 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

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exposed to the atmosphere of the chamber. The door of the growth chamber was modified by installation of a window and a pair of access ports fitted with rubber gloves. The window was designed so as to be opened from either side. Thus, the investigator could remove samples from the chamber environment without disrupting the chamber atmosphere. The door and window were then sealed, using RTV[R] sealant. Sample collection began at 1500 hours on the first day of the sweetgum study and 1200 hours on the first day of the pine study and continued at 3 hour intervals for a period of 48 hours. Samples of chamber air, leaves, nutrient solution, control bed water were collected. Approximately 7.2 cubic feet/minute of chamber air was drawn out for a period of 8 minutes by a vacuum pump which led to a series of 3 Bechman Value Vials[R] 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 nutrient solution, control bed water and chamber atmospheric samples were mixed with 10 mls of Amersham-Searle PCS[R] 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 and thawed several times to disrupt the cell walls. Subsequently, they were thawed and treated with 2 mls of Amersham-Searle NCS[R] 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[R]. Activity was measured with a Beckman LS 250[R] liquid scintillation detector using a wide window tritium isoset and programmed for 1% error. Each sample was counted at least 6 times to reduce errors from chemoluminescence and color quench.

Two specific sets of environmental conditions were used to study transpiration of each of the 2 tree species, namely, a vapor pressure deficit of 1.84 mm Hg. and a vapor pressure deficit of 6.74 mm Hg. 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

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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.A., 30 year average). In each instance, the plants were subjected to a constant illumination of about 1310 foot candles from both flourescent 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, adjusted for the difference in the size of the original ^3H_2O spike.

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RESULTS

Nutrient solutions exhibited decreased radioactivity with time in all cases (Fig.2). Activity declined more rapidly during the sweetgum studies than during the pine studies.

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 sweetgum experiment at 1.84 V.P.D., air tritium concentrations exhibited a high initial value of 2.46×10^{-3} uCi/ml, but this decreased almost 80% in the following 6 hours to 5×10^{-4} uCi/ml. Subsequently, air activity generally leveled off and then began to exhibit a series of peak increases at 6 hour intervals. A similar but more strongly defined 6 hour cycle of peaks appeared when the chamber environment was held at 6.74 V.P.D. during the sweetgum experiment after an initial erratic period (Fig. 5b). In the pine studies at 1.84 and 6.74 V.P.D. air tritium levels initially rose, dropped precipitously, and then increased erratically throughout the remainder of the experiment (Fig. 5c-d). No evidence of a cycle was apparent.

Sweetgum leaves from trees at 1.84 V.P.D. contained varying amounts of tritium (0 to .037 uCi/gm) (Fig. 5a). Leaves from trees at 6.74 V.P.D. contained tritium concentrations 3 times greater than those from trees held at 1.84 V.P.D. (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 as that observed in the chamber atmosphere also appeared.

Pine needles from trees held at 1.84 and 6.74 V.P.D. both revealed a 9 hour cycle of peak retention of ^3H_2O, in contrast to the absence of a cyclic pattern in the chamber air. Tritium levels in the pine needles appeared to reach their greatest concentrations every 9 hours in trees held at either of the 2 chamber conditions. Two of the peaks occurred simul-

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taneously 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, based upon the amount of water present in leaf tissue (Table 2). It was found that the transpiration rate of sweetgum was 5 times greater than that of pine at 1.84 V.P.D. and 8 times greater at 6.74 V.P.D. Transpiration rates for both species increased at the higher V.P.D. In the case of the sweetgum trees, rates at the 6.74 V.P.D. were 3 times greater than at 1.84 V.P.D. while pine rates were twice as high at 6.74 as at 1.84 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

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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 trees 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 trees 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 at 6.74 than at 1.84 V.P.D. These differences are consistent with known differences in 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.

