Letter to the Editor

Global Warming and Nonlinear Growth: How Important are Changes in Average Temperature?

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Increasing concentrations of greenhouse gases, particularly CO_2, in the lower atmosphere have led to concern about global changes in temperature and precipitation patterns. It has been estimated that mean surface air temperature will rise at a rate of ~0.3–0.4 C per decade because of the increased greenhouse effect (2,10). These projections are based on outputs from General Circulation Models (GCMs). GCMs are coupled ocean–atmosphere models that simulate the transfer of heat, mass, and momentum in the lower atmosphere. They are reliable tools for simulating climate on large temporal and spatial scales, but they have two important drawbacks that may limit their usefulness for estimating the potential impact of global warming on biological processes.

First, impact assessments based on GCMs so far have focused on changes in average temperature, although changes in climate variability may be equally or more important (9,12). A theoretical study by Katz and Brown (9) showed that changes in climate are more closely associated with shifts in the frequency of meteorological extremes than with shifts in the mean. Furthermore, global warming may be associated with an asymmetric diurnal temperature increase, by which daily minima increase while daily maxima remain unchanged (7,8,12). Therefore, impact assessments that rely on scenarios involving only shifts in the mean may be misleading. Second, the low temporal and spatial resolution of GCM outputs makes it difficult to link projections of global warming to biological response models, such as crop growth or plant disease models, which require daily or subdaily data as input (3,16,19). Bonan (3) reviewed several studies that contained sensitivity analyses of ecosystem models to climate change and/or global warming. Results from models based on simple, semi-empirical parameterizations of growth at monthly or annual resolutions differed substantially from more detailed models that explicitly accounted for biophysical and physiological processes on daily or subdaily time scales. As recent advancements in computer modeling make it possible to scale down from monthly averaged GCM outputs to daily or hourly data with stochastic weather generators (16,19), the use of more detailed (and presumably more accurate) biological models for impact assessment of global warming will probably increase. The computational demands will be high, however, given the long-term scope of such studies (3).

Interactions between plant pathogens and their hosts occur on subdaily time scales. For example, spores of many fungal pathogens can germinate and infect in less than 12 h. Furthermore, growth and developmental responses of plant pathogens (e.g., to temperature) are often nonlinear (1,15). Nonlinearity may lead to biased results if averaged data are used for estimating responses to changes in meteorological conditions (15). This bias may be amplified by the projected asymmetric increase of daily minimum and maximum temperatures. Therefore, to arrive at realistic predictions about the potential impact of global warming on plant diseases, it may be necessary to specify projected changes in climate to a resolution that is compatible with the time scale of the underlying biological processes. Thus, projections with subdaily resolution may be needed to accurately model the potential impact of global warming on plant pathosystems.

The objective of this communication is to direct attention to problems resulting from the use of averaged data as input for biological models when response functions are nonlinear. Because only a few published impact assessments of global warming focus on plant pathology (4), our study's purpose is to make plant pathologists aware of the potential for improving impact assessments by accounting for changes in variability of temperature as well as changes in mean temperature.

SIMULATION STUDIES

Consider a hypothetical plant pathogen whose constant-temperature growth curve is unimodal and skewed to the left (Fig. 1A), with minimum, optimum, and maximum temperatures of 0, 20, and 30 C, respectively. Temperature response functions

