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Comparison of modelling approaches to simulate the phenology of the European corn borer under future climate scenarios

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ABSTRACT

The phenological development of insects is simulated predominantly via models based on the response of the organisms to air temperature. Despite of a large body of literature supporting the evidence that the organism physiological response to temperature is nonlinear, including a declining phase, most of these models calculate the rate of development using a linear approach, implying that air temperatures mostly does not fall outside of the linear region of response to temperature of the organism. Another simplification is represented by the calculation of the rate of development using daily mean air temperature, which has already been demonstrated being a reliable method only in limited conditions. It can be hypothesized that the use of developmental models based on linear developmental rates, which can be successfully applied under climate conditions to which organisms are well adapted, could be inadequate under either future climatic scenarios or when extreme events occur (e.g., heat waves). In such contexts, linear responses might lead to interpretations of climate effects not consistent with the real organism physiological response to temperature.

In this work the case of *Ostrinia nubilalis* Hübner (European corn borer, ECB) development was taken as an example to compare (i) a nonlinear approach with hourly air temperature as input (HNL approach), (ii) a linear based approach with hourly air temperature as input (HL approach), (iii) a linear based approach with daily air temperature as input (averaging method, DL approach), and (iv) a linear based approach using a cutoff temperature with daily air temperature as input (DL_{cutoff} approach). The comparison was performed under the IPCC (Intergovernmental Panel for Climate Change) emission scenario A1B, and three time frames in Europe: 1995–2004 (baseline–2000s), 2015–2024 (2020s), and 2045–2054 (2050s). The SRES A1B was selected as one of those for which the projected raise of temperature is estimated to be one of the highest, although the projected difference comparing to the other SRES is estimated as evident in the 2050s time frame, among the ones considered.

Using degree-days as a proxy for the rate of development, results showed that the DL approach predicts more than the HNL in all the time frames in almost all Europe with the exception of Southern Italy and the Mediterranean coasts of France and Spain where the differences were negligible. These effects were due (i) to the linear relationship used by the DL approach, and partially (ii) to the averaging operation that decrease the effects of high temperatures in regions with high (but not extreme) warm temperatures. The HNL and HL approach predicted the same pattern of degree-days accumulation in all Europe with the exception of the regions of Southern Iberian peninsula (across all the timeframes), Balkans, and Turkey (under the 2050 scenario). This effect was due to the different HNL and HL accumulation of degree-days at temperatures higher than the ECB optimum temperature. The comparison between the DL_{cutoff} and the HNL approaches showed similar results to the DL vs HNL approach in central and Northern Europe, while in Southern Europe a negative difference (more DD accumulated for the HNL approach) were observed: in regions characterized by high temperatures, the cutoff temperature, setting a limit to the maximum temperatures diminished the calculated average temperature and as a consequence the calculated degree-days.

The results of this work showed that according to the method chosen for simulations, different results can be obtained, hence leading to different conclusions about the effect of a warming climate on pest development. These results stress the need of reconsidering the appropriateness of models to be used, which cannot be assumed as correct on the basis of their effectiveness under current conditions.

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1. Introduction

The poikilothermic characteristic (i.e., the variation of internal temperature as a consequence of variation in the ambient environmental temperature) of many insects has been used for developing operational temperature-driven models applied in the integrated management of many agricultural pests (Régnière and Logan, 2003). The thermal time approach (also known as degree-days) is one of the most widely used method to simulate phenological development of insects: it represents the accumulation of heat units above a minimum temperature threshold required for an organism to develop from one stage to another in its life cycle, usually calculated on a daily basis (Honek, 1996; Trudgill et al., 2005). Despite a large body of literature supporting the evidence that the response of biological organisms to temperature is nonlinear (e.g., Stinner et al., 1974; Curry et al., 1978; Briere et al., 1999; Allen and Jason, 2000), thermal time based models adopt a linear approach to model the relationship between degree-day and the whole range of air temperature. The assumption of linearity has been widely accepted assuming adaptation of the insects to local climatic conditions, and that their exposure to extreme temperatures is rare in the field (Campbell et al., 1974). This formalization suggests that these models work properly only when air temperature do not fall outside of the linear region of the organism thermal response (Régnière and Logan, 2003). Furthermore, the application of these methods requires that consideration must be given to the geographical location, climate conditions and biology of the specific organism under study (Roltsch et al., 1999).

Another simplification used by some thermal time models is the adoption of the averaging method (i.e., rectangle method; Arnold, 1960) which calculates degree-days starting from the daily mean air temperature. Roltsch et al. (1999) and Maiorano (2011) demonstrated that this method is less accurate than other approaches which take into account daily temperature fluctuations. In addition, Worner (1992) suggested that using mean air temperature, without considering daily fluctuations, is inappropriate to simulate insect response to temperature because their developmental rates at constant or variable temperatures are deeply diverse. The limit in the application of such methods is marked when daily air temperature exceeds the lower and upper threshold temperatures.

