# Response of Fusarium solani to Constant and Fluctuating Temperatures and Its Relationship to Fusarium Canker of Sugar Maple

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## ABSTRACT

Fusarium solani, a cause of an annual canker of sugar maple, develops during the dormant season. Studies of the temp response of the organism indicated that the threshold for linear growth was about 6 C, and that an average of 100 effective day-degrees was necessary for 20 mm of linear mycelial growth in a fluctuating temp regime similar to that observed in nature. Growth was greater in a fluctuating temp regime than at the constant median about which temp fluctuated. During the spring and fall of 1968, temp beneath the bark of sugar maples was recorded at three heights on four tree faces. Approximately 600 effective day-degrees were available for fungus growth during this period. Although there were differences in temp among faces and heights, there were no differences in total effective day-degrees during this period. When the rate of mycelial growth in vitro was extrapolated for 600 day-degrees, the amount of linear growth approximated the average length of cankers observed in nature. Canker incidence has been reported to be greater on some tree faces than on others and to vary inversely with height. While the results indicate temp is limiting, it is not the only factor responsible for distribution of cankers on tree stems.

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*Fusarium solani* (Mart.) Appel. & Wr. emend Snyd. & Hans. is a pathogen of sugar maple (*Acer saccharum* Marsh.) in Pennsylvania where it is found inhabiting forest soils and the bark of healthy trees. The fungus induces cankers and/or rots on a wide variety of hardwoods such as eastern cottonwood (3), musizi (4), tupelo (23), yellow-popular (7), trembling aspen (13), elm (18), oak (24), and sugar maple (19). Cankers on sugar maple originate and develop during the dormant season of the host (19). Temperature regimes beneath the bark favorable to the pathogen are unknown with respect to both amplitudes of fluctuation on given days and number of day-degrees that favor growth.

Effects of temp on fungal growth usually have been determined at constant temp. It is not known if such organisms respond similarly to constant and fluctuating temp. Since *F. solani* is subjected to a fluctuating temp regime in nature, it is important to know how the fungus responds to fluctuating vs. constant temp. Effects of fluctuating temp on growth rates of other fungi or on the progress of disease have been studied (5, 8, 10, 11, 12, 21).

Studies on temp summations or cumulative temp effects are not of recent origin. Platenius (15) employed Vant Hoff's Rule involving $Q_{10}$ to predict storage life of fresh vegetables. Stevens (22) calculated temp efficiency, which was essentially a temp summation. He assumed a minimum (threshold) temp for fungal growth and, each day, added the difference between the assumed minimum and the mean temp for that day, to the previous summation. Andrewartha and Birch (1) used a similar approach to explain the distribution and abundance of animals in nature.

Objectives of this study were to determine: (i) the effect of fluctuating temp on growth of *F. solani*; (ii) the threshold temp for growth of *F. solani*; (iii) the temp summation response of *F. solani* at constant and fluctuating temp, and (iv) the number of effective day-degrees beneath the bark of sugar maple trees available for pathogen development during the dormant season.

MATERIALS AND METHODS.—*Constant temperature.*—Two virulent isolates of *F. solani* were obtained from forest soil. Forty ml of potato-dextrose agar was placed in each of 33 cm × 1.27 cm diam linear growth tubes closed at one end. Single spores were transferred to one end and incubated in darkness for 24 h at 21 C. Three replicates of each isolate then were placed in constant temp of 2, 10, 15, 18, 21, 24, 27, and 35 C. Isolates were maintained in darkness throughout this and the fluctuating temp study to approximate conditions beneath bark of the suscept. Linear growth measurements were made daily for 18 days, and mean growth rates were determined for each temp.

A factorial analysis of variance of a randomized block design was made to determine if there was a significant interaction between isolates and temp and if differences existed between temp, isolates, and replications within isolates. A Duncan's multiple range test was used to test the significance of mean differences.

Temperature thresholds were determined over five temp ranges for the time required to reach 10, 15, and 20 mm of mycelial growth, using the technique employed by Chapman (6) and Elliot and Wilcoxson (8). The threshold was determined by the formula $Y(X-A) = Y' (X'-A)$,

where Y is the time period required for a certain quantity of fungus growth at a given temp (X). Y' is the time period for the same quantity of fungus growth at a second temp (X'). The equation is then solved for A, the threshold temp.

