Environmental Cues

Introduction

Dormancies are controlled chiefly by seasonal periodicities at the earth’s surface, or by other periodicities that give seasonal information. This chapter briefly introduces terrestrial seasonality, and then considers each of the possible controlling factors in the environment in more detail. This treatment will be compared in the next two chapters with experimental findings about the responses of insects to seasonal cues.

Seasonality

Factors that directly limit life on the earth’s surface stem from geographical and seasonal variations in the long-term pattern of physical conditions we know as climate. The basic elements of climate are controlled by global temperatures which depend on solar heat. Energy from the sun passes through the earth’s atmosphere and is absorbed by the earth. This warms the surface of the ground, which in turn warms adjacent layers of air. The heat gained depends chiefly on the ground’s orientation to the sun, and the gain is greatest when the plane of the surface is directly perpendicular to the sun’s rays. When the sun is at a low angle to the ground (or has set) little or no heat is absorbed, and heat may re-radiate away. As a result, regions near the equator receive more heat than those near the poles. Although global patterns of atmospheric circulation driven by these temperature differences modify regional temperatures, areas at higher latitudes are therefore colder.

In addition, sites at higher elevation (altitude) are colder than those at lower elevations. Temperature decreases with height because the atmosphere is warmed by terrestrial re-radiation rather than direct absorption of the sun’s rays. Other factors being equal, the difference amounts to about 1°C per 100 m of elevation.

Seasonal variations in the capture of heat result from the fact that the earth’s axis is inclined at an angle of 23°27’ to the perpendicular in its orbit around the sun (Fig. 4). As a result, the region where the sun is overhead at midday varies between 23°27’N (the tropic of Cancer) and 23°27’S (the tropic of Capricorn). When the sun is over the tropic of Cancer, in other words when the north pole has its greatest tilt toward the sun, maximum heat is contributed to the northern hemisphere; this is the summer solstice (21 June). Overhead at noon at 23°27’S, the sun provides its minimum heat of the year to the northern hemisphere (the winter solstice, 22 December), because the north pole then tilts away from the sun. When the sun is over the equator during its apparent journey north (21 March), it is the spring or vernal equinox; as the sun’s apparent position crosses the equator toward the south (22 September) it is the autumnal equinox. The dates of these invariable events are exactly reversed in the seasons of the southern hemisphere. The earth’s orbit is actually slightly elliptical, but for general purposes (as in Fig. 4) can be treated as exactly circular.
A second result of these seasonal progressions is that daylength (see the following section) changes steadily from a winter minimum (at the solstice) to a summer maximum, reinforcing the differential heating between seasons because the shortest day coincides with the lowest solar elevation.

These basic patterns are complicated by the fact that the ground warms up relatively slowly. As a result, the earth re-radiates less heat than it receives for the first part of the summer in a given region, so that temperatures at the earth's surface (and in the lower atmosphere) reach their maximum significantly later than the summer solstice, often several weeks later. Similarly, the earth cools down relatively slowly as the supply of solar heat diminishes, so that the minimum annual temperature occurs significantly later than the winter solstice.

These key changes in temperature modify conditions for life both directly and through interactions with the supply of moisture, the availability of plant or animal food, and so on.

The fact that the earth's surface consists of continents separated by large oceans also modifies regional climates. The sea warms and cools more slowly than the land, and so reduces temperature variations at the edges of the continents. Small islands in the oceans have, relative to large land masses, and depending on their latitude, very moist and stable climates. At the other extreme, lands unmodified by oceanic influences, as in the centre of continents, have true “continental climates” at temperate latitudes: cold winters and hot dry summers.
These global and regional differences are integrated by the basic type of vegetation — such as coniferous trees, deciduous trees, or grasses — that grows in a particular region. Especially for small poikilotherms like insects, however, temperature and other effects are modified on a still smaller scale by particular features of local habitats and microhabitats.

Environmental cues

As indicated in Chapter 4, the possible environmental controls for seasonal events can be divided into two classes. Some factors can themselves render conditions unsuitable and may directly enforce quiescence or regulate development. These factors include temperature, moisture, food, oxygen, water-turbulence, predators, competitors, lack of habitats, or phenological stage of foodplant. Such factors also may have caused diapause or indirect developmental stimulation or inhibition to have been selected for. Other factors such as photoperiod correlate predictably with such limiting seasonal progressions, but are not themselves limiting ("cues"). Some factors, such as temperature or food, might act in both ways at different levels, but experiments have not usually been designed to distinguish the effects of limiting levels from those of non-limiting levels that act as seasonal cues.

