Rapid Estimation of Heat Accumulation from Maximum and Minimum Temperatures
Author(s): G. L. Baskerville and P. Emin
Source: *Ecology*, Vol. 50, No. 3 (May, 1969), pp. 514-517
Published by: Wiley
Stable URL: http://www.jstor.org/stable/1933912
Accessed: 24-07-2016 17:59 UTC

RAPID ESTIMATION OF HEAT ACCUMULATION FROM MAXIMUM AND MINIMUM TEMPERATURES

G. L. BASKERVILLE AND P. EMIN

Forestry Branch, Department of Fisheries and Forestry, Fredericton, N. B.

and

University of New Brunswick Computing Centre, Fredericton, N. B.

(Received April 27, 1968; accepted for publication November 25, 1968)

Abstract. A method is presented for estimating heat accumulation by using daily maximum and minimum temperatures and assuming the sine curve as an approximation of the diurnal temperature curve. A table is given for estimating heat accumulation for a given day, and a computer program is described for accumulating heat units over a 1-year period. The technique permits the use of an upper as well as a lower threshold and has a precision in the order of $\pm$ 5%.

INTRODUCTION

Ecologists often use heat accumulation above a given threshold to measure or predict the effect of temperature on biological processes. This heat accumulation is most commonly expressed in degree-days and is estimated by measuring the area contained above a threshold temperature and under the trace on a thermograph chart. The procedure is time consuming, but most of the simpler graphical methods are not sufficiently precise. Arnold (1960) devised a method of estimating accumulated heat units by means of daily maximum and minimum temperatures only. Although his system greatly extends the data available for computing accumulated heat, it is limited to a narrow range of maximum and minimum temperatures and does not allow for the introduction of an upper temperature threshold. Arnold's method has been extended so that these limitations no longer apply, and a computer program has been produced that greatly facilitates calculations. The method is outlined in the following section.

METHOD

The principal assumption of the method is that the diurnal temperature curve, which is typically skewed to the right and contains minor variations, is similar to the trigonometric sine curve, which is symmetrical and smooth. Under this assumption the daily mean temperature, which is necessary to the computation, is taken to be the average of the maximum and minimum, whereas with the actual curve this is not always true. However, Arnold has shown that for any given day the area under a sine curve, the amplitude of which has been adjusted to the daily maximum and minimum temperatures, closely approximates the area under the temperature curve.

In extending Arnold's method four situations were considered: two involving a lower temperature threshold only (as in Arnold's paper) and two involving both an upper and a lower threshold.

Case 1: Daily minimum above lower threshold (K1); no upper threshold

This is the simplest case (Fig. 1, A), and the heat units are calculated directly from the difference between the mean daily temperature and the threshold.

Case 2: Daily minimum below lower threshold (K1); no upper threshold

This situation and the equation giving the area are shown in Fig. 1, B. Table 1 provides an array of solutions for this case for any combination of minimum temperatures from 0°F to 50°F and maximums from 52°F to 120°F over a lower threshold of 51°F. The heat units accumulated on a given day over a base of 51°F are estimated by entering the table at the appropriate maximum and minimum temperatures for that day and reading the degree-days from the body of the table—e.g., maximum = 80°F, minimum = 47°F, heat units = 13.

Heat units above a threshold other than 51°F can be obtained in one of two ways: by shifting the maximum and minimum scales by the difference between the required threshold and 51°F or by adding the algebraic difference (51°F—required threshold) to the daily maximum and minimum temperatures. This procedure is similar to that given by Arnold, but Table 1 allows for a wider range of maximums and minimums and hence for a greater range of threshold temperatures.

Case 3: No restriction on daily minimum; daily maximum exceeds upper threshold (K3); horizontal cutoff at upper threshold

This situation and the equation for computation are shown in Fig. 1, C. The application of the upper threshold in this manner is somewhat artificial in that heat is accumulated at a constant rate for the period when the temperature exceeds the upper limit (K3). The technique has proven useful, however, where temperatures above the upper threshold diminish rather than arrest a process. Calculation of heat units may be made from Table 1 as follows: first, the total heat units for the day are read from the table without regard to the upper limit (K3); the scales are then shifted (or a constant is added to the temperatures) so that the new base temperature becomes the upper limit K3. The heat units between the two limits K1 and K3 are given by the difference between the two values.

