

## Role of water and moisture in diapause development (A review)

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**Abstract.** While observational studies led to the assumption that water or moisture (W/M) is a prerequisite for diapause development, the experimental research indicates rather the opposite: usually W/M is needed as late as for the post-diapause resumption of morphogenesis. Recent examples for this type of regulation of dormancy are given: Eggs of the tettigoniid *Stictophaula armata*, eggs of the grasshopper *Oedaleus senegalensis*, adults of the bruchid *Bruchidius atrolineatus*, adults of the endomychid *Stenotarsus subtilis* (= *S. rotundus*). In the late diapause of the noctuid *Busseola fusca* and in eggs of the chrysomelid *Homichloda barkeri*, moisture is assumed to be the diapause terminating cue. Fall in temperature is assumed decisive for termination of pupal diapause in the saturniid *Schausiella santarosensis*, although the effect of intense rain after a long dry period has not yet been excluded. Effects of intense changes in environmental conditions and of gradual decrease in diapause intensity with time have often been neglected.

### INTRODUCTION

Most studies of seasonal ecology of insects focus on photoperiod and temperature as principal regulating cues (Tauber et al., 1986; Danks, 1987). Although particularly photoperiod has an essential role due to the high reliability of its precise repetition year after year, moisture should not be underestimated - as was rightly indicated by Tauber et al. (1998). Detailed experimental protocols for the study of moisture were suggested in the mentioned forum paper, but not many such experiments have been performed since then. A serious survey can nevertheless be based on several detailed and precise experimental studies and a quite long series of observations.

There is an obvious causal relation between the regrowth of vegetation, produced by rain after a period of drought, and the resumption of the active phase of insect life. The principal function of diapause is to assure synchronization of these two phenomena. These facts represent the basis for a widely accepted assumption that moisture or water (M/W) is the factor regulating the development of such diapauses that are in some way related to alternation of periods of drought and high humidity. It appears that the impact of moisture on dia-

pause development is not so simple. It is, in fact, so complex that often the interpretation of findings remains ambiguous.

Andrewartha's (1952) remark, that it is difficult to unravel the true causal relationships between water and diapause, is certainly true. According to his opinion "the absorption of water is rarely if ever the primary stimulus which initiates diapause development".

### NEGATIVE VS. POSITIVE INFLUENCE OF WATER/RAIN

Increasing relative humidity and precipitation was recorded as a seasonal signal for annual vertical migration of arthropods to trees in flooded plains of central Amazonia (Adis & Junk, 2002). The ascent to tree trunks occurs 3–4 months before forest inundation. The reproduction of arthropods (that are usually univoltine), such as tiger beetles (*Pentacomia egregia*), is postponed to the terrestrial phase after inundation (Table 1).

Not only flooding, but also very high humidity can endanger the development of descendants and delay oviposition to the post-rain season (Table 1, below). The females of a Mexican bruchid beetle, *Acanthoscelides obtectus*, spend the wet period between April and

TABLE 1. Examples of multiple relations of insects to water.

signal		examples	reference
+	SYNCHRONISATION		
	with host-plant regrowth	after winter diap. <i>Leptinotarsa 10-lineata</i> (Chrysomelidae)	Tauber et al. (1994)
		after dry season <i>Hypolimnas bolina</i> (Nymphalidae)	Kemp (2001)
	with growth of fungi	“ <i>Stenotarsus rotundus</i> (Endomychidae)	Tanaka et al. (1987a, b)
–	ESCAPE		
	from water	inundation regions <i>Pentacomia egregia</i> (Cicindellidae)	Adis & Junk (2002)
	from moisture	seed eating larvae <i>Acanthoscelides obtectus</i> (Bruchidae)	Hodek et al. (1981)

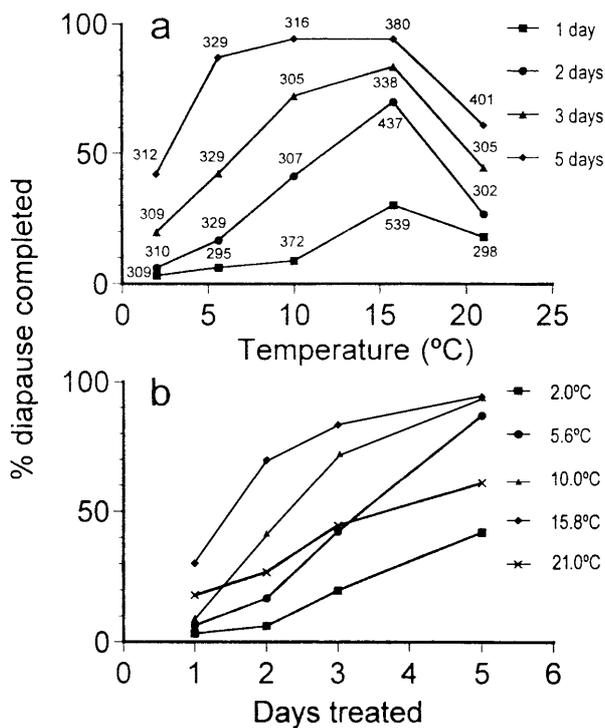


Fig. 1. Effect of temperature on completion of the summer diapause of *Delia antiqua*. (Before experiments, diapause was induced at 25°C, 16L : 8D.) a – percentage of diapause completion obtained when individuals were exposed to five temperatures, for time intervals indicated on the right margin. Values near the symbols indicate the numbers of puparia used; b – effect of five temperatures, indicated on the right margin, on completion of diapause in respect to the duration of treatment. (Ishikawa et al., 2000)