Possible seasonal cues vary in their reliability (= predictability), frequency (number of opportunities that the insect has to monitor them as it prepares to respond) and ease of recognition (the precision with which cues can be used depends on the ability of insects monitoring them to recognize critical differences).

These properties may also vary according to whether absolute or relative perceptions are to be employed. Thus the absolute daylength indicates a seasonal position; but seasonal cues are also given by comparisons from day to day of the magnitude, and especially the direction, of change of daylength.

Table 16 summarizes the features of major cues that would be available for use in the control of dormancy by temperate insects. These and some other less significant potential cues are discussed below. Three main phases of diapause — induction, diapause development and completion (Table 2) — are potentially cued to these environmental signals. Some cues are geophysical, and are related chiefly to properties of the earth as a planet. Other cues are both globally and locally determined, derived from physical factors such as temperature, or from biotic ones such as vegetation or other organisms.

The components of the "reliability" of particular cues have been considered in more detail in several theoretical and statistical discussions (e.g. Colwell 1974; Stearns 1981). These reflect attempts to specify the "predictability" or reliability of particular phenological patterns in terms of their "constancy" (lack of change with season), and "contingency" (temporal consistency with which seasonal changes are repeated).

Photoperiod

Seasonal and geographic patterns

1. Daylength

The astronomical relationships that govern the seasonal supply of heat from the sun (see above), together with the diel rotation of the earth on its own axis, result
Table 16. The qualities of some environmental cues that can indicate seasonal position in temperate regions

<table>
<thead>
<tr>
<th>Cue</th>
<th>Reliability</th>
<th>Frequency</th>
<th>Ease of recognition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Absolute (correlation with seasonal position)</td>
<td>Relative (predictability of seasonal change)</td>
<td>Absolute (availability of sensors)</td>
</tr>
<tr>
<td><strong>Physical</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Photoperiod(^a)</td>
<td>High</td>
<td>High</td>
<td>Daily</td>
</tr>
<tr>
<td>Thermoperiod(^b)</td>
<td>Fairly high</td>
<td>Fairly high</td>
<td>Daily</td>
</tr>
<tr>
<td>Temperature level(^c)</td>
<td>Low in short term, except in certain habitats, high in long term</td>
<td>Low in short term, except in certain habitats, high in long term</td>
<td>Continuous</td>
</tr>
<tr>
<td>Moisture(^d)</td>
<td>Low to high</td>
<td>Fairly low? Low to moderate</td>
<td>Continuous</td>
</tr>
<tr>
<td>Sunshine(^d)</td>
<td>Low</td>
<td>Low or none</td>
<td>Intermittent</td>
</tr>
<tr>
<td>Wind(^d)</td>
<td>Low or none</td>
<td>Low or none</td>
<td>Intermittent</td>
</tr>
<tr>
<td><strong>Non-physical</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Occurrence of other organisms(^e)</td>
<td>None to high</td>
<td>None to high</td>
<td>Variable</td>
</tr>
<tr>
<td>Food (e.g. state of foodplant)(^f)</td>
<td>Often high</td>
<td>Often high</td>
<td>Variable or continuous</td>
</tr>
<tr>
<td>Metabolic state of host(^g)</td>
<td>Often high</td>
<td>Often high</td>
<td>Continuous</td>
</tr>
</tbody>
</table>

\(^a\) Least affected by microhabitat.
\(^b\) Usually correlated with photoperiod.
\(^c\) Can also be limiting.
\(^d\) Not seasonal everywhere.
\(^e\) In parasites.

in precise seasonal changes in daylength (Fig. 5). The sidereal day, or real period of the earth’s rotation, is nearly 4 minutes shorter than the solar day of exactly 24 hours: the apparent position of the sun moves as the earth travels in solar orbit by a distance equivalent to about 4 minutes of rotation. The symmetry of the latitudinal and seasonal patterns is modified, albeit only slightly, because the earth is not an exact sphere, because its orbit is not exactly circular, because its axis of rotation has a slight wobble, and for other astronomical reasons. Table 17 summarizes the length of day at different latitudes at the solstices and equinoxes and on intervening dates. At the equinoxes, of course, the axis of the earth’s rotation is perpendicular to the sun’s rays, so that theoretically equal daylengths occur everywhere on earth. The slight differences shown are due partly to the way in which sunrise and sunset are defined (see Table 17). Between the poles and the arctic and antarctic circles at latitude 66°33′ (which corresponds to the angle between the earth’s axis and the plane of its orbit, i.e. 90° – 23°27′) continuous daylight (in summer)
Fig. 5. Scheme showing the effect of the inclination of the earth's axis and the plane of solar orbit on seasonal photoperiod. Note the long nights during winter in the northern hemisphere.

