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Title: OXYGEN CONSUMPTION BY *Dendroctonus pseudotsugae* HOPKINS

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Oxygen uptakes of Douglas-fir beetles collected during November 1969 through April 1970 were measured at different experimental temperatures. The oxygen uptakes of adult beetles increased at each experimental temperature as the seasons progressed from winter to spring.

The larval and pupal Douglas-fir beetles, collected in February 1970, had lower oxygen uptake levels at 10°, 20° and 30°C than did the adults, but the proportional changes in these uptake levels were not significantly different.

Dendroctonus pseudotsugae, *D. ponderosae* and *D. valens*, collected in November 1969, had different levels of oxygen uptake at the three experimental temperatures, but the proportional changes in the log oxygen uptakes with changing temperature were not significantly different. The larger species, *D. valens*, respired at a lower level than did either of the smaller species. The oxygen uptake levels of

the larval *D. ponderosae* were not significantly different than those of the adults.

Oxygen Consumption by *Dendroctonus pseudotsugae* Hopkins

by

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INTRODUCTION

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, is the most destructive insect pest of mature Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in western North America (Wright and Lejeune, 1967). Many biological and ecological features of this beetle have been studied and reported. Among this abundance of literature, some of the more noteworthy studies are those of McMullen and Atkins (1962), Daterman, Rudinsky and Nagel (1965), Cowan and Nagel (1965), and Schmitz and Rudinsky (1968). There has been a shift in emphasis in the more recent studies from the areas of basic biology to the more specialized subject of chemical attractants (Jantz and Rudinsky, 1966; Borden, Silverstein, and Brownlee, 1968; Kinzer *et al.*, 1969; and Pitman and Vite, 1970).

A survey of these and other studies reported in the literature on the family Scolytidae indicated that no work had been done on the oxygen consumption of any of these bark beetles. Measurements of the oxygen uptake of these beetles at different test temperatures could provide reliable estimates of the seasonal changes in their metabolic rates. As the season progresses from winter to spring the beetles might be expected to acclimate to the higher environmental temperatures. This acclimation should be evidenced by an increasing rate of oxygen uptake at each test temperature.

Prosser and Brown (1961) show that the metabolic rate of many organisms may, under controlled conditions, fluctuate as a function of time. Petitpren and Knight (1970) conclude that initial metabolic studies should take into consideration these seasonal effects.

The primary objectives of this study were to determine the effect of temperature on the rate of oxygen uptake by the Douglas-fir beetle and the degree to which seasonal changes will modify this rate. Secondary objectives were to determine whether similar responses would be observed in other species of the genus *Dendroctonus*.

MATERIALS AND METHODS

Douglas-fir beetles (Plate lb.) were collected in a slash residue area resulting from a selective cutting operation at an elevation of 1,500 feet on the northeast slope of Bull Run ridge in the Siuslaw National Forest (Plate 2a.).

Red turpentine beetles, Dendroctonus valens Lec. (Plate lc.) were collected from a standing ponderosa pine tree, Pinus ponderosa Dougl., five miles northwest of Sisters, Oregon, in the Deschutes National Forest (Plate 4.).

Mountain pine beetles, Dendroctonus ponderosae Hopk. (Plate la.) were collected from a standing sugar pine tree, Pinus lambertiana Dougl., three miles north of the Taft Mountain ski area in the Umpqua National Forest.

The Douglas-fir beetles were collected monthly, during November 1969 through April 1970 (Table 1), from log sections of Douglas-fir trees located within the slash area (Plate 2b.). Bark sections were removed from the log (Plate 3a.) and the beetles were placed on moist paper toweling in a plastic box (Plate 3b.). This box was placed in a styrofoam cooler and transported to the laboratory. It was transferred to an incubator set at a temperature equal to that of the under-bark temperature recorded during the collection. Table 1 shows a range of 5 °C for the under-bark temperatures from

December 1969 to April 1970.

The morning following collection the adult beetles were randomly placed into 14 groups, each consisting of five beetles. Five of these groups were removed from the incubator, weighed on a type H16 Mettler balance and placed into five model GME-130 reaction vessels. A 1.0 ml. capacity syringe was used to place 0.2 ml. of 10% potassium hydroxide into the side arm of each reaction vessel (Umbreit, Burris and Stauffer, 1964). Each arm was then closed with a model GME-9 venting plug. The five reaction vessels were then attached to a model GRP-14 Gilson differential respirometer (Gilson, 1963) set at 10° C with a shaking frequency of 80 oscillations per minute (Plate 5.).

The system was allowed to stand open for one hour to allow the beetles to adjust to the new temperature and to allow the pressure in the system to equalize. The system was then closed and the oxygen uptake of the beetles in each vessel was measured in microliters and recorded every 30 minutes for 2 1/2 hours. This same procedure was followed using five of the remaining nine groups at 20° C and the final four groups at 30° C. Oxygen uptake data of the beetles in the initial group of five vessels were measured and recorded at 10°, 20° and 30° C. The oxygen uptake data of the second group of beetles were measured and recorded at 20° and 30° C and those of the third group were measured and recorded only at 30° C.

The three temperatures used in this study are each significant for the Douglas-fir beetle. It has been shown that these beetles exhibit well organized activity between 10° and 34° C, and that within this range there are two distinct temperature thresholds. The condition required for flight is a temperature between 18° and 22° C and the optimum temperature for regulated locomotion is between 26° and 32° C (Rudinsky and Vite, 1956).

The mountain pine beetles and the red turpentine beetles were collected during November 1969. The limited number available necessitated a different procedure. Groups of five individuals were used to test the mountain pine beetles, and the red turpentine beetles were tested using three individuals per group. The oxygen uptake values for all of the beetles and larvae collected were measured and recorded at 10°, 20° and 30° C. The readings were made at 30 minute intervals for 2 1/2 hours. The system was allowed to stand open for one hour between tests to allow the beetles to adjust to each 10° C increase in temperature and to allow the pressure in the system to equalize.

The larval and pupal Douglas-fir beetles were tested with methods similar to those used for the mountain pine beetles. They were tested in groups of five individuals with each group being subjected to each test temperature.