A temp summation was then calculated for growth levels of 10, 15, and 20 mm. In determining effective temp for growth, the threshold temp was calculated and the amount added to the summation each day was the difference between the threshold temp and the "mean" temp for that day (22). Day-degrees were calculated with the formula $K = Y(T-A)$, where Y is the time required for a certain amount of growth, T is the temp, and A, the threshold. Day-degrees, or K, is a thermal constant based on the summation of effective temp (T-A) required for an organism to complete a certain stage of development (1).

*Fluctuating temperature.*—The same isolates and method of preparation were employed as in the constant temp study. However, growth tubes were slanted in wire baskets and thus not in contact with the floors of the temp cabinets as in the previous experiment. Five replicates of each isolate were incubated in a fluctuating temp regime and at constant temp of 4.4, 10, and 15.5 C.

Effects of fluctuating temp were studied in an ISCO controlled environment chamber having a cam-type temp programmer. The cam was cut, based on the fluctuating temp regime observed beneath sugar maple bark, to have an asymmetric diurnal fluctuation of 5.5 C about the median of 10 C. The fluctuating temp regime, as established in the laboratory, is shown in Fig. 1.

Linear growth measuremtns were recorded daily for 28 days and the data were analyzed using a factorial analysis of variance. A Duncan's test was used to detect significant differences between the means. Temperature summations were calculated in the same manner as described previously, except that at the fluctuating temp regime, (T-A) was determined for each hour and a mean value for (T-A) was calculated for the day. The number of day-degrees, K, was computed with the following formula:

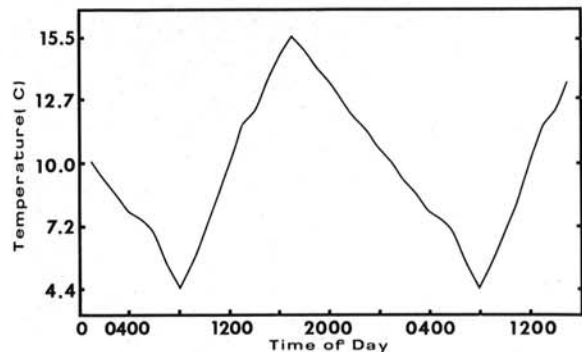$$K = \frac{\sum\limits_{i=1}^{24} (T-A)_i}{24}.$$



**Fig. 1.** Fluctuating temp regime used to program controlled environment chamber.

*Field temperatures.*—Temperatures were recorded beneath the bark of healthy sugar maple trees at 0.6, 3.0, and 5.5 m aboveground on the north, east, south, and west faces of six trees in Clearfield County, Pennsylvania. Temperatures were recorded every 2 h during selected days of March through mid-May and mid-September through mid-December of 1968 (Table 1).

Copper constantan thermocouples (24-gauge) were inserted beneath the bark to the cambial region and upward approximately 5 cm above the point of entrance (Fig. 2). At each height one thermocouple was exposed to ambient temp at the north face about 2 mm from the bark

TABLE 1. Bark temp sampling periods during 1968

|  | Dates[a] | Days (no.) | Temp measurements (no.) |
|---|---|---|---|
| March | 10-12 | 3 | 3,240 |
|  | 17-19 | 3 | 3,240 |
|  | 21-31 | 11 | 11,880 |
| April | 1-30 | 30 | 32,400 |
| May | 1-15 | 15 | 16,200 |
| September | 16-24 | 9 | 9,720 |
| October | 1-18 | 18 | 19,440 |
|  | 20-27 | 8 | 8,640 |
|  | 29-31 | 3 | 3,240 |
| November | 1 | 1 | 1,080 |
|  | 3-30 | 28 | 30,240 |
| December | 1-9 | 9 | 9,720 |
| Total |  | 138 | 149,040 |

