infection[12], it is reasonable to suggest that the virus may be contributing to the production of chromosomal anomalies in these cells.

An important role has been attributed to the papilloma virus in the development of epithelial neoplasias both in animals and in man[16-20]. The transformation of benign lesions induced by the virus into malignant tumors seems to depend on an interaction with other factors. If the epithelial cells of the digestive and urinary tracts are also exposed to the clastogenic action of *P. aquilinum*, then the plant may induce chromosome rearrangements in these cells. Perhaps the induction of chromosome rearrangements in cells infected by the papilloma virus is one of the cofactors needed for the malignant transformation of papillomas through oncogenic activation. Alternatively, the transformation of cultured cells infected with bovine papilloma virus is known to be induced by 12-O-tetradecanoyl-phorbol-13 acetate (TPA). The use of TPA as a chemical promoter induces transcription of the viral genome both in vivo and in vitro[21]. It is possible that substances present in bracken fern may act in a similar manner by promoting genome expression of the virus and thus contribute to the malignant transformation of the papillomas.

The bladder and digestive tract tumors of cattle represent a convenient model for the study of papilloma virus (BPV2 and BPV4) in terms of the induction of benign neoplasias that may turn malignant through the direct or indirect action of chemical agents present in bracken fern. While the virus seems to play a role only in tumor initiation[22], bracken fern may contribute to the maintenance and progression of these tumors either by inducing mutations and/or chromosome aberrations or by promoting viral gene activity in the infected cells.

1 Acknowledgments. We are grateful to Dr F. J. Benesi, Dr J. L. Guerra and Dr I. L. Sinhorini for performing some of the clinical and pathological analyses; O. P. Ferraz, L. A. Tadeu Dias, L. F. Feitosa and A. M. N. Paiva for technical assistance; and to Dr N. H. C. Castro and Dr C. de Araujo Peres for critical and statistics review, respectively. Research was supported by CNPq FAPESP and CAPES.

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0014-4754/88/090785-04$1.50 + 0.20/0

Photoperiodic diapause induction suppressed at low temperatures in a long-day insect

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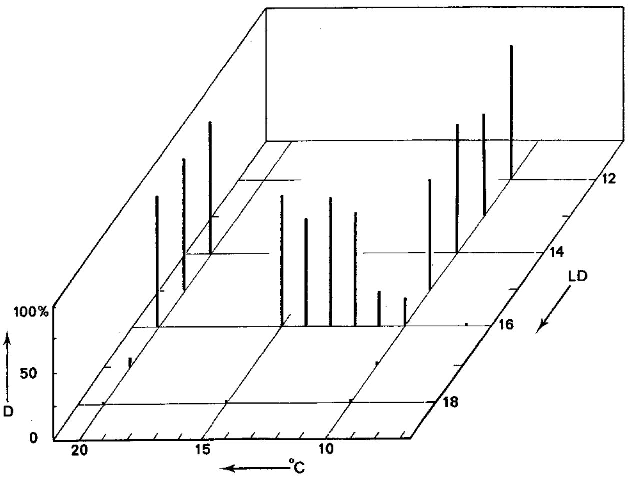
Received 7 January 1988; accepted 6 May 1988

Summary. The long-day insect *Yponomeuta vigintipunctatus* was subjected to various combinations of temperature and photoperiod. The photoperiodic induction curve at 10 °C resembled the one at 20 °C, but with a shift of the critical photoperiod towards the shorter day-length. Such unusual averting of diapause at lower temperatures in combination with intermediate long-day photoperiods has still been described in only few insect species of the temperate zone.
Key words. Yponomeuta vigintipunctatus; Lepidoptera; Yponomeutidae; diapause; photoperiodic induction curves; low temperature influence.

In most long-day insects it has been found that the photoperiodic induction curve shifts to longer day-length when the temperature at which they are reared is lowered[2]. Preliminary laboratory studies with the small ermine moth of orpine, *Yponomeuta vigintipunctatus* Rez., however, revealed the opposite effect of low temperatures on diapause induction: at LD 16:8 almost all the pupae enter diapause between 20 °C and 13 °C; diapause induction is suppressed to a large extent within the range from 12 to 7.5 °C. In this paper I report the effects of various combinations of larval rearing temperatures and photoperiods on the incidence of diapause in the small ermine moth of orpine. This species has two generations a year and hibernates as a pupa in diapause.

Material and methods. All experiments were performed with larvae of the F1 generation obtained from parents collected in the field in the autumn of the foregoing years. They originated from three different localities in The Netherlands. Copulation and oviposition took place under long-day conditions (LD 17:7, 20 °C)[3]. The larvae were equally distributed over each of the three groups of treatments (in total 19) presented in the figure. They were fed until pupation with leaves of orpine, *Sedum telephium* L., the only host-plant of this monophagous species[4].