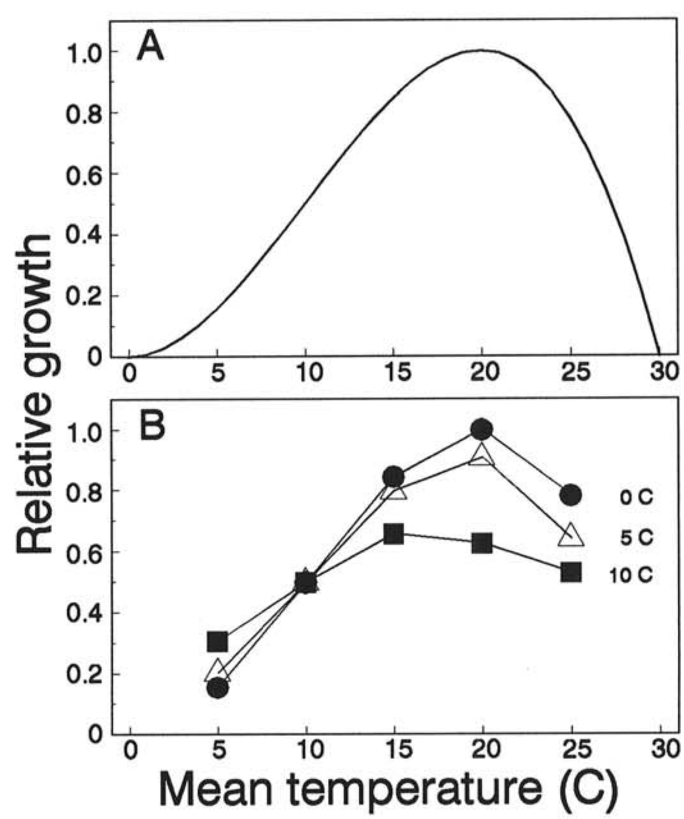

Fig. 1. A, Simulated constant-temperature growth curve of a hypothetical plant pathogen. The curve was generated using equation 1 (see text) with the parameter values $T_{min} = 0$ C, $T_{max} = 30$ C, $m = 1.0$, and $n = 2.0$. **B,** Simulated variable-temperature growth curves for the pathogen shown in **A.** The curves were generated using equation 1 with sinusoidally fluctuating temperatures as input. Amplitudes were 0 C (solid circles), 5 C (open triangles), and 10 C (solid squares).

with this shape and similar cardinal values are typical for many plant pathogenic fungi (1,5,11). They can be described mathematically with various nonlinear models (18), of which we chose the BETE function (1):

$$y = p(T - T_{\min})^n (T_{\max} - T)^m \quad (1)$$

with

$$p = \frac{(n+m)^{n+m}}{n^n m^m}. \quad (2)$$

Here, y is relative growth (on a scale from 0 to 1); T is temperature; $T_{\min}$ and $T_{\max}$ are temperature minima and maxima of the organism, respectively; and n and m are positive parameters. The latter two parameters influence the curvature (nonlinearity) of the growth curve and the location of the temperature optimum relative to minimum and maximum temperatures (1).

Suppose next that temperature fluctuates sinusoidally with a period of 24 h, a mean of 5, 10, 15, 20, or 25 C, and an amplitude of 0, 5, or 10 C; and that hourly temperature values are used in equation 1 to simulate the growth response of the pathogen. When growth is then plotted against daily mean temperature, the resulting curves are flatter than at constant temperatures (Fig. 1B). The magnitude of this effect increases with increasing diurnal temperature amplitude (Fig. 1B). The magnitude is greatest at temperatures near the optimum and smallest at the inflection point of the constant-temperature growth curve (where the growth response is approximately linear).

It is evident from Figure 1B that there may be large differences between growth at constant vs. fluctuating temperatures, and that data on mean temperature without knowledge of the amplitude of the temperature fluctuation may not be adequate for predicting growth. For example, if mean temperature increased from 15 to 20 C, growth could either increase (if the amplitude was 0 or 5 C) or decrease (if the amplitude was 10 C). At a mean temperature of 20 C, relative growth could vary between 1.0 and 0.6, again depending on the amplitude of the temperature fluctuations. Thus, it would be impractical to predict the growth response of the pathogen shown in Figure 1 based on information about mean temperature only.

Growth curves can differ in several features, for example in the location of their cardinal temperatures and/or in the general shape of the curve. In the following, we systematically, although not exhaustively, analyze the effects of changes in some of these factors on simulated growth at fluctuating temperatures. In all calculations, we employed the same temperature scenarios as described above.