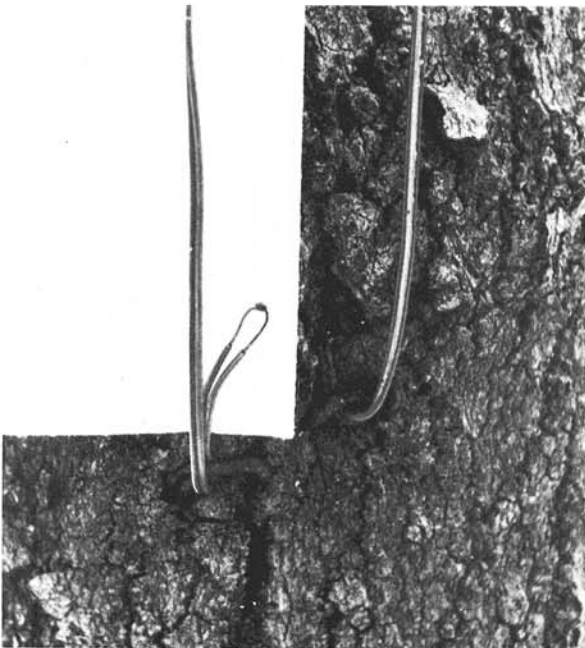[a]Temp were measured at 2-h intervals.



**Fig. 2.** Copper constantan thermocouples in place beneath the bark and near the bark surface.

surface. Thermocouple leads 1.4 m long were attached by a Quick-Konnect thermocouple jack and plug (16) to 20-gauge field wire which ranged from 9 to 61 m in length. Field wires were connected to an electronic multi-point logger system. The recording system, described by Schmidt and Wood (16, 17), consisted of a strip-chart recording potentiometer, two 48-point rotary stepping switches and a junction box control panel. The system was controlled by an automatic reset timer that could record temp from −32 to 52 C from 96 sensors in approximately 4 min.

A factorial analysis of variance of a randomized block design and a Duncan's test of the means were made comparing temp at various heights and tree faces.

A summation of effective temp was calculated for each face at each height on each of the six trees sampled for the 138 days that temp were recorded. Day-degrees, or K, were computed with the following equation:

$$K = \frac{\sum_{i=1}^{N} (T-A)_i}{N}.$$

K was calculated for each day, and the individual K's were summed. The number of recorded temp above the threshold was not the same for each day, hence N varied from day to day.

RESULTS.—*Constant temperature.*—The optimum temp for linear growth of the two isolates in vitro was determined to be near 27 C. There was a significant interaction between temp and isolates, but at no time were optimum temp different for the two isolates. There was a highly significant temp effect and growth rates between isolates differed significantly, but no differences existed among replications within isolates on any given day during the growth period. There were significant differences in response to temp treatments in all comparisons except between 21 and 35 C (Fig. 3).

The average threshold temp for growth, calculated over five different temp ranges, was 5.5 C (Table 2). Differences among individual threshold temp were not significant.

Effective temp summations for accumulated growth of 20, 15, and 10 mm were determined to be 78.2, 61.7, and 40.3 day-degrees, respectively. Each figure represents the average day-degrees of tests at 10, 15, 18, 21, and 27 C.

*Fluctuating temperature.*—The threshold temp for growth was calculated at 6.0 C based on determinations made between the constant temp controls of 10 and 15.5 C (Table 2).

Average effective temp summations for accumulated growth of 20, 15, and 10 mm for both isolates at the constant temp were 101.7, 77.4, and 51.4 day-degrees, respectively. Effective temp summations for the same amounts of growth at the fluctuating temp were 100.1, 73.8, and 48.1 day-degrees, respectively.

Rate of growth in both fluctuating and constant regimes was linear as recorded daily (Fig. 4). There were highly significant differences in growth response among temp treatments and an equally significant temp × isolate interaction on several days. There were no significant differences between isolates or among replicates within isolates. The amount of linear mycelial growth was significantly different, ($P = 0.01$), when any two temp regimes were compared.

*Field temperatures.*—On four of the six trees monitored, there were significant differences ($P = 0.05$) among temp on the various faces and on a fifth, a significant difference, $P = 0.10$. On three of the six trees there were very highly significant differences ($P = 0.005$) among temp at the various heights. There were no significant interactions between face and height.

There were consistent differences in mean temp between the south and north faces, between the west and north faces on two trees, between the south face and ambient temp at the surface of the north face on two trees. In each comparison, the face mentioned first had the higher temp. Mean bark temp were 7.5, 7.3, 7.2, 7.2, and 7.0 C for the south, west, east, ambient, and north faces, respectively.