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Analysis of the labelled water changes in the nutrient solution and control bed further supports these hypotheses. Nutrient solution values in all cases displayed a general decrease with time, presumably because of uptake of nutrient solution by the transpiring trees. (Since the experimental bed was thoroughly sealed, there was no other possible way in which the ^3H_2O could have escaped). However, the amount of labelled water remaining in the nutrient solution declined much more slowly when pine trees were growing in it than when sweetgum trees were present, which agrees with the hypothesis of a slower transpiration rate for pine trees. The control bed solutions all gained radioactivity throughout the experiments. At 6.74 V.P.D., control bed values at the end of the collection period were 6 times higher than initial activity values when sweetgum trees were studied, whereas they were only 3 times higher when pine was studied. 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 l/hr at a 1.84 V.P.D., based on the results of this study. Under more severe environmental stress, it would transpire more than 7500 l/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 l/hr at a 1.84 V.P.D. and 3800 l/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 possibly suggesting that they may be endogenous rhythms. Both air and leaf values support this idea.

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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 at 1.84 V.P.D. and 0300 hours at 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 failed to show any evidence of cyclic activity.

Leaf samples taken during the 1.84 V.P.D. sweetgum experiment revealed varying amounts of tritium with 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 so much lower.

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

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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 physiological and marphological differences. These 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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TABLE 1. Statistical results of the three level nested analysis of variance conducted on the data obtained from all experiments.

	df	SS	MS	F
group (species)	1	40.155	40.155	42.245 sig.
subgroups (V.P.D.s)	2	1.775	.8875	43.822 sig.
subsubgroups (sample type)	12	466.703	38.892	1.071 not sig.
within subsubgroups	16	666.519	41.657	

df - degrees of freedom

SS - Sum of Squares

MS - Mean Square

F - F test value

sig. - significant

TABLE 2. Transpiration rates computed for sweetgum and loblolly pine under controlled conditions based on water content of leaf tissue.

Species	V.P.D.	Rate ml/hr/gm
sweetgum	1.84	4.95
sweetgum	6.74	15.99
pine	1.84	1.03
pine	6.74	2.19

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FIGURE 1. Diagrammatic representation of the sealed plant bed containing the trees and the hydroponic nutrient solution.

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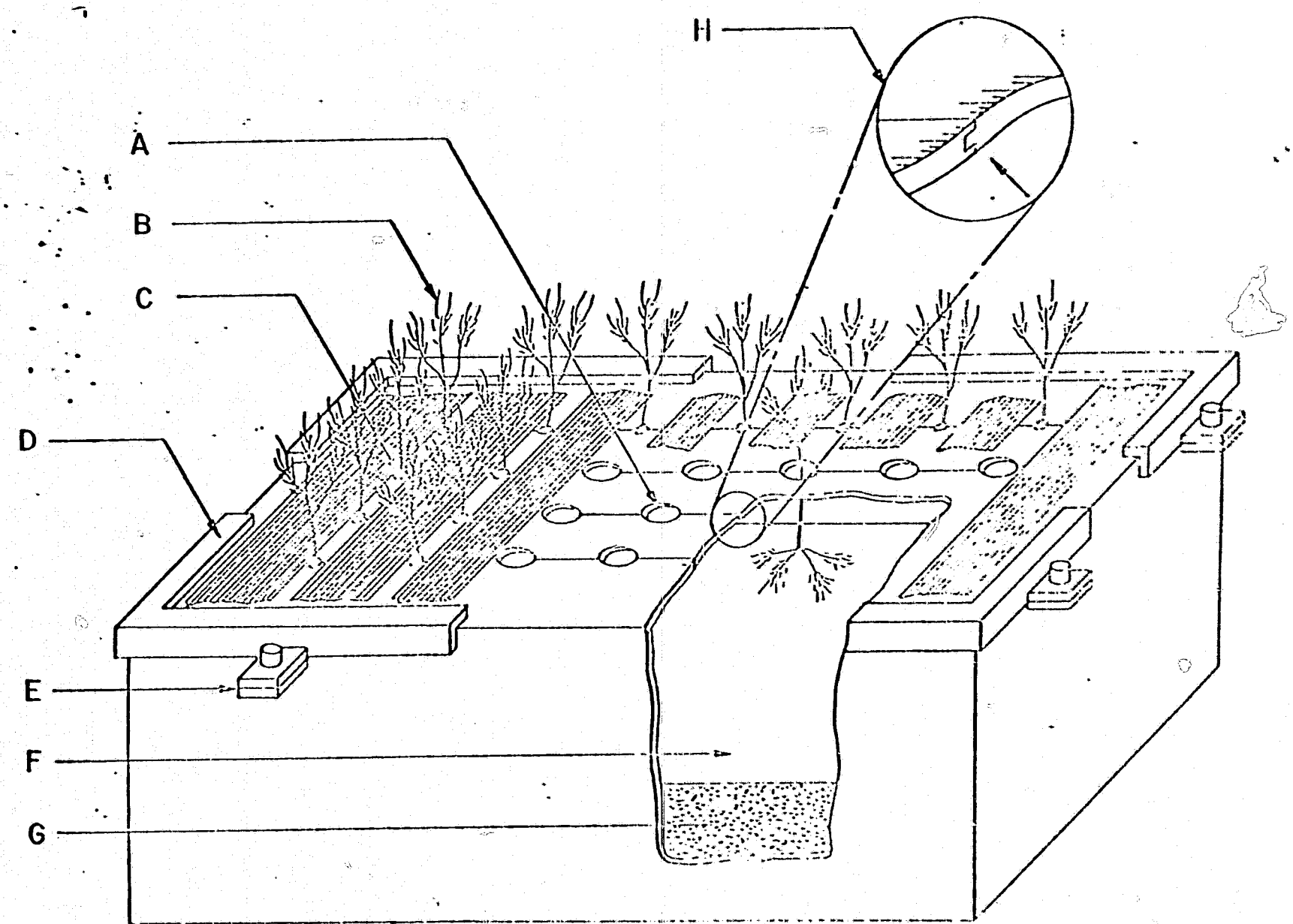
H
A
B
C
D
E
F
G