Case 4: No restriction on daily minimum; daily maximum exceeds upper threshold (K2); vertical cutoff at upper threshold

This situation and the expression for computation are shown in Fig. 1, D. Here no heat units are accumulated for the period when the temperature exceeds the upper threshold (K2). This approach is useful where temperatures in excess of the upper threshold arrest a process. This case does not lend itself to tabular presentation, and the computation is best accomplished by using a computer.

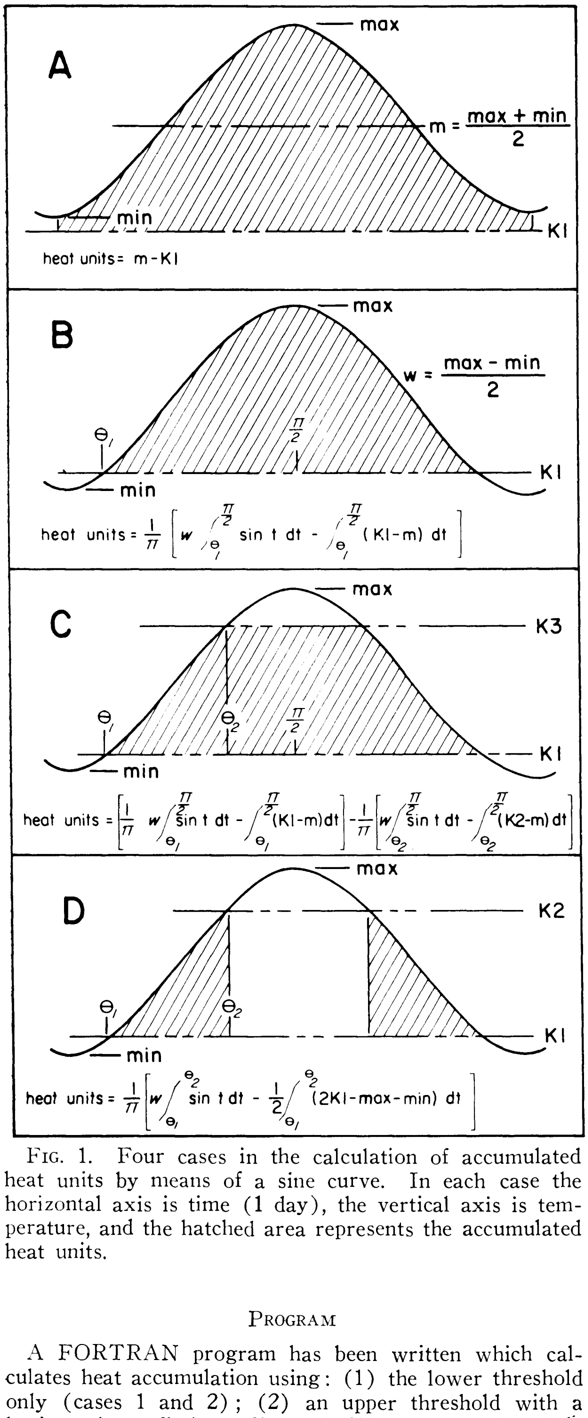

FIG. 1. Four cases in the calculation of accumulated heat units by means of a sine curve. In each case the horizontal axis is time (1 day), the vertical axis is temperature, and the hatched area represents the accumulated heat units.

PROGRAM

A FORTRAN program has been written which calculates heat accumulation using: (1) the lower threshold only (cases 1 and 2); (2) an upper threshold with a horizontal cutoff (case 3); and (3) an upper threshold with a vertical cutoff (case 4). The input consists of a serial listing of daily maximum and minimum temperatures. The output is a 12 (month) $\times$ 31 (day) table giving the total accumulated heat units (to nearest whole degree-day) at the end of each day. The lower threshold K1 and the upper thresholds, K3 for a horizontal cutoff and K2 for a vertical cutoff, are set by the user for each run. The program tests the magnitude of each pair of maximum and minimum temperatures against the assigned values of K1, K2, and K3 and uses the appropriate method for calculating degree-days. An IBM 1620II can compute and print the three heat-accumulation patterns for a 6-month period in about 3 min. Prints of the program with control specifications are available from the Forest Research Laboratory of the Department of Fisheries and Forestry, Fredericton, N. B.