Wet weights, dry weights, ash-free dry weights or percentage of organic nitrogen are the units usually used for expressing metabolic rates. The live weights of the beetles were used in this study. Keister and Buck (1964) advocate the use of unit whole body live weights for expressing metabolic rates of insects. They point out that the use of dry weights may encourage the misconception that water is metabolically inert and that tissue hydration necessarily changes with changing body water content.

RESULTS

The monthly respiratory response curves for the Douglas-fir beetles are shown in Figure 1. These curves pass through the mean oxygen uptake values observed for each set of five (or four) vessels at each test temperature. The curves ascend with greater rapidity as temperature increases. Logarithmic transformations of these oxygen uptake values, plotted as functions of temperature, were fitted by the regression equations shown in Table 2. Data transformed by this device are said to be rectified (Snedecor and Cochran, 1968). The graphs of these regression lines are shown in Figure 2.

It was seen that, in general, the oxygen uptake of adult Douglas-fir beetles at a given temperature increases with the progression of the seasons after December 1969 (Figure 1). Table 3 shows the parameters of the regression equations fiting oxygen uptakes of adult Douglas-fir beetles at each of the three experimental temperatues to the passage of time. Figure 3 shows the graphs of these equations together with the mean oxygen uptake values actually observed for each collection date from December 1969 through April 1970. These regression lines were calculated to give the least squares fit of a straight line to the observed values of the oxygen uptakes as functions of time in number of days with day zero being November 1, 1969.

Figure 4 (uniform scale) shows the respiratory responses for

February 1970 of adult, pupal and larval Douglas-fir beetles to temperature changes (lines d, e and f). These data, rectified and fitted by the regression equations shown in Table 4, are graphed on the logarithmic scale of Figure 4 (lines a, b and c).

The respiratory response curves of the adult and larval mountain pine beetles collected in November 1969 are graphed on the uniform scale of Figure 5 (lines c and d). The regression equations of these rectified data are shown in Table 5, and graphed on the logarithmic scale of Figure 5 (lines a and b).

The respiratory response curves for the adults of three species of Dendroctonus bark beetles are shown on the uniform scale of Figure 6 (lines d, e and f). These beetles were collected during November 1969. The regression equations of these rectified data, presented in Table 6, are graphed on the logarithmic scale of Figure 6 (lines a, b and c).

The respiratory response curves shown in Figure 1 indicate that from November to December oxygen uptake decreased at all three test temperatures, and that it increased as the seasons progressed from December through April. Exceptions to this trend are seen in the response at the April II 10 °C test, and the response at 30 °C in February. These two responses are less than those of the previous months.

The curves in Figure 1 are exponential in appearance and have the characteristic that the increase in oxygen uptake rate with temperature is proportional to the rate already attained. They could be represented by the regression equation $Y = (A)(B^x)$, where Y = oxygen uptake, x = temperature, and A and B are constants to be estimated. Applying logarithms to this equation, it becomes $\log Y = \log A + (\log B) X$ (Snedecor and Cochran, 1968).

Table 2 shows the log A and log B values for the regression equations relating the log oxygen uptake to temperature of adult _D. pseudotsugae_. These equations were calculated to give the least squares fit of straight lines to the rectified uptake data (Figure 2). The resulting regression lines fit their data points with unusual fidelity. The correlation coefficients (r) between log oxygen uptake and temperature ranged from 0.923 to 0.979.

The OSU-21 *SIMLIN program (Yates, 1969) was used to calculate these log A, log B and r values via a remote teletype terminal connected to the CDC 3300 computer. This program produces the log A and log B constants, sample correlation coefficients and an analysis of variance table for the rectified data of the equation $Y = A + BX$. It fits the log oxygen uptakes versus temperature to a straight line by the least squares method.

The slope of the regression line for December is 0.010 less than the April I value (Table 2). The hypothesis Ho: $B_1 - B_2 = 0$ was tested, where B_1 is the log B value of April I and B_2 is the log B value for December. The test statistic was

$$t = \frac{B_1 - B_2}{S\sqrt{\frac{1}{SSX_1} + \frac{1}{SSX_2}}}$$

where S is equal to the pooled standard deviation and SSX is equal to the mean sum of squares for temperature (Wine, 1964).

The computed value was t = 0.574, which is less than the tabular value of $t_{0.05(24)} = 1.711$. The hypothesis Ho: $B_1 - B_2$ was not rejected and it was concluded that the variation in slope between April I and December is not statistically significant at the 95% level. This would indicate that the change in log oxygen uptake per degree change in temperature was not significantly different between December 1969 and April 1970.

Figure 3 represents the regression of the oxygen uptake rate on time in days after November 1969 for each test temperature. The oxygen uptake data were not rectified and the lines were fitted by least squares analysis. The plotted points indicate the mean response level for each collection date.

The hypothesis Ho: $B_1 - B_2 = 0$ was tested where B_1 is the slope of the 20° C line and B_2 is the slope of the 10° C line (Table 3). The test statistic was the same as that shown above. The computed value was t = 3.850 which is greater than the tabular value of

$t_{0.05\ (52)} = 1.675$. The hypothesis Ho: $B_1 - B_2 = 0$ was rejected and it was concluded that the variation in the slope between the 10° and 20° C lines is statistically significant. The hypothesis Ho: $B_1 - B_2 = 0$ was tested where B_1 is the slope of the 30° C line and B_2 is the slope of the 20° C line. The computed value was t = 1.850 which is greater than the tabular t-value. The hypothesis was rejected and it was concluded that the variation in slope between the 20° and 30° C lines was statistically significant.

Figure 3 shows that the oxygen uptake of adult Douglas-fir beetles at any given temperature increases with the passage of winter. The above statistical tests indicate that these rates of increase are significantly greater at the higher test temperatures. The correlation coefficients (r) for these regression lines are: 10° C r = 0.665, 20° C r = 0.826, and 30° C r = 0.914. Sendecor and Cochran (1968) estimate that with an r value of 0.7 about 50% of the variation in Y (oxygen uptake rate) is due to changes in X (temperature acclimation through time) while at an r value of 0.9, variation in X is responsible for about 80% of the variation in Y.

