Phenology/Degree-Day and Climate Suitability Model Analysis – Jan. 2021

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Egyptian cottonworm ***Spodoptera littoralis*** **(Boisduval)** **(Lepidoptera: Noctuidae)**

Hosts: Highly polyphagous (cotton, maize, potato, rice, soybean, vegetables, ornamentals) Native to: Palearctic Region

Goal: Develop a phenology model and temperature-based climate suitability model using available literature and weather data analysis

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Thresholds, degree-days, events and climate suitability params used in Egyptian cottonworm model:

Parameter abbr.	**Description**	**degF**	**degC**	**DDF**	**DDC**
eggLDT	egg lower dev threshold	53.0	11.67	-	-
eggUDT	egg upper dev threshold	95.0	35.0	-	-
larvaeLDT	larvae lower dev threshold	53.0	11.67	-	-
larvaeUDT	larvae upper dev threshold	95.0	35.0	-	-
pupaeLDT	pupae lower dev threshold	53.0	11.67	-	-
pupaeUDT	pupae upper dev threshold	95.0	35.0	-	-
adultLDT	adult lower develpmental threshold	53.0	11.67	-	-
adultUDT	adult upper dev threshold	95.0	35.0	-	-
eggDD	duration of egg stage in DDs	-	-	89	49
larvaeDD	duration of larva stage in DDs	-	-	424	236
pupaeDD	duration of pupa stage in DDs	-	-	274	152
adultDD	duration of adult stage to mid-OV in DDs	-	-	45	25
OWlarvaeDD	DDs until OW larvae first pupation	-	-	435	242
eggEventDD	DDs into egg stage when hatching begins	-	-	88	49
eggEventLabel	egg hatch	-	-	-	-
larvaeEventDD	DDs until mid-larval deveopment	-	-	212	118
larvaeEventLabel	larval development	-	-	-	-
pupaeEventDD	DDs until mid-pupal development	-	-	137	76
pupaeEventLabel	pupal development	-	-	-	-
adultEventDD	DDs until first oviposition	-	-	45	25
adultEventLabel	adult activity (flight and egg laying)	-	-	-	-

coldstress_threshold	cold stress threshold	50.0	10	-	-
coldstress_units_max1	cold stress degree day limit when most individuals die	-	-	1710	950
coldstress_units_max2	cold stress degree day limit when all individuals die	-	-	4050	2250
heatstress_threshold	heat stress threshold	98.6	37	-	-
heatstress_units_max1	heat stress degree day limit when most individuals die	-	-	1440	800
heatstress_units_max2	heat stress degree day limit when all individuals die	-	-	1980	1100
distro_mean	average DDs to OW larvae first pupation	-	-	435	242
distro_var	variation in DDs to OW larvae first pupation	-	-	9000	5000
xdist1	minimum DDs (°C) to OW larvae first pupation	-	-	158	88
xidst2	maximum DDs (°C) to OW larvae first pupation	-	-	712	396
distro_shape	shape of the distribution	-	-	normal	

PHENOLOGY MODEL ANALYSIS

A) Analysis of temperature-development data

1. Baker, C.R.B. and G.W. Miller. 1974. Some effects of temperature and larval food on the development of *Spodoptera littoralis* (Boisd.) (Lep., Noctuidae). Bull. Entom. Res. 63:495-511.

- Studied development of eggs, larvae, and pupae in controlled-enviro cabinets under constant & cycling temps between 15-30C (initial stock of eggs came from Canary Islands)
- Larvae tested on 3 food plants (development faster on lucerne than on 2 cultivars of chrysanthemum)
- Concluded that minimum constant temp for normal development in all life stages is between 13-14C
- At 13C all stages were capable of some development but eggs failed to hatch, larvae died after 3rd instar, and no viable adults emerged from pupae exposed to 13C for 56 days
- At 15C only 1 larva pupated
- A Tlow of 13C seems too high when compared to data from other studies (see summary table below)

Regression each diet separately (w/ forcing)

* Results for chrysanthemum are not included in final results because these plants have insecticidal properties and slow development

** The authors note that larval food plant may have affected pupal development, at least for males (only female data are reported here). However they apparently pooled data from pupae raised on both diets.

Egg development

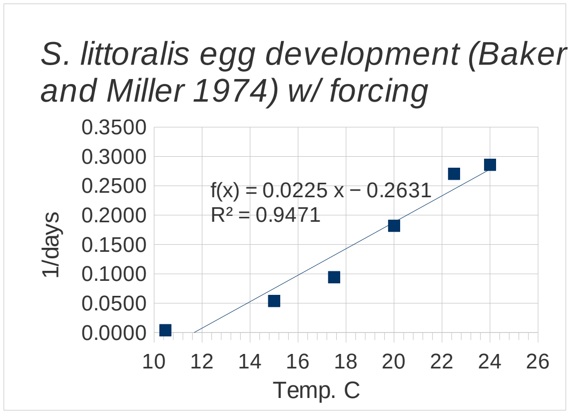
Temp C	Days	1/days
10.47	250	0.0040
15	18.6	0.0538
17.5	10.6	0.0943
20	5.5	0.1818
22.5	3.7	0.2703
24	3.5	0.2857
	slope	0.0225
	y-intercept	-0.2631
	R-sq	0.9471
	Tlow (-a/b)	11.67
	DD req. (1/slope)	44

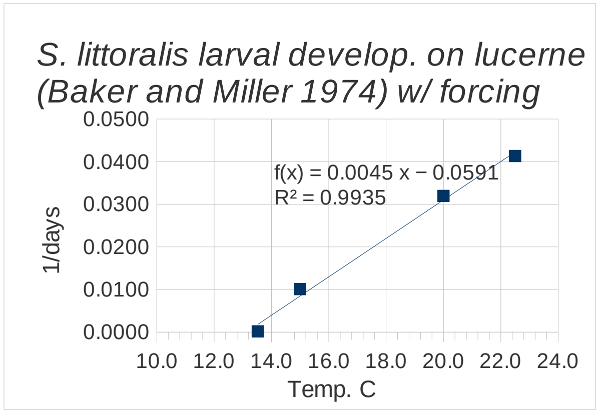
Larval development (lucerne diet)

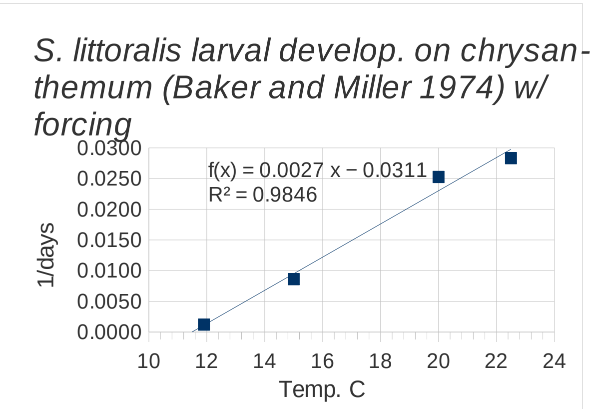
Temp C	Days	1/days
13.52	5000	0.0002
15	99	0.0101
20	31.3	0.0319
22.5	24.2	0.0413
	slope	0.0045
	y-intercept	-0.0526
	R-sq	0.9987
	Tlow (-a/b)	11.67
	DD req. (1/slope)	222