FIGURE 2. Tritium concentrations of the nutrient 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.

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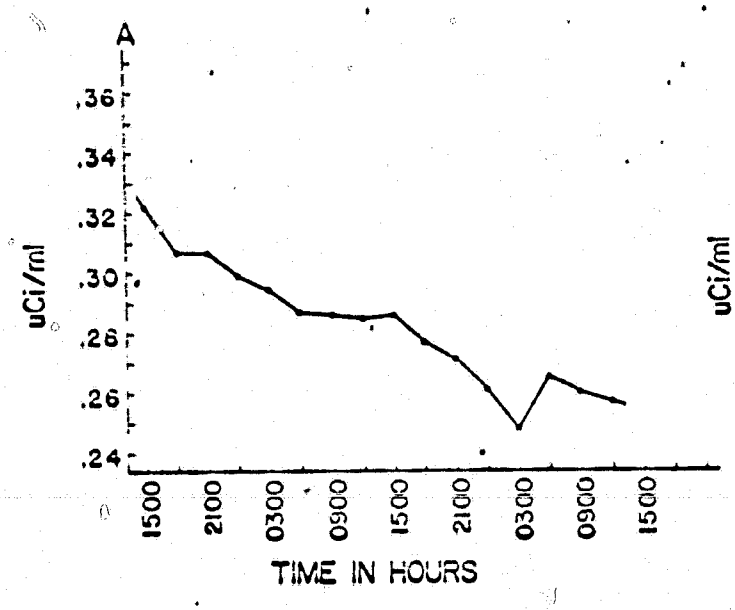
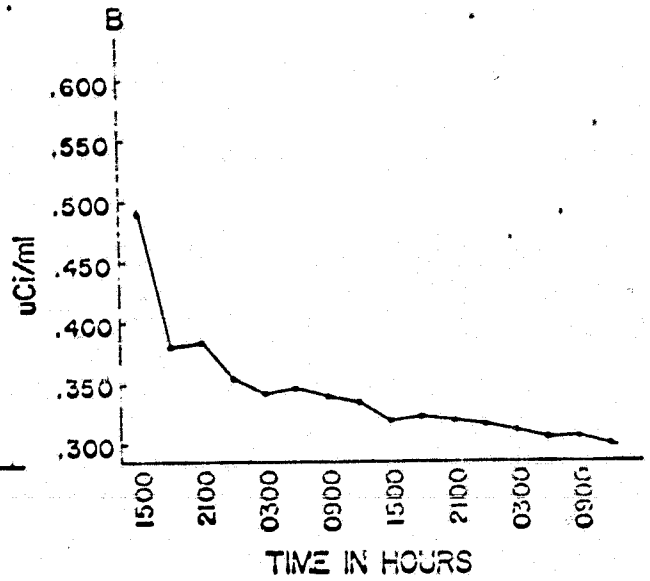
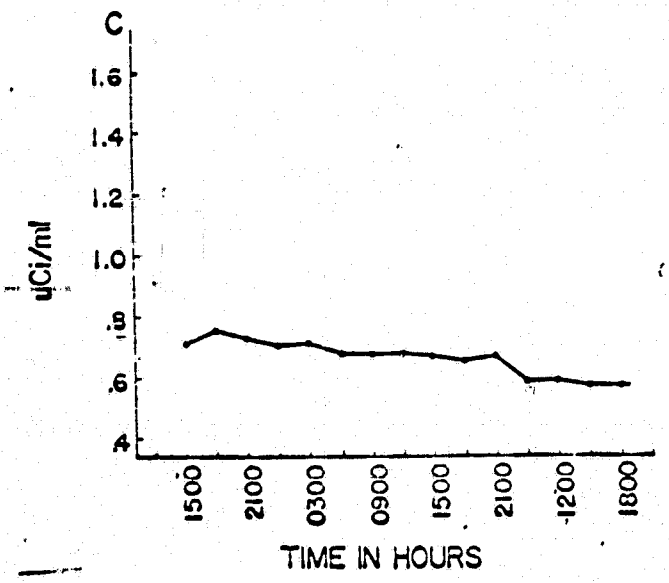