Table 17. Daylengths at different northern latitudes during the solstices and equinoxes and on intermediate dates. Nightlengths in the southern hemisphere are essentially the same (from United States Naval Observatory 1945)

<table>
<thead>
<tr>
<th>Date</th>
<th>Daylength (h.min) at latitude °N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td>21 March</td>
<td></td>
</tr>
<tr>
<td>6 May</td>
<td></td>
</tr>
<tr>
<td>21 June</td>
<td></td>
</tr>
<tr>
<td>6 August</td>
<td></td>
</tr>
<tr>
<td>22 September</td>
<td></td>
</tr>
<tr>
<td>7 November</td>
<td></td>
</tr>
<tr>
<td>22 December</td>
<td></td>
</tr>
<tr>
<td>7 February</td>
<td></td>
</tr>
</tbody>
</table>

* Daylength is the interval between apparent sunrise and sunset (when the upper edge of the sun just appears above or disappears below the horizon), as viewed from the earth's surface.
and continuous darkness (in winter) occur for varying periods depending on the latitude.

The day is a few minutes longer than might be expected chiefly because of the way sunrise and sunset are defined with reference to the top edge rather than the centre of the sun, and because the atmosphere refracts light especially when the sun is low in the sky.

As viewed at the earth's surface, the sun's apparent position is raised by this refraction by an amount equivalent to a few minutes of daylength at both dawn and dusk. Thus the equatorial day, theoretically exactly 12 hours, is about 12 hours and 7 minutes (cf. Table 17). For the same reason, the sun can still be seen during the continuous polar "night" above 67° rather than at 66°33'.

Two further features of these basic patterns relate to the possible use of photoperiod as a seasonal signal.

2. Daylength versus signal length

The daylengths just cited are based on the times at which the sun rises above and drops below the horizon. However, a period of significant illumination — "twilight" — persists beyond this time. *Civil* and *nautical twilights* are the periods during which the sun passes from the horizon to 6° or to 12° below it in the evening (vice versa in the morning). Astronomical twilight (until the sun is 18° below the horizon, at which time no trace of solar illumination remains) is of no significance in insect photoperiodism, as Beck (1980) pointed out. However, the day perceived by an insect may not be symmetrical with respect to the light intensities defined by equal solar elevations at the beginning and end of the day: some species respond at different intensities at dawn and dusk (Chapter 11).

The duration of twilight also changes seasonally, depending on latitude. Its duration depends on the angle that the trajectory of the rising or setting sun makes with the horizon, which is 90° only at the equator. Twilight therefore is longer at higher latitudes where the sun climbs or drops obliquely (see Table 18). Nautical twilight normally is somewhat more than twice as long as civil twilight (the latter begins when the centre of the sun is already below the horizon).

<table>
<thead>
<tr>
<th>Date</th>
<th>Duration of civil twilight* at latitude 40° N (h.min)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td>21 March</td>
<td>Spring equinox</td>
</tr>
<tr>
<td>6 May</td>
<td></td>
</tr>
<tr>
<td>21 June</td>
<td>Summer solstice</td>
</tr>
<tr>
<td>6 August</td>
<td></td>
</tr>
<tr>
<td>22 September</td>
<td>Autumn equinox</td>
</tr>
<tr>
<td>7 November</td>
<td></td>
</tr>
<tr>
<td>22 December</td>
<td>Winter solstice</td>
</tr>
<tr>
<td>7 February</td>
<td></td>
</tr>
</tbody>
</table>

* Civil twilight is the interval between the time of sunrise or sunset and the time when the centre of the sun is 6° below the horizon.
Table 19. Minimum and maximum rates of change of photoperiod at different latitudes

<table>
<thead>
<tr>
<th>Latitude (°N or S)</th>
<th>Difference (minutes) between successive days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Equinoxes</td>
</tr>
<tr>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>30</td>
<td>2</td>
</tr>
<tr>
<td>45</td>
<td>4</td>
</tr>
<tr>
<td>60</td>
<td>5–6</td>
</tr>
<tr>
<td>75</td>
<td>11–12</td>
</tr>
</tbody>
</table>

3. Rate of change of photoperiod

The daily change in daylength varies with the time of year and latitude: changes are most rapid about the time of the equinoxes, and negligible during the solstices; changes are greater at higher latitudes (Table 19). In the major zones of insect habitation, therefore, daylengths change each day by between about 0 and 6 minutes, which is apportioned more or less equally between the beginning and end of each day. This means that in little more than one week during March and during September, the daylength at latitudes near 60°N changes by about an hour.