PRECISION

The computer program (and Table 1) gives the area under the sine curve with amplitude specified by any given pair of maximum and minimum temperatures. Error in the method stems from the assumption that the area under the sine curve is identical to that under the diurnal temperature curve. Arnold (1960) compared the sine curve area with areas from thermograph traces and found the difference to be extremely small (2–4% of the total of accumulated heat units). Although he suggested procedures for refining the estimates in critical cases, he concluded that the technique was generally satisfactory. The introduction of the upper temperature thresholds with either a horizontal or a vertical cutoff does not seem to affect precision. The areas under thermograph traces for a 6-month period were measured and compared the accumulated heat units with those computed from daily maximum and minimum temperatures for the same station. Even with horizontal or vertical cutoffs, the difference between the four methods never exceeded 5% of the total of accumulated heat units.

INTERPRETATION

The foregoing sections have dealt with the mechanics of an efficient technique for the estimation of heat accumulation. A caveat with respect to interpretation of such data is in order. There are two limitations to interpretation regardless of the level of refinement in the estimation of heat accumulation. First, the method provides, at best, a measure of only one of the many environmental parameters. Clearly one cannot expect heat accumulation alone to explain all variation in a biological response. Second, there are two assumptions implicit in the use of heat-accumulation units:

1) It is assumed that the response of the plant or animal to temperature is linear and that this response is constant over a growth period.

2) It is assumed that biologically meaningful temperature thresholds for various age classes of the subject organism are available. These limitations are critical to any biological interpretation of heat accumulation and users of the technique, including the refinement presented here, should have a clear awareness of this fact. A more complete consideration of the problems inherent in the interpretation of the response of organisms to temperature is provided by Wang (1960) for plants and by Andrewartha and Birch (1954, p. 129–205) for animals.

CONCLUSION

The estimation of heat units by measuring the area under a sine curve as proposed by Arnold is an efficient tool of considerable value to ecologists. The precision of the estimate is not affected by the introduction of upper temperature thresholds and is well within the tolerances imposed by the ability of the ecologist to make biological interpretations of the data. The technique is simple and greatly increases the number of stations that

MINIMUM (degree days)