A
uCi/ml
.36
.34
.32
.30
.28
.26
.24
1500
2100
0300
0900
1500
2100
0300
0900
1500
TIME IN HOURS


B
uCi/ml
.600
.550
.500
.450
.400
.350
.300
1500
2100
0300
0900
1500
2100
0300
0900
TIME IN HOURS


C
uCi/ml
1.6
1.4
1.2
1.0
.8
.6
.4
1500
2100
0300
0900
1500
2100
1200
1800
TIME IN HOURS

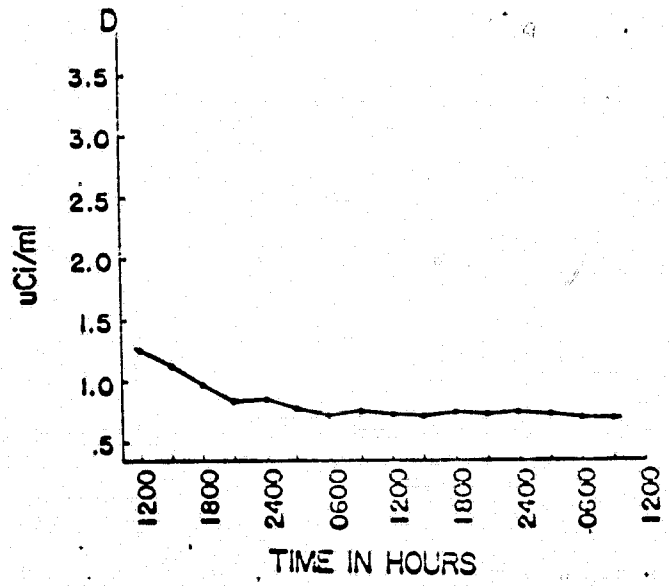

D
uCi/ml
3.5
3.0
2.5
2.0
1.5
1.0
.5
1200
1800
2400
0600
1200
1800
2400
0600
1200
TIME IN HOURS

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.