November in reproductive diapause in rolled dead leaves hanging from plants, and postpone the oviposition (mid-November to late December), i.e. to the period when precipitation is below 50 mm per month (Hodek et al., 1981). The larvae developing inside bean seeds may thus be saved from the highly probable dying in decaying beans. A contrasting example of synchronization of reproduction with high humidity can be mentioned. The reproduction in the tropical endomychid beetle, *Stenotarsus subtilis* (= *S. rotundus*; Roubik & Skelley, 2001) occurs in May, i.e. the first month of the wet season (Tanaka et al., 1987a, b; Tanaka, 2000; Table 1, above; see also the last chapter). It

feeds most probably on fungi like the other beetles from this family, but a direct evidence is still missing. The difference in food requirements of larvae could explain the contrasting timing of reproduction in relation to rainy seasons in the above two species of beetles.

#### EFFECT OF PHOTOPERIOD AND TEMPERATURE IN SUMMER DIAPAUSE

Before proceeding to cases where a more or less active role of M/W in diapause termination was recorded (or at least supposed) it should be stressed that in many summer diapauses no decisive effect was found. Diapause termination has often been reported to be governed rather by decrease in photophase and temperature (Masaki, 1980; Tauber et al., 1986; Danks, 1987; Hodek, 1996, 2002).

A recent example of summer diapause completed by low temperature is *Delia antiqua* (Ishikawa et al., 2000; Fig. 1). Sometimes, however, diapause in tropical insects is terminated by several days exposure to high temperature (25°C), as was reported in parasites of *Drosophila* (Carton & Claret, 1982) or in sarcophagids (Denlinger, 1986). These relations were already discussed in the classic reviews of Masaki (1980) and Denlinger (1986). In Table 2 some recent examples are given. It should, however, be indicated that in most cases the effect of M/W was not excluded.

In a detailed study on *Stenotarsus subtilis* (= *S. rotundus*) (Tanaka et al., 1987 a, b; Tanaka, 2000; see the last chapter), where the resumption of activity and dispersal from dormancy sites were recorded at the beginning of rainy period, the role of photoperiod was not only observed in the field, but also proved by experiments as decisive. An experimental proof that the photoperiod and not moisture is the decisive factor for diapause development was given for two chrysomelids, *Chrysolina hyperici* and *C. quadrigemina* (Schops et al., 1996; Fig. 2). It also was proved by experiments in prepupae of the Mediterranean arctiid moth *Cymbalophora pudica* (Kostal & Hodek, 1997) that photoperiod is the decisive factor for diapause development. In this moth the action of M/W and temperature was excluded.

TABLE 2. Species in which summer diapause is terminated by other factor than water/moisture.

Larva		
<i>Elcysma westwoodii</i>	short days	Gomi & Takeda, 1992
<i>Anagrus takeyanus</i> , Kyoto popul.	short days, low T°	Tsukuda, 1999
Adult		
<i>Omalium rivulare</i>	short days, low T°, also the intrinsic ovarian development	Topp, 1986
<i>Leptocarabus kumagaii</i>	short days, low T°	Sota, 1987
<i>Heteronympha merope</i>	short days, low T°	James, 1988
<i>Chelymorphia alternans</i>		Pullin & Knight, 1992
<i>Hypera postica</i>	short days, T° neutral	Elden, 1995
<i>Chrysolina hyperici</i>	short days	Schops et al., 1996
<i>Chrysolina quadrigemina</i>	short days	Schops et al., 1996