MAX	50	49	48	47	46	45	44	43	42	41	40	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	-1	MAX
120	34	34	33	33	33	32	32	32	31	31	31	30	30	30	30	30	29	29	29	29	28	28	28	28	28	27	27	27	27	27	27	26	26	26	26	26	26	25	25	25	25	25	25	25	25	24	24	24	24	24	24	24	120
119	34	33	33	32	32	32	31	31	31	31	30	30	30	29	29	29	29	29	28	28	28	28	28	27	27	27	27	27	26	26	26	26	26	26	25	25	25	25	25	25	25	24	24	24	24	24	24	24	24	23	23	23	119
118	33	33	32	32	32	31	31	31	30	30	30	30	29	29	29	29	28	28	28	28	27	27	27	27	27	27	26	26	26	26	26	26	25	25	25	25	25	25	24	24	24	24	24	24	24	24	23	23	23	23	23	23	118
117	33	32	32	31	31	31	30	30	30	30	29	29	29	29	28	28	28	28	27	27	27	27	27	26	26	26	26	26	26	25	25	25	25	25	25	24	24	24	24	24	24	24	23	23	23	23	23	23	23	23	23	22	117
116	32	32	31	31	31	30	30	30	29	29	29	29	28	28	28	28	27	27	27	27	27	26	26	26	26	26	25	25	25	25	25	25	24	24	24	24	24	24	24	23	23	23	23	23	23	23	23	22	22	22	22	22	116
115	32	31	31	30	30	30	29	29	29	29	28	28	28	28	27	27	27	27	26	26	26	26	26	25	25	25	25	25	25	24	24	24	24	24	24	24	23	23	23	23	23	23	23	22	22	22	22	22	22	22	22	22	115
114	31	31	30	30	30	29	29	29	28	28	28	28	27	27	27	27	26	26	26	26	26	25	25	25	25	25	24	24	24	24	24	24	24	23	23	23	23	23	23	23	22	22	22	22	22	22	22	22	21	21	21	21	114
113	31	30	30	29	29	29	28	28	28	28	27	27	27	27	26	26	26	26	26	25	25	25	25	25	24	24	24	24	24	24	23	23	23	23	23	23	23	22	22	22	22	22	22	22	21	21	21	21	21	21	21	21	113
112	30	30	29	29	29	28	28	28	27	27	27	27	26	26	26	26	25	25	25	25	25	24	24	24	24	24	24	23	23	23	23	23	23	22	22	22	22	22	22	22	22	21	21	21	21	21	21	21	21	21	20	20	112
111	30	29	29	28	28	28	27	27	27	27	26	26	26	26	25	25	25	25	25	24	24	24	24	24	23	23	23	23	23	23	22	22	22	22	22	22	22	21	21	21	21	21	21	21	21	21	20	20	20	20	20	20	111
110	29	29	28	28	28	27	27	27	26	26	26	26	25	25	25	25	24	24	24	24	24	24	23	23	23	23	23	22	22	22	22	22	22	22	21	21	21	21	21	21	21	21	20	20	20	20	20	20	20	20	20	19	110
109	29	28	28	27	27	27	26	26	26	26	25	25	25	25	24	24	24	24	24	23	23	23	23	23	23	22	22	22	22	22	22	21	21	21	21	21	21	21	20	20	20	20	20	20	20	20	20	19	19	19	19	19	109
108	28	28	27	27	27	26	26	26	25	25	25	25	24	24	24	24	24	23	23	23	23	23	22	22	22	22	22	22	21	21	21	21	21	21	21	20	20	20	20	20	20	20	20	19	19	19	19	19	19	19	19	19	108
107	28	27	27	26	26	26	26	25	25	25	24	24	24	24	23	23	23	23	23	22	22	22	22	22	22	21	21	21	21	21	21	21	20	20	20	20	20	20	20	19	19	19	19	19	19	19	19	19	18	18	18	18	107
106	27	27	26	26	26	25	25	25	24	24	24	24	23	23	23	23	23	22	22	22	22	22	21	21	21	21	21	21	21	20	20	20	20	20	20	20	19	19	19	19	19	19	19	19	18	18	18	18	18	18	18	18	106
105	27	26	26	25	25	25	25	24	24	24	23	23	23	23	23	22	22	22	22	22	21	21	21	21	21	21	20	20	20	20	20	20	20	19	19	19	19	19	19	19	19	18	18	18	18	18	18	18	18	18	17	17	105
104	26	26	25	25	25	24	24	24	23	23	23	23	23	22	22	22	22	21	21	21	21	21	21	20	20	20	20	20	20	19	19	19	19	19	19	19	19	18	18	18	18	18	18	18	18	18	17	17	17	17	17	17	104
103	26	25	25	24	24	24	24	23	23	23	22	22	22	22	22	21	21	21	21	21	20	20	20	20	20	20	19	19	19	19	19	19	19	18	18	18	18	18	18	18	18	18	17	17	17	17	17	17	17	17	17	17	103
102	25	25	24	24	24	23	23	23	23	22	22	22	22	21	21	21	21	21	20	20	20	20	20	19	19	19	19	19	19	19	18	18	18	18	18	18	18	18	17	17	17	17	17	17	17	17	17	17	16	16	16	16	102