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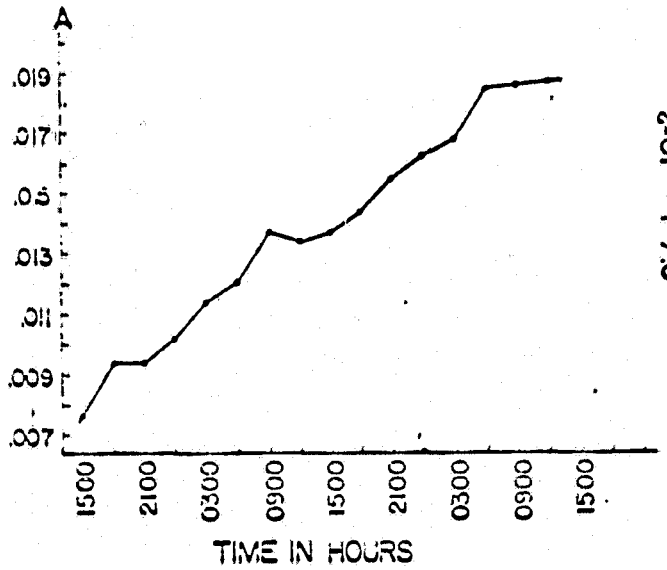
A
.019
.017
.015
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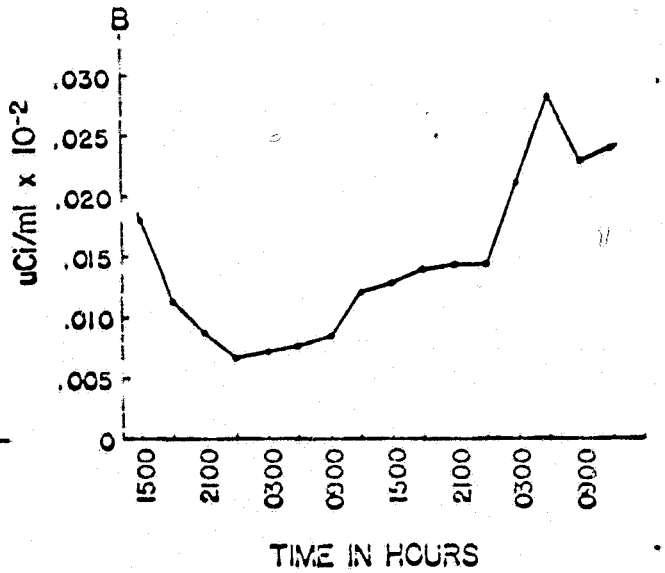
.011
.009
.007
1500
2100
0300
0900
1500
2100
0300
0900
1500
TIME IN HOURS


B
uCi/ml x 10-2
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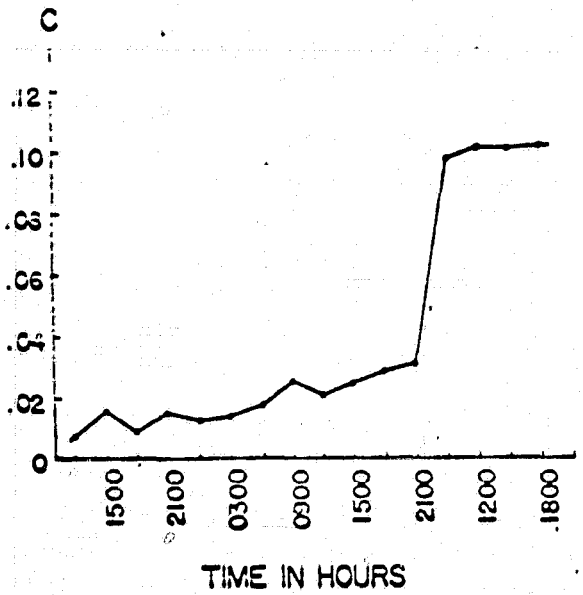
.005
0
1500
2100
0300
0900
1500
2100
0300
0900
TIME IN HOURS


C
.12
.10
.08
.06
.04
.02
0
1500
2100
0300
0900
1500
2100
1200
1800
TIME IN HOURS

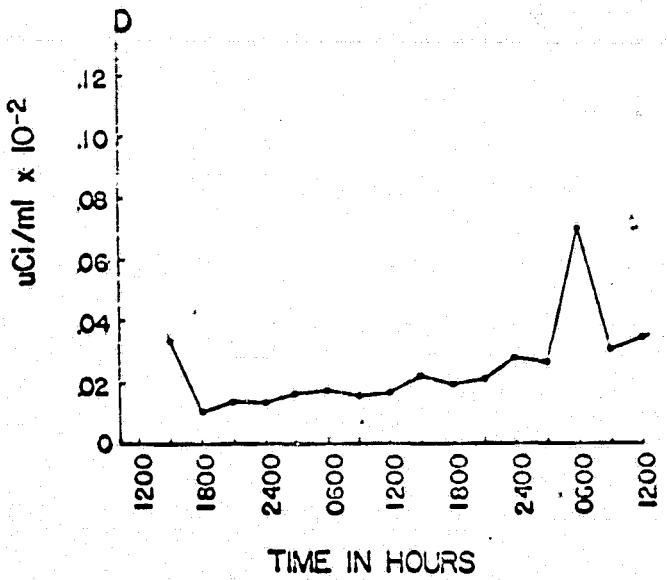

D
uCi/ml x 10-2
.12
.10
.08
.06
.04
.02
0
1200
1800
2400
0600
1200
1800
2400
0600
1200
TIME IN HOURS

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.