Photoperiod as a seasonal signal

The preceding information shows that daylength is a highly reliable and frequent cue to seasonal position. In both absolute and relative terms, the cues are more conspicuous farther north or south of the equator. At 45°N, for example, the photoperiod varies between 8 h 46 min and 15 h 37 min, or if the full extent of morning and evening civil twilight is included, between 9 h 54 min and 16 h 51 min (cf. Tables 17, 18). However, temperatures are too low for activity in most habitats at latitudes farther north when daylengths are shortest (Fig. 6).

Photoperiod is a simple cue to assess because it can be monitored from the presence or absence of light at particular times of the day, or from the two rapid daily changes of signal level (light–dark and dark–light). Furthermore, as De Wilde (1969, p. 263) and others have pointed out, responses to photoperiodic seasonal tokens may be physiologically ‘old’ responses that developed before differentiation of specialized sense organs. Thus, for example, endogenous diel periodicities — driven by circadian rhythms — of metabolism, activity, etc., are found in most organisms in nature. If such periodicities are a basic property of living systems, as has been generally supposed (e.g. Pittendrigh 1960 table 1, and references cited there; Farner 1970), the “time-measuring” machinery involved in response to photoperiodic cues may be almost universal. The direct response of the brain to photoperiodic signals (see Chapter 11) supports this point of view. Paietta (1982) has suggested that these universal periodicities may have been selected because light was potentially directly damaging to evolving eukaryotic organisms through photo-oxidative effects on metabolic processes and cell systems.

The duration of the absolute signal “photoperiod” perceived by an insect depends on the mechanisms used to monitor it. In particular, the perceived duration depends on the response threshold of light receptors (see Chapter 11), that is on the intensity
across which a change is interpreted as an "on" or "off" signal.

Information on light intensities in the evening and at night is shown in Table 20. These figures apply to ideal conditions only, for example unobstructed terrain, clear skies, and the moon directly overhead illuminating a plane at right angles. In practice, values would nearly always be somewhat to considerably lower. Unfortunately, data are available chiefly in lux units, which apply to human visual responses; some wavelengths are excluded. This means, for example, that although the full moon is 1/450,000th as bright as the sun to human eyes, its total intensity is only 1/650,000th as great.

Different light conditions in the field have not been interpreted in terms of the visual responses of insects. Furthermore, because of scattering by the atmosphere,

Table 20. Comparisons of light intensity at the earth's surface under ideal conditions (from various sources)

<table>
<thead>
<tr>
<th>Situation</th>
<th>Light intensity (lux)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sunset</td>
<td>395</td>
</tr>
<tr>
<td>End of civil twilight</td>
<td>3.55</td>
</tr>
<tr>
<td>End of nautical twilight</td>
<td>0.015</td>
</tr>
<tr>
<td>Full moon</td>
<td>0.25</td>
</tr>
<tr>
<td>First quarter moon</td>
<td>0.021</td>
</tr>
<tr>
<td>Starlight</td>
<td>0.0009</td>
</tr>
</tbody>
</table>
the spectral composition of light changes with solar elevation, so that the setting sun, for instance, contributes more longer wavelengths than does the sun overhead.

The crep, a time unit reflecting illumination for the period around twilight, was introduced by Neilsen (1963), and the decline of illumination treated in this way was graphed by Beck (1980) and by Dreisig (1980). The duration of civil twilight is one crep, from 0 (sunset or sunrise) to + 1 crep; the purpose of this scheme is to provide an index that is insensitive to regional and seasonal variations in the duration of twilight, allowing universal comparisons based only on illumination (log lux units), including extensions into the regions either side of twilight that are lighter (negative crep) or darker (crep values greater than + 1). The rate of change of illumination at dawn and dusk is greatest when the sun is about four-fifths of the way toward its position 6° below the horizon, that is at 0.8 crep (see Dreisig 1980, fig. 1). The response threshold is therefore somewhat more likely to be crossed around this time than at times when the light is changing less rapidly. There is no reason to suppose, however, that any particular response threshold would be universal. Any reasonably low threshold could be used reliably in temperate regions. Even in summer at arctic latitudes, moreover, there is enough change in solar elevation to cause significant changes in light intensity through the diel, though these changes are much modified by cloud (Corbet 1966). The threshold of fully exposed insects is unlikely to be lower than full moonlight (0.25 lux), since this could erratically alter the perceived daylength. (Individuals are seldom “fully exposed”, however, and much lower thresholds have been reported, see Chapter 11.)