Larval development (chrysanthemum diet)

Temp C	Days	1/days
11.9	825	0.0012
15	116	0.0086
20	39.6	0.0253
22.5	35.3	0.0283
	slope	0.0027
	y-intercept	-0.0315
	R-sq	0.9651
	Tlow (-a/b)	11.67
	DD req. (1/slope)	370

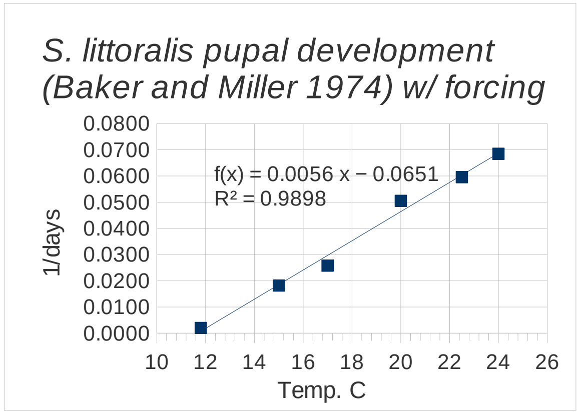






Pupal development (female only) w/ forcing

Temp C	Days	1/days
11.8	500	0.0020
15	55	0.0182
17	38.8	0.0258
20	19.8	0.0505
22.5	16.8	0.0595
24	14.6	0.0685
	slope	0.0056
	y-intercept	-0.0651
	R-sq	0.9898
	Tlow (-a/b)	11.67
	DD req. (1/slope)	179



Results: With forcing of x-intercept through 11.67C, DD requirements were 44, 222, and 179 DD for eggs, larvae, and pupae. DD requirements for pupae are higher than other studies, which is consistent with the authors' suggestion that diet also influenced pupal development, so this result is ignored. Development of larvae on chrysanthemum is much slower than lucerne (as expected), so this result is also ignored.

2. Bhatt, N.S., and A.K. Bhattacharya. 1976. Development of *Spodoptera littoralis* (Boisd.) (Lepidoptera, Noctuidae) at constant temperatures on two host plants. Z. Angew. Entomol. 80:201-206.

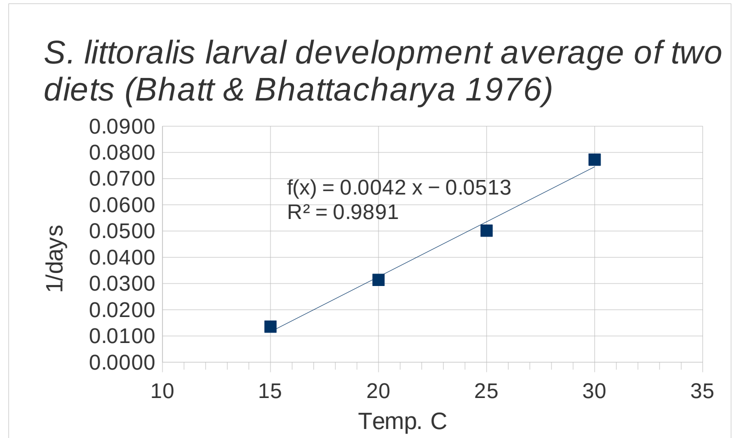
- Studied larval growth and development on two host plants, soybean and green gram, at 4 constant temps with alternating 12hr light vs dark photoperiods
- Lab study was in India, but unclear if stock culture of larvae was derived from field collected individuals
- At 20C, larvae had maximum body weight and survival (pupation was maximal)
- Larvae had an extra moulting at lower temps (15C), also found by Miyashita (1971) Jap. J. Appl. Ent., indicating this low temp is unsuitable

Data from Table 1 [Larval period at different temps (female data only)]

Regression (avg. of two diets; no forcing)

	Soybean	**Green gram**		
Temp C	1/days	Days	Days	Avg
15	0.0136	67.8	79.8	73.8
20	0.0314	31.2	32.5	31.85
25	0.0501	21.3	18.6	19.95
30	0.0772	13.3	12.6	12.95

Tlow (-a/b)	12.23	slope	0.0042
DD req. (1/slope)	238	y-intercept	-0.0513
		R-sq	0.9891



Regression (avg. of two diets; with forcing)

Temp C	Days	1/days
11.70	470	0.0021
15	73.8	0.0136
20	31.85	0.0314
25	19.95	0.0501
30	12.95	0.0772

Tlow (-a/b)	11.67	slope	0.0040
DD req. (1/slope)	249	y-intercept	-0.0469
		R-sq	0.9908

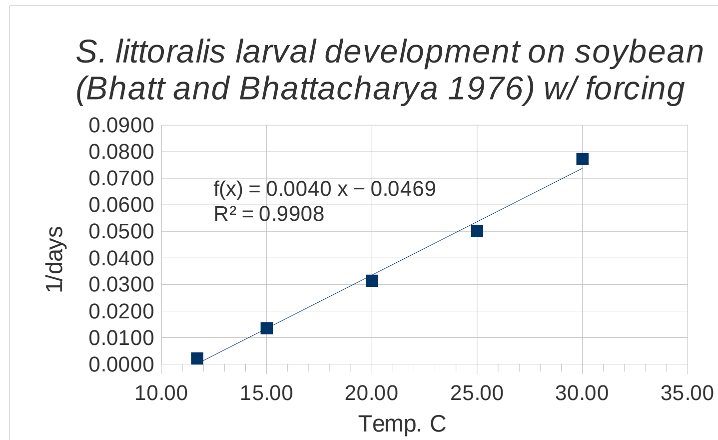
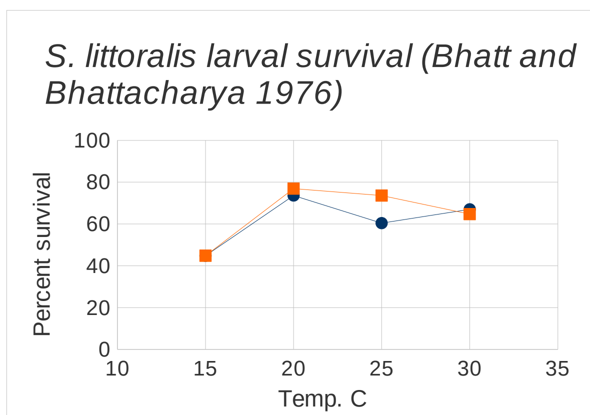


Table 2. Survival response of larvae (percent that reached pupation)

	Percent survival	
Temp C	Soybean	Green gram
15	44.8	44.8
20	76.9	73.6
25	73.6	60.4
30	64.7	67



Results: For larvae reared on 2 plant diets, with no forcing x-intercept was 12.23C. Larval development using a forced x-intercept of 11.67C required 249 DDC. Larval survival sharply declined below 20C.

3. Dahi, H.F. 2005. Egyptian cotton leafworm *Spodoptera littoralis* development on artificial diet in relation to heat unit requirements. The Third International Conference on IPM Role and Integrated Crop management and Impacts on Environment and Agricultural Products. Plant Protection Research Institute, ARC, Dokki, Giza, Egypt.