When temp differences existed between heights, temp at 5.5 m were consistently higher than at 0.61 m and on two trees, 5.5-m temp were significantly higher than those at 3.05 m. Mean bark temp were 7.4, 7.2, and 7.2 C for 5.5, 3.05, and 0.61 m aboveground, respectively. Since there were no significant interactions among treatments, the faces were compared over all heights and the heights over all faces.

Comparisons of temp at different hours of the day before foliation in the spring, after foliation in the spring, and after defoliation in the fall indicated that in general there were no appreciable lag periods during which temp remained at a given level at one face longer than on another. This was particularly true when there was no foliage; a slight lag did exist at the 3.05- and 5.5-m levels during sunny days in mid-summer.

The mean number of effective day-degrees at any of the monitored points on any of the six trees was determined at 616 (Table 3). Although there were slight differences in effective day-degrees from face to face (Table 3) and height to height (Table 4), a chi-square test of homogeneity of variance among the various temp summations showed that the data were homogeneous. Therefore, no significant differences were detected in the effective day-degrees among faces or heights. This may be explained by the fact that the trees studied were located in a dense forest stand and no doubt monitoring points were often shaded by other stems and subsequently by foliage. Although the east face had a slightly higher mean temp than the ambient point, the latter had a slightly higher temp summation than the east face beneath the bark. All other rankings of effective day-degrees at the various faces and heights followed the same trend as the means for their faces and heights.

DISCUSSION.—The most recent reports involving effects of fluctuating temp on fungus or disease development are those of Burgess and Griffin (5), Jensen and Reynolds (11, 12), and Smith (20, 21). Burgess and Griffin incubated cultures of *Gibberella zeae* (Schw.) Petch., *Cochliobolus sativus* (Ito and Kur.) Drechsler ex Dastur, and *C. spicifer* Nelson in darkness and concluded that, in some instances, growth at a fluctuating temp may be greater or less than at the median around which temp fluctuated. Smith incubated cultures of *Macrophomina phaseoli* (Maubl.) Ashby in continuous light and attributed much of the variation in growth to the amplitude of the temp fluctuation and concluded that (i) fluctuations with small amplitudes enhanced the growth

rate, (ii) that the higher the mean temp, the greater the detrimental effect of large fluctuations, and (iii) that the greater the amplitude of fluctuation over a series of different means, the lower the mean temp at which maximum growth occurs.
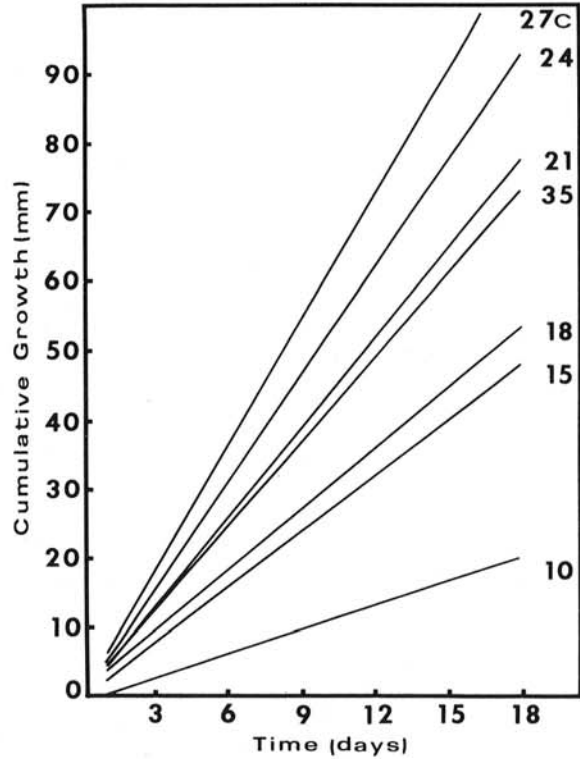


Fig. 3. Rate of linear growth of *Fusarium solani* at constant temp.