Table 4 shows the log A and log B values for the rectified oxygen uptake data graphed on the uniform scale of Figure 4. The slopes of the adult, larval and pupal regression lines, shown on the log scale of Figure 4, were not significantly different when tested with the test statistic shown above.

The hypothesis Ho: $A_1 - A_2 = 0$ was tested where A_1 is the log A for the adults and A_2 is the Log A value for the larvae. The test statistic was

$$t = \frac{A_1 - A_2}{S\sqrt{\frac{\Sigma X_1^2}{n_1 SSX_1} + \frac{\Sigma X_2^2}{n_2 SSX_2}}}$$

where ΣX^2 is equal to the sum of the squares of the temperature values, with the other values being the same as those shown above (Wine, 1964). The computed t-value was 2.72 and the tabular value of $t_{0.05\,(29)}$ was 1.70. The hypothesis was rejected and it was concluded that there is a significant difference between these intercepts. The test of the hypothesis Ho: $A_1 - A_2 = 0$, where A_1 was the log A value for the larvae and A_2 was the log A value for the pupae, resulted in a computed t-value of 0.23. The tabular value of $t_{0.05}$ (20) was 1.725 and the hypothesis was not rejected.

These tests indicate that the adult Douglas-fir beetles have a significantly higher log oxygen uptake, as a function of temperature, than do the larvae or pupae, but that the changes in these uptakes in response to temperature changes are not significantly different.

The respiratory responses of the adult and larval mountain pine beetles are shown on the uniform scale of Figure 5. These data were rectified and the log A and log B values of the regression lines, plotted against the logarithmic scale of Figure 5, are listed in Table 5. The hypotheses Ho: $B_1 - B_2 = 0$ and Ho: $A_1 - A_2 = 0$ were tested using the test statistics shown above. The computed t-values for the test of slopes was 0.412 and was less than the tabular t-value of 1.706. The computed t-value for the intercepts was 0.844 and which was less than the tabular t-value. The hypotheses were not rejected and it was concluded that there is no significant difference between the larval and adult mountain pine beetles respiratory responses at the three test temperatures.

The November respiratory response curves shown on the uniform scale of Figure 6 indicate that D. pseudotsugae has a higher response level than either D. ponderosae or the D. valens. Statistical t-tests of the log A and log B values for these rectified data (Table 6) indicated that the intercepts differed significantly, but that no significant difference occurred between the slopes. This would indicate that the three species responded at different levels, but that there was no significant difference in the proportional changes in the log oxygen uptakes at the three test temperatures.

DISCUSSION

Douglas-fir beetles occur throughout the range of Douglas-fir trees, in the Pacific Coast region from California into British Columbia, and in the Rocky Mountain region, from northern Mexico into southern Canada (Lejeune and Wright, 1967).

The beetles have only one generation per year throughout their range, but there is considerable variation in the seasonal history between the cold interior climates of the Rocky Mountains and the warmer regions of the Pacific Coast range. The seasonal extremes in temperature and humidity between the Coastal and Rocky Mountain portions of the beetles range are considerably different.

The adult Douglas-fir beetles used in this study had significantly higher respiratory responses to temperature as the seasons progressed from winter to spring. The higher response levels observed in the spring were probably related to an acclimation of the beetles to the changing environmental conditions. The relative humidity in the microhabitat of these beetles was nearly 100% during the rainy winter and early spring months in the Coastal range of western Oregon. The under-bark temperature, however, increased from a low of 9 ° C in December to a high of 14 ° C in April. This 5 ° C increase in temperature could have been responsible for the observed acclimation.

In the interior regions the winter temperatures drop to well below 0 ° C, and the beetles would enter a dormant stage within the frozen resins of the standing Douglas-fir trees. The respiratory responses of these beetles would probably be quite low if measured at their environmental temperature. They would likely respire at levels similar to those observed in this study as the seasons progressed from winter to spring in these interior regions.

The ability of the Douglas-fir beetle to acclimate to such a wide range of temperatures is undoubtedly related to their success in persisting throughout the range of their primary host.

The three species of Dendroctonus bark beetles used in this study showed different levels of oxygen uptake at different temperatues, but the proportional changes in the log oxygen uptakes with changing temperature were not significantly different. This variation could be explained on the basis of different temperature histories between the three collection areas, or the relative difference in size of the three beetle species. The larger species, D. valens, respired at a lower level than did either of the smaller species.

The larvae of both the Douglas-fir and mountain pine beetles respired at lower levels than did the adults, but the statistical tests indicated that this difference in the mountain pine beetles was not significant.

The proportional change in the respiratory response to temperature between the adult and larval Douglas-fir beetles was not significantly different, which would indicate that the larvae acclimate at the same rate, but at a lower response level than do the adults. This could explain the existence of two beetle emergences in the warmer regions of their range. The second emergence, in the middle to late summer, would consist of those individuals that over-wintered as larvae. They would complete their development as the environmental temperatures increased during the spring and early summer months, to emerge as adults in mid- to late summer.

PLATE 1

Magnification 1.5X

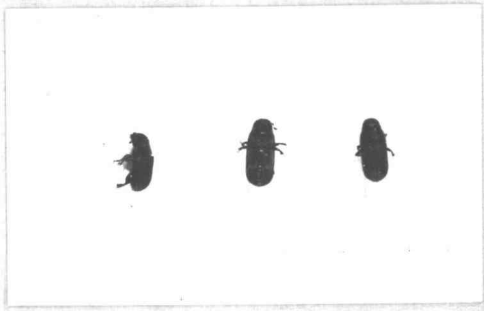

Plate 1a. Dendroctonus ponderosae Hopk. adults.

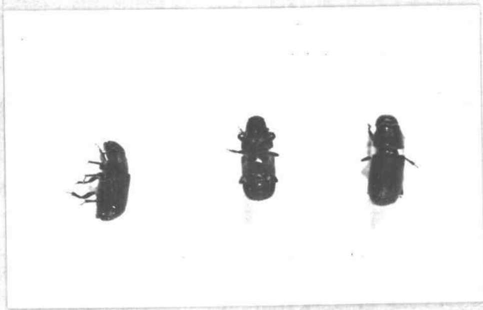

Plate 1b. Dendroctonus pseudotsugae Hopk. adults.