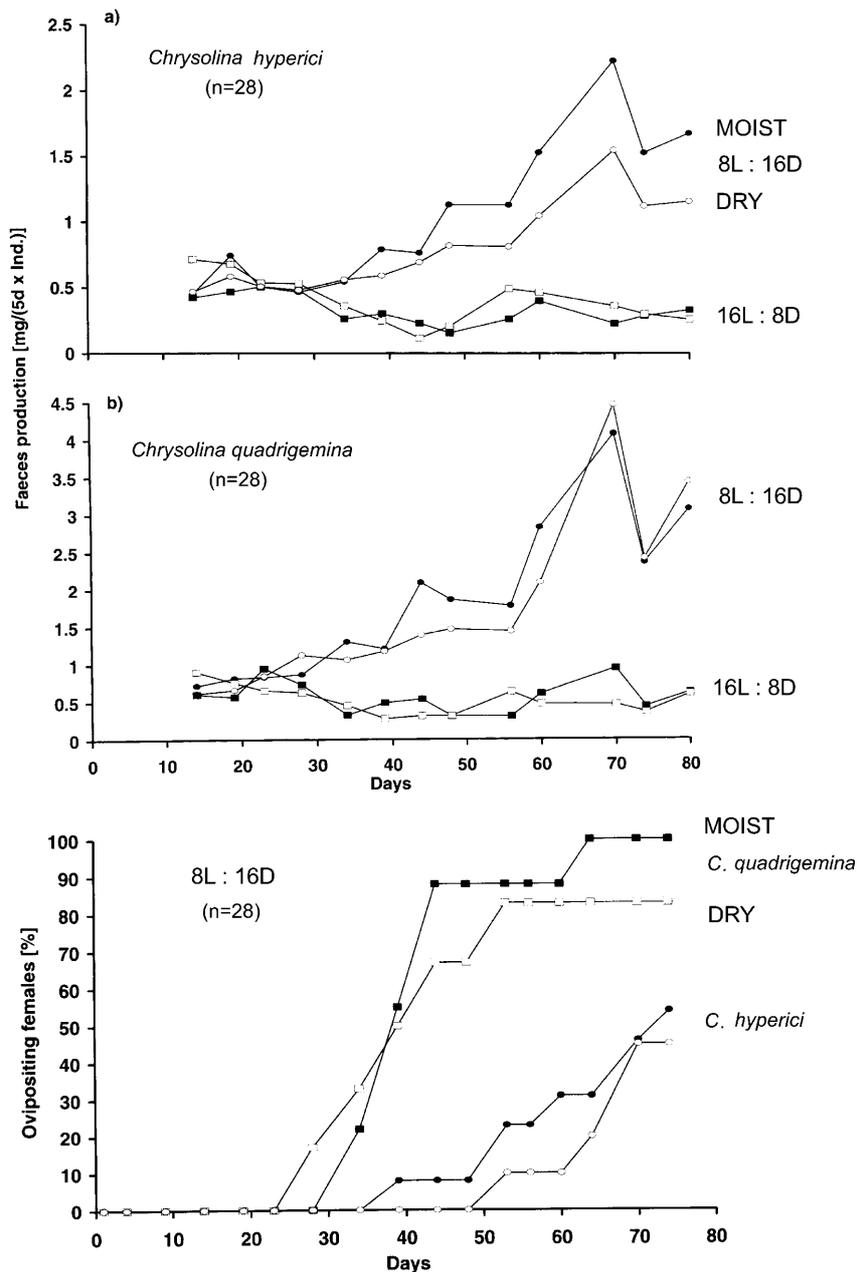


Fig. 2. Termination of summer diapause in females of two *Chrysolina* spp. under contrasting photoperiod and humidity conditions, recorded by production of faeces (a, b) and cumulative proportion of ovipositing females (c). (Schops et al., 1996)

#### ROLE OF MOIST AND DRY PERIODS IN DIAPAUSE DEVELOPMENT

Tropical borers have been the most popular example of diapause terminated by rains.

In spite of several studies, the role of water in termination of larval diapause in several species of African borers remained only partially understood until the series of clever experiments on the noctuid *Busseola fusca* performed in Kenya by Okuda (1988, 1990, 1991). Larvae of this sorghum stem borer spend 6 to 8 months in diapause in dry stalks and pupate after the onset of rains in spring. Okuda (1991) found that water stimulates pupation only in late diapause and he proved by experiments that a previous exposure to drought is a prerequisite for the stimu-

latory effect of wetting (Figs 3 & 4). Diapause development evidently proceeds at dry conditions, while wet conditions are then needed for the resumption of development and pupation. Okuda (1990) was also able to find out that the stimulation is produced rather by a continuous contact with moist surroundings than through drinking. When diapausing larvae were provided with water by means of a pipet no pupation was recorded - when they did not become wet (Okuda, 1990). The drinking larvae did not pupate although their constant weight indicates that they had higher water content than the wet larvae (Fig. 5).

Similar positive effect of a dry period was found in Thailand in diapausing eggs of a tettigoniid *Stictophaula*

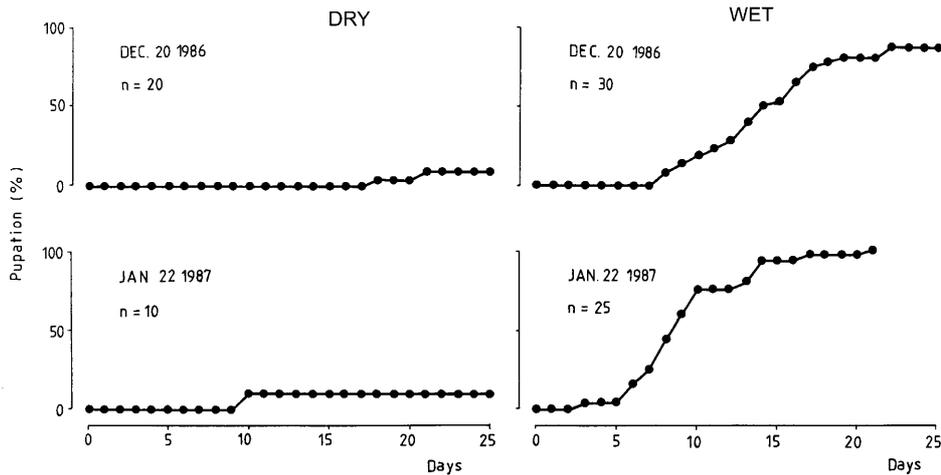


Fig. 3. Pupation of larvae of *Busseola fusca*, diapausing from July and transferred in December and January to laboratory dry and wet conditions. (Okuda, 1988)

*armata* by Ingrisich (1996). While the apparently post-diapause “dry” eggs (after 6 months = 180 day storage) hatched early after wetting (the peak of hatching was after about 4 wk), the constantly moist eggs had a bimodal hatching, with only about 30% of (probably non-diapause) eggs hatched within 5 weeks. Hatching of the other 30% was delayed until about 200–300 days. The pre-hatch period of the second mode of constantly moist eggs was thus longer than in the case of eggs that spent

about 180 days in low RH (Fig. 6). Moreover, in another experiment, Ingrisich (1996) achieved the same effect after only 2–3 months storage in 60% RH, as after 6 months.