TABLE 2. Threshold temp for growth of *Fusarium solani* calculated for constant temp within five temp ranges

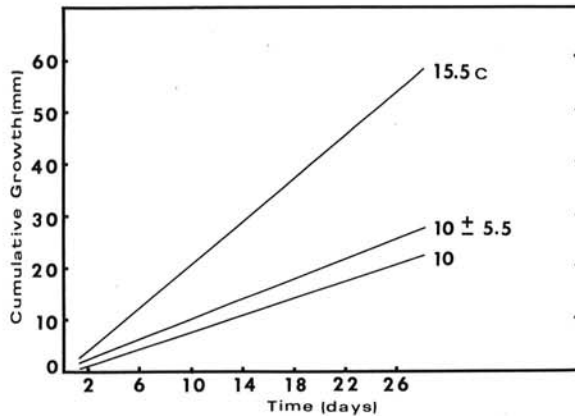| Cumulative growth (mm) | Temp range (C) | Threshold temp (C) | Mean temp (C) |
|---|---|---|---|
| 20 | 15-24 | -0.7 | 3.5 |
| 15 | 15-24 | 6.4 | |
| 10 | 15-24 | 4.7 | |
| 20 | 15-27 | 3.2 | 5.9 |
| 15 | 15-27 | 7.8 | |
| 10 | 15-27 | 6.7 | |
| 20 | 10-15.5 | 5.9 | |
| 15 | 10-15.5 | 5.9 | 6.0 |
| 10 | 10-15.5 | 6.1 | |
| 20 | 10-24 | 5.2 | 5.8 |
| 15 | 10-24 | 5.9 | |
| 10 | 10-24 | 6.0 | |
| 20 | 10-27 | 5.9 | 6.3 |
| 15 | 10-27 | 6.4 | |
| 10 | 10-27 | 6.5 | |

**Fig. 4.** Rate of linear growth of *Fusarium solani* at constant and fluctuating temp.

TABLE 3. Average effective temp summations by tree face

| Thermocouple position | Day-degrees at tree number | | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | Mean |
|---|---|---|---|---|---|---|---|
| South face | 630 | 641 | 679 | 671 | 634 | 636 | 648 |
| West face | 631 | 632 | 636 | 639 | 605 | 638 | 630 |
| Ambient (North face) | 599 | 599 | 646 | 616 | 603 | 626 | 615 |
| East face | 613 | 572 | 611 | 616 | 573 | 618 | 600 |
| North face | 593 | 557 | 598 | 594 | 566 | 601 | 585 |

TABLE 4. Average effective temp summations by height aboveground

| Height aboveground (m) | Day-degrees at tree number | | | | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | Mean |
|---|---|---|---|---|---|---|---|
| 5.5 | 609 | 633 | 642 | 658 | 630 | 643 | 636 |
| 3.05 | 612 | 593 | 650 | 623 | 587 | 617 | 614 |
| 0.61 | 619 | 575 | 610 | 600 | 570 | 612 | 598 |

To determine if temp fluctuations per se influence the growth rate of *F. solani*, linear mycelial growth was plotted over temp and extrapolations and calculations were made regarding the observed and predicted growth at any particular temp in the fluctuating regime. Observed and predicted values were approximately the same at 9.75 C. Below this temp only slightly more mycelial growth was observed at any given temp (as extrapolated from a curve based on constant temp) than was predicted from growth rates based on fluctuating temp. Therefore, at temp between the threshold and 9.75 C, fluctuation in temp appeared to increase mycelial growth somewhat. However, at temp above 9.75 C fluctuations per se appeared to have an opposite effect, decreasing significantly the amount of observed growth at fluctuating temp below that expected value at corresponding constant temp for the same length of time. Between 11 C and 15 C, fluctuations seemed to cause

progressively less linear mycelial growth as temp increased. It appears, therefore, that temp fluctuation per se exerts some influence on the linear growth of *F. solani* in vitro. Jensen and Reynolds (11), using a mean of 21 C, showed that fluctuations of 5.5 and 11 C about this mean increased the growth of *F. solani*, but a fluctuation of 22 C decreased growth. They also concluded (12) that temp fluctuation by itself in some cases may cause an increase in growth.

Burgess and Griffin (5), working in temp ranges similar to those in nature found a trend of increased growth rate associated with magnitudes of fluctuation when mean temp about which fluctuations were set were below optimum. They concluded that the trend was attributed to the relationship between temp and growth rate not being linear over the temp range studied.

However, Smith (21) found that increases in fluctuation amplitudes of soil temp resulted in an increase in the severity of charcoal root disease of sugar pine *(Pinus lambertiana* Dougl.) even though peak temp were well into the sublethal range of the pathogen. Effects of such temp regimes on the host were not determined.