- Interlibrary loan could not acquire this article and it is not available online except for the abstract
- DD requirements are all slightly higher than most estimated by other studies

Estimated Tlow and DD req

Stage	Tlow degC	DD req.
Egg	11.86	53.2
Larva	7.69	314.7
Pupa	12.34	155.6
PreOV	10.66	27.5
Generation	10.3	537.20

4. El-Malki, Kh. Gh. 2000. Thermal requirements and prediction models of cotton leafworm *Spodoptera littoralis* (Boisd). Pages 1019-1021 *in* Proceedings of the 2000 Beltwide Cotton Conferences, Memphis, TN.

- Reported results of lab development study and a trapping study of moths in middle Egypt

Laboratory study - estimation of Tlow for each stage (diet = castor oil leaves)
- Eggs didn't hatch at 10C and 37.5C, and larvae and pupae exhibited high mortality at 37.5C
- A logistic model most accurately expressed the temperature - development relationship

Table 2. Their estimated thresholds and DD requirements for each stage

Stage	Tlow C	Thigh C	DD req.
Egg	11.81	36	49
Larva	12.5	37	199
Pupa	11.33	35.5	145.5
Pre-oviposition	10.66	36.5	16
Oviposition	10.8	37.5	77.5
Generation	12.6	36	366
Avg. of stages	11.42	36.5	

Population study
- Population peaks occurred in cycles of ca. 480 DDCs
- Assuming a Jan 1 start date:

	DDC	DD accum.	Peaks
	488	488	1st gen
	495	983	2nd gen
	488.6	1471.6	3rd gen
	485.9	1957.5	4th gen
	489	2446.5	5th gen
Avg.	489.3		

Re-analysis of original data (Table 1) using a forced x-intercept

* Author only presented rates, not durations in days

** Data for "adult" in Table 1 are not reported because they seem much too high to be adult longevity, and they are not summarized in Table 2

Egg development (w/ forcing)

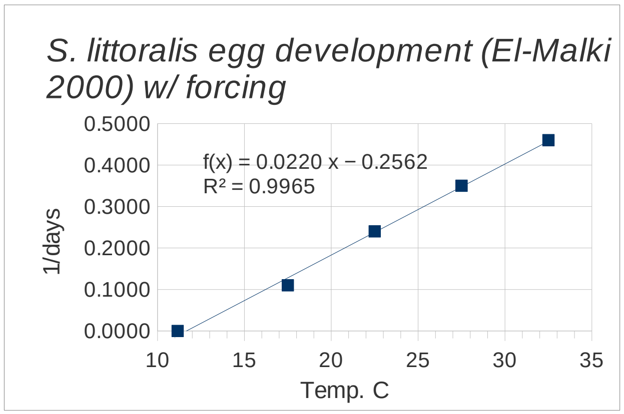
Temp C	Rate eggs	Days
11.16	0.0001	10000.00
17.5	0.1100	9.09
22.5	0.2400	4.17
27.5	0.3500	2.86
32.5	0.4600	2.17
slope	0.0220	
y-intercept	-0.2562	
R-sq	0.9965	
Tlow (-a/b)	11.67	
DD req. (1/slope)	46	

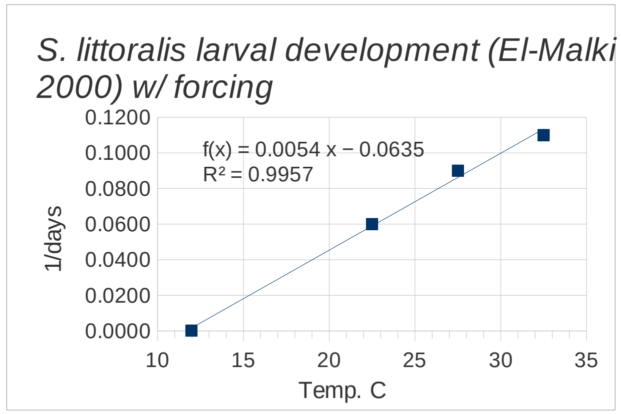
Larval development (w/ forcing)

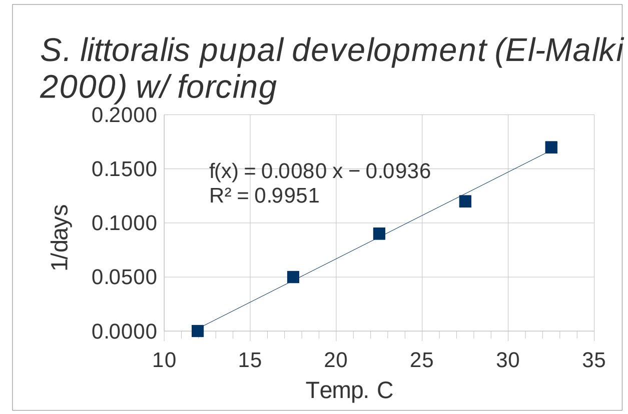
Temp C	Rate larva	Days
11.97	0.0002	5000.00
17.5		
22.5	0.0600	16.67
27.5	0.0900	11.11
32.5	0.1100	9.09
slope	0.0054	
y-intercept	-0.0635	
R-sq	0.9957	
Tlow (-a/b)	11.67	
DD req. (1/slope)	184	

Pupal development (w/ forcing)

Temp C	Rate pupa	Days
11.95	0.0001	10000.00
17.5	0.0500	20.00
22.5	0.0900	11.11
27.5	0.1200	8.33
32.5	0.1700	5.88
slope	0.0080	
y-intercept	-0.0936	
R-sq	0.9951	
Tlow (-a/b)	11.67	
DD req. (1/slope)	125	







Pre-oviposition time (w/ forcing)

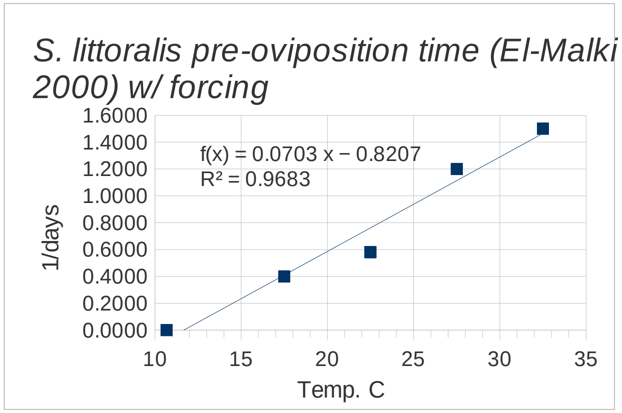
Temp C	Rate preOV	Days
10.67	0.0001	10000
17.5	0.4000	2.5
22.5	0.5800	1.72
27.5	1.2000	0.83
32.5	1.5000	0.67
slope	0.0703	
y-intercept	-0.8207	
R-sq	0.9683	
Tlow (-a/b)	11.67	
DD req. (1/slope)	14	

