INTERNAL REPORT 103

TREE PHYSIOLOGICAL PROCESS STUDIES AT THE ALLEN E. THOMPSON RESEARCH CENTER: A 1972 PROGRESS REPORT

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INTRODUCTION

A basic knowledge of tree physiological processes is mandatory to IBP's goals of understanding and predicting values of terrestrial plant productivity and forest stand production. These goals necessitate an understanding of plant CO2 assimilation and those factors which influence assimilation rates, such as environmental factors and plant water status. During the past decade, numerous investigations at the University of Washington have formed a solid foundation on which to base such studies. Many of these investigations have been recently reviewed by Walker et al. (1972). Presently, research into these areas has proceeded under the auspices of the Coniferous Forest Biome, U. S. Analysis of Ecosystems, International Biological Program. Preliminary research and development of primary productivity investigations have been reported elsewhere (Salo et al. 1971, 1972a,b, Scott and Lassoie 1971ab, Walker et al. 1971, Lassoie and Scott 1972, Lassoie submitted). Basically, these studies have investigated and reported on cuvette design and testing, net assimilation rates as affected by temperature, light, stomatal aperture and plant water stress, stem circumference fluctuations due to internal water deficits, and the water relations of vine maple (Acer circinatum).

The following is a progress report of net assimilation, water relations, and dendrometry research conducted during 1972 in conjunction with the cooperative work being done at the Allen E. Thompson Research Center, Cedar River Watershed. Also presented are recent developments not, at this time, presented elsewhere. It must be noted that the research results presented in this paper are only preliminary in nature and represent only an example of the general types of data collected during the year. When additional information becomes available from other research groups working at the Research Center, additional analysis and interpretation will be presented. Developments noted in this paper will also be presented in more complete fashion at a later time.

METHODS

This study was conducted at the Allen E. Thompson Research Center located about 55 km southwest of Seattle at an elevation of about 1200 m in the foothills of the Washington Cascades. The Center is an intensive research site for IBP. The vegetation, climate, geology, and soils of this area have been generally described by Cole and Gessel (1968) and will not be

described in this report. The exact location of the study trees was near the lysimeter tree installation site described by Fritschen (1972). The principal study tree (tree #3) was a dominant Douglas-fir (Pseudotsuga menziesii) about 28 m tall and 41 cm in diameter at 1.4 m. Although other trees in this area representing different crown classes were also investigated, the concentration of effort was on the lysimeter tree and study tree #3. For this reason the data presented in this report are from work associated with these two trees.

Measurement of tree water status included measurements of transpiration, sap velocity, stomatal aperture, and water potential. Actual measurements of evapotranspiration (ET) were available for the lysimeter tree located about 4.5 m north of study tree #3. Description, installation, and sensitivity of this weighing lysimeter have been described by Fritschen (1972). This lysimeter enabled monitoring continuously the weight of the soil and tree, yielding a continuous absolute measurement of weight loss (evapotranspiration) or gain (precipitation and/or plant growth). Heat pulse velocity (HPV) measurements were taken automatically every half hour using techniques and a heat pulse velocity meter described in an earlier publication (Scott and Lassoie 1971b). Measurements were taken from the north side of the stem (tree #3) at a height of about 1.5 m and a depth of 10 mm into the xylem. These measurements were used to estimate stem sap velocities. Branch water potentials (Ps) were estimated periodically during a data collection period using the pressure chamber technique (Scholander et al. 1965). At least three separate measurements were taken, corrected for hydrostatic pressure differences (all to zero height from soil surface), and averaged for each sample period. Relative stomatal apertures were estimated using the needle infiltration technique (Scholander et al. 1965). At least three separate measurements were taken, corrected for hydrostatic pressure differences (all to zero height from soil surface), and averaged for each sample period. Relative stomatal apertures were estimated using the needle infiltration technique (Fry and Walker 1967). At least five stomatal infiltration pressure (SIP) measurements were taken per sample period and averaged.

Net assimilation (NA) measurements were taken using thermoelectrically cooled cuvettes and an open system which has been described in other publications (Salo et al. 1971, 1972a,b). For these studies two cuvettes were used, one located at about 17 m and the other near 20 m of the north side of the crown (tree #3). Measurements were taken semi-continuously during a data collection period. These measurements were used to calculate net assimilation rates based on a needly dry weight basis. Besides data collection, further developments were made in the area of net assimilation measurement techniques (see Appendix A).

