

Thus, we demonstrated that the system of JH degradation in flies of line ts403 responds to a stressful agent by a sharp reduction in JH-hydrolyzing activity. The response of the system of OA metabolism to the action of the stressor was also strongly manifested in individuals of line ts403. It may be concluded that impairment of the synthesis of the HSPs in this line does not result in perturbation in any one of the links of the hormonal stress reaction we studied. It may be inferred that the heat shock response presumably is not a trigger link of the stress reaction and that the two adaptive mechanisms to unfavorable conditions in insects are triggered independently or in parallel, being under the common central control of a, so far, unknown factor.

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References: Arking, R., 1975, *Genetics* 80: 519-523; Cymborowski, B., 1991, *Hormones and Metabolism in Insect Stress*. CRC Press, Boca Raton, pp. 99-114; Hammock, B.D., and T.C. Sparks 1977, *Analyt. Biochem.* 82: 573-579; Evgen'ev, M.B., and O.M. Denisenko 1990, *Russian J. of Genetics* 26: 266-271; Lindquist, S., 1993, *Translational Regulation of Gene Expression 2*, Plenum Press, New York, pp. 279-320; McCaman, M.W., R.E. McCaman, and G.J. Lees 1972, *Analyt. Biochem.* 45: 242-252; Rauschenbach, I.Yu, 1991, *Hormones and Metabolism in Insect Stress*. CRC Press, Boca Raton, pp. 115-148; Rauschenbach, I.Yu, T.M. Khlebodarova, N.A. Chentsova, N.E. Gruntenko, L.G. Grenback, E.I. Yantsen, and M.L. Filipenko 1995, *J. Insect Physiol.* 41: 179-189; Sukhanova, M. Jh., I.A. Ankilova, N.E. Gruntenko, T.M. Khlebodarova, L.Z. Kaidanov, and I.Y. Rauschenbach 1997, *Biochem. Genet.* 35: 91-103.

Frugivorous *Drosophila simulans* begins to exploit *Opuntia ficus-indica* cladodes.

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The introduction of exotic plants creates potential new niches for endemic animals. European tradespeople brought the cactus *Opuntia ficus-indica* in the 16th century from Mexico to Europe to serve as substrate for the cochineal insect (*Dactylopius coccus*), which is used for the production of red dye. Cosmopolitan frugivorous *Drosophila* species as *D. melanogaster*, *D. simulans*, and *D. hydei* are known to use the fruits of this exotic plant (Carson, 1965; Haouas *et al.*, 1984, Santos *et al.*, 1999). Whereas the cactophilic species *Drosophila buzzatii* is not known to breed outside its plant-specific niche, *i.e.* decaying cladodes and cactus fruits (Carson, 1965), we show that *D. simulans* made a start to adapt to the non-fruit part of *O. ficus-indica*. (A) Naturally rotting *O. ficus-indica* pads were collected in a semi-abandoned *O. ficus-indica* plantation in southern Spain, 3 km north of Carboneras (37° 01'N, 1° 52'W) (Eisses and Santos, 1997). These pads yielded low but increasing numbers of *D. simulans* in two successive years (Table 1). In a few cases (3/10), the frugivorous *D. simulans* outnumbered the cactophilic *D. buzzatii*. Inherently to cactophilic *Drosophila*, *D. buzzatii* emerged from rotting pads in much higher numbers, *e.g.* in September 1993 and 1994 up to 1109, and 1861, respectively, per cladode. (B) The non-accidental occurrence of *D. simulans* in cladodes was tested by placing baits in the field in June 1995 (Table 1). Fresh *O. ficus-indica* cladodes were cut into discs (7 cm diameter) and placed on moist vermiculite in plastic plant-breeding trays. After about 100 h in the field, the cladode-discs were brought back to Barcelona, and checked for emerging flies (Table 1). All 39 *D. simulans* emerged from 6/12 discs placed near a flowering *Agave ricana* and a solitary *O. ficus-indica* at one of the six sites. Only one of these discs produced both *D. buzzatii* and *D. simulans*. The mature *D. simulans* and *D. buzzatii* were very small compared with those emerging from standard laboratory medium or *O. ficus-indica* fruits. In contrast with the normal situation, some *D. simulans* males were bigger than females. Emerging *D. simulans* males and females were paired and placed on standard laboratory medium to check their fertility: all pairs produced offspring. The fresh cladode discs yielded only a total of 33 adult *D. buzzatii*. (C) Discs, which did not yield flies but continued to decay, were used for additional experiments in the