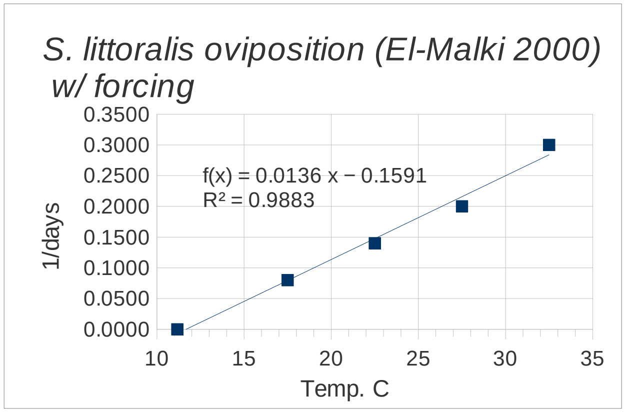
Oviposition time (w/ forcing)

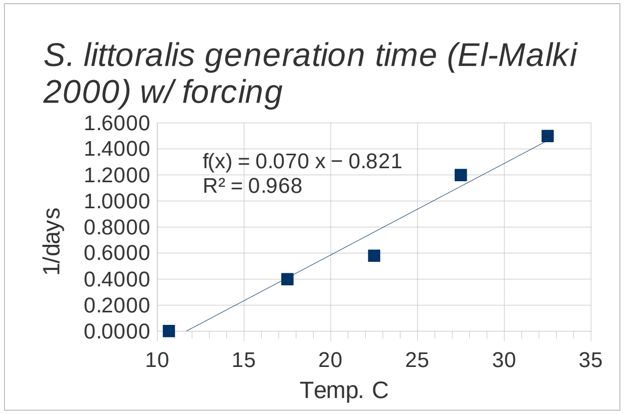
Temp C	Rate OV	Days
11.17	0.0001	10000.00
17.5	0.0800	12.50
22.5	0.1400	7.14
27.5	0.2000	5.00
32.5	0.3000	3.33
slope	0.0136	
y-intercept	-0.1591	
R-sq	0.9883	
Tlow (-a/b)	11.67	
DD req. (1/slope)	73	

Generation time (w/ forcing)

Temp C	Rate generati	Days
10.56	0.0001	10000.00
17.5	0.0120	83.33
22.5	0.0300	33.33
27.5	0.0400	25.00
32.5	0.0600	16.67
slope	0.0027	
y-intercept	-0.0317	
R-sq	0.9794	
Tlow (-a/b)	11.67	
DD req. (1/slope)	368	







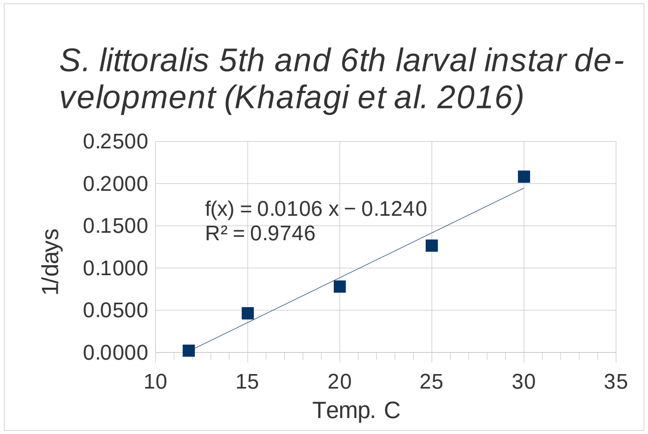
Results: With forcing of x-intercept through 11.67C, DD requirements were 46, 187, 125, 14, 73, and 368 DD for eggs, larvae, pupae, pre-oviposition, oviposition, and generation time. These values aligned very well with the durations reported by this study.
A Tupper of 36C is similar to results of other studies, although slightly higher at least for larvae (Sidibe and Lauge 1977, Nasr and Nassif 1974)

5. Khafagi, W.E., E.M. Hegazi, and N.A. Aamer. 2016. Effects of temperature on the development, food consumption and utilization parameters of the last two larval instars of *Spodoptera littoralis* (Boisd.). Journal of Agricultural Science and Food Technology 2:93-99.

- Studied development of last larval instars at 15, 20, 25 and 30C in the lab (raised on artificial diet)
- In Egypt it may have 4 generations on clover, 2 to 3 generations on cotton, and 1 generation on maize
- Larvae had highest digestion efficiency at 25C, indicating this temp was optimal

Temp C	5th instar Days	6th instar Days	5th + 6th inst.	1/rate
11.8	230	241.8	471.8	0.0021
15	8.9	12.7	21.6	0.0463
20	5.5	7.3	12.8	0.0781
25	3.1	4.8	7.9	0.1266
30	1.9	2.9	4.8	0.2083

slope	0.0106
y-intercept	-0.1240
R-sq	0.9746
Tlow (-a/b)	11.67
DD req. (1/slope)	94



6. Nasr, E.S.A., and F.M. Nassif. 1974. Response of various stages of the cotton leafworm, *Spodoptera littoralis* (Boisd.) to temperature and relative humidity (Lepidoptera: Noctuidae). Bull. Soc. Entomol. Egypte 58:123-131.

- Studied the influence of temperature (15-35C) and RH (69-90%) on different stages under controlled conditions in Egypt between 1968-1971
- Used 100 newly hatched larvae from egg masses laid in the lab
- Fed all larvae castor oil leaves except for insects kept at 35C which were fed sweet potato leaves (this likely biases the results)
- Development of all stages was faster at RH = 69%, which is consistent with other studies that high levels of RH slow development
- Similar to other studies, they documented non-linear development at 35C (even lower for larvae - 30C)
- They estimated a much lower Tlow for larvae than other studies - forcing the x-intercept did not work well in this case
- Nasr (1962) documented the slowest rate of larval and pupal development at RH = 0% and temp = 30C, consistent w/ results of Rivnay and Meisner (1966)
- However RH had little impact on adult longevity
- Concluded that 25C was the most optimum temp; egg fertility and avg. number of eggs laid was highest

Estimated Tlow

Stage	Tlow degC (RH = 69%)	
Egg	12	
Larva	8.25	
Pupa	12	Females (males = 12.25C)
Generation	11.18	Not reported, but estimated from unforced regression

Egg development at different RHs

Data points highlighted in red were removed because temperature - development relationship became non-linear

Egg development at RH = 69%

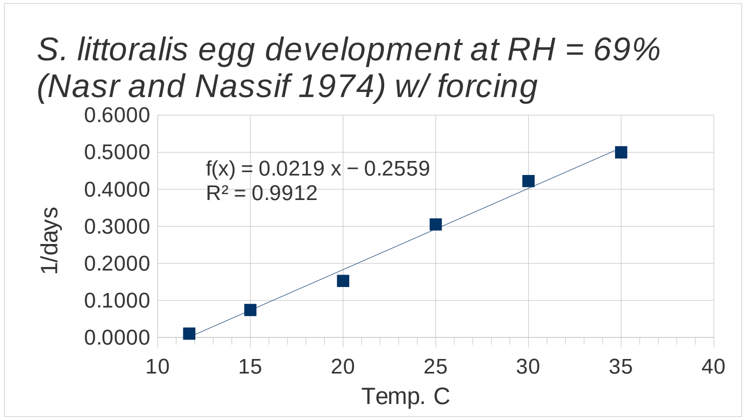
Temp C	Days	1/days
11.7	100	0.0100
15	13.5	0.0741
20	6.56	0.1524
25	3.28	0.3049
30	2.37	0.4219
35	2	0.5000