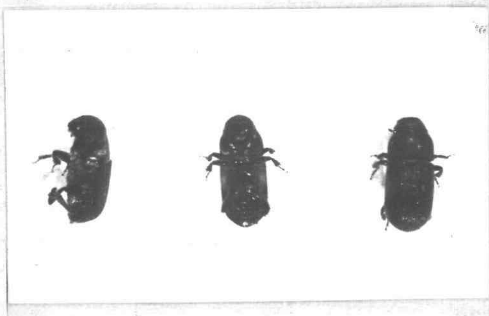

Plate 1c. Dendroctonus valens Lec. adults.

PLATE 2

Plate 2a. Collection area of Douglas-fir beetles.

Plate 2b. Pseudotsugae menziessi (Mirb.) Franco. log section infested with Douglas-fir beetles.

Plate 3a. Bark section showing Douglas-fir beetle gallery.

Plate 3b. Plastic collection box showing Douglas-fir beetles on moist paper toweling.

PLATE 4

Plate 4. Collection area of red turpentine beetles.

PLATE 5

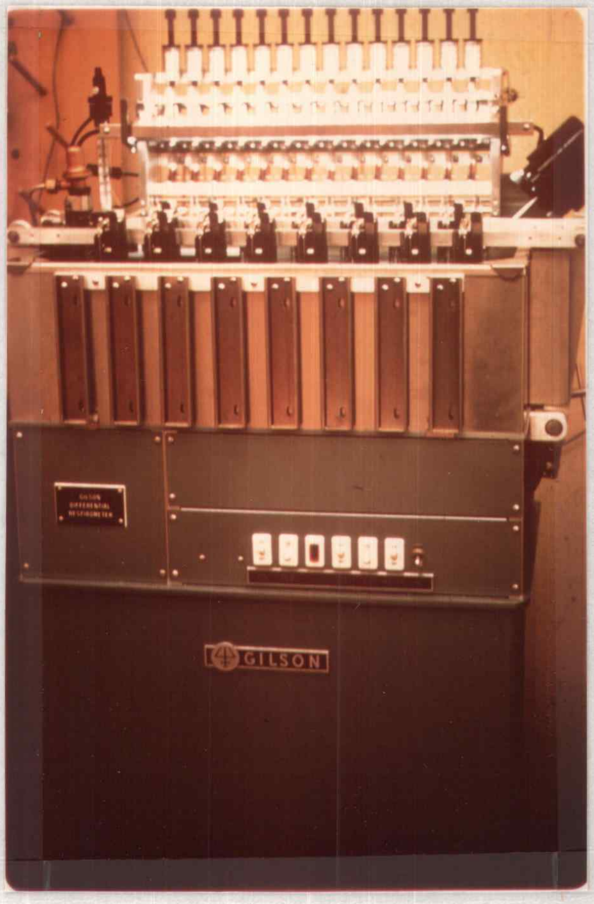

Plate 5. Gilson differential respirometer Model GRP-14.

Table 1. Collection dates for D. pseudotsugae and under-bark temperatures at the Bull Run Ridge collection area.

Month	Collection Date	Under-bark Temperature
November	11/14/69	12°C
December	12/16/69	9°C
January	1/23/70	10°C
February	2/13/70	11°C
March	3/17/70	11°C
April I	4/4/70	13°C
April II	4/29/70	14°C

Table 2. Regression equations fitting log O_2 uptakes of D. pseudotsugae adults at different temperatures. Log A and B values of equation Y = A + B * X (Y = Log O_2 uptake, X = temperature, A = Log A, B = Log B). Experimental temperatures were 10, 20 and 30° C.

Month	Log A	Standard Error	Log B	Standard Error	Correlation Coefficient
November	2.076	0.045	0.037	0.002	0.958
December	1.808	0.100	0.038	0.004	0.923
January	2.041	0.051	0.038	0.002	0.979
February	2.000	0.053	0.038	0.002	0.976
March	2.244	0.087	0.040	0.004	0.941
April I	2.015	0.089	0.048	0.004	0.955
April II	2.180	0.081	0.045	0.003	0.963

Table 3. Regression equations fitting oxygen uptakes of D. pseudotsugae adults at experimental temperatures to passage of time. A and B values of equation Y = A + B * X (Y = oxygen uptake, X = number of days after November 1, 1969).

Temperature	A	Standard Error	B	Standard Error	Correlation Coefficient
$10^{\circ}C$	121.514	39.286	1.374	0.308	0.665
$20^{\circ}C$	-109.245	157.249	9.406	1.237	0.826
$30^{\circ}C$	39.783	170.446	15.739	1.393	0.914

Table 4. Regression equations relating log O_2 uptake of D. pseudotsugae adults, larvae and pupae to temperature. A and B values of equation Y = A + B * X (Y = Log O_2 uptake, X = temperature, A = Log A, B = Log B). Beetles collected in February, 1970.

	Log A	Standard Error	Log B	Standard Error	Correlation Coefficient
Adults	2.006	0.046	0.037	0.002	0.979
Larvae	1.756	0.068	0.036	0.003	0.944
Pupae	1.674	0.098	0.036	0.004	0.970

Table 5. Regression equations relating log O_2 uptake of D. ponderosae adults and larvae to temperature. A and B values of equation Y = A + B * X (Y = Log O_2 uptake, X = temperature, A = Log A, B = Log B). Beetles collected in November 1969.

	Log A	Standard Error	Log B	Standard Error	Correlation Coefficient
Adults	1.872	0.135	0.041	0.006	0.902
Larvae	1.531	0.104	0.048	0.005	0.929

Table 6. Regression line relating log O_2 uptake of three species of Dendroctonus bark beetles to temperature. A and B values of equation Y = A + B * X (Y = Log O_2 uptake, X = temperature, A = Log A, B = Log B). Beetles collected in November 1969.