laboratory. These experiments showed that *D. simulans* was able to develop in one-third of rotting cladode-discs (Tables 1 and 2). Several hundreds of *D. buzzatii*, *D. simulans*, and *D. melanogaster* were put into a population cage (25 × 25 × 35 cm) together with the rotten discs for one day. *Drosophila simulans* and *D. melanogaster* made up about one-quarter of the total number of flies. All experimental flies descended from flies emerging from cactus fruits (prickly pears) collected in Carboneras in September 1993 (A. Galiana, Universitat Autònoma de Barcelona). A second experiment was performed with 24 more or less rotten cladode discs, which had been in the field for 6¼ days in September 1995. These discs did not produce any insects within 2 months of being brought into the laboratory. During 96 h three cages contained approximately 350 *D. buzzatii* and *D. simulans* (10:1) (progeny

of flies that emerged from prickly pears collected in September 1995, Santos *et al.*, 1999). *D. simulans* outnumbered or equalled *D. buzzatii* in three discs, and developed in 8/21 (Table 2). The correlation coefficient between the total number of emerged flies per patch and the weight of the 18 rotten cladode-discs at the start of the experiment was 0.785 ($F_{(1,16)} = 25.75$, $P < 0.0001$), whereas the correlation coefficient with the original fresh weights in September was -0.212 ($F_{(1,16)} = 0.75$, NS). The average residual weight, expressed as percentage of fresh weight remaining after 2 months were: green discs: $71.3 \pm 3.8\%$, rotting discs $55.3 \pm 8.5\%$. After larval growth the averages had dropped to $41.5 \pm 15.4\%$ (green cladode-discs), and to $20.3 \pm 6.9\%$ (rotten discs). Table 3 shows the average ambient temperatures and the averages of the mean developmental times in the three experiments with cladode discs. Egg-to-adult development of *D. buzzatii* varied from 14 to 43 days, whereas *D. simulans* developed in 12 to 25 days. Long developmental times were not due to second generation flies.

D. simulans emerging from *O. ficus-indica* cladode material proved to be not accidental, although this species is well known as frugivorous (Carson, 1965; Atkinson and Shorrocks, 1977), and has been reported as developing only on fruits of various *Opuntia* species (Carson, 1965; Atkinson and Shorrocks, 1984; Haouas *et al.*, 1984). The relative frequency of *D. simulans* in natural rots increased more than six-fold from September to November 1994, and the percentage of cladode-discs yielding *D. simulans* doubled. *D. simulans* appears to be able to use a broader range of yeast species than *D. melanogaster* (Parsons, 1975). Some of the yeasts associated with rotting cladodes are also found in *Opuntia* fruits, though three times less commonly (Ganter *et al.*, 1989). The low content of free sugars in cladodes compared with cactus fruits (Fogleman and Abril, 1990) accounts at least partly for the much slower decay (Starmer and Aberdeen, 1990). In fruits, fast-developing species such as *D. melanogaster* and *D. simulans* will have a selective advantage over slowly-developing species as *D. buzzatii* and *D. hydei* because of the relatively fast degradation of the fruits. However, in rotting cladodes, larvae can survive only if they can tolerate the slow release of nutrients the decay of cactus material

Table 1. Number of emerged cactophilic *D. buzzatii* and other *Drosophila* species from a number (n) of natural rotting cladodes of *O. ficus-indica* or cladode-discs. Collections were made in different years.

Date	n	<i>D. buzzatii</i>	Other species
Natural rotting cladodes			
March 1978*	34	325	0
June 1981**	40/400**	666	0
September 1993*	34	5,897	1 <i>D. simulans</i>
September 1994	52/91**	13,915	15 <i>D. simulans</i> (1/3)*
November 1994	42/63**	4,421	24 <i>D. simulans</i> (2/7)*
Cladode-discs in the field			
June 1995	12/144**	33	39 <i>D. simulans</i> (5/6)*
Cage experiments			
1) July 1995	7/7**	805	18 <i>D. simulans</i> (0/2)* 3 <i>D. melanogaster</i> (0/3)
2) November 1995	21/24**	600	22 <i>D. simulans</i> (3/8)*

*Unpublished data from M. Santos, A. Leibowitz, J. Quezada-Diaz and H. Laayouni.

**Data from Ruiz *et al.*, 1986.

*The number of cladodes in which *D. simulans* formed the majority of the emerged *Drosophila* or equalled *D. buzzatii* over the number of cladodes or cladode-discs containing *D. simulans*.

**Cladodes or cladode-discs with emerging *Drosophila* over the total number of collected cladodes or experimental cladode-discs, including those without any *Drosophila* emerging.