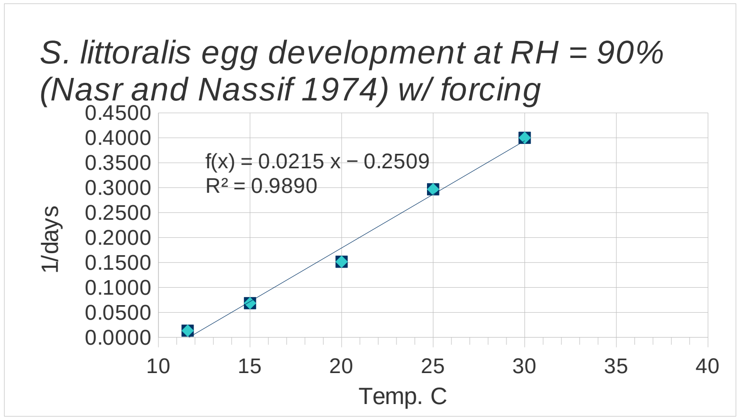
Tlow (-a/b)	11.67	slope	0.0219
DD req. (1/slope)	46	y-intercept	-0.2559
		R-sq	0.9912

Egg development at RH = 90%

Temp C	Days	1/days
11.6	75	0.0133
15	14.6	0.0685
20	6.6	0.1515
25	3.37	0.2967
30	2.5	0.4000
35	2.23	

Tlow (-a/b)	11.67	slope	0.0215
DD req. (1/slope)	47	y-intercept	-0.2509
		R-sq	0.9890





Larval development at different RHs

Larval development at RH = 69%

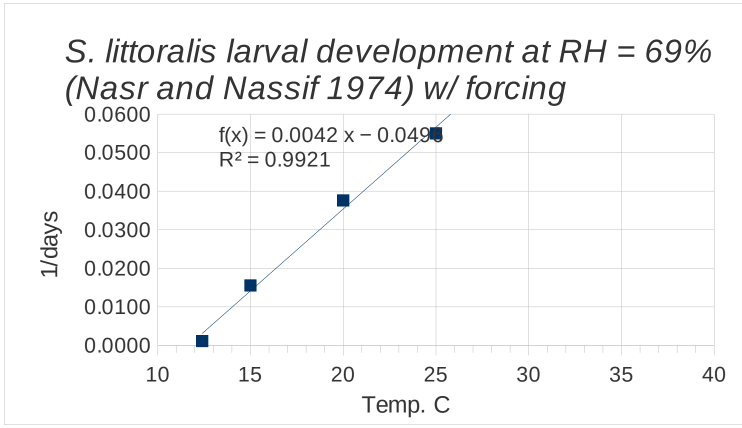
Temp C	Days	1/days
12.4	900	0.0011
15	64.29	0.0156
20	26.6	0.0376
25	18.18	0.0550
30	14.31	
35	13.42	

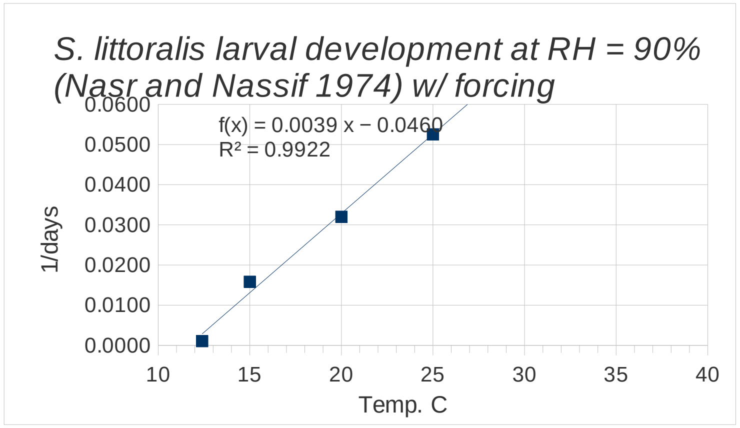
Tlow (-a/b)	11.67	slope	0.0042
DD req. (1/slope)	235	y-intercept	-0.0496
		R-sq	0.9921

Larval development at RH = 90%

Temp C	Days	1/days
12.4	950	0.0011
15	63.14	0.0158
20	31.24	0.0320
25	19.04	0.0525
30	15.24	
35	13.25	

Tlow (-a/b)	11.67	slope	0.0039
DD req. (1/slope)	254	y-intercept	-0.0460
		R-sq	0.9922





Pupal development at different RHs (females)

Pupal development at RH = 69%

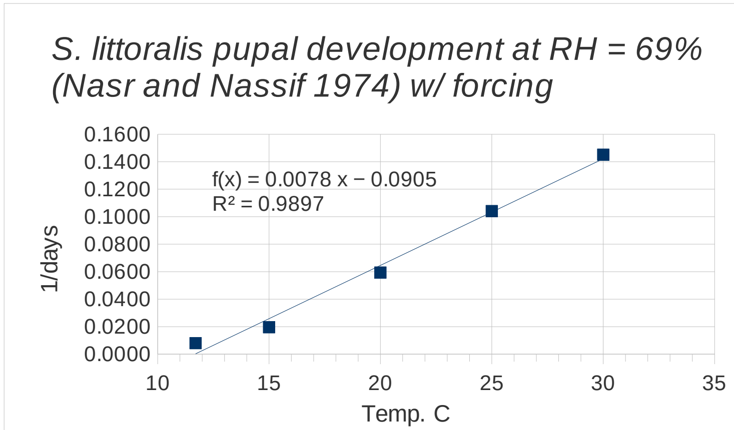
Temp C	Days	1/days
11.7	125	0.0080
15	51	0.0196
20	16.85	0.0593
25	9.61	0.1041
30	6.89	0.1451
35	6.15	

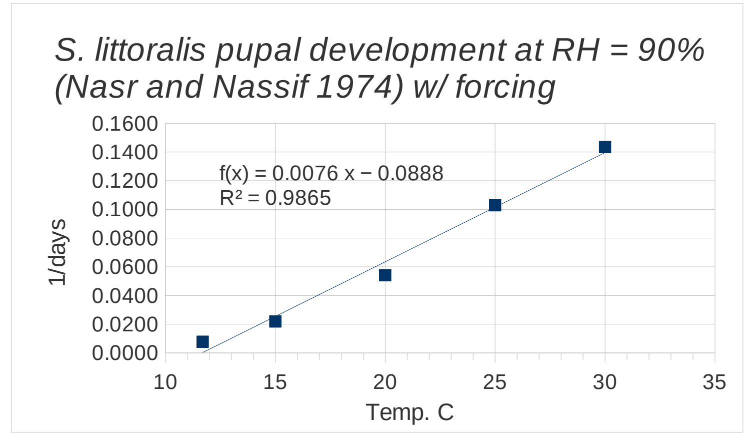
Tlow (-a/b)	11.67	slope	0.0078
DD req. (1/slope)	129	y-intercept	-0.0905
		R-sq	0.9897

Pupal development at RH = 90%

Temp C	Days	1/days
11.7	128	0.0078
15	45.62	0.0219
20	18.48	0.0541
25	9.72	0.1029
30	6.97	0.1435
35	6	

Tlow (-a/b)	11.67	slope	0.0076
DD req. (1/slope)	131	y-intercept	-0.0888
		R-sq	0.9865