Measurements of diurnal fluctuations in tree stem circumference (CIRCUM) were taken every hour using automated band dendrometers (Scott and Lassoie 1971a, Lassoie submitted). Bands were located at about 1.4 and 9.0 m on the study tree (#3). These bands along with other located on numerous other trees throughout the study site were monitored and recorded automatically once every hour using a 100-channel data recording system (see Appendix B). Further development of a new dendrometry system are described in Appendix B.

Standard meteorological data were collected and processed by Dr. L. J. Fritschen in conjunction with micro-meteorological studies being conducted at the site (Fritschen 1972). These data included measurements of solar and net radiation, dew point, wind speed and direction, air temperature, and precipitation at the top of the canopy. These types of data were also taken at various heights in the canopy by Mr. P. C. Doraiswamy. At the time of writing (December 1972), much of this data had not been processed and therefore, was not available. These data will be incorporated with our findings as soon as they become available.

Needle temperatures (T_L) inside the cuvettes were measured during the study periods. Measurements were made with small clip-on thermocouples (copper-constantan) whose construction and description have been described by Fry (1965).

RESULTS AND DISCUSSION

As mentioned earlier, the data presented in this paper are representative of the type of data collected during August, September, and October of 1972 at the lysimeter tree site, Cedar River Watershed. These results typify general tree responses to primarily clear and sunny days experienced during the study period.

Water loss from the tree due to an evaporative demand results in the development of internal water deficits. These deficits can cause a reduction in net assimilation rates due to stomatal closure and/or by increasing internal resistances to carbon dioxide fixation. In the middle of the summer, under periods of high tree water stress, positive net assimilation rates were essentially non-existent (Figure 1). During periods of slightly lower stresses, an early morning peak in positive net assimilation rates was observed (Figure 2). Stomata typically opened quickly early in the morning and then gradually closed throughout the remainder of the day. Higher leaf temperatures were generally associated with low net assimilation rates.

On all days reported in this paper, tree water stresses and stomatal aperture trends and magnitudes were somewhat similar. In the fall, tree water stresses were high but unlike the summer, net assimilation rates were also relatively high most of the day (Figure 3). Similar results not reported in this paper were found to occur in October. Leaf temperatures were generally lower. Until further supportive data becomes available the above discrepancies are difficult to adequately explain.

These preliminary data, however, suggest a few possibilities: Other factors (quite possibly affecting internal resistances) must be important in regulating net assimilation rates in Douglas-fir. Preconditioning, both on a molecular and structural basis, differences in 400-700 nm radiation flux densities, and the different leaf temperatures are all possible causes for the above discrepancies.

Other factors such as ambient carbon dioxide and oxygen concentrations may also have been involved, although this seems unlikely. When support data becomes available more definite answers should quickly follow.

Even though the trends and magnitudes in stomatal infiltration pressures were quite similar during the study period, the actual leaf diffusion resistances may have been different accounting for the above mentioned divergent results. This possible problem will be examined in the field during the next research summer using an aspirated diffusion porometer (Turner et al. 1969).

When water loss exceeds uptake, plant water stresses develop and internal water reserves are drawn upon. One of these reserves seems to be in the area near the cambium. High water losses result in the development of tree water stresses and the dehydration and shrinkage of these tissues. This results in tree stems decreasing in dimension during the periods of high transpiration and water stresses. Diurnal fluctuations in stem circumference (at about 9 m) for the days examined showed basic trends which were quite similar in shape and magnitude (Figure 1, 2, and 3). Stem shrinkage began soon after sunrise, continued into the afternoon and began to increase in the evening. This trend is quite typical of periods of high transpiration and low water potentials (Lassoie, submitted). During periods of low transpirational water loss and higher water potentials, not reported in this paper, stem shrinkage was considerably less.

Evapotranspiration rates, based on preliminary data from the lysimeter, were generally greater in mid-summer (Figure 1 and 2) than later in the year (Figure 3). This is no doubt due to differences in evaporative demands during the study period. Measurements of heat pulse velocity (estimation of sap velocities) were quite disconcerting (Figure 2). Rates on August 29 can be seen to peak near noon and then decline during the afternoon while remaining quite low during the night. This general trend has been found on clear and sunny days both with Douglas-fir (Lassole, submitted) and vine maple (Lassole and Scott 1972). The following day, however, velocities remain quite low and variable during the entire day (Figure 2). Leaf temperatures and actual transpiration weight loss from the lysimeter suggested that a similar trend should have resulted. At this time an understanding of this discrepancy is not evident. Additional investigations are planned to examine this feature of the heat pulse velocity technique in order to see if this is a biological or an instrumentational phenomenon.