Table 2. Emergence and developmental times of the cactophilic species *D. buzzatii* and the frugivorous species *D. simulans*. Adult flies of both species were mixed and put in population cages from 16-20 November 1995, together with cladode-discs in various stages of decay.

<i>D. simulans</i>		<i>D. buzzatii</i>	
No. of flies	First and last day of emergence (mean)	No. of flies	First and last day of emergence (mean)
Green cladode-discs*			
-	-	8	27-29 (28.0)
-	-	18	32-40 (35.7)
-	-	17	23-33 (26.3)
3	12-14 (12.7)	82	14-30 (19.5)
1	13	70	23-43 (33.6)
Rotting cladode-discs*			
1	15	1	26
-	-	4	23-30 (25.0)
-	-	20	26-37 (30.9)
-	-	20	19-30 (24.6)
-	-	17	30-43 (34.8)
9	13-14 (13.7)	6	21-24 (22.0)
1	13	65	20-32 (25.9)
-	-	74	17-26 (21.8)
-	-	71	17-33 (24.9)
-	-	4	31-40 (35.8)
3	14-19 (16.0)	59	19-31 (23.7)
-	-	9	27-36 (31.0)
1	13	42	20-33 (26.0)
-	-	3	33-42 (36.0)
3	13-14 (13.3)	3	36-41 (38.0)
-	-	7	26-36 (31.6)

*One green and two rotting cladode-discs did not yield adult flies.

provides, which is one of the adaptations made by cactophilic *Drosophila* species. *D. simulans* from the Carboneras area showed a broad range of development times in fresh and rotting cladode patches. Comparative experiments with *D. simulans* strains from geographically separate areas would show whether these results apply only to adaptations of a local race of *D. simulans* or to *D. simulans* in general. The fact that *D. simulans* can develop into viable adults utilizing the resources in cladodes probably allows it to persist in the area between the successive fruiting seasons. Flies were trapped in the Carboneras area in April 1995, when no prickly pears were present: *D. simulans* was present in similar numbers to *D. buzzatii*. The beginning of a niche expansion by *D. simulans* may have been witnessed in the arid area of Carboneras.

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References: Atkinson, W., and B. Shorrocks 1977, *Oecologia* 29: 223-232; Atkinson, W.D., and B. Shorrocks 1984, *Am. Natur.* 124: 336-351; Carson, H.L. 1965, In: *The Genetics of Colonizing Species* (H.G.

Table 3. The averages of the mean developmental times and standard deviation of *D. buzzatii* and *D. simulans* in cladode-discs under ambient laboratory conditions with average temperatures and standard deviations in different periods of the year 1995.

Period	Average temperature (°C)	Mean developmental times $\pm$ SD (days)		
		<i>D. buzzatii</i>	<i>D. simulans</i>	<i>D. melanogaster</i>
June 1995	25.2 $\pm$ 2.5	20.4 $\pm$ 3.6 (7)	16.6 $\pm$ 1.8 (6)	-
July 1995	26.5 $\pm$ 2.9	20.8 $\pm$ 4.5 (7)	15.2 $\pm$ 1.5 (2)	16.3 $\pm$ 1.5 (3)
November 1995	21.0 $\pm$ 2.7	28.6 $\pm$ 5.5 (21)	13.7 $\pm$ 1.2 (8)	-
Fast-cladode-discs		24.4 $\pm$ 2.4 (12)	13.9 $\pm$ 1.3 (6)	-
Slow-cladode-discs		34.1 $\pm$ 2.5 (9)	13.2 $\pm$ 0.2 (2)	-

Baker, and G.L. Stebbins, eds.), Academic Press, New York and London, pp. 503-531; Eisses, K.Th., and M. Santos 1997, *Dros. Inf. Serv.* 80: 25-29; Fogleman, J.C., and J.R. Abril 1990, In: *Ecological and Evolutionary Genetics of Drosophila* (J.S.F. Barker, W.T. Starmer, and R.J. McIntyre, eds), Plenum Press, New York, pp. 121-143; Ganter, P.F., F. Peris, and W.T. Starmer 1989, *Am. Midl. Natur.* 121: 331-340; Haouas, S., Y. Carton, M. Marrakchi, and J. David 1984, *Acta Oecol. Oecol. Gener.* 5: 175-179; Parsons, P.A., 1975, *Quart. Rev. Biol.* 50: 151-169; Ruiz, A., A. Fontdevila, M. Santos, M. Seoane, and E. Torroja 1986, *Evolution* 40: 740-755; Santos, M., K.T. Eisses, and A. Fontdevila 1999, *Evolution* 53:175-186; Starmer, W.T., and V. Aberdeen 1990, In: *Ecological and Evolutionary Genetics of Drosophila* (J.S.F. Barker, W.T. Starmer and R.J. McIntyre, eds), Plenum Press, New York, pp. 145-160.