	Log A	Standard Error	Log B	Standard Error	Correlation Coefficient
D. pseudotsugae	2.333	0.043	0.028	0.002	0.939
D. ponderosae	1.872	0.135	0.041	0.006	0.902
D. valens	1.834	0.046	0.040	0.002	0.982

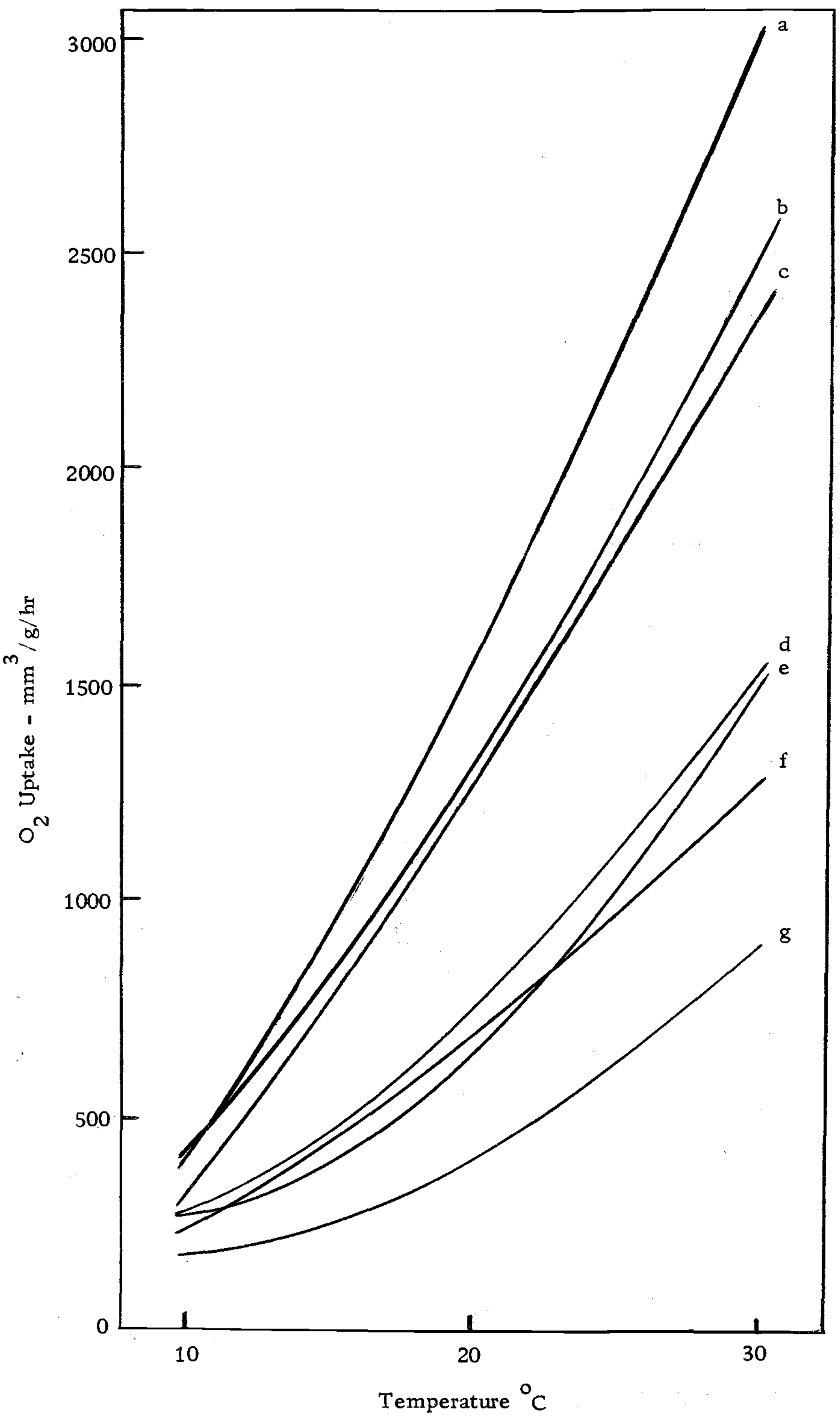

Figure 1. Mean oxygen uptakes of D. pseudotsugae adults at different temperatures. Beetles collected in a) April II, b) March, c) April I, d) November, e) January, f) February and g) December.