The interpretation of these similar results by the two authors is not the same. While Okuda (1991) suggested that a tachytelic moist completion of diapause followed after a period of horotelic processes of diapause, Ingrisich (1996) assumed that a post-diapause hygric quiescence was terminated by water. He also suggested that “drought as a proximate factor for the elimination of diapause has been rarely discussed” and “could be more commonly

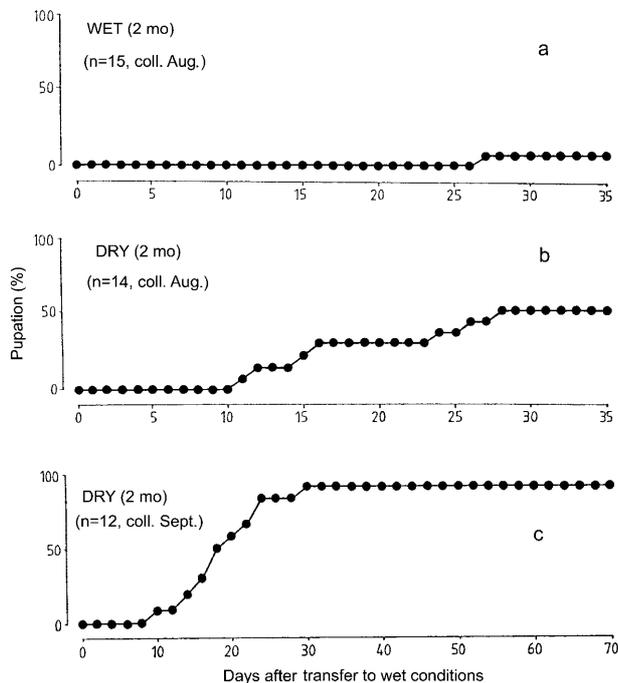


Fig. 4. Pupation of larvae of *Busseola fusca*, diapausing from July and transferred in August and September to laboratory wet conditions. Before the experiment the insects were always stored for 2 months; at either wet conditions (a), or at dry conditions (b, c). (Larvae in the September sample lived one month longer in the field drought than the August sample.) (Okuda, 1991)

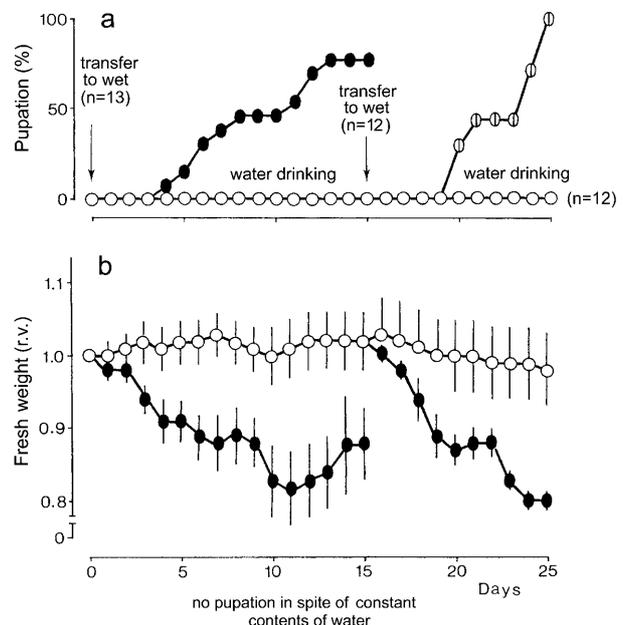


Fig. 5. a – pupation of larvae of *Busseola fusca* (diapausing from July, collected in mid January, n = 37), when drinking water without contact to moist environment (○) vs. in contact with moist environment (wetted, ●); b – fresh weight of larvae under the two experimental procedures as indicated in (a). (Okuda, 1990)