Increasing nonlinearity (proportional increases in n and m in equation 1) results in greater differences between growth at constant temperatures and growth at fluctuating temperatures when all other factors remain constant (Fig. 2). A similar effect is observed as nonlinearity increases and the relative location of the temperature optimum is shifted to the right (Fig. 3). (This can be achieved by increasing the value of n in equation 1 while keeping m, $T_{\min}$, and $T_{\max}$ constant.) Differences between simulated growth at constant vs. fluctuating temperatures decrease with increasing values of $T_{\max}$ (Fig. 4) and increase slightly with increasing values of $T_{\min}$ (data not shown). When the entire growth curve is shifted to the right by simultaneously increasing $T_{\max}$ and $T_{\min}$ by the same increments and keeping n and m constant, the differences are also reduced (Fig. 5) if the temperature treatments remain otherwise unchanged. In summary, differences between growth at constant temperatures and growth at fluctuating temperatures are greatest when the mean temperature is close to the cardinal temperatures of the organism and/or when the temperature range over which the growth response is approximately linear is narrow. This suggests that errors resulting from the use of mean temperature for estimating growth are greater for cold-adapted organisms than for warm-adapted organisms, and for organisms with a highly nonlinear growth curve compared to those with a wide temperature range at which the growth response is linear.

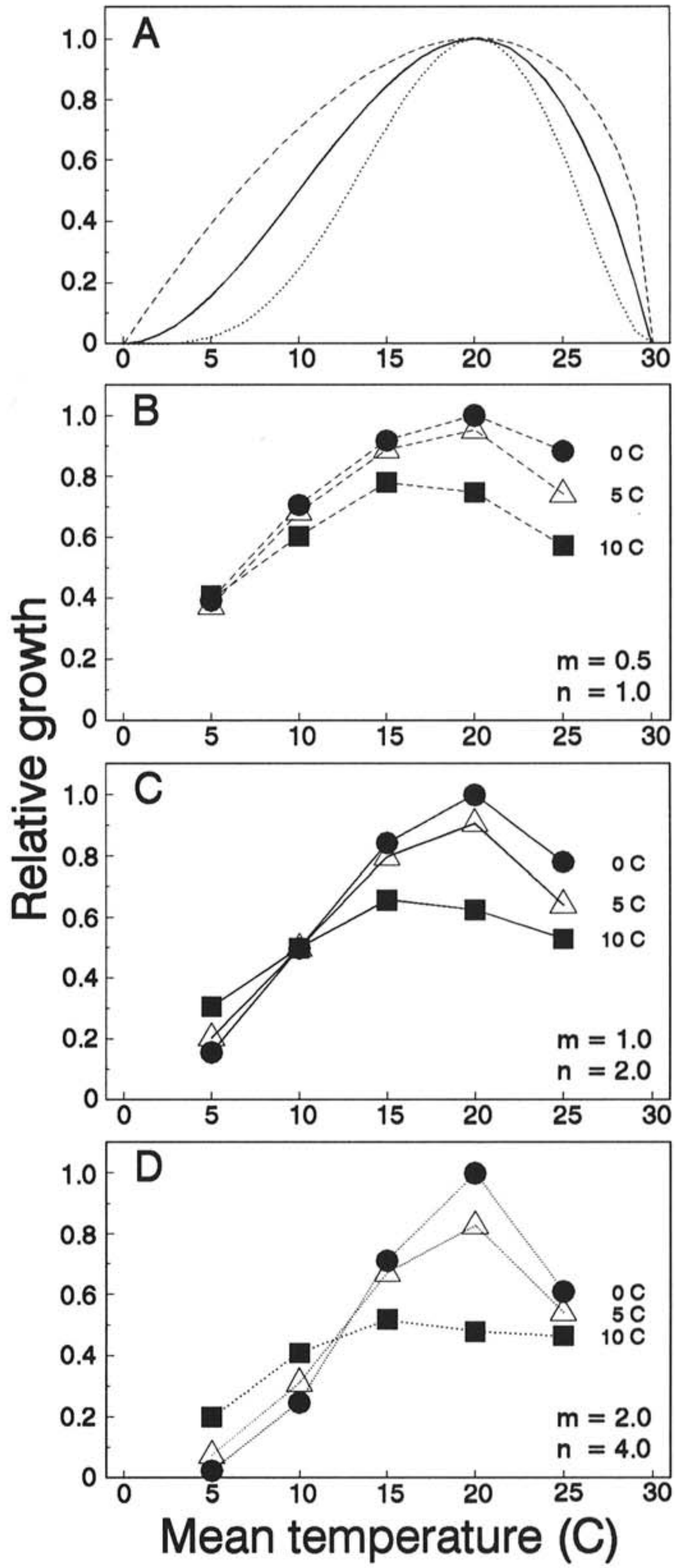

Fig. 2. Effects of increasing nonlinearity of the growth curve on relative growth at constant vs. fluctuating temperatures. **A,** Simulated constant-temperature growth curves for different combinations of the parameters n and m (broken line $m = 0.5$, $n = 1.0$; solid line $m = 1.0$, $n = 2.0$; dotted line $m = 2.0$, $n = 4.0$). **B–D,** Simulated variable-temperature growth curves for different combinations of the parameters n and m. All other parameter values as in Figure 1. The curves were generated using equation 1 (see text) with sinusoidally fluctuating temperatures as input. Amplitudes were 0 C (solid circles), 5 C (open triangles), and 10 C (solid squares).