At mid-temperate latitudes, relative or day-to-day changes in photoperiod are greatest at the equinoxes, though the direction of change is reversed either side of the solstices. However, because photoperiod normally changes by only a few minutes from one day to the next even at the equinoxes (Table 19), this relative seasonal factor would not usually be easy to recognize. This may be partly compensated for in the case of photoperiod because the seasonal changes are so regular, and in fact cues around the solstice seem to be especially important in some species (Killian and Lutz 1985; King and Benjamin 1965; Tauber and Tauber 1975).

Finally, photoperiodic signals may be modified by habitat. The change of up to 400 lux during civil twilight is large enough that daylength could be interpreted with an error of 30 minutes or less at most latitudes even in habitats into which only a few percent of the light penetrates. For example, Malicky and Winkler (1974) reported that certain limnephilid caddisflies that aestivate in caves remain in the region of weak illumination, rather than entering total darkness, suggesting that the basic light–dark signal can be monitored precisely (given a low response threshold) even in habitats where the signal is very faint.

Other geophysical cues

The interactions of the sun, the earth and the moon produce several other “astronomical” periodicities in addition to the 365 1/4 day solar year and the 24 hour solar day already dealt with. These include the lunar day (24.8 h), the lunar period for one circuit of the moon about the earth (about 27.3 d), the synodic month, when the sun and moon are in line and which controls the phases of the moon (29.5 d),
and the tidal period or lunar half day (12.4 h). There are many other constant but less conspicuous geophysical periodicities with periods of a year or less, such as the rotation of the sun, that can be measured by instruments devised by man. Except for tidal and lunar periodicities in some invertebrates, including marine chironomids (review by Neumann 1980; Neumann and Heimbach 1984), and terrestrial millipedes (Saha and Mukhopadhyaya 1981), most of these features do not seem to have been used as cues for temporal control, although Brown (1972, etc.) has argued that weak electromagnetic fields are the primary, invariable, signals that are the basis of "biological clocks" (Chapter 12). For additional discussion of such potential cues see Sollberger (1965) and Brown (1972, 1976).

Temperature

Seasonal and geographic patterns

Seasonal patterns of temperature are governed by inputs of solar radiation, but unlike photoperiod they are much modified at the earth's surface on a large scale because of atmospheric (air mass) movements, and to a lesser extent because of ocean currents. Moreover, on to the characteristic trend of decreasing temperatures and increasing seasonal differences at higher latitudes are superimposed greater extremes at the centres of the continents than at coastal sites modified by the proximity of the ocean.

Monthly mean temperatures for some maritime and continental sites at different latitudes are shown in Fig. 7. This information demonstrates the very clear seasonal and geographic patterns of temperature, especially at higher latitudes. Temperatures are also modified locally by topography, vegetation, and other regional factors (which confuse geographic patterns), but at any given site clear seasonal patterns of monthly mean temperatures are retained.

Unlike geophysical factors, however, temperatures vary from day to day around these mean values in an unpredictable way — the seasonal temperature signal is very "noisy". Figure 8 compares daily, weekly, and monthly mean air temperatures, as experienced by insects on vegetation, for example, for 3 months during a single year at a single site at 45°N. In addition, note that mean daily air temperatures are derived by averaging daily maxima and minima, which themselves may differ (in this example) by as much as 17°C (see thermoperiod and Fig. 10 below).

Figure 8 shows that unless air-temperature cues are integrated over fairly long periods, as in the regular seasonal patterns of monthly mean temperatures shown by Fig. 7, they would normally be unreliable. Integration of this sort could perhaps be made directly by the insect; it can also be made indirectly by certain habitats, as in the case of soil temperatures at 10 cm depth, representing a relatively sheltered insect habitat, that are shown in Fig. 9.

Thermoperiod

Diurnal temperatures broadly follow the elevation of the sun, so that patterns of daily temperature in most habitats are relatively predictable and approximate a sine-wave. This daily temperature cycle has a period of exactly 24 hours. Its amplitude
Fig. 7. Mean monthly screen air temperatures at selected sites. 0°N: A. Libreville, Gabon (maritime; elevation 39 m); B. Yangambi, Zaire (modified continental; elevation 1378 m). 30°N: C. Jacksonville, Fla. (maritime; elevation 18 m); D. San Antonio, Texas (modified continental; elevation 792 m). 45°N: E. Halifax, N.S. (modified maritime; elevation 26 m); F. Ottawa, Ont. (modified continental; elevation 80 m). 60°N: G. Bergen, Norway (maritime; elevation 141 m); H. Fort Smith, N.W.T. (continental; elevation 205 m). Note especially that seasonal minima are lower, and temperatures more variable, as latitude increases. Note also that conditions in maritime sites are less extreme, to a striking degree in the case of Bergen (G), which is adjacent to a warm current.
Fig. 8 (top). Course of seasonal air temperature at Ottawa, Ontario (45°N), July–September 1970. Daily (solid line), weekly (dashed line) and monthly (stars) means of screen air temperatures show that the considerable daily fluctuations are masked by the weekly or monthly means.