Adult longevity at different RHs (females)

Note: removed values at lowest and highest temps (15 and 35C) for RH=69%, at lowest temp only at RH = 90%

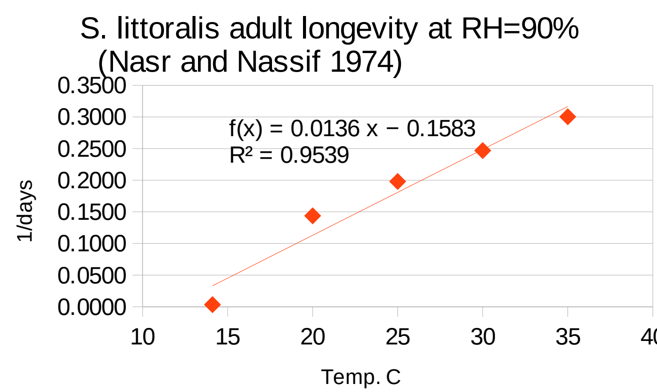
Adult longevity at RH = 69%

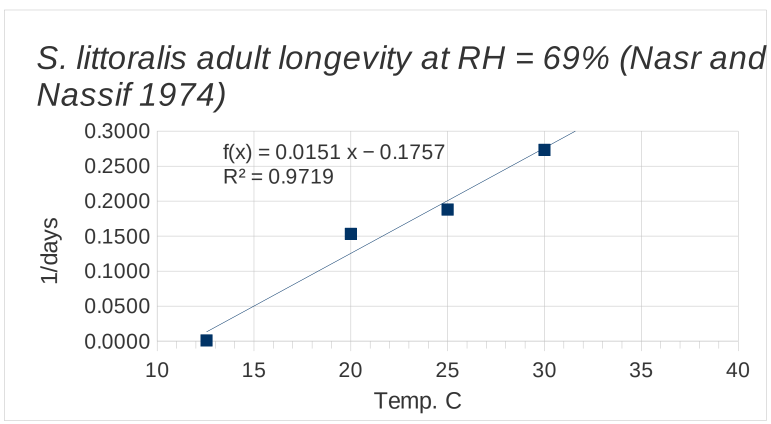
Temp C	Days	1/days
12.55	1000	0.0010
15	10.16	
20	6.53	0.1531
25	5.32	0.1880
30	3.66	0.2732
35	3.16	

Tlow (-a/b)	11.67	slope	0.0151
DD req. (1/slope)	66	y-intercept	-0.1757
		R-sq	0.9719

Adult longevity at RH = 90%

Temp C	Days	1/days
14.11	300	0.0033
15	11.2	
20	6.96	0.1437
25	5.05	0.1980
30	4.05	0.2469
[illegible]	[illegible]	[illegible]





Generation time (females) – NOTE: this publication fails to clearly define what they mean by "total life cycle (generation period)"

normally we would assume that, with what is available in this study, would be egg+larvae+pupae+ca. 50% female longevity:

(using RH=69%): **443** but, this value is rather different than the value 491 solved for from this Table III

Generation time at RH = 69%

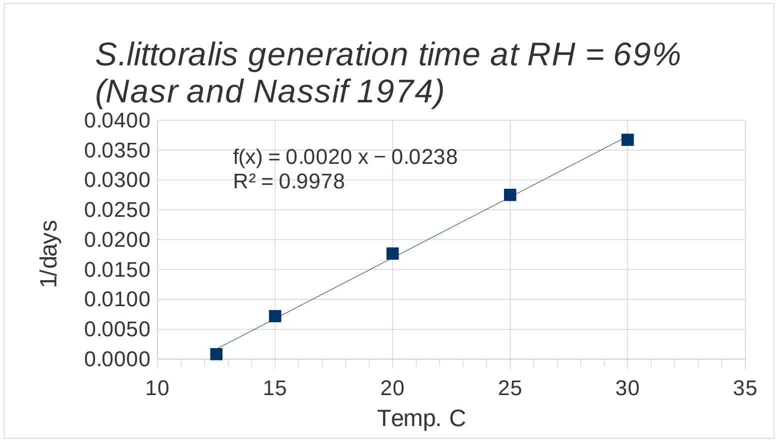
Temp C	Days	1/days
12.5	1200	0.0008
15	138.97	0.0072
20	56.54	0.0177
25	36.39	0.0275
30	27.23	0.0367
35	24.73	

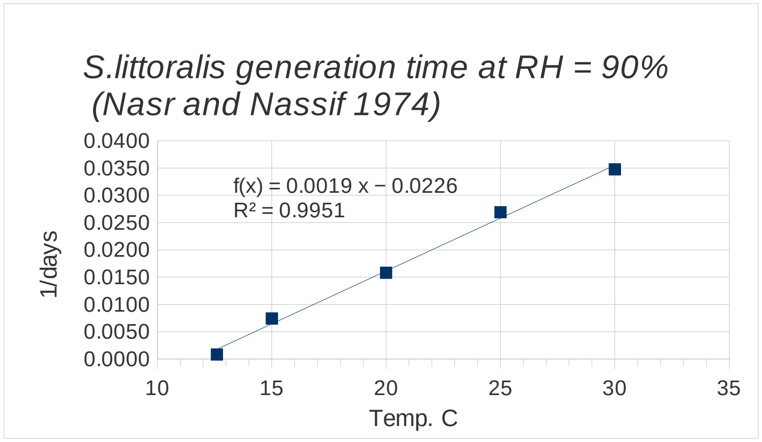
Tlow (-a/b)	11.67	slope	0.0020
DD req. (1/slope)	491	y-intercept	-0.0238
		R-sq	0.9978

Generation time at RH = 90%

Temp C	Days	1/days
12.6	1200	0.0008
15	134.56	0.0074
20	63.28	0.0158
25	37.18	0.0269
30	28.77	0.0348
35	25.06	

Tlow (-a/b)	11.67	slope	0.0019
DD req. (1/slope)	516	y-intercept	-0.0226
		R-sq	0.9951





Results: using data collected at RH = 69% (ideal for development) and a forced intercept of 11.67C, the DD requirements for eggs, larvae, pupae, and generation time was 46, 235, 129, and 491 DDC, respectively.

7. Nasr, E-S, M. Tucker, and D. Campion. 1984. Distribution of moths of the Egyptian cotton leafworm, *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae), in the Nile Delta interpreted from catches in a pheromone trap network in relation to meteorological factors. Bulletin of Entomological Research 74:487-494.

- Checked 46 pheromone traps in or near the Nile Delta in Egypt in 1979 and 1980
- As shown in other studies there were fairly regular seasonal increases and decreases, suggesting local build-up rather than migration events
- Rapid succession of generations in the summer (approx. 1 month per gen in summer) explains build-up

-Could do a rough validation of phenology/generation time using Fig. 3 but would only have access to recent year data.

- No early spring flight included that would help with determining OW requirements
- Moths captured in all months indicating no diapause in Nile Delta.