Plant water potentials for the days examined were fairly similar in trends and magnitudes. Since the lysimeter tree was periodically irrigated, its water potential was sometimes higher than tree #3 (Figure 2) and was about the same at other times (Figure 3). Tree water potentials generally decreased during the morning, reached a minimum in the early afternoon, and increased in the late afternoon, reaching a maximum near sunrise of the following day. This basic trend is quite typical of clear and sunny days (Scott and Lassoie 1971, Lassoie submitted).

Stomata opened quickly in the early morning and then closed slowly during the rest of the day. This trend was quite evident in the middle of the summer (Figure 1 and 2). Later in the fall, stomata seemed to open quickly at times but also began to close immediately (Figure 3). This seasonal trend in stomatal aperture has been observed before in Douglas-fir (Swank 1972).

CONCLUSIONS

The results of the past year's work suggest that the actual relationships between tree physiological factors such as net assimilation, stem shrinkage, and water status and environmental factors are quite complex. Preliminary analysis suggests that the trends and magnitudes of net assimilation and stem shrinkage are related to transpirational water loss and internal water deficits, which are in turn influenced by the soil and atmospheric environment. Discrepancies in net assimilation rates and heat pulse velocities suggest further investigations into these areas. The relationship between stomatal infiltration pressures and actual diffusion resistances will also be investigated.

At the present time, investigations of net assimilation, stem shrinkage, and tree water status in small trees is being conducted under controlled environmental conditions at the University of Washington, Botany Greenhouse. Further field investigations are planned for this spring and summer. These studies, as well as further analysis of past data, will hopefully elucidate the basic trends and discrepancies reported in this progress report. The final phase of this work will be the use of these data in the development of mathematical models for primary production processes in the Coniferous Biome (Reed and Webb, 1972).

APPENDIX A

The Development of a New Plant Gas Exchange System

Since March, work has progressed through the conception, design, and now the assembly of a new plant gas exchange system. With this system we plan to estimate variations in net assimilation between different crown classes of Douglas-fir under natural stand conditions. This new system was designed to take periodic samples of carbon dioxide and water vapor at six tree canopy positions during a single data collection period. The system developed last year (Salo et al. 1971, 1972a,b) presently allows the use of only one cuvette without the manual switching of gas lines. Briefly, the new system entails a pneumatic circuit, infrared carbon dioxide and water vapor gas analysers, cuvettes, and environmental transducers. A short description of this system follows.

The pneumatic circuit (schematic in Figure 4) consists of twelve sample lines which take one ambient and one cuvette air sample at each of six cuvettes. Both lines at each cuvette are sampled essentially at the

same time. There is a twelve minute cycle for the entire system, each cuvette sample being analysed for both water vapor and carbon dioxide for a one-minute period. This enables us to obtain simultaneously, net assimilation and transpiration estimated in each cuvette and thus allows us to calculate boundary layer plus stomatal resistance. It also supplies necessary data for a leaf level net assimilation model (Reed and Webb 1972).

Gas analysis is to be accomplished using two infrared gas analysers. Water vapor analysis is to be done with a MSA "LIRA" model 200 while $\rm CO_2$ will be measured using a URAS I after the water vapor has been removed. However, due to sensitivity and accuracy problems with the water vapor analyser, an investigation is presently underway as to the possible use of Hygrodynamics "Hygrometer" system for measuring water vapor.

Cylindrical, stirred, 8x8 cm cuvettes, made from a "Plexiglass" frame covered with "Propafilm C" were designed for this system. The small size and simple construction of these cuvettes is an essential requirement for their use in a broad sampling scheme. Extensive testing of these cuvettes under controlled environmental conditions in comparison to the thermoelectrically cooled cuvettes (Salo et al. 1971, 1972a,b) is presently underway. Leaf temperatures will be measured with contact leaf thermocouples (copper-constantan) as described by Fry (1965). This system allows the estimation of leaf temperature within ± 1.0°C.

Light measurements will be made with Lambda "Quantum Sensors". These sensors only act as transducers for the electromagnetic wave range affecting the light reaction of photosynthesis (400-700 mm). Such sensors were tested for their applicability in the field during the past year.