101	25	24	24	23	23	23	23	22	22	22	22	21	21	21	21	20	20	20	20	20	20	19	19	19	19	19	19	18	18	18	18	18	18	18	17	17	17	17	17	17	17	17	17	16	16	16	16	16	16	16	16	16	101
100	24	24	23	23	23	22	22	22	22	21	21	21	21	20	20	20	20	20	19	19	19	19	19	19	18	18	18	18	18	18	18	17	17	17	17	17	17	17	17	16	16	16	16	16	16	16	16	16	16	16	15	15	100
99	24	23	23	22	22	22	22	21	21	21	21	20	20	20	20	19	19	19	19	19	19	18	18	18	18	18	18	18	17	17	17	17	17	17	17	17	16	16	16	16	16	16	16	16	16	15	15	15	15	15	15	15	99
98	23	23	22	22	22	21	21	21	21	20	20	20	20	19	19	19	19	19	18	18	18	18	18	18	17	17	17	17	17	17	17	17	16	16	16	16	16	16	16	16	16	15	15	15	15	15	15	15	15	15	15	15	98
97	23	22	22	21	21	21	21	20	20	20	20	19	19	19	19	19	18	18	18	18	18	18	17	17	17	17	17	17	16	16	16	16	16	16	16	16	16	15	15	15	15	15	15	15	15	15	15	14	14	14	14	14	97
96	22	22	21	21	21	20	20	20	20	19	19	19	19	18	18	18	18	18	18	17	17	17	17	17	17	16	16	16	16	16	16	16	16	15	15	15	15	15	15	15	15	15	15	14	14	14	14	14	14	14	14	14	96
95	22	21	21	20	20	20	20	19	19	19	19	18	18	18	18	18	17	17	17	17	17	17	16	16	16	16	16	16	16	15	15	15	15	15	15	15	15	15	14	14	14	14	14	14	14	14	14	14	14	13	13	13	95
94	21	21	20	20	20	19	19	19	19	18	18	18	18	18	17	17	17	17	17	16	16	16	16	16	16	16	15	15	15	15	15	15	15	15	14	14	14	14	14	14	14	14	14	14	14	13	13	13	13	13	13	13	94
93	21	20	20	20	19	19	19	18	18	18	18	17	17	17	17	17	16	16	16	16	16	16	16	15	15	15	15	15	15	15	15	14	14	14	14	14	14	14	14	14	13	13	13	13	13	13	13	13	13	13	13	13	93
92	20	20	19	19	19	18	18	18	18	17	17	17	17	17	16	16	16	16	16	16	15	15	15	15	15	15	15	14	14	14	14	14	14	14	14	14	13	13	13	13	13	13	13	13	13	13	13	12	12	12	12	12	92
91	20	19	19	19	18	18	18	17	17	17	17	17	16	16	16	16	16	15	15	15	15	15	15	15	14	14	14	14	14	14	14	14	13	13	13	13	13	13	13	13	13	13	12	12	12	12	12	12	12	12	12	12	91
90	19	19	18	18	18	17	17	17	17	16	16	16	16	16	15	15	15	15	15	15	14	14	14	14	14	14	14	14	13	13	13	13	13	13	13	13	13	13	12	12	12	12	12	12	12	12	12	12	12	12	11	11	90
89	19	18	18	18	17	17	17	16	16	16	16	16	15	15	15	15	15	14	14	14	14	14	14	14	13	13	13	13	13	13	13	13	13	12	12	12	12	12	12	12	12	12	12	12	12	11	11	11	11	11	11	11	89
88	18	18	17	17	17	16	16	16	16	16	15	15	15	15	15	14	14	14	14	14	14	13	13	13	13	13	13	13	13	12	12	12	12	12	12	12	12	12	12	12	11	11	11	11	11	11	11	11	11	11	11	11	88
87	18	17	17	17	16	16	16	15	15	15	15	15	14	14	14	14	14	14	13	13	13	13	13	13	13	12	12	12	12	12	12	12	12	12	12	11	11	11	11	11	11	11	11	11	11	11	11	11	10	10	10	10	87
86	17	17	16	16	16	15	15	15	15	15	14	14	14	14	14	13	13	13	13	13	13	13	12	12	12	12	12	12	12	12	12	11	11	11	11	11	11	11	11	11	11	11	10	10	10	10	10	10	10	10	10	10	86
85	17	16	16	16	15	15	15	15	14	14	14	14	13	13	13	13	13	13	13	12	12	12	12	12	12	12	12	11	11	11	11	11	11	11	11	11	11	10	10	10	10	10	10	10	10	10	10	10	10	10	10	9	85
84	16	16	15	15	15	15	14	14	14	14	13	13	13	13	13	13	12	12	12	12	12	12	12	11	11	11	11	11	11	11	11	11	11	10	10	10	10	10	10	10	10	10	10	10	10	9	9	9	9	9	9	9	84
83	16	15	15	15	14	14	14	14	13	13	13	13	13	12	12	12	12	12	12	11	11	11	11	11	11	11	11	11	10	10	10	10	10	10	10	10	10	10	10	10	9	9	9	9	9	9	9	9	9	9	9	9	83