Cytological localization of the *Drosophila melanogaster* *Dhr38* gene.

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The *Dhr38* gene codes for a protein belonging to superfamily of steroid hormone receptors and plays an important role in regulation of metamorphosis processes at late developmental stages in *D. melanogaster*

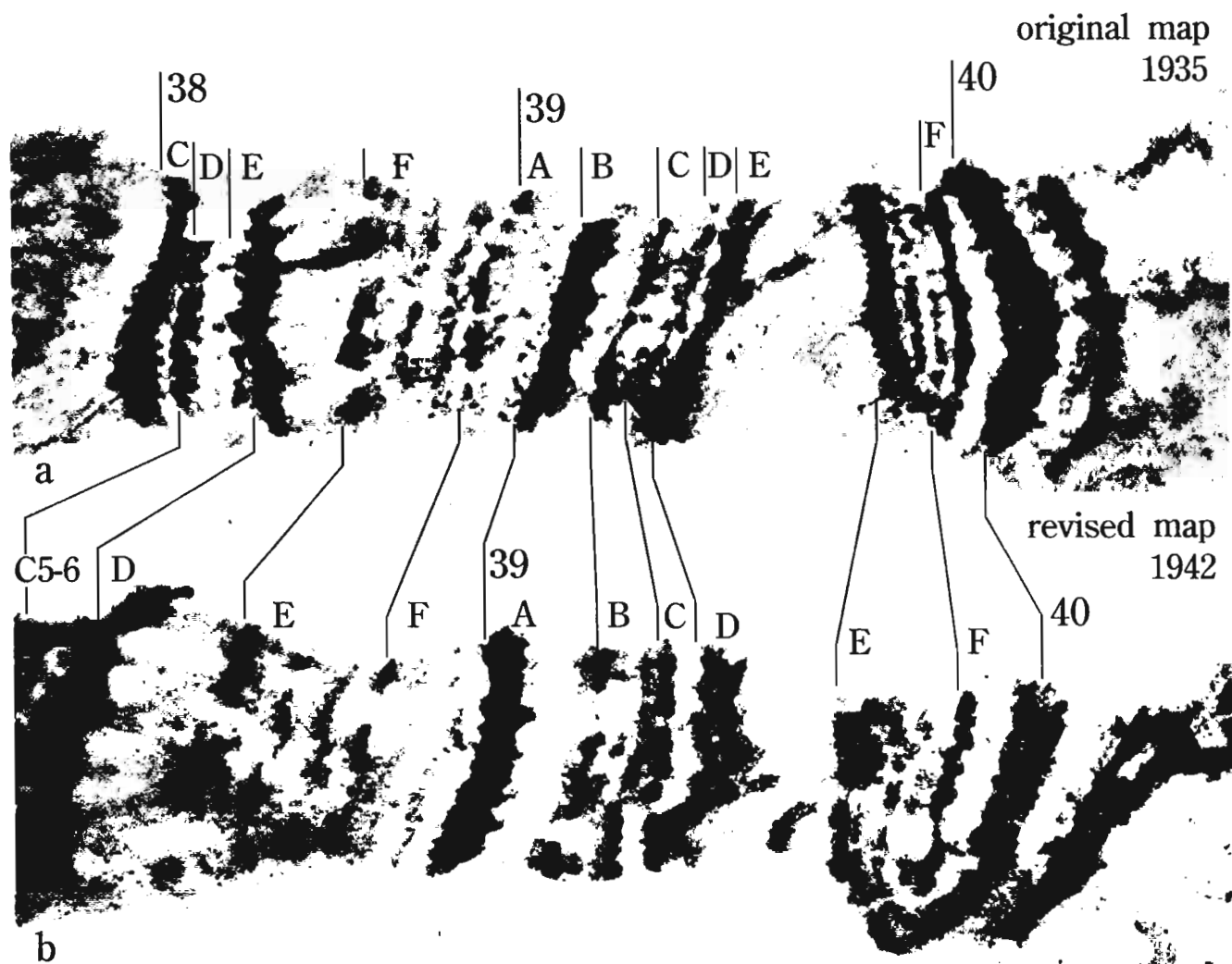


Figure 1. Electron microscopical map of 38C-39F region. Batumi L strain. Sections and subsections are designated according to C.B. Bridges, 1935(a) and P.N. Bridges, 1942(b).