Immediately after pupation all individuals were placed at 20 °C, LD 17:7 to secure diapause termination. For each of the 19 combinations the percentages diapausing and non-



Diapause commitment (in percentages = D) in *Y. vigintipunctatus*. The low temperature effect is measured at LD 16:8. That a temperature of 10 °C causes a shift in critical photoperiod only of about 1 h is clearly demonstrated. The dots on the LD 18:6 line denote 0%, as do the two other dots shown.

diapausing were assessed by a method in which three criteria (developmental time, decrease in pupal weight and eye pigmentation) were taken into account. This procedure will be dealt with in full in the near future. In most cases a developmental time below 14 days was found for non-diapausing pupae[5]. As in earlier experiments no differences between the sexes as regards diapause behavior was observed the data for males and females were pooled. The number of pupae varied among groups between 22 and 277. At 7.5 °C, however, only 9 specimens reached the pupal stage.

Results and discussion. As can be concluded from Veerman and Herrebout's work and the figure the critical photoperiod for diapause induction at 20 °C is to be found between LD 16:8 and 17:7. At 15 °C and LD 16:8 100% diapause is still obtained. With a further decrease in temperature, however, there is a gradual decrease of the incidence of diapause to little more than 20% at 10 °C, LD 16:8 and even 0% at 7.5 °C, LD 16:8. At the lower temperatures larval development time increased considerably (three to four times as long in comparison with the 20 °C treatment) and larval mortality increased to as high as 90% at 7.5 °C. This will be dealt with in detail elsewhere.

That the photoperiodic responsiveness as such is not suppressed or even eliminated at these low temperatures is nicely demonstrated by the abrupt increase in diapause incidence when the photoperiod was shortened at 10 °C from LD 16 : 8 to 15:9. The induction curve at 10 °C resembles the one at 20 °C (fig.), but the critical photoperiod is shifted and lies between LD 15:9 and 16:8.

Suppression of diapause by low temperatures has been found in relatively few insects. In the oriental fruit moth, *Laspeyresia molesta,* diapause is induced only at medium temperatures (20–26 °C). Higher or lower temperatures result in continuous development, irrespective of the light conditions[6]. The south-western corn borer, *Diatraea grandiosella,* has a similar narrow temperature range for photoperiodic diapause induction[7]. The most relevant example is the cotton-boll worm, *Chloridea obsoleta*[8]. Under natural conditions a large percentage of this species of which the larvae had developed in early autumn at temperatures above 20 °C were diapausing. The incidence of diapause progressively decreased with the steadily decreasing autumn and winter temperatures. It is speculated[2] that this reaction – the opposite of what one would expect in autumn in the temperate zone – is a relict of the southern origin of the species.

Two non-lepidopteran examples of insects in which low temperature acts as a diapause-averting stimulus are, firstly, the soil-inhabiting scarab *Anomala cuprea,* of which the mature larvae enter diapause when reared at 22 °C under any photoperiod. A rearing temperature of 5 °C, however, applied to late second-instar or third-instar larvae averts diapause[9]. Secondly, in the linden bug *Pyrrhocoris apterus* diapause induction occurs at 26 °C, but not at 15 °C. Here also the termination of diapause was restrained at this low temperature[10].

Although the above-mentioned examples differ greatly in rearing regimes (and concern laboratory versus field observations), as well as in taxonomic position, all except the linden bug have one feature in common; they are of tropical or subtropical origin. *Yponomeuta vigintipunctatus* also inhabits suptropical regions within its geographical range; the southern part of Japan[11]. The ecological significance of the low temperature effect may then be sought in the specific nature of the temperature regimes during (sub)tropical autumn and winter.

In contrast to temperate zone insects those living in (sub)tropical regions are characterized by their reliance on relatively subtle changes in photoperiod and temperature as diapause-inducing stimuli[12]. This may account for the gradual decrease in diapause commitment when the rearing temperature is lowered from 15 °C to 7.5 °C in *Y. vigintipunctatus* without changing the photoperiodic conditions. More support for the assumption that the low temperature effect may come from the (sub)tropics might be derived from the observation that decreasing the photoperiod at 10 °C from LD 16:8 to LD 12:12 again raises the percentage of diapause from 20.6% to 98.2%. Thus, here the low temperature as such does not restrain the summation of diapause promoting photoperiods as is found for *Pyrrhocoris apterus*[10]. This latter phenomenon meets the criticism[2,13] that the low temperature effect is caused by a weakening or even abolishment of the insect's reaction to photoperiod. The physiological mechanism underlying the low temperature effect awaits further investigation.

1 The author thanks W. M. Herrebout, A. Veerman and M. C. M. de Jong for valuable suggestions and for correcting the manuscript, and J. Herzberg for drawing the figure.
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