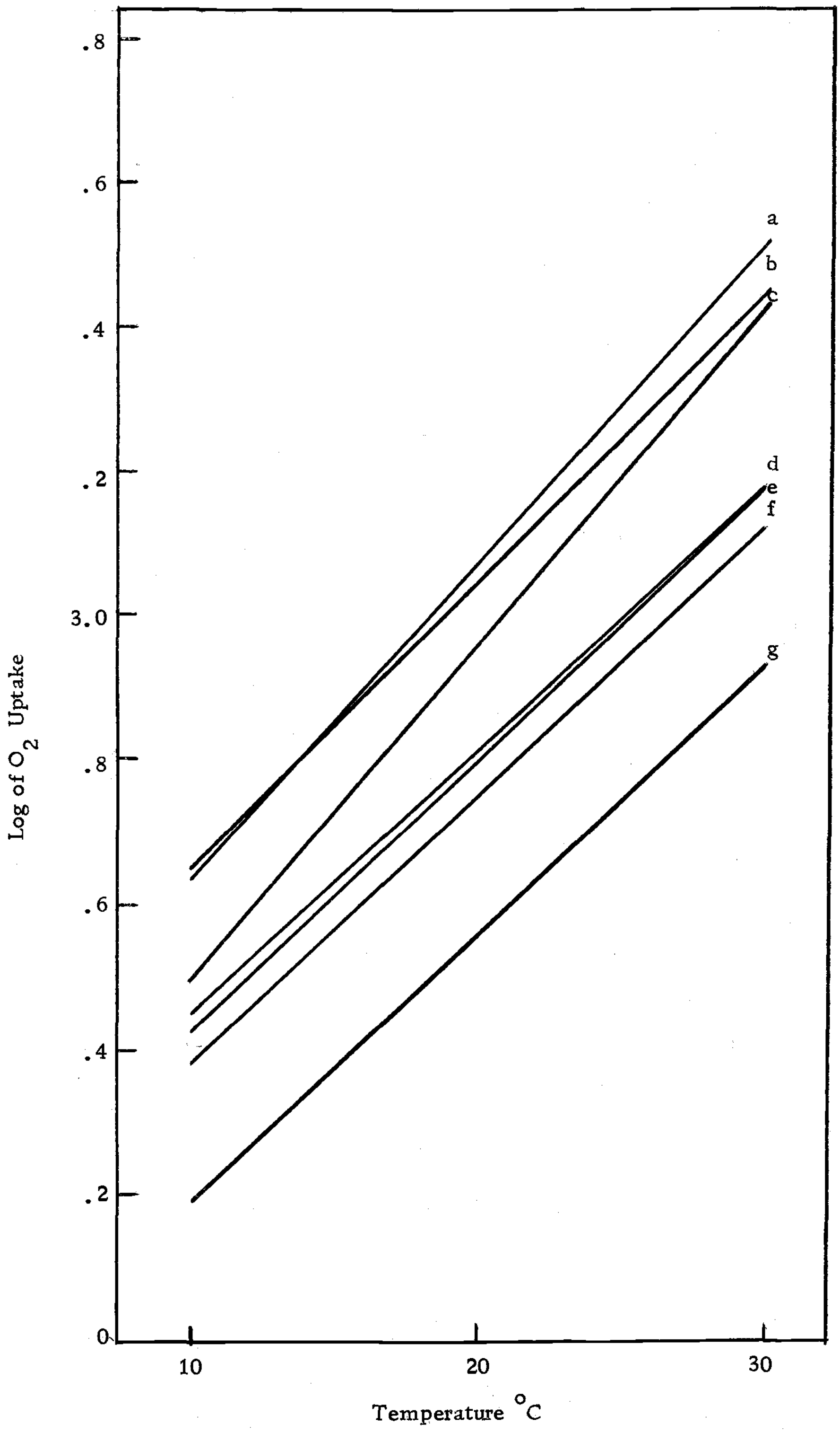

Figure 2. Regression lines fitted by least squares analysis of log O_2 uptakes at different temperatures for D. pseudotsugae adults. Beetles collected in a) April II, b) March, c) April I, d) November, e) January, f) February and g) December.

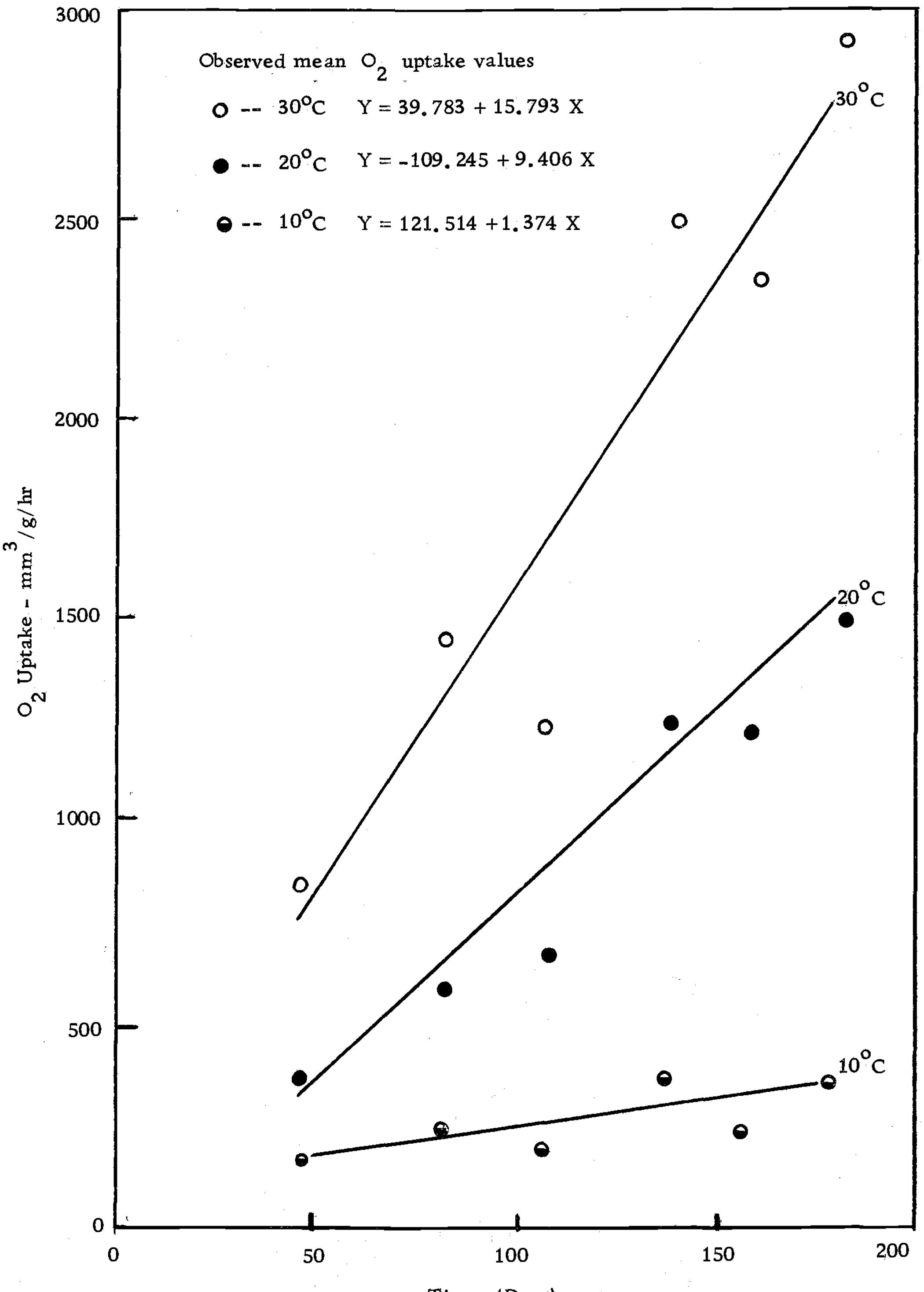

Figure 3. Increase in oxygen uptake by D. pseudotsugae adults at different temperatures versus passage of time. Day 0 = November 1, 1969.