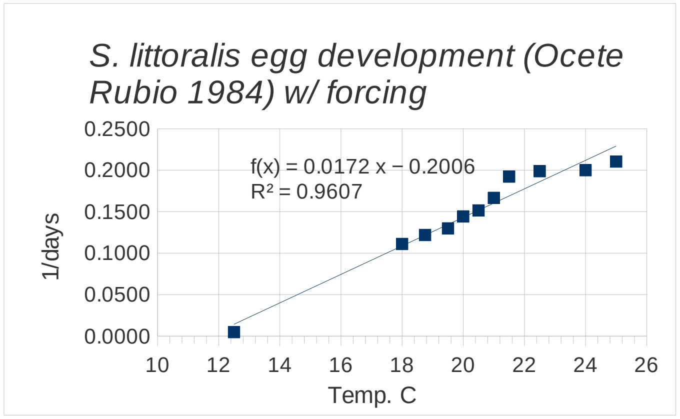
8. Ocete Rubio, E. 1984. Study of the biological cycle of *Spodoptera littoralis* at different temperatures Lepidoptera Noctuidae. Graellsia 40:195-206.

- Species has up to 7 generations in Egypt; it has 3 generations in Seville Province of Spain where this study took place
- Studied development and survival of larvae that were reared on lucerne, at temps between 18 and 36C (+/- 2 C) (unknown RH)
- Stage durations were calculated as the mean of the first and last day across 10 groups (100 larva per group)
- They present a table of results of previous studies, showing the diversity of estimated stage durations
- Re-analysis of their data using a forced x-intercept method is below - data for high temps excluded because of non-linearity
- Male pupae had slightly lower rates of development, consistent with other studies (Jarczyk and Hertle 1960)
- Survival to adulthood was highest at 20-25C (40-90%) and declined between 25-30C (15%); it was lowest at 30-36 (3%)

Egg development

Temp C	Days	1/days
12.5	210	0.0048
18	9	0.1111
18.75	8.2	0.1220
19.5	7.7	0.1299
20	6.93	0.1443
20.5	6.6	0.1515
21	6	0.1667
21.5	5.2	0.1923
22.5	5.03	0.1988
24	5	0.2000
25	4.75	0.2105
26	4	
30	4	
32	4	
36	2	

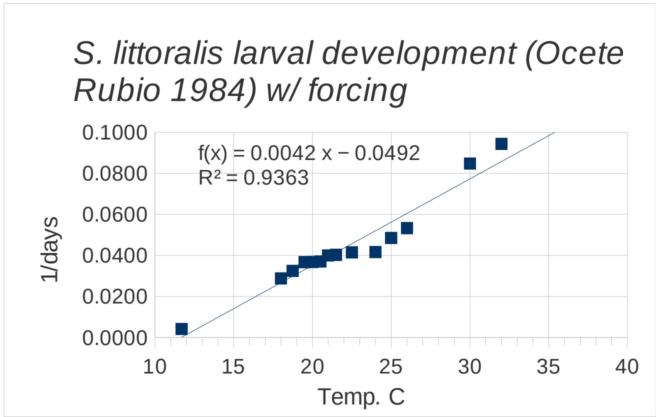
Tlow (-a/b)	11.67	slope	0.0172
DD req. (1/slope)	58	y-intercept	-0.2006
		R-sq	0.9607



Larval development

Temp C	Days	1/days
11.7	240	0.0042
18	34.72	0.0288
18.75	30.8	0.0325
19.5	27.24	0.0367
20	27.16	0.0368
20.5	27	0.0370
21	25	0.0400
21.5	24.8	0.0403
22.5	24.08	0.0415
24	24.02	0.0416
25	20.62	0.0485
26	18.77	0.0533
30	11.8	0.0847
32	10.6	0.0943
36	10	

Tlow (-a/b)	11.67	slope	0.0042
DD req. (1/slope)	237	y-intercept	-0.0492
		R-sq	0.9363

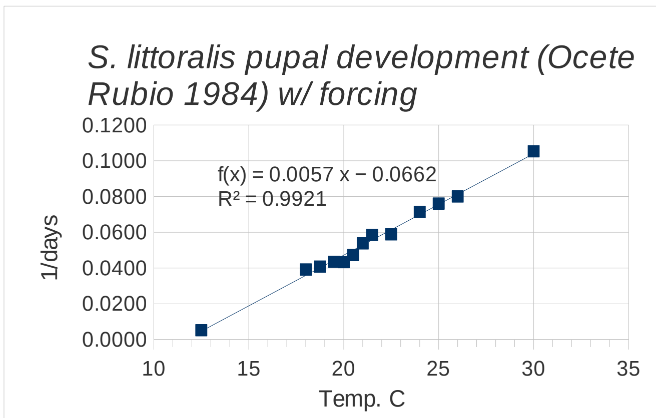


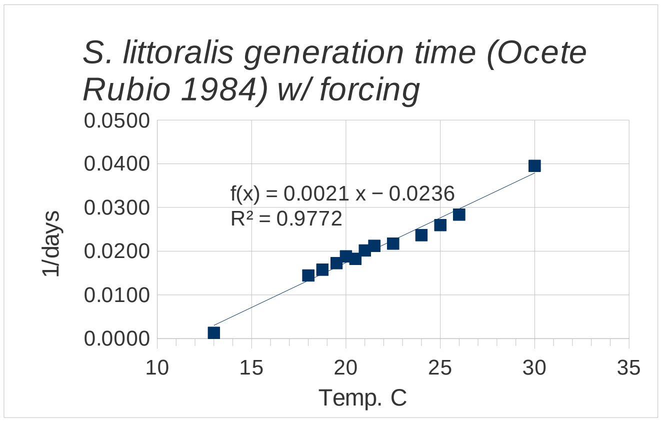
Pupal development (females)

	Temp C	Days	1/days
	12.5	190	0.0053
	18	25.5	0.0392
	18.75	24.5	0.0408
	19.5	23	0.0435
	20	23.09	0.0433
	20.5	21.15	0.0473
	21	18.6	0.0538
	21.5	17.1	0.0585
	22.5	17	0.0588
	24	14	0.0714
	25	13.15	0.0760
	26	12.5	0.0800
	30	9.5	0.1053
	32	9.7	
	36	7.8	
Tlow (-a/b)	11.67	slope	0.0057
DD req. (1/slope)	176	y-intercept	-0.0662
		R-sq	0.9921

Generation time (females)

	Temp C	Days	1/days
	13	750	0.0013
	18	69.22	0.0144
	18.75	63.5	0.0157
	19.5	57.94	0.0173
	20	53.13	0.0188
	20.5	54.75	0.0183
	21	49.6	0.0202
	21.5	47.1	0.0212
	22.5	46.05	0.0217
	24	42.3	0.0236
	25	38.52	0.0260
	26	35.27	0.0284
	30	25.3	0.0395
	32	24.3	0.0412
	36	19.8	
Tlow (-a/b)	11.67	slope	0.0020
DD req. (1/slope)	494	y-intercept	-0.0236
		R-sq	0.9837





Results: Forcing through an x-intercept of 11.67C, DD requirements for eggs, larvae, pupae and a full generation were 58, 237, 176, and 494 DD, respectively. Results for eggs and pupae are rather high compared to other studies.

9. Rivnay, E. and J. Meisner. 1966 The effects of rearing conditions on the immature stages and adults of *Spodoptera littoralis* (Boisd.). Bull. Entom. Res. 56:623-634.