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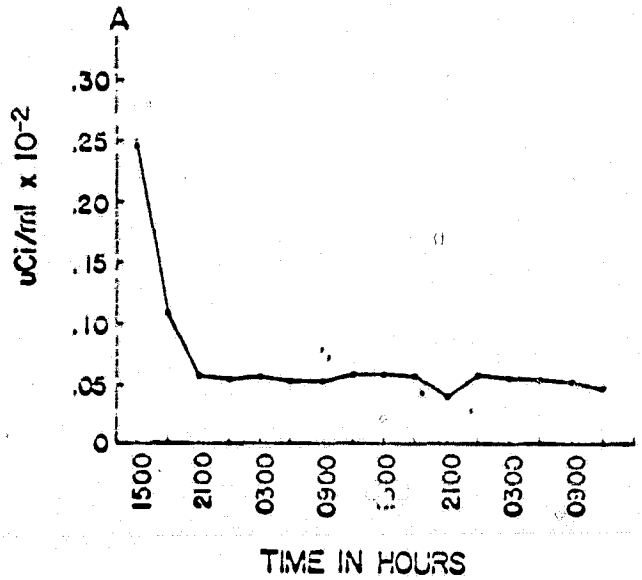
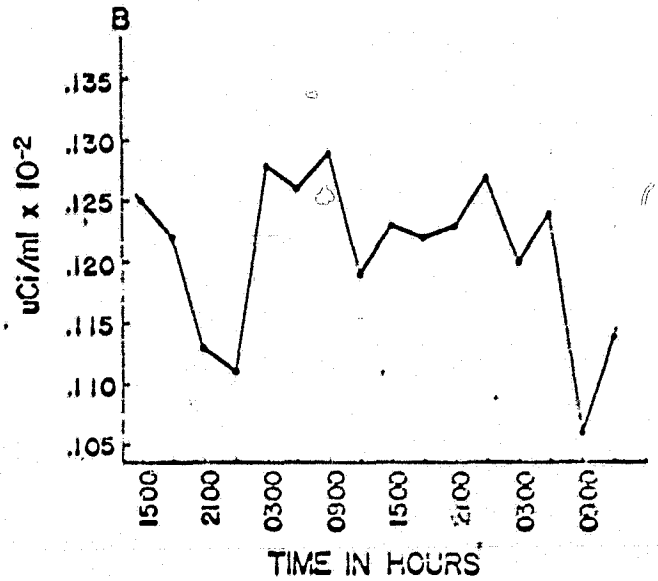

A
uCi/ml x 10-2
.30
.25
.20
.15
.10
.05
0
1500
2100
0300
0900
2100
0300
0900
TIME IN HOURS


B
uCi/ml x 10-2
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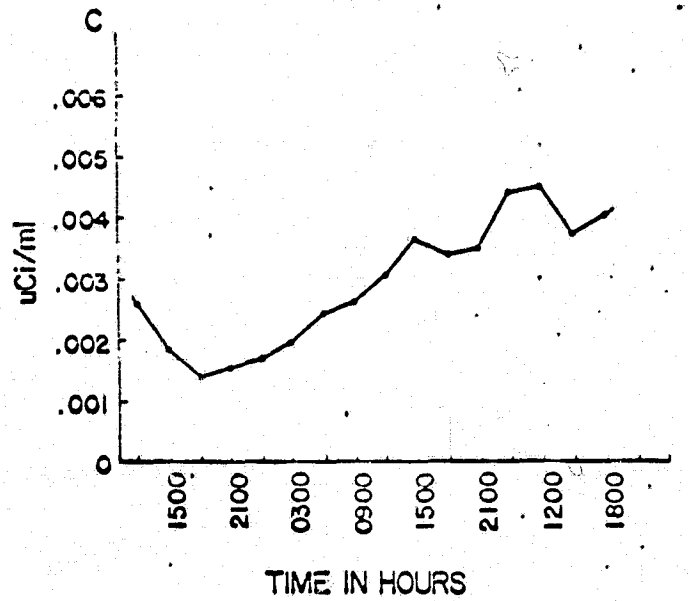
.130
.125
.120
.115
.110
.105
1500
2100
0300
0900
1500
0300
TIME IN HOURS