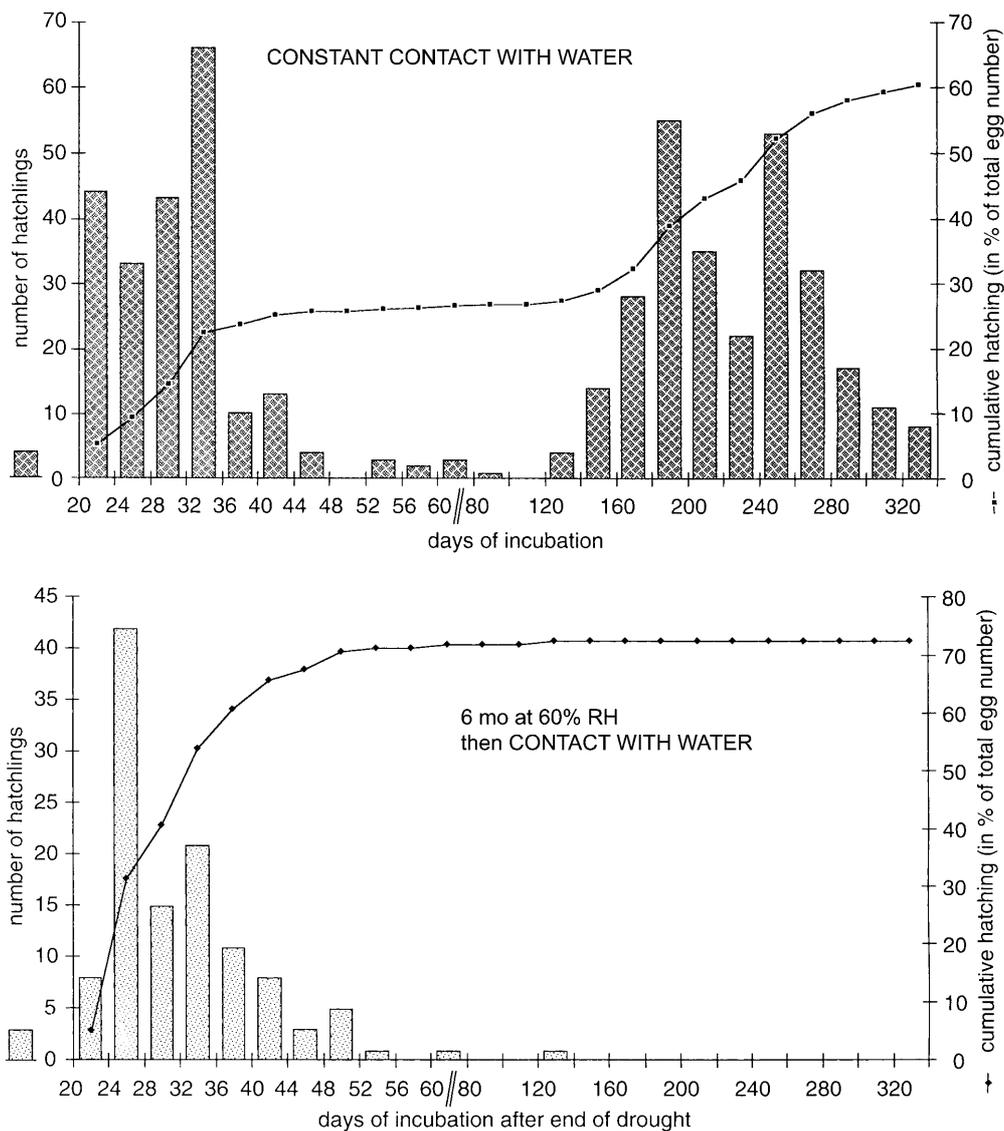


Fig. 6. Hatch of diapause eggs in *Stictophaula armata*; above - when in constant contact with water; below - placed into contact with water after 6 month of 60% rel. humidity (this represents drought for *S. armata* eggs). (Ingrisch, 1996)

detected in areas with a pronounced dry season, if it was looked for”.

The importance of dry periods - although in a different sense - was clearly shown also in egg diapause of the African chrysomelid *Homichloda barkeri* introduced to Australia (Nahrung & Merritt, 1999). Significantly higher hatch rate was recorded under the regime of alternated wetting and drying than under constant moisture. A similar proportion of larvae hatched from eggs wetted daily and from those wetted every 23rd day. In the latter group hatching lasted more than six times longer (Fig. 7). It was evident that each subsequent wetting stimulated development of a further proportion of embryos. The constant period of 12–14 days between wetting and eclosion indicates that at each wetting, embryos within the developing cohort begun development at the same stage of embryogenesis. In *Homichloda*, diapause development was thus completed within only 2 to 4 weeks through daily wetting and the delay in the cohort with less frequent wetting events was due only to longer intervals

between wetting events. For the same total hatching rate, however, much less wetting events were needed (9) compared to the daily wetting regime (27). Two factors had a complementary role: Wetting events and the passage of time. It may be suggested that horotelic processes of diapause development alternated with tachytelic activation events. The authors consider wetting events per se responsible for “breaking” diapause. They assume thus that diapause of *Homichloda* is in this aspect different from that of *Diabrotica virgifera* (Krysan, 1978) where moisture triggers development after a previous spontaneous diapause termination.

There are many cases similar to *Diabrotica*, in which the completed diapause development is followed by a quiescence due to low moisture. The post-diapause morphogenesis is not resumed until water content is replenished to/above a critical level. Thus, e.g., the larvae of the wheat blossom midges, *Contarinia tritici* and *Sitodiplosis mosellana* need high soil moisture for pupation after the