Given all these considerations, there is the risk that using models based on linear developmental rates, which can be successfully applied under 'standard' climate conditions, could be inadequate under future changed climatic conditions or when extreme events occur (e.g., heat waves), possibly leading to interpretations of climate effects not consistent with the real organism physiological response to temperature. This problem is expected to be even more pronounced when using mean temperatures (i.e., the averaging method).

In the last decade some studies were performed using thermal time methods to simulate insect development under climate change scenarios (Porter, 1995; Bergant et al., 2005; Trnka et al., 2007; Diffenbaugh et al., 2008; Luedeling et al., 2011). In this study we have chosen to analyze the case of the European corn borer (*Ostrinia nubilalis* Hübner, ECB). The ECB is a species of great concern for all the maize growers of Europe and North America. This pest develops through four stages of development: egg, larva (five instars), pupa, and the adult stage. Each generation is completed after the accumulation of around 670 degree-days (calculated from the occurrence of 50% adult first flight to the 50% of second flight, estimated from Bessin, 2003). It diapauses as a last instar larva and both induction and termination of diapause are photoperiodically controlled (Beck, 1962; Skopik and Bowen, 1976). In Europe, the ECB has been reported from the south of Spain to Finland. In almost all Southern Europe, the Balkans, Greece and Turkey, ECB can develop from two to three generations. In Central and Northern Europe usually one generation is observed.

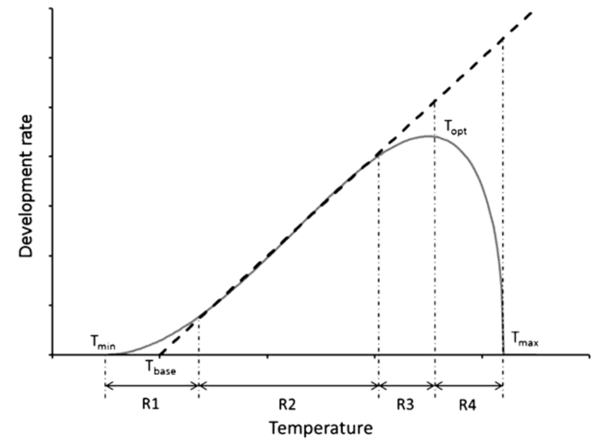

Fig. 1. Differences between linear (black dotted line) and nonlinear (grey full line) approaches for representing the relationships between temperature and development. Four regions (R1–R4) are represented. The nonlinear approach is based on three cardinal temperature: T_{min}, T_{opt} and T_{max} which are the minimum, the optimum and the maximum temperature of development, respectively. T_{base} is the base temperature of the linear approach.

The studies so far conducted (Porter et al., 1991; Porter, 1995; Trnka et al., 2007; Diffenbaugh et al., 2008) agree in predicting an increase in the number of generations in all the areas where the ECB is already endemic and a northward extension (both in Europe and USA) of the limits of ECB. These works have been conducted using a linear approach to simulate the response to temperature, assuming that a rise in temperature of any magnitude results in one-sided more favourable conditions for the ECB.

The objectives of this work were: (i) to show that different approaches to simulate ECB phenological development under actual and future climate can lead to different results and consequently to different considerations about the effect of climate warming, and (ii) to underline the importance of choosing the most appropriate approach while assessing ECB response to climate scenarios diverse from the one in which the organism is well adapted.

2. Materials and methods

The hourly nonlinear degree-day approach proposed by Maiorano (2011) was compared to the degree-day methods that have been used to model the ECB development: (i) averaging method (Porter et al., 1991; Porter, 1995); (ii) averaging method with cutoff temperature (Trnka et al., 2007), and the hourly linear approach (Got and Rodolphe, 1989; Diffenbaugh et al., 2008).

2.1. Linear vs nonlinear approaches

Fig. 1 shows a graphical example of the linear (L, black dotted line) and the nonlinear (NL, dark grey solid line) approaches to reproduce the response to temperature of biological organisms. The nonlinear one is based on three parameters: the minimum (T_{min}), the optimum (T_{opt}), and the maximum (T_{max}) cardinal temperatures for development and it is described by an exponential phase at low temperatures, which increases up to T_{opt} and then it is followed by a decline to T_{max}. Four regions can be observed in Fig. 1 (indicated from R1 to R4). The first region (R1) is bounded by T_{min} and the starting point of the almost linear development. In R1, the NL approach calculates a higher development rate than the L approach. Moreover, the L approach assumes that the organism development starts from T_{base}, which is an extrapolation from the exponential phase of development.