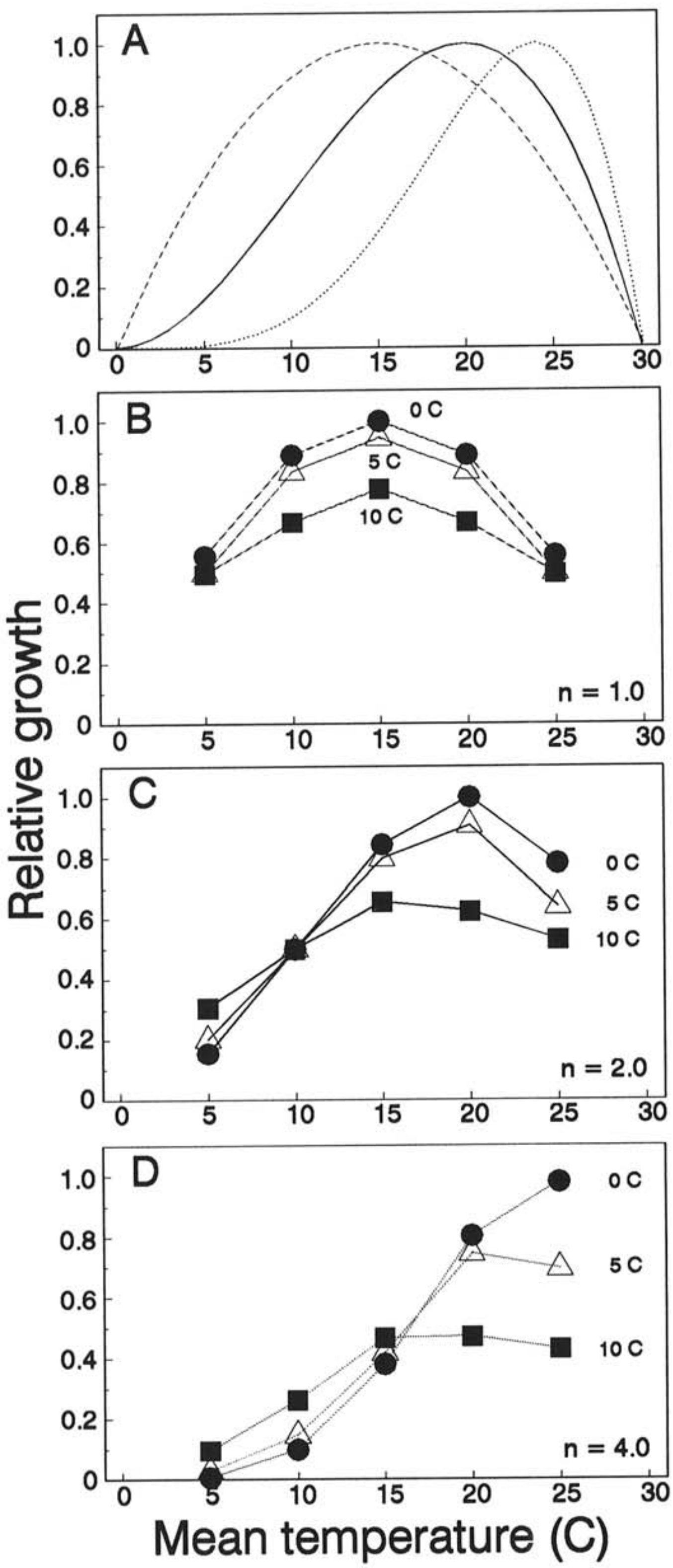

Fig. 3. Effects of increasing nonlinearity of the growth curve and shifts in the temperature optimum of the pathogen on relative growth at constant vs. fluctuating temperatures. **A,** Simulated constant-temperature growth curves for different values of the parameter n (broken line $n = 1.0$; solid line $n = 2.0$; dotted line $n = 4.0$). **B–D,** Simulated variable-temperature growth curves for different values of the parameter n. All other parameter values as in Figure 1. The curves were generated using equation 1 (see text) with sinusoidally fluctuating temperatures as input. Amplitudes were 0 C (solid circles), 5 C (open triangles), and 10 C (solid squares).