Smith (20) showed that growth of *M. phaseoli* increased at two fluctuating temp regimes which apparently did not extend into the sublethal range. In the present study, conducted at temp well below optimum, growth rate of *F. solani* in the fluctuating temp regime was greater than at the median about which fluctuations were centered; growth was not as great as that at the constant optimum. It is possible that different organisms respond differentially to similar fluctuating temp regimes, but the authors attribute greater growth to fluctuations approaching the optimum. Also, since the fluctuating temp regime was asymmetric in the present study (Fig. 1), the test isolates experienced slightly more time above the median than below it. This could account for the greater growth at the fluctuating temp than at the median; there were also more effective day-degrees available to the fungus in the fluctuating temp regime.

In calculating temp summations, Stevens (22) used a minimum temp as a starting point and summed the differences between the minimum and the mean daily temp. Such a calculation does not accurately reflect the effective heat load on a given day since effective temp are those above the minimum, the threshold in this study, but which have not exceeded the optimum. Glenn (9) accounted for temp in the upper sublethal range by subtracting twice the number of day-degrees above optimum from day-degrees above the lower threshold. He termed the resulting figure, "effective day-degrees". In our study, we observed very few records above the optimum throughout the dormant season and even when present, such temp did not persist for more than 2 h at any specific sampling point. Since the total number of day-degrees is based essentially on averages per day, such infrequent temp above optimum would contribute very little to the total day-degrees over the entire sampling period. Consequently, special calculations for such temp were not made and they were averaged in the total day-degree calculations.

Slightly different mean temp thresholds were calculated in the constant and fluctuating temp studies. This discrepancy was due to the temp between tubes that

were slanted and those that were placed on the incubator floor; those placed on the floor of the cabinet were warmer. However, there was a high degree of consistency among calculated temp summations for the different studies.

In the fluctuating temp regime, 100 effective day-degrees were necessary for the fungus to attain 2.0 cm of linear growth. The average total temp summation at any point beneath the bark on a tree stem in the field was determined as 616 day-degrees. This suggests that enough heat energy was available during the dormant season for the pathogen to grow 12.3 cm, on the average. When cankers, induced during pathogenicity tests in a previous study, were measured, the average size of a canker induced by *F. solani* was 3.2 cm wide × 10.5 cm long with a range of from 2.7-5.5 cm wide × 4.5-24.5 cm long.

Temperature alone probably does not account for more cankers being located near the bases of trees, since temp were nearer the optimum for fungal growth higher on a given tree. Likewise, there was no significant difference in total effective heat load either at different heights or on different faces. However, the available heat energy on the lower portions of the stem was adequate for fungus growth and there is no knowledge of what the bark temp were when cankers were initiated years ago. Borger (2) found spring temp near the ground to be significantly different from those at higher elevations and suggested that wounds due to freezing might occur more frequently at points nearer the ground.

Massie and Peterson (14) have postulated that higher summer temp reduce the viability of *Fusarium lateritium* Nees and, therefore, account for the annual nature of cankers of *Sophora japonica*. The same workers found temp at the bark surface to be 6 to 8 C higher than air temp while in the present study differences between ambient air temp and temp beneath bark were as great as 7 C. At certain times there were, beneath the bark on different faces, temp differences as great as 12 C. Wood and French (25) observed temp of cankered bark of aspen as much as 13 C above ambient air temp.

Borger (2) concluded that at the surface of sugar maple bark, temp at the rim of a fissure were not significantly different from temp near the bottom of the respective fissures. He found no significant differences among fall temp at 0, 10, 20, and 30 ft aboveground outside the bark.

We concluded from our study that during the period of the year that cankers develop, adequate heat energy for growth of *F. solani* is available in the microenvironment of the pathogen. Immediately following reasonably cold weather the pathogen can develop for brief periods when the lower threshold temp is exceeded. However, most fungal growth probably occurs in the fall and spring when conditions favorable for growth persist for prolonged periods.

We showed that growth rates of *F. solani* differ between the constant median and fluctuating temp regimes. It is probable that more growth will result with fluctuating temp than at the constant median, if the amplitude of fluctuation does not extend into the sublethal range.

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