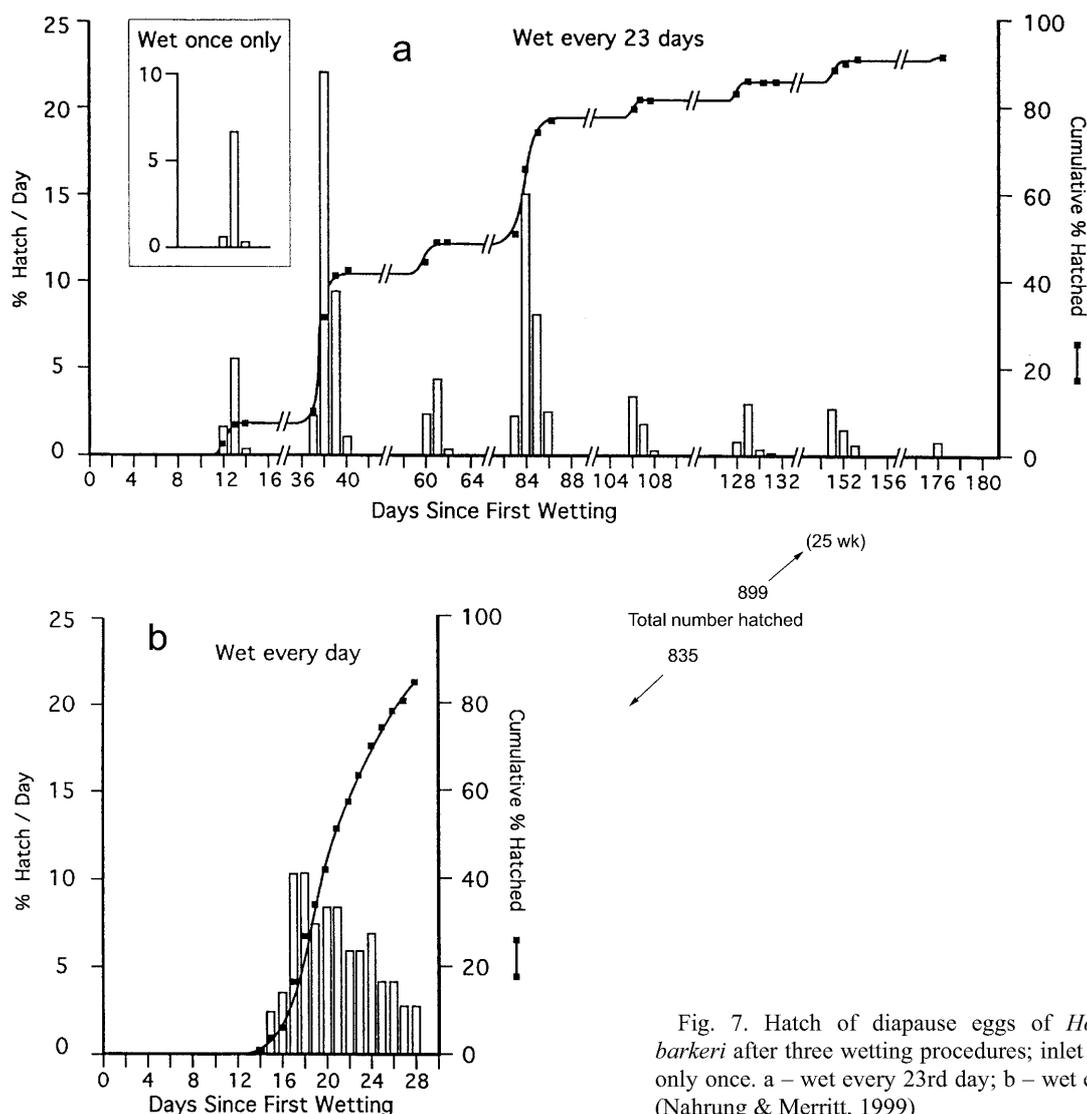


Fig. 7. Hatch of diapause eggs of *Homichloda barkeri* after three wetting procedures; inlet in (a) wet only once. a – wet every 23rd day; b – wet every day. (Nahrung & Merritt, 1999)

temperature regulated diapause development (Basedow, 1977).

Another example of such a sequence of low moisture quiescence after diapause completion was reported as one of the possible developmental pathways in eggs of the Australian plague locust, *Chortoicetes terminifera* (Acrididae). The development of the so called “second quiescent stage”, that is morphologically indistinguishable from the previous diapause stage, cannot start without replenishing about 10% of moisture lost during diapause (Wardhaugh, 1988). Diapause development lasts 30–60 days at 10–15°C and hatching occurs in warmth in spring. Also Gehrken & Doumbia (1996) concluded from detailed observations in Mali that the eggs of the grasshopper *Oedaleus senegalensis* complete diapause development after 7–8 months and remain thereafter dormant in “a state of postdiapause quiescence until the return of moist conditions”.

In addition to other environmental cues (mainly short days) also high humidity (70–80 %) was needed for termination of reproductive diapause in the Sahelian bruchid *Bruchidius atrolineatus* (Lenga et al., 1993; Glitho et al., 1996). Vitellogenesis was considered here as a criterion

of diapause termination. Most probably the dormancy scenario could be similar in the bruchid adults and in the cases mentioned earlier, eggs of orthopterans or larvae of the stem borer: Also here diapause development was completed during the long dry season and the cues of the rainy season (high humidity and pollen of host plants) switched on the post-diapause development.

Action of several environmental factors is apparently combined in the already classical model of tropical diapause, the adult dormancy of the endomychid beetle *Stenotarsus subtilis* (= *S. rotundus*) in Panama (Tanaka, 2000). This beetle spends a long, up to 10 months (6 months of the wet season and 4 months of the dry season) dormancy within large aggregations (Fig. 8). While the breeding sites and food requirements of the beetle probably still remain unknown, experiments with dormant beetles reveal the role of environmental cues, namely photoperiod, in diapause development, and moisture in the resumption of post-diapause development. Although at the low latitude of Panama (9°N) the difference between the longest and shortest day is only one hour, the increasing photophase appears to stimulate from March the early weak growth of CA, primary oocytes and flight