Fig. 9. Course of seasonal soil temperature at Ottawa, Ontario (45°N), July–September 1970. Daily (solid line), weekly (dashed line) and monthly (stars) mean temperatures at a depth of 10 cm. Note that the fluctuations are smaller in the more sheltered soil habitat than in the air (compare Fig. 8).
Fig. 10. Daily maxima and minima of temperatures in the air (solid lines) and at 10 cm depth in the soil (dashed lines) at Ottawa, Ontario (45°N), during September 1970. Note that the daily ranges of screen air temperatures are quite wide relative to the means (e.g., 5 to 17 degrees of amplitude when means are about 8-22°C); but that the ranges are much reduced in the sheltered soil habitat (e.g., 0 to 4 degrees of amplitude when means are about 13-19°C).

depends, like mean temperatures, on various factors including habitat (see Fig. 10), and varies from day to day. For example, during August and September 1970 at Ottawa (45°N), daily maximum and minimum temperatures differed by 4 to 17 Centigrade degrees during August (mean amplitude 11.6, median 11 degrees) and by 3 to 17 degrees during September (mean 9.2, median 9). The daily pattern may
be disturbed on unusual days, for example if an incursion of warm air causes significant warming overnight, but such disturbances are rare especially during summer. According to Taylor (1981), the mean daily amplitude (unlike the annual amplitude) does not change greatly with latitude. However, the daily amplitude of temperature is more pronounced at lower than at higher elevations (e.g. a mean of 19°C versus 9°C over less than 2000 m in elevation at two sites at 35°N), which may modify latitudinal trends (Taylor 1981).

The parts of the 24-hour period that are “warm” and “cool” respectively vary in a very similar way to, but less precisely than, photoperiod. Such thermoperiods are potential daily cues of high reliability.

**Temperature as a seasonal signal**

The preceding information suggests that, although temperature follows regular seasonal patterns, its daily and day-to-day variations make absolute or relative temperature cues unreliable over the short term in many habitats. Nevertheless, temperature levels would be more reliable in sheltered microsites such as soil (Figs. 9, 10) and many freshwaters, even quite shallow ones. For example, screen air temperatures differed by 12.5°C between July and October (monthly means 20.3° and 7.8°C) at St. Catharines, Ont. in 1976, but also varied by 12.4°C during July alone (maximum and minimum daily means 26.6° and 14.2°C). In shallow ponds in the same area, on the other hand, the corresponding differences (at a water depth of 1 m) were 12°C between July and October (approx. monthly means 21° and 9°C), but only 3°C between July maxima and minima (19.7° and 22.7°C) (pers. obs. for one of two shallow ponds showing a similar pattern). Conversely, seasonal or daily changes in air temperatures may be amplified at the soil surface, so that this less stable habitat provides especially conspicuous temperature signals. These signals might be of particular seasonal value (notably as thermoperiods) in tropical areas where temperature changes are small (Tauber *et al.* 1986, p. 230).

Since rates of metabolism are temperature-dependent, there is reason to suppose that temperatures can be measured rather easily in poikilotherms (cf. Hoffman 1969). Moreover, reception of essentially continuous signals such as temperature can be simplified by receptor response at successive thresholds. Theoretically, for example, a given minimum temperature could be used as a seasonal index, as could the time spent at a minimum temperature, the time spent below a threshold temperature, or the number of days in succession at an average temperature below a certain threshold (cf. Bariola and Henneberry 1980, p. 379). Summing of temperature, using information from a large number of cue events, would also be expected to be more reliable than a simple threshold response (Giesel 1976, p. 71).

Thermoperiodic cues could be received in ways very similar to those for photoperiod, including simple threshold temperatures to define the cryophase and thermophase. Other ways might require comparison rather than measurement of extremes, however, because nighttime (cool) temperatures at some times of the year are the same as daytime (warm) levels at other times. For example, maximum and minimum mean daily screen air temperatures at Ottawa are about 26° and 13°C in August, and 13°C and 3°C in October. Alternating temperatures can be read in many other ways besides the amplitude and the upper and lower extremes, however, including the number of cycles, the times at upper and lower limits, and the rates of
warming and cooling (e.g. Totterdell and Roberts 1980). Moreover, these attributes are interdependent (cf. Roberts 1981).

