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Geography of photoperiodic response in diapausing mosquito

IN temperate latitudes, many arthropods rely on photoperiod to cue their seasonal development. Although the relationship between critical photoperiod and latitude is well illustrated, that between critical photoperiod and altitude remains obscure[1,2]. I wish to consider photoperiodic control of dormancy in the pitcher-plant mosquito, *Wyeomyia smithii*, and quantify the relative effects of altitude and latitude on the photoperiodic response of an organism.

W. smithii is found from the Gulf coast to Labrador and northern Manitoba[3–6] where it confines its breeding site to the water-filled leaves of a single species of plant, *Sarracenia purpurea*. The larvae overwinter in the pitchers in a state of developmental arrest. Short days evoke and maintain, while long days avert or terminate this diapause[7,8]. The photoperiod which promotes 50% development and initiates or maintains 50% diapause is known as the critical photoperiod[4,7,9,10]. In *W. smithii*, the critical photoperiod is the same for the initiation and termination of diapause among larvae reared in the laboratory and for the termination of diapause among larvae collected during early autumn[7]. I have collected larvae north of 38°N latitude only during the autumn (autumn larvae) and south of this latitude only during the winter (winter larvae). I packed the autumn larvae in ice on the day of capture and maintained them on ice until they reached the laboratory where I stored them in an ordinary refrigerator at 4±2 °C until the start of experiments. All experiments were begun within 45 d of capture. Since the winter larvae received unknown chilling in nature which might have affected the critical photoperiod[11,12], I reared them in the laboratory and determined the critical photoperiod for the initiation of diapause in the F_1 generation. Whether considering the maintenance of diapause among autumn larvae or the initiation of diapause among the F_1 of winter larvae, I exposed them to a range of LD 10 : 14 to LD 17 : 7 in 30-min increments at 25±1 °C. Rearing procedures and the criteria for diapause and development were the same as in previous studies[7,13].

I determined the critical photoperiod for 22 populations of *W. smithii* collected over a range of 19° latitude, 20° longitude and 1,200 m altitude. The critical photoperiods ranged from 12 to 16 h of light per day (Fig. 1) and were closely correlated with latitude ($t=14.26$; $P<0.001$) and altitude ($t=9.25$; $P<0.001$) but not longitude ($t=1.71$; $P>0.10$). Latitude accounted for 80.5% of the variation in critical photoperiod and altitude an additional 15.5%. Critical photoperiod may then be estimated from latitude and altitude by the least-squares regression equation

$$\text{critical photoperiod} = 6.51 + 0.185 \text{ latitude} + 0.00129 \text{ altitude}$$

To correlate critical photoperiod with climatic variables, I modelled the growing season (mean number of freeze-free days) for 26 cities in the United States north of latitude 30°N and east of longitude 90°W (ref. 14). Although city temperatures are not the same as in bogs, they are presumably correlated[15]. I found that growing season was closely correlated ($r=0.97$) with latitude ($t=15.39$; $P<0.001$) and altitude ($t=4.59$; $P<0.001$) but not longitude ($t=0.42$; $P>0.60$). I then calculated the growing season for each locality in Fig. 1 using its latitude and altitude and the least-squares regression equation relating growing season to these parameters

$$\text{growing season} = 585.93 - 9.33 \text{ latitude} - 0.094 \text{ altitude}$$

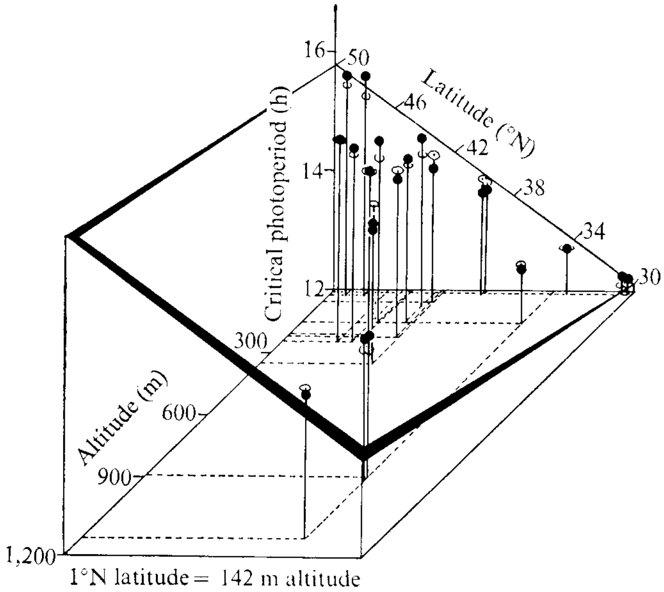

Fig. 1 Relationship between critical photoperiod, altitude and latitude. Circles on the regression plane indicate where the projections of the data points cross that plane. $r = 0.98$; $P < 0.001$.

I found that growing season calculated in this manner was an excellent predictor of critical photoperiod in *W. smithii* (Fig. 2). This degree of correlation between an ecogeographic character and a specific climatic variable is unprecedented. In many other studies[16–20], the ecogeographic characters being examined are affected by a wide range of environmental influences which may be changing independently of geography. The photoperiodic response of *W. smithii* tracks climate so closely for several reasons. First, photoperiodism is a physiological adaptation concerned mainly with the timing of seasonal development; second, the low variation in microhabitat offered by the leaves of *Sarracenia purpurea* over a wide geographic range permits a more direct expression of this adaptation. Third, critical photoperiod in *W. smithii* is a continuous variable over the range considered, rather than a discontinuous variable as in some other insects[21,22].

To account for geographic differences in the timing of phenological events, including seeding and harvest dates of winter wheat and insect emergence, Hopkins proposed a bioclimatic law[23] equating a 1° increase in latitude with a

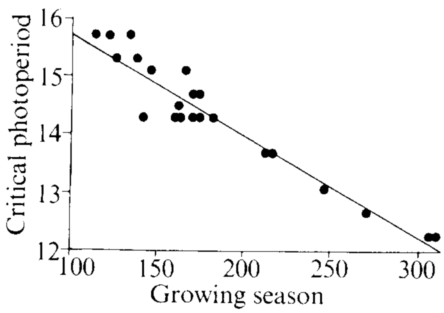

Fig. 2 Correlation of critical photoperiod with growing season. Freeze-free days for each locality were calculated from a least-squares regression equation relating number of freeze-free days of 26 cities in eastern North America to latitude and altitude. $r = 0.96$; $P < 0.001$.

rise in altitude of 122 m, or somewhat less than my estimate of 142 m per °N. My results are not grounds for modifying Hopkins' law and its prediction of phenological events, but rather point to the departure from this law by the photoperiodic cues which mediate seasonal development. The disparity between Hopkins' law and critical photoperiod in *W. smithii* relates to the observation that, for a given date between the spring and autumnal equinox, daylengths are longer in the north than in the south[24]. Consequently, insects on a southern mountain should use a shorter daylength to enter diapause on a given calender date than will those in a population further north which enters diapause on the same date. One would then have to go higher up the mountain than predicted from the bioclimatic law to find a locality where the mosquitoes are using the same critical photoperiod as the northern population. Hopkins' bioclimatic law in temperate and north-temperate latitudes may thus be expected to underestimate the effect of altitude on photoperiodism.

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