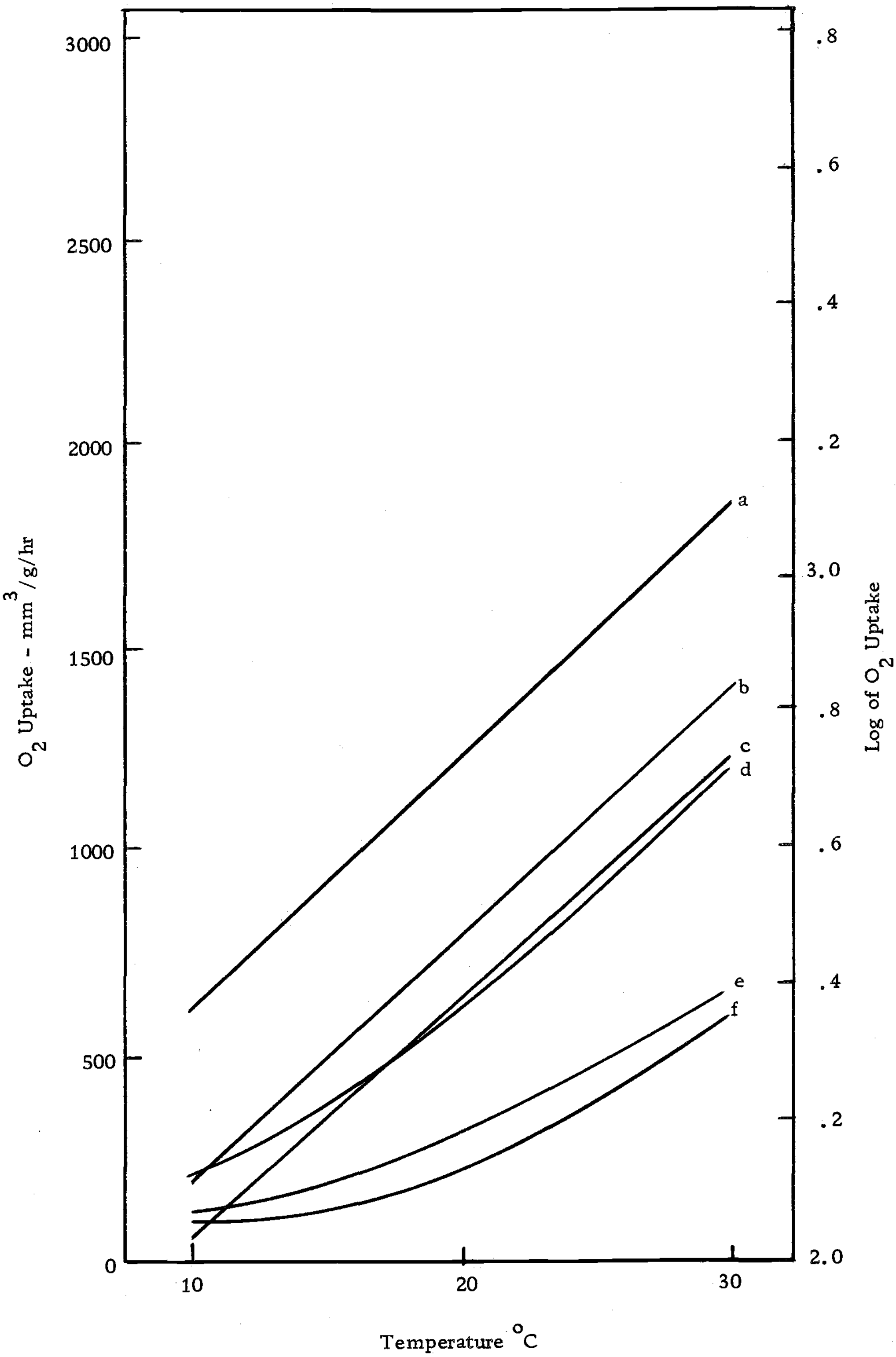

Figure 4. Mean oxygen uptakes of D. pseudotsugae (uniform scale; d. adults, e. larvae, f. pupae) at different temperatures. Regression lines of rectified uptake data fitted by least squares analysis (log scale; a. adults, b. larvae, c. pupae). Beetles collected in February 1970.