C
uCi/ml
.006
.005
.004
.003
.002
.001
0
1500
2100
0300
0900
1500
2100
1200
1800
TIME IN HOURS

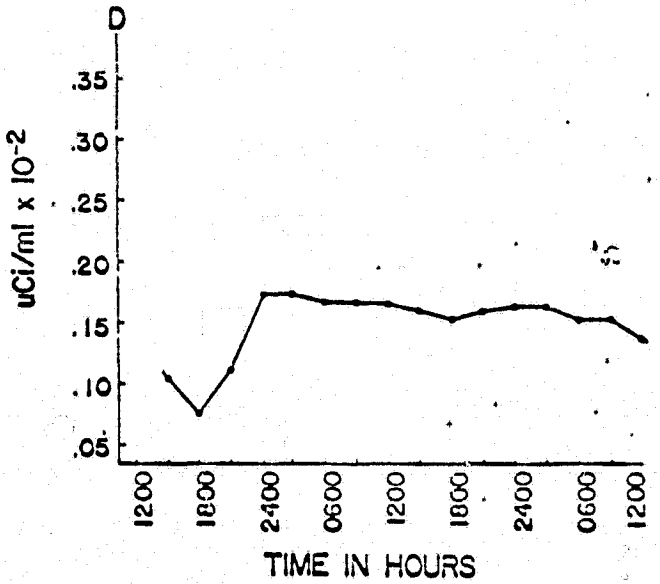
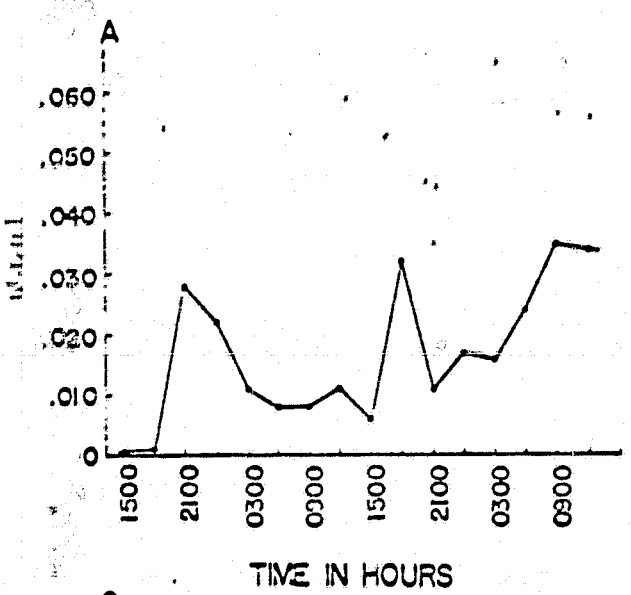

D
uCi/ml x 10-2
.35
.30
.25
.20
.15
.10
.05
1200
1800
2400
0600
1200
1800
2400
0600
1200
TIME IN HOURS