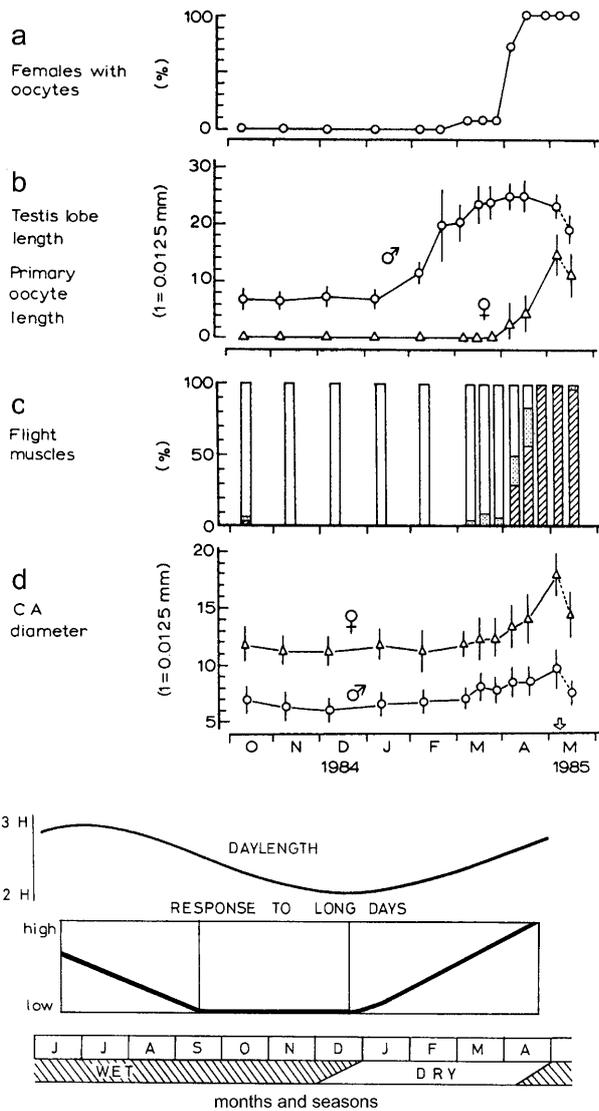


Fig. 8. Changes in gonads (a, b), flight muscles (c) and corpora allata (d) in diapausing adults of *Sienotarsus rotundus*. Below - photoperiod and humidity conditions at the Panaman site, with the assumed sensitivity to photoperiod. (Tanaka et al., 1987a, b; Tanaka, 2000)

muscles. Similar to many species, it is difficult in *S. subtilis* (= *S. rotundus*) to pin-point when diapause development is completed and the post-diapause quiescence begins. Mating and dispersal coincide with the onset of rains. Usually a short early period of rain during the rainy season is sufficient for triggering dispersal, but in some years dispersal may be bimodal (Tanaka, 2000). Probably the beetles with still less developed flight muscles “wait” for the next rain. Effects of exposures of 2 months to contrasting relative humidities of 100 vs. 75% confirmed the existence of stimulation by the higher humidity on early development of several organs: Ovaries, male accessory glands and flight muscles (Denlinger, 1994; Tanaka, 2000). It seems that moisture stimulates post-diapause development in only those beetles that had already completed diapause development before the start of experimental humidity exposures in mid-February. Another sample was collected more than 2 months earlier, at the

#### SEASONS IN A COSTA RICAN TROPICAL DRY FOREST

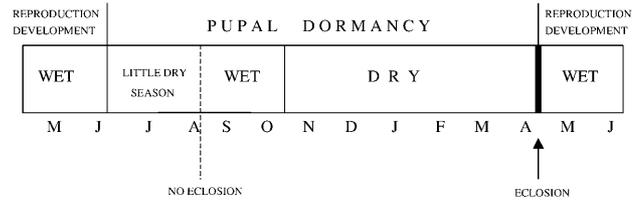


Fig. 9. Life cycle of *Schausiella santarosensis* and environmental conditions in the Costa Rican site. (After Janzen, 1987)

end of wet season, in early December (Tanaka et al., 1987a, b) and exposed for the same period of 2 months to the identical high humidity. A comparison of the development of organs between these two samples indicates that an important progress of diapause development occurred already during 10 weeks of dry season.

The humidity exposures did not affect the size of testes in *S. subtilis* (= *S. rotundus*). This parameter is not important for monitoring its diapause, because reproductive diapause in coleopteran males involves the accessory glands rather than testes, as was shown in coccinellids (Hodek & Ceryngier, 2000).

In a detailed study on seasonality of Lepidoptera in a Costa Rican tropical dry forest, Janzen (1987) is suspicious to the widely accepted assumption that rains are the cue for pupal eclosion. He suggests on the contrary that the cue is the “temperature and/or its changes, rather than the actual moisture brought by rainfall”. Thus, e.g., an experimental exposure to moisture does not re-initiate development in the pupae of the saturniid *Schausiella santarosensis*. The about 2–4 months old pupae remain dormant also through the “little wet season” (before the subsequent 6 month dry season) but the pupae eclose at the beginning of the second wet season, when they are about 8 months old. A dramatic drop in temperature at the beginning of the second rainy season occurs about a week before “really soaking” rains arrive (Fig. 9). Also several other saturniids were observed to eclose after a series of exceptionally cool days with nocturnal lows of 17–18°C (Janzen, 1987). Janzen’s assumption sounds quite plausible. However, two other possibilities remain to be excluded. (1) In the 2–4 month old pupae the horotelic processes of diapause development are, most probably, not yet progressed enough, i.e. diapause development is not completed. (2) The effect of contrast in physical conditions (heavy rains after the long dry period) can play an important role, similar to the effect of contrasts in photoperiod or temperature, suggested in temperate diapauses (Hodek, 1978, 1983, pp. 19–24, 2002; Zaslavsky, 1978).