All data outputs form the above equipment are to be collected on three Leeds and Northrup strip chart recorders. One 10 inch, 0 to 2 millivolt "Speedomax G" will record the output from the light and temperature sensors. A second "Speedomax G" (6 to 9 millivolt range) will be used to record the URAS I data. The water vapor analyser output will be recorded on a "Speedomax H" with a range of 0 to 100 millivolts.

The cuvettes designed for this new gas exchange system are easily portable and light weight, but they lack an effective cooling device. Under conditions of high solar radiation flux densities increased cuvette temperatures may decrease their usefulness. At such times, use will be made of the thermoelectrically cooled cuvettes (Salo et al. 1971, 1972a,b) which can be easily incorporated into the new system.

APPENDIX B

The Development of an Automated Band Dendrometer System

For the study reported in this paper and preliminary studies (Scott and Lassoie 1971a; Lassoie submitted), linear motion potentiometers were used

as dendrometer band transducers. These transducers and their control circuitry were similar to those described by Dobbs (1969). Due to their initial expense, only 18 dendrometer bands were available for these early investigations. Preliminary results have indicated that more dendrometer bands would be necessary in order to adequately sample different species and crown classes at various heights along their stems. Therefore, a set of criteria were established for a new dendrometry system. It was felt that the new system must be (1) sensitive to changes of less than 0.001 inch. (0.0254 mm) in stem circumference, (2) able to control a large number of dendrometer bands, (3) easy to install and maintain in the field, (4) relatively inexpensive, (5) easily expandable, and (6) capable of providing easy data collection and management. The following is a brief report on the development of such a system.

The automated dendrometer bands developed used rotary potentiometers as voltage dividers which enabled minute changes in stem circumference to cause slight shaft rotation and a change in voltage. The original use of these types of dendrometer bands was by Dr. J. N. Woodman, Weyerhaeuser Research Center, Centralia, Washington in conjunction with his studies of tree growth (Woodman 1971a,b, 1972). The mounting brackets are constructed of standard aluminum angle and strip. The dendrometer transducers are Bourns potentiometers model 3585-a-598-502, 7/8 inch diameter, single-turn servo-mount wirewound element with a resistance of 5000 ohms.

Shaft rotation is accomplished by a stainless steel wire which makes one loop around the potentiometer shaft, is fixed to an invar-36 (an iron-nickel alloy) band which wraps around the tree at one end, and is spring-loaded at the other end. Installation of these dendrometer bands on tree stems in the field is similar to that described by Dobbs (1969).

Since the dendrometer band transducers act as voltage dividers they must be placed in an appropriate circuit with a fixed voltage source and a millivolt data recording system (Figure 5). The control circuitry enables an electrical output of 0 to 100 millivolts responding to an electrical resistance change of 0 to 5000 ohms as the shaft rotates. The control circuitry along with the regulated power supply, a dendrometer input panel, and a connector receptacle for output to the data recording system were packaged in a compact unit.

Compared to earlier dendrometry systems this system was relatively inexpensive, with 100 complete dendrometer bands and their control circuitry costing about \$3,000.

These dendrometer bands and their control circuitry were designed in order to be monitored using a 100-channel data recording system. Besides the dendrometer band inputs this system is presently available and is maintained as a data recording system for any dc millivolt signal

(0 to 100 millivolt range). Output from this system is in paper punch tape which can be processed on the main computer at the University of Washington.

Since these dendrometer bands measure changes in linear distance using rotary motion of the potentiometer shaft they must be calibrated so that a change in millivolt output (0 to 100 millivolts) corresponds to certain linear distance. Ten dendrometer band assemblies were randomly chosen and calibrated by rotating the shaft a known distance and recording the change in millivolt output. A single turn of the potentiometer shaft was found to correspond to a linear motion about 0.42 inches (10.67 mm). With the data recording system described earlier, the sensitivity of these transducers was found to be better than 0.0004 inches (0.0102 mm). Linearity also proved to be quite good especially between the range of 10 to 90 millivolts. Some of these transducers were also tested in a controlled environment chamber under various temperature and humidity regimes. Output from these proved to be unaffected by changes in temperature and humidity corresponding to natural ranges.