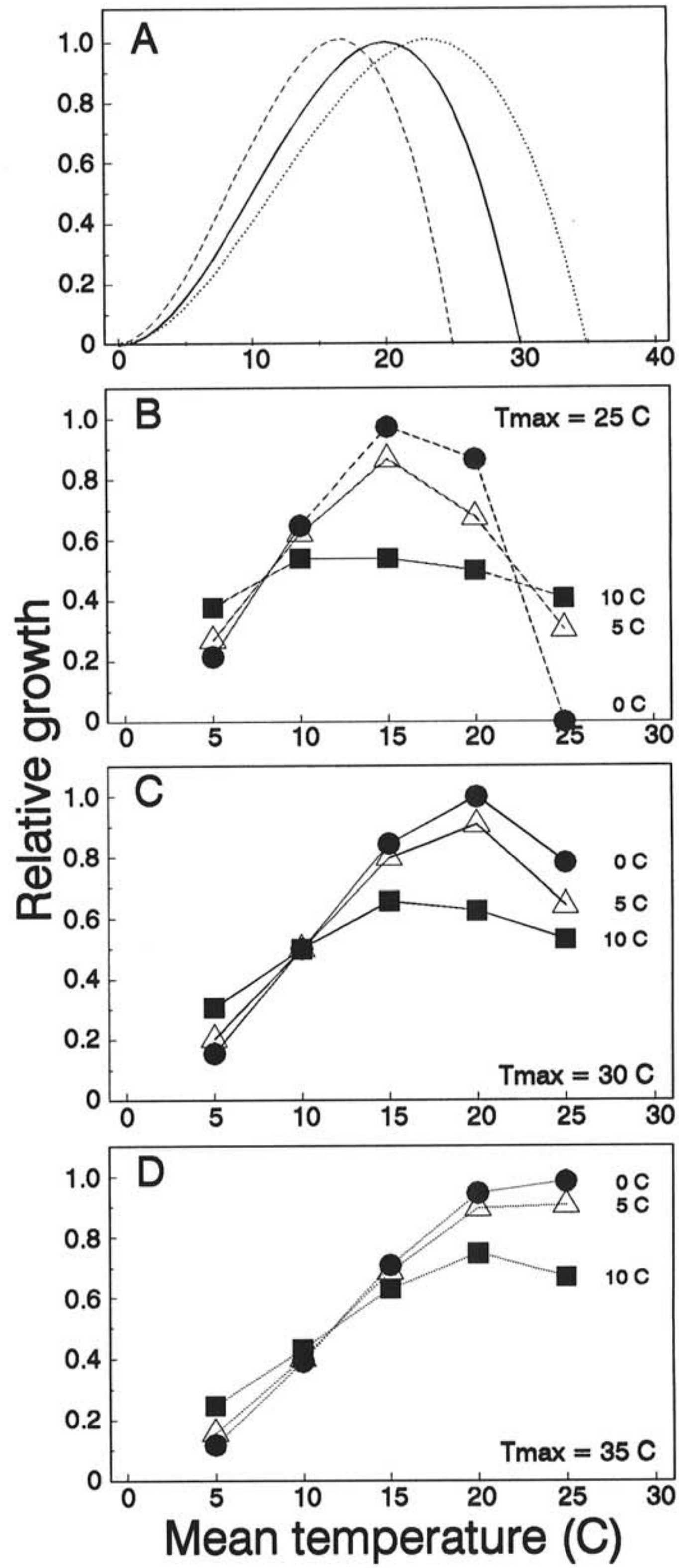

Fig. 4. Effects of increasing maximum temperature (T_{max}) of the pathogen on relative growth at constant vs. fluctuating temperatures. **A,** Simulated constant-temperature growth curves for different values of T_{max} (broken line $T_{max} = 25$ C; solid line $T_{max} = 30$ C; dotted line $T_{max} = 35$ C). **B–D,** Simulated variable-temperature growth curves for different values of T_{max}. All other parameter values as in Figure 1. The curves were generated using equation 1 (see text) with sinusoidally fluctuating temperatures as input. Amplitudes were 0 C (solid circles), 5 C (open triangles), and 10 C (solid squares).