**Moisture**

*Seasonal and geographic patterns*

Moisture regimes depend on precipitation and also on the humidity of air masses, which is usually correlated with precipitation. Globally, several characteristic precipitation regimes can be identified (Fig. 11). Especially at low latitudes, precipitation regimes may be markedly seasonal (e.g. Libreville, Fig. 11C).

![Graphs showing seasonal rainfall patterns](image)

**Fig. 11.** Seasonal pattern of rainfall (long-term monthly means) at selected sites: A. Ottawa, Ont. (45°N). Thin bars and bar breaks indicate also the rainfall during 1970 for comparison with the mean; B. Saskatoon, Sask. (52°N, continental, elevation 520 m); C. Libreville, Gabon (0°N).
"Equatorial" regimes have two rainy seasons (corresponding to the times the sun is overhead on its apparent northward and southward passages). Tropical regimes have a pronounced dry winter. Monsoonal regimes occur where the summer rainfall maximum is very marked and the dry season very long. In Mediterranean climates most rain occurs in winter or in late autumn and early spring. Winter rain prevails also on temperate west coasts (e.g. Vancouver), but in the continental interior at temperate latitudes summers are more rainy than winters (e.g. Saskatoon, Fig. 11B). Elsewhere, precipitation may be more evenly distributed (e.g. Ottawa, Fig. 11A).

Such patterns of precipitation often are relatively consistent on a monthly basis, but records for a single year for Ottawa (included in Fig. 11A) show that rainfall can be well above or below the monthly average (e.g. September, June). In addition, precipitation varies considerably over shorter time periods. In many temperate regions it may or may not rain at all in a given week, for example. Highly reliable seasonal cues would therefore be provided by rainfall in relatively few regions, those with a very marked dry or wet season.

A second moisture-related cue is humidity or some measure of the drying power of the air, such as saturation deficit or potential evapotranspiration. Such indices depend also on temperature. Seasonal patterns of this sort can be detected in most regions, and often reflect the "dryness" of the summer more strikingly than measures of precipitation alone, but again they are subject to substantial daily and year-to-year variations. For example, mean potential evapotranspiration at Ottawa varies from month to month during the frost-free season by less than a factor of two, but successive days may differ by an order of magnitude or more.

**Moisture as a seasonal signal**

Receptors for moisture should be virtually universal: the spiracular system and exoskeleton of terrestrial insects represent adaptations to conserve moisture, to which the organisms are often sensitive. However, rainfall and humidity are not especially reliable seasonal signals except when the dry and wet seasons are very pronounced (see above). Moreover, some insects live in moist microsites which are much less susceptible to seasonal changes. Longer-term moisture conditions can be integrated by living plants, which might serve as an index of moisture supply (see Chapter 7).

**Other physical cues**

The general effects of physical factors are very pervasive. Seasonal and shorter-term patterns persist even in the deep ocean, in currents (Dickson *et al.* 1982; Hollister *et al.* 1984), and probably in other cues (cf. Tyler *et al.* 1982). Several other physical conditions vary seasonally and might serve as seasonal signals to terrestrial insects. These include sunshine (Fig. 12) and wind (Fig. 13). Such factors change only slowly through the season (e.g. Randal 1970 for sunshine) and can be detected reliably only over the long term. Specific seasonal responses by insects to these factors would therefore not be expected. However, peaks of radiation near the equinoxes in the tropics apparently can influence certain trees (Longman 1969, p. 478).
Biotic cues

Plants and other animals provide insects with supplies of living or formerly living food, and these organisms may change in ways that broadly indicate seasonal position. In addition, the population density of some species may alter on a seasonal basis. Among different species, possible changes in food or density are very diverse. Explicit summaries similar to those already presented for some geophysical and physical factors therefore cannot be given for potential biotic cues, which are treated here in very general terms.

Food resources

Food sources (which can also be limiting) are easily perceived and might often be highly reliable indicators of seasonal position. Foods may give clues to the season not only from their quantity or abundance, but also from their quality, either through their value as food, or through other seasonal tokens.

Other organisms used as food, including foodplants, host animals and prey, vary quantitatively through the summer. Most species change in abundance through their active season; for part of the year they are absent in a particular stage or in a particular habitat, depending largely upon their own seasonal programmes. The seasonal restriction as well as the clarity of such cues would be greatest for individual species,
and seasonality based on cues from food resources should therefore be most evident among specialists. Nevertheless, non-living organic matter may also vary seasonally. For example, leaves of certain trees decay slowly and persist in streams until temperatures rise in spring, whereas those kinds of leaves that decompose rapidly are available in particulate form during winter (Kaushik and Hynes 1971). Again, in certain kinds of running water, detritus is removed more or less completely by the spring spate, so that food supplies for detritivores are markedly seasonal.