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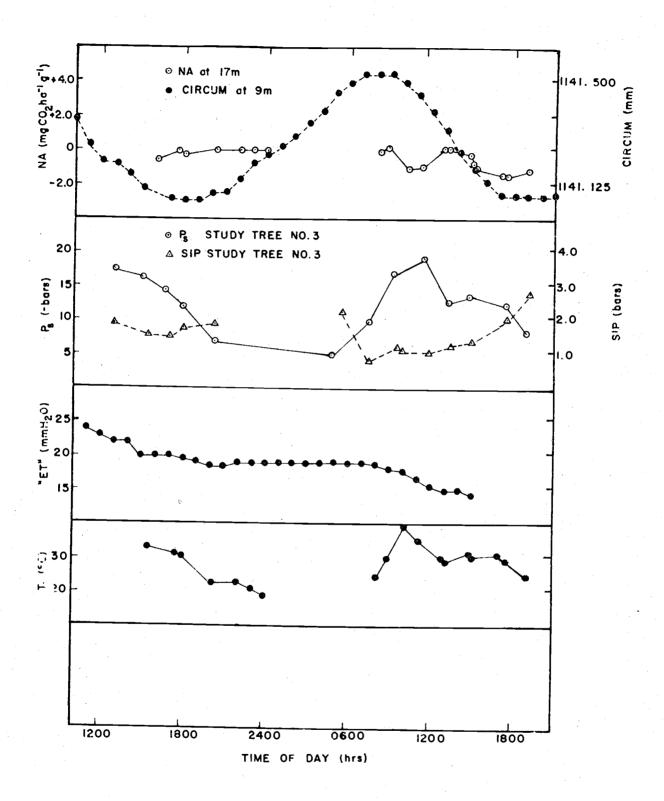


Figure 1. Diurnal trends in net assimilation (NA), fluctuations in stem circumference (CIRCUM), plant moisture stress, (Ps), stomatal infiltration pressures (SIP), evapotranspiration ("ET"), and leaf temperature on 7 and 8 August 1972 at A. E. Thompson Research Center.

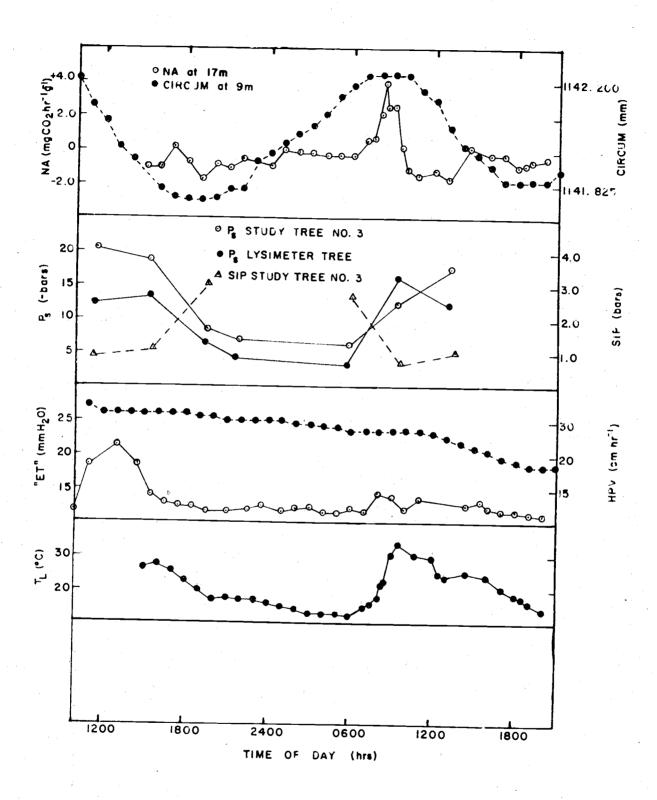


Figure 2. Diurnal trends in net assimilation (NA), fluctuations in stem circumference (CIRCUM), plant moisture stress (Ps), stomatal infiltration pressures (SIP), evapotranspiration ("ET"), heat pulse velocity (HPV), and leaf temperature on 29 and 30 August 1972.