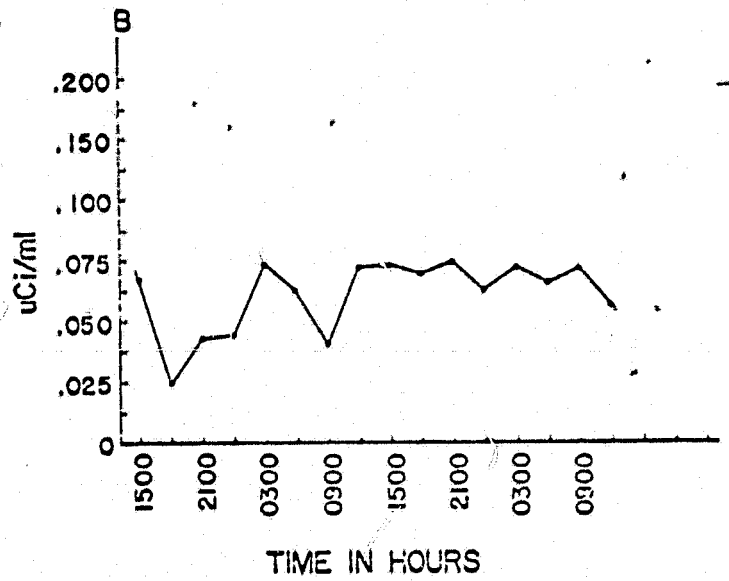
FIGURE 5. Leaf sample activity in uCi/gm from the:

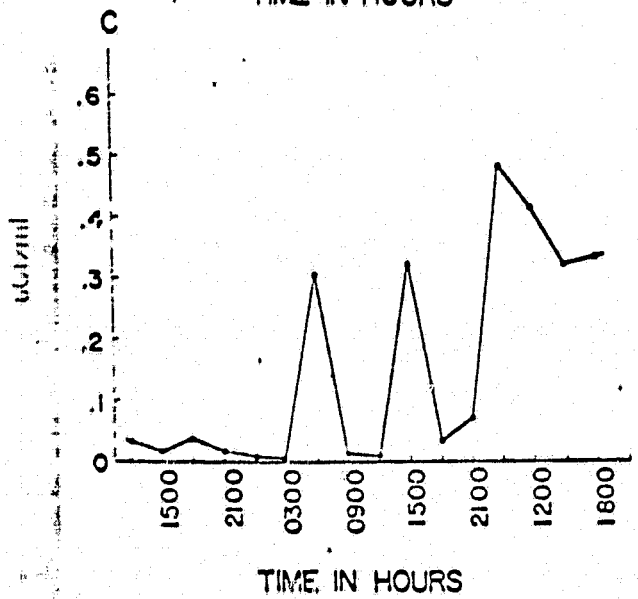
a) 1.84 V.P.D. sweetgum experiment,

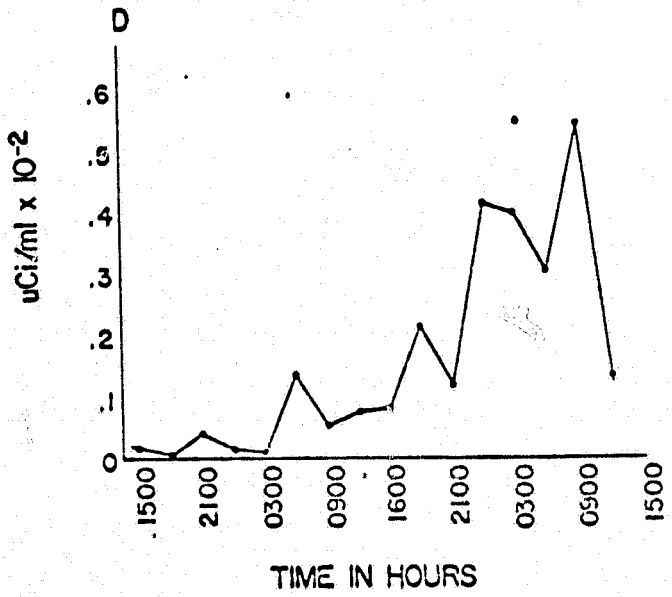
b) 6.74 V.P.D. sweetgum experiment,

c) 1.84 V.P.D. pine experiment, d) 6.74 V.P.D. pine experiment.


A
.060
.050
.040
.030
.020
.010
0
1500
2100
0300
0900
1500
2100
0300
0900
TIME IN HOURS


B
.200
.150
.100
.075
.050
.025
0
uCi/ml
1500
2100
0300
0900
1500
2100
0300
0900
TIME IN HOURS


C
.6
.5
.4
.3
.2
.1
0
1500
2100
0300
0900
1500
2100
1200
1800
TIME IN HOURS


D
.6
.5
.4
.3
.2
.1
0
uCi/ml x 10-2
1500
2100
0300
0900
1600
2100
0300
0900
1500
TIME IN HOURS