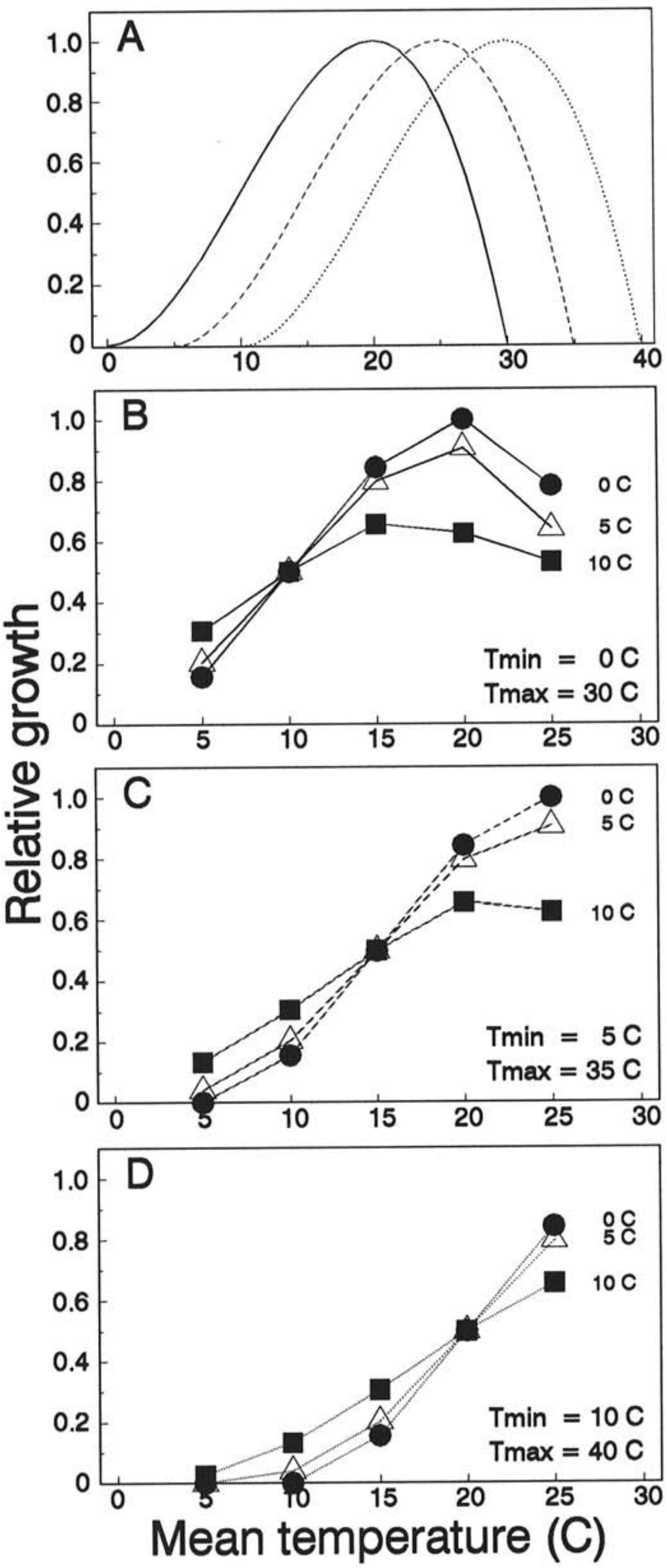

Fig. 5. Effects of increasing minimum (T_{min}) and maximum temperature (T_{max}) of the pathogen on relative growth at constant vs. fluctuating temperatures. **A,** Simulated constant-temperature growth curves for different values of T_{min} and T_{max} (broken line T_{min} = 0 C, T_{max} = 30 C; solid line T_{min} = 5 C, T_{max} = 35 C; dotted line T_{min} = 10 C, T_{max} = 40 C). **B–D,** Simulated variable-temperature growth curves for different values of T_{min} and T_{max}. All other parameter values as in Figure 1. The curves were generated using equation 1 (see text) with sinusoidally fluctuating temperatures as input. Amplitudes were 0 C (solid circles), 5 C (open triangles), and 10 C (solid squares).

CONCLUSIONS

Two general conclusions can be drawn from the examples given in this communication. First, there may be substantial differences between the growth of plant pathogens at constant temperatures and the growth at fluctuating temperatures. And second, data on mean temperature without information about the amplitude of the temperature fluctuations may not be sufficient for predicting growth. On the first point, differences between growth or development at constant vs. fluctuating temperatures have been found experimentally for insects (6,20), microorganisms (13,14), and plants (17). Mostly, variable-temperature growth curves were flatter than constant-temperature growth curves. We reported recently that temperature had only a small effect on the latent period of lettuce downy mildew (*Bremia lactucae* Regel) at fluctuating temperatures, although a strong interaction between temperature and latent period was observed in experiments with constant temperatures (14). As shown in the present study, these observations can be explained, at least in part, with a basic property of nonlinear growth: average inputs (e.g., in temperature) will not result in average outputs (e.g., in growth). On the second point, it may be impractical to predict the magnitude and direction of the growth response of an organism if only information about changes in mean temperature is available. This applies particularly to cold-adapted organisms and to organisms with a highly nonlinear growth curve. This result has implications for all assessment studies of climate change and/or global warming, in which projections with averaged data are used to estimate or simulate biological responses that are nonlinear. Researchers need to become more aware of scaling problems imposed by nonlinearity, which may constrain their ability to translate large-scale, low-resolution data (such as GCM outputs) into information that is relevant to biological or physiological processes (such as interactions between plants and their pathogens). It will be a challenge for climate change researchers to reconcile physiological and biophysical approaches to modeling biological processes with the long-term approach to modeling global warming.

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