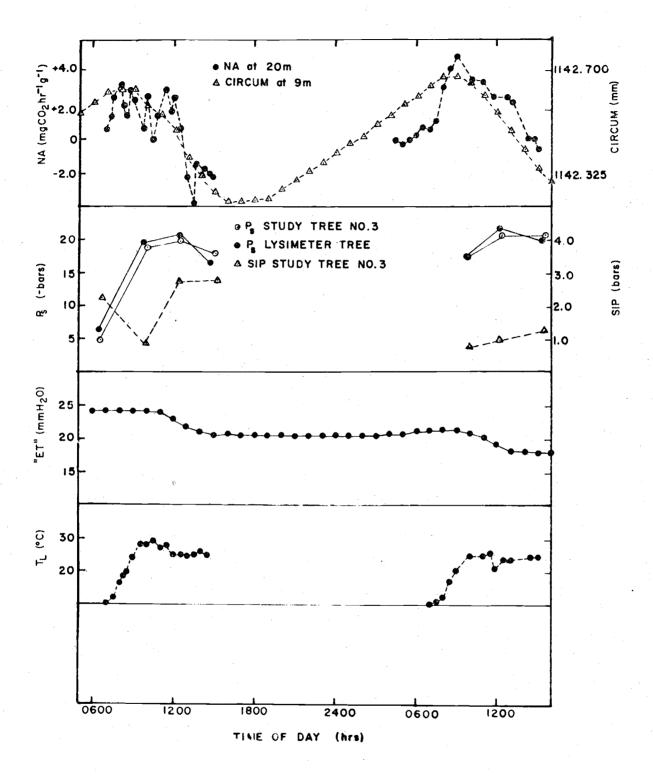


Figure 3. Diurnal trends in net assimilation (NA), fluctuations in stem circumference (CIRCUM), plant moisture stress (Ps), stomatal infiltration pressures (SIP), evapotranspiration ("ET"), and leaf temperature on 14 and 15 September 1972.

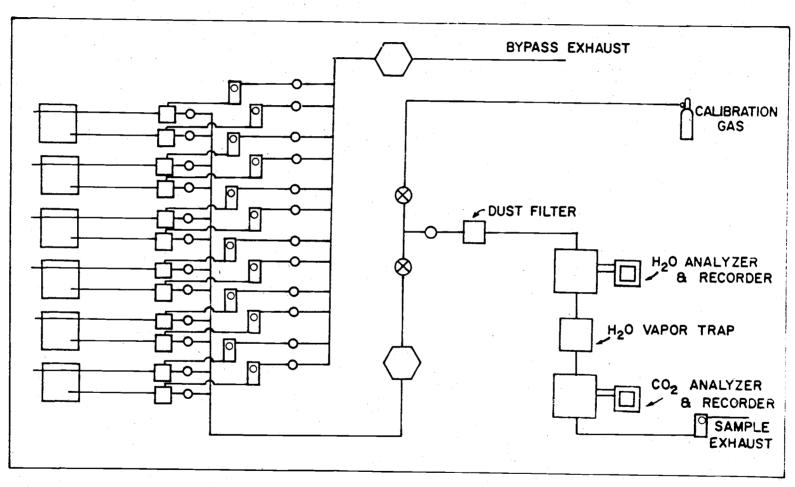


Figure 4. Schematic diagram of pneumatic circuit.

 $(\bigotimes = \text{on-off value}, \bigcirc = \text{needle value}, \bigcirc = \text{flow meter},$

= diaphragm pump, = solonoid value.)

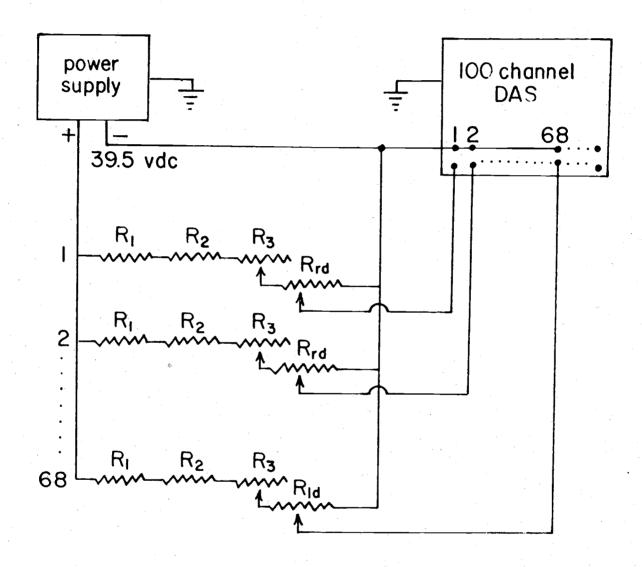


Figure 5. Schematic diagram of dendrometer band transducer control circuitry. R_1 and R_2 are, respectively, 1 M, and 960 K ohms \pm 1.0% high stability metal film resistors. R_3 is a 100 K ohms wirewound potentiometer. R_{rd} and R_{ld} are, respectively, 5 K ohms rotary and linear potentiometers used as dendrometer band transducers. The power supply is a dc-regulated Sorensen model QRD 40-0.75. Output from the dendrometer band transducers is recorded on paper punch tape automatically every hour by a 100-channel NLS data acquisition system (DAS).