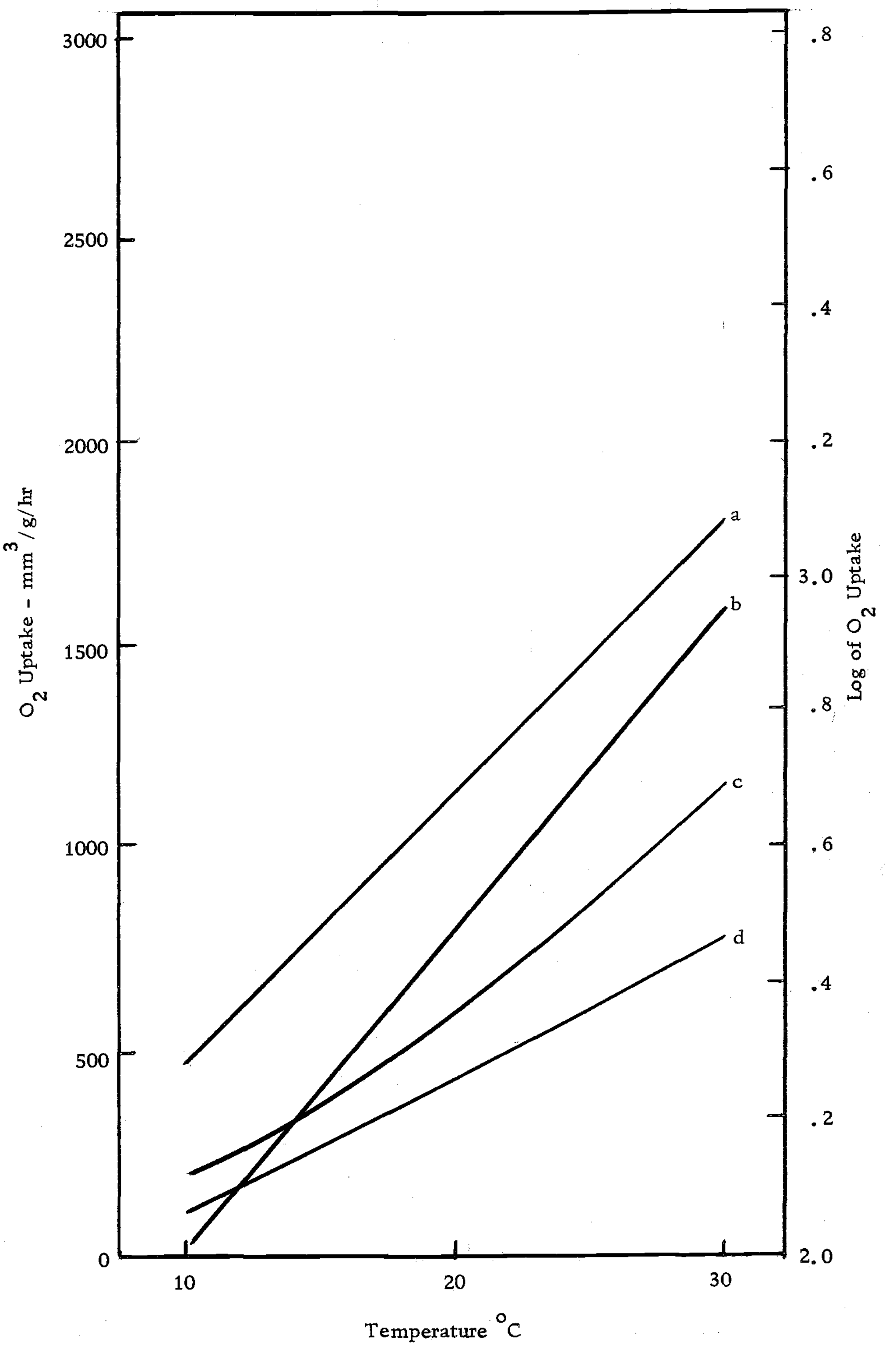

Figure 5. Mean oxygen uptakes of D. ponderosae (uniform scale; c. adults, d. larvae) at different temperatures. Regression lines of rectified uptake data fitted by least squares analysis (log scale; a. adults, b. larvae). Beetles collected in November 1969.

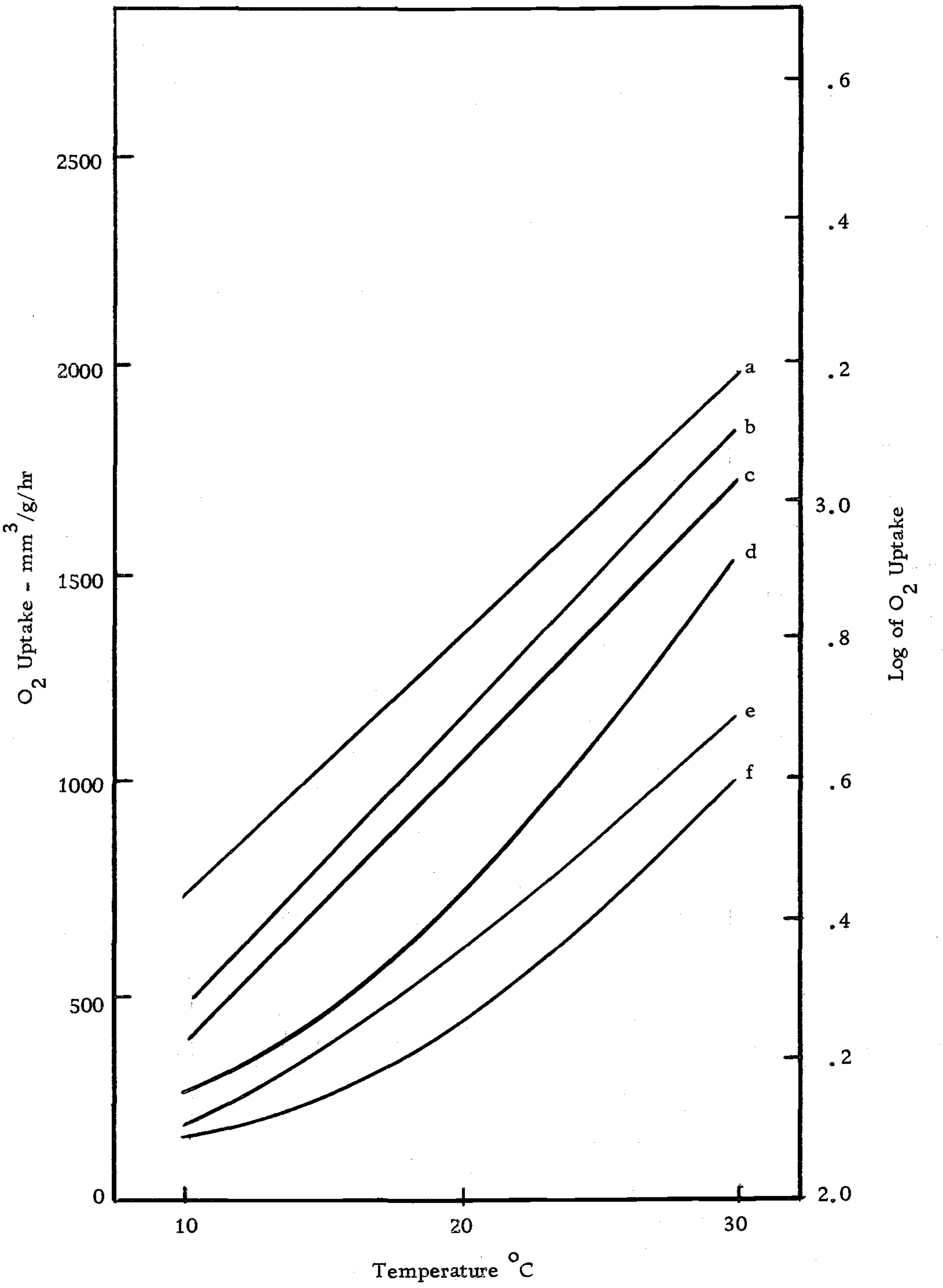

Figure 6. Mean oxygen uptakes of three Dendroctonus species adults at different temperatures (uniform scale; d, e and f). Regression lines of rectified uptake data fitted by least squares analysis (log scale; a, b and c). D. pseudotsugae (lines a and d), D. ponderosae (lines b and e) and D. valens (lines c and f). Beetles collected in November 1969.

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