82	15	15	14	14	14	14	13	13	13	13	12	12	12	12	12	12	11	11	11	11	11	11	11	11	10	10	10	10	10	10	10	10	10	10	10	9	9	9	9	9	9	9	9	9	9	9	9	9	8	8	8	8	82
81	15	14	14	14	13	13	13	13	12	12	12	12	12	11	11	11	11	11	11	11	10	10	10	10	10	10	10	10	10	10	9	9	9	9	9	9	9	9	9	9	9	9	9	8	8	8	8	8	8	8	8	8	81
80	14	14	13	13	13	13	12	12	12	12	12	11	11	11	11	11	11	10	10	10	10	10	10	10	10	10	9	9	9	9	9	9	9	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	8	8	8	80
79	14	13	13	13	12	12	12	12	11	11	11	11	11	11	10	10	10	10	10	10	10	10	9	9	9	9	9	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	7	7	7	7	79
78	13	13	12	12	12	12	11	11	11	11	11	10	10	10	10	10	10	10	9	9	9	9	9	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	8	8	7	7	7	7	7	7	7	7	7	7	7	78
77	13	12	12	12	11	11	11	11	10	10	10	10	10	10	10	9	9	9	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	8	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	77
76	12	12	11	11	11	11	10	10	10	10	10	10	9	9	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	8	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	6	6	6	6	6	6	76
75	12	11	11	11	10	10	10	10	10	9	9	9	9	9	9	8	8	8	8	8	8	8	8	8	8	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	6	6	6	6	6	6	6	6	6	6	6	6	75
74	11	11	10	10	10	10	9	9	9	9	9	9	8	8	8	8	8	8	8	8	8	7	7	7	7	7	7	7	7	7	7	7	7	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	74
73	11	10	10	10	9	9	9	9	9	8	8	8	8	8	8	8	8	7	7	7	7	7	7	7	7	7	7	7	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	5	5	5	5	5	73
72	10	10	9	9	9	9	9	8	8	8	8	8	8	7	7	7	7	7	7	7	7	7	7	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	72
71	10	9	9	9	8	8	8	8	8	8	7	7	7	7	7	7	7	7	6	6	6	6	6	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	71
70	9	9	8	8	8	8	8	7	7	7	7	7	7	7	6	6	6	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	4	4	4	4	4	70
69	9	8	8	8	8	7	7	7	7	7	7	6	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	69
68	8	8	8	7	7	7	7	6	6	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	68
67	8	7	7	7	7	6	6	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	5	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	3	3	3	3	67
66	7	7	7	6	6	6	6	6	5	5	5	5	5	5	5	5	5	5	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	66
65	7	6	6	6	6	5	5	5	5	5	5	5	5	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	65
64	6	6	6	5	5	5	5	5	5	4	4	4	4	4	4	4	4	4	4	4	4	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	64
63	6	5	5	5	5	5	4	4	4	4	4	4	4	4	4	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2	63
62	5	5	5	4	4	4	4	4	4	4	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	62
61	5	4	4	4	4	4	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	61
60	4	4	4	3	3	3	3	3	3	3	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	60
59	4	3	3	3	3	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	59
58	3	3	3	3	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	58
57	3	2	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	57
56	2	2	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	56
55	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	55
54	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54
53	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	53
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	52