#### CONCLUSION

It can be concluded from detailed experimental studies that the assumption of positive direct effects of W/M on the processes of diapause development is mostly erroneous - when based merely on observations. On the contrary, diapause development is often completed spontaneously during a dry period and is followed by a

TABLE 3. Species in which moisture was reported as an environmental cue for diapause termination; mostly for post-diapause resumption of activity/development, but also diapause development.

<b>Egg</b>		
<i>Allonemobius fasciatus</i>	wetting	Tanaka, 1987
<i>Chortoicetes terminifera</i>	rain	Wardhaugh, 1988
<i>Trirhabda geminata</i>	wetting	Bethke & Redak, 1996
<i>Oedaleus senegalensis</i>	1% soil moisture is satisf.	Gehrken & Doumbia, 1996
<i>Stictophaula armata</i>	water contact	Ingrisch, 1996
<i>Homichloda barkeri</i>	wetting	Nahrung & Merritt, 1999
<i>Deois flavopicta</i>	water	Pires et al., 2000
<b>Larva</b>		
<i>Contarinia tritici</i>	rain, soil moisture	Basedow, 1977
<i>Sitodiplosis mosellana</i>	rain, soil moisture	Basedow, 1977
<i>Contarinia sorghicola</i>	rain, soil moisture	Forrester, 1987
<i>Busseola fusca</i>	water contact	Okuda, 1988, 1990
“	intensive rain	Moyal, 1998
<i>Coniesta ignefusalis</i>	continuous rain	Tanzubil et al., 2002
<b>Pupa</b>		
<i>Schausiella santarosensis</i>	rain? T° decrease, rain	Janzen, 1987
<i>Manduca dilucida</i>	rain	Janzen, 1987*
<b>Pharate adult in cocoon</b>		
<i>Crioceris</i> sp.	submersion (30s)	Witt & Edwards, 2002
<b>Adult</b>		
<i>Agabus disintegratus</i>	inundation	Garcia & Hagen, 1987
<i>Stenotarsus rotundus</i>	100% R.H.	Tanaka et al., 1987a, b
<i>Zygogramma bicolorata</i>	monsoon rains	Jayanth & Bali, 1993
<i>Bruchidius atrolineatus</i>	increase to 80% R.H.	Lenga et al., 1993
<i>Leptinotarsa decemlineata</i>	rain, soil moisture	Tauber et al., 1994
<i>Dicladispa gestroi</i>	rain	Delucchi, 2001
<i>Hypolimnas bolina</i>	rain	Kemp, 2001

\*more lepidopteran species discussed in this paper.

hygric quiescence. It is during this second part of dormancy, in early post-diapause, when the loss of water is replenished and the resumption of morphogenic development is enabled (Tables 3 & 4).

In discussions on the role of various factors in completion of diapause, three factors are mostly invoked, photo-

period, temperature and water or moisture (W/M), while two further factors are almost always neglected, a necessary passage of time and the effect of contrast. In many insect species the horotelic processes of diapause development cannot be substituted by activation too early; diapause development simply needs to be completed

TABLE 4. Assumptions on the role of moisture/water in diapause termination.

MOISTURE NEEDED for <b>POST-DIAPAUSE DEVELOPMENT</b>
Ando, 1972 - <i>Atrachya menetriesi</i> - egg
Krysan, 1978 - <i>Diabrotica virgifera</i> - egg (moisture allowing development to continue after diapause terminates spontaneously)
Tanaka, 1987 - <i>Allonemobius fasciatus</i> - egg (termination of summer diapause independent of water absorption)
Forrester, 1987 - <i>Contarinia sorghicola</i> - larva - (rains no effect until diapause requirements .... satisfied)
Wardhaugh, 1988 - <i>Chortoicetes terminifera</i> - egg - (post-diapause 2 <sup>nd</sup> quiescent stage)
Gehrken & Doumbia, 1996 - <i>Oedaleus senegalensis</i> - egg
Ingrisch, 1996 - <i>Stictophaula armata</i> - egg
Pires et al., 2000 - <i>Deois flavopicta</i> - egg - (water did not enhance the rate of diapause development)
MOISTURE NEEDED for <b>DIAPAUSE DEVELOPMENT</b>
Okuda, 1988, 1990 - <i>Busseola fusca</i> - larva - (only in late diapause)
Nahrung & Merritt, 1999 - <i>Homichloda barkeri</i> - egg

before the post-diapause development is resumed under influence of W/M (Janzen, 1987). It seems that a previous period of drought predisposes the insects to the effect of the increase in moisture.

The difficulty to discriminate easily between these two periods of dormancy leads some authors to avoid the problem by using the ambiguous term "termination" of diapause (to include both diapause development and post-diapause development) against which Tauber et al. (1986, 1998) and Danks (1987) rightly warned. When we misuse this term, we elude the challenge to understand how the two certainly different phases of dormancy - diapause vs. post-diapause quiescence are regulated. We should strive to elucidate this problem by well focussed experimental studies. The methodical viewpoint paper by Tauber et al. (1998) could help in planning such trials.

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