Changes in the quality of food may also give reliable seasonal signals, either by direct effects on growth through modified nutritional value, or simply by providing chemical indicators of the time of year. Many plants, for example, change in nutritive value as leaves become senescent, fruit or seeds ripen, or seeds and other parts lose water. Other biochemical changes, such as the absolute or relative quantities of substances such as fats or proteins, could indicate seasons directly (through nutritional quality) or indirectly. Finally, organisms might be able to “read” the physiological state of their hosts from the host’s diapause or other physiological response to seasonal cues.

Density

Studies of behaviour and communication suggest that intraspecific density can often be measured directly or through its effect on food supply. However, density is probably not especially reliable as a seasonal signal in most species. A characteristic density
will seldom be reached at a given time of year, because the growth of most populations depends largely on chance happenings at a local and general level. Rather, if density controls diapause or rate of development, it is likely to serve as a means of avoiding over-exploitation at any time of year, or as a means of increasing synchrony within a given subpopulation. Density alone seems almost as likely to distort as to enhance coincidence with a given season. It would therefore be expected to favour an immediate response ("social facilitation" or "irritation") more often than it serves strictly as a seasonal cue.

**Interaction of cues**

Some of the factors considered in these separate discussions interact with one another in characteristic ways, for example, photoperiod with temperature, and temperature with moisture.

Because the earth warms up slowly in spring, the seasonal maximum temperature is reached after the summer solstice (see above). Figure 14 exemplifies this relationship (see also, for example, Denlinger 1972b, fig. 1; Sanburg and Larsen 1973, fig. 1).

![Graph showing seasonal patterns of daylength and long-term mean screen air temperature](image)

**FIG. 14.** Seasonal patterns of (A) daylength and (B) long-term mean screen air temperature, at Ottawa, Ont. Note the seasonal lag of temperature, which continues to rise in June-July when photoperiod is decreasing.
Fig. 15. Seasonal patterns (long-term monthly means) of rainfall (solid lines) and screen air temperature (dashed lines) at: A. Libreville, Gabon; B. San Antonio, Texas. Note that both regions have a midsummer dry period of high temperatures and lower rainfall even though their climates are very different.

It means that photoperiods begin to decrease in summer while mean temperatures are still rising, and that photoperiods are quite short in autumn before temperatures fall too low for insect activity. Therefore, at least in theory, fall and spring conditions can easily be distinguished by the "constant" values of both photoperiod and temperature.

Temperature and moisture interact in some regions to produce more marked aridity in summer than would be expected from rainfall patterns alone. Figure 15 exemplifies relationships of this sort (see also, for example, climatic diagrams in Walter and Lieth 1967).

Such relationships, and the fact that other factors can provide seasonal information more or less independently, lead to the expectation that cues act in concert, increasing the reliability of the overall response.

Conclusions

Many of the features by which an insect might measure season or its suitability have similar seasonal characteristics everywhere. Table 16 and the discussion in this chapter indicate that the most reliable cue for both absolute and relative use normally is photoperiod. Thermoperiod shares a similar though less marked reliability. Short-term perception of temperature normally does not indicate seasonal position reliably,
except in stable habitats where habitat temperatures approximate the longer-term averages of air temperatures and therefore follow a regular seasonal pattern. However, temperatures continue to rise in the second half of the summer when daylengths have begun to shorten. Overall patterns over long periods are fairly reliable in all habitats.

The reliability of temperature, moisture and other cues may be reduced by their spatial variation if the insect moves between different microhabitats and thereby introduces additional ‘noise’ into the seasonal pattern; but there are relatively few habitats in which photoperiodic cues cannot be perceived reliably. Although the ease of recognition of a particular cue depends on the capabilities of a given species, sensory or other equipment in insects is available to monitor most of the cues listed in Table 16.

This discussion leads to the strong expectation that if precise responses were necessary, absolute photoperiod would normally be the overriding cue in the control of diapause in temperate areas, with the possibility that day-to-day changes in photoperiod might sometimes be used. It would further be expected that control of diapause by daily temperatures would operate only in a rather general way, except in very stable habitats, though thermoperiod might be more precisely used. Rainfall, food quantity and quality, and other factors could sometimes indicate seasonal position reliably, but only for some species in certain regions or habitats. To what extent these expectations are borne out is considered in the next two chapters.