TABLE 1. The estimation of degree-days from maximum and minimum temperatures when the minimum is below a threshold temperature of 51°F (cases 2 and 3)

can be used, as only maximum and minimum temperatures are required. This method in conjunction with a computer program greatly speeds the estimation of accumulated heat units without appreciable loss in precision.

Literature Cited

Andrewartha, H. C., and L. C. Birch. 1954. The distribution and abundance of animals. Univ. Chicago Press, Chicago, Ill. 782 p.

Arnold, C. Y. 1960. Maximum-minimum temperatures as a basic for computing heat units. Proc. Amer. Soc. Hort. Sci. **76**: 682–692.

Wang, J. Y. 1960. A critique of the heat unit approach to plant response studies. Ecology **41**: 785–789.

CALORIC VALUE OF WET TROPICAL FOREST VEGETATION

Frank B. Golley

Institute of Ecology and Department of Zoology, University of Georgia, Athens, Ga.

(Accepted for publication January 27, 1969)

Abstract. Energy values of tropical forest vegetation collected in the Republic of Panama differed significantly depending upon the type of forest and the vegetation part sampled. The pattern of difference was complex, with maximum values varying with the plant part and the forest type. Mangrove generally had higher values than other tropical forests. These observations support the earlier conclusion that tropical vegetation has lower energy values than temperate or alpine vegetation.

Introduction

A comparison of the caloric values of vegetation in alpine, temperate, and tropical communities showed that tropical vegetation had the lowest average caloric content (Golley 1961). For example, tropical rain forest averaged 3,897 cal/g dry weight, compared to 4,790 gcal in alpine juncus dwarf heath. It was suggested that the observed differences were due to the storage of high energy reserves such as lipids in the plants growing in alpine environments. While this conclusion is logical, it is based on a relatively limited number of observations. In 1966 the University of Georgia Institute of Ecology subcontracted with Battelle Memorial Institute, Columbus, Ohio, to carry out studies in Darien Province, Republic of Panama, as part of a sea-level canal feasibility study. Samples of vegetation collected during that study were used to expand the analysis of caloric value to a wider variety of tropical vegetation.

Samples were collected from tropical moist forest near Santa Fe, premontane forest at the Summit line camp on the continental divide, gallery forest along the Chucunaque River at Ortiga, and red mangrove forest near Boca Grande line camp on the Gulfo de San Miguel. Each of these sites was near a camp of the Interoceanic Canal Studies Commission. The forests are described by Child (1968) and Golley (1968). Briefly, the tropical moist forest is mostly deciduous with few epiphytes. The premontane forest is evergreen and has an abundance of epiphytes. The gallery forest, located along the main river of Darien Province, is very tall (over 150 ft) and has the greatest total biomass of all the forest types studied (1,208 metric tons/hectare). The red mangrove forest is also very tall and has characteristic large, branching prop roots in response to a mean tidal fluctuation of 5–7 m.

Methods

In each forest the vegetation on ¼ hectare was harvested and live weight determined for canopy leaves, canopy tree stems, understory leaves, understory stems, epiphytes, fruits and flowers, litter, and roots. At least two samples of material from each vegetation compartment were dried at 60°C, ground in a Wiley mill, and shipped to the United States for caloric analysis. At the Savannah River Ecology Laboratory the dried samples were redried at 100°C for 24 hr and prepared for caloric determination.

Calories per gram were determined by burning samples in a Parr adiabatic bomb calorimeter. At least two sets of duplicate samples were tested for each compartment. Weight of the ash residue was determined so that gram calories could be expressed per gram dry biomass or per gram ash-free dry weight.

Results

An analysis of variance of caloric value by compartments, forests, and comparment-forest interaction showed that each source of variation was significant for both calories per gram and calories per gram ash-free weight. Duncan's multiple range test of differences between forests and compartments showed that the caloric values per gram of tropical moist with premontane and of premontane with gallery forests were not different at the .05 level of significance, but the calories per gram ash-free weight in all forests were different. Considering calories per gram for the vegetation compartments in all forests combined, canopy stems were not different from understory fruit, and canopy leaves, canopy fruit, understory stems, understory fruit, epiphytes, litter, and roots were not different. Understory leaves were different from all other compartments. Considering calories per gram ash-free weight, epiphytes were different from all but canopy leaves, and canopy leaves were different from canopy fruits and flowers, understory leaves, and understory stems. The other compartments were not different from each other.

Analysis of the differences between compartments within forests showed that compartments accounted for a significant amount of the variability at least at the .05 level of probability. Since the results of statistical analysis were the same for calories per gram and calories per gram ash-free weight, the latter data will not be described in detail. The value of calories per gram dry weight was 93.8% of the value of calories per gram ash-free dry