- Measured duration of OV period, length of life, proportion of barren females, no. of eggs laid, and proportion of non-viable eggs after exposing larvae to various temps
- Rearings began with 1-2 day old larvae from the field in Israel or from lab colonies
- Larvae and pupae kept at constant RH of 60-70 and 70-80%, respectively

- Experiment 1: Larvae exposed to different temps (22-34C), and pupae were raised at a constant temp of 24C, to measure effect on adult life span and egg viability
- Experiment 1 results: exposure to higher temps increased proportion of non-viable eggs, where 25% were inviable at 26C, and nearly all were inviable at 34C (Fig. 1)
- Experiment 2: Larvae reared at 22-24C, whereas pupae were raised at different temps (20-34C) to measure effect on adult life span and egg viability
- Experiment 2 results: little effect of temp on adult life span - mean adult life span was longest at 20C and lowest at 34C (Fig. 1)
- Experiment 3: measured direct effects of temperatures on pupal development and mortality (pupae were fed clover)
- Exeriment 3 results: all pupae dead when examined after 155 days at 10C; almost all died at 16C; and above 16C the pupal period shorted w/ inc. temps
- Experiment 4: measured effects of exposure of pupae to different RH on adults (constant temp of 20-21C)
- Experiment 4 results: adults from pupae kept at 95% RH had shorted lifespan; longest life spans and egg viability were at 76% RH
- Experiment 5: measured direct effects of RH on pupal development and mortality
- Experiment 5 results: pupal mortality was lowest at 55% RH, and only slightly higher from 76 to 95% RH, but very high at 32%
- Other experiments included effects of density on larval development, where development was faster and mortality was lower with a lower larval density

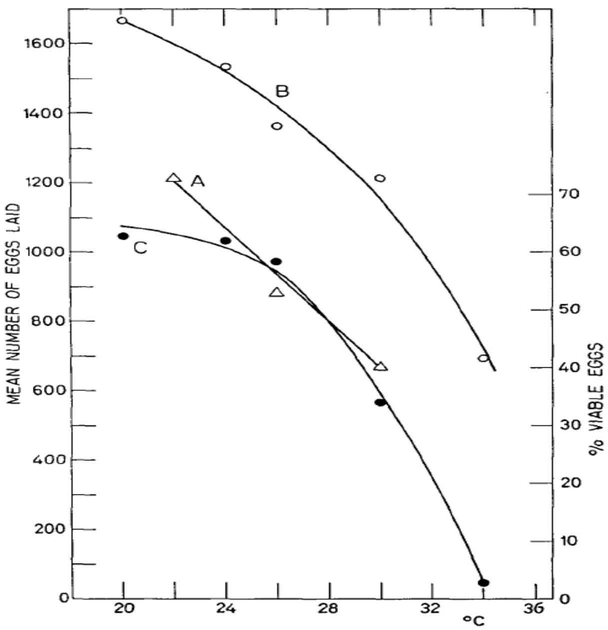


Fig. 1.—Effects of rearing temperature on the fecundity of adults

Effects of temp on fecundity of adults and on viability of eggs (Experiments 1 and 2; Fig. 1)

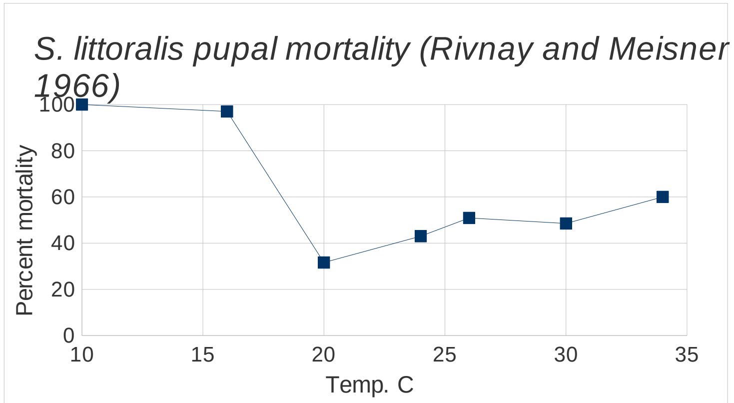
Line A: effect of exposure of larva to different temps on egg viability (Experiment 1)

Line B: effects of different pupal temperatures on egg viability (Experiment 2)

Line C: effects of different pupal temps on percentage of egg viability

Effects of temperature on pupal period and mortality of pupae after 155 days (Experiment 3) - data from Table 3

Temp C	No. pupae observed	No. adults produced	Pupal mortality
10	60	0	100
16	66	2	97
20	38	26	31.6
24	70	51	43
26	55	27	50.9
30	60	31	48.5
34	60	24	60



Pupal development (no forcing)

Temp C	Days	1/days
16	53.5	0.0187
20	20.5	0.0488
24	12.7	0.0787
26	9.8	0.1020
30	7.9	0.1266
34	7.3	0.1370

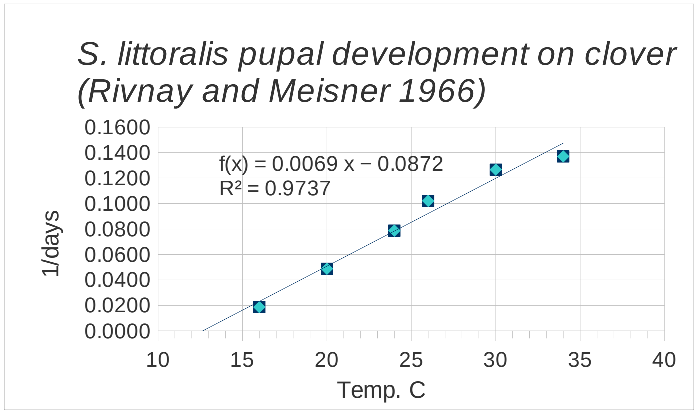
slope	0.0069
y-intercept	-0.0872
R-sq	0.9737
Tlow (-a/b)	12.64
DD req. (1/slope)	145

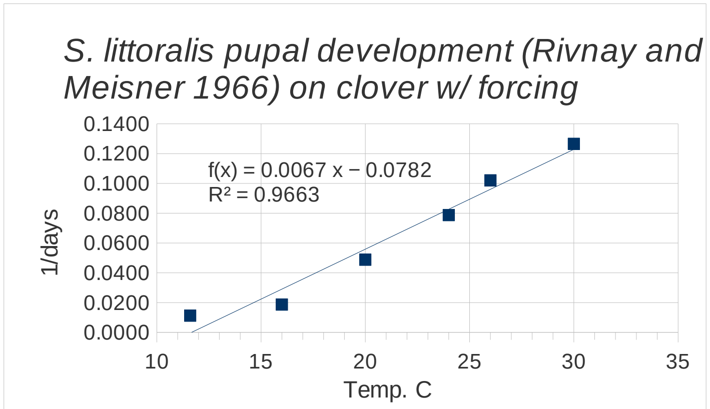
Pupal development (w/ forcing)

Temp C	Days	1/days
11.6	89	0.0112
16	53.5	0.0187
20	20.5	0.0488
24	12.7	0.0787
26	9.8	0.1020
30	7.9	0.1266
34	7.3	

slope	0.0067
y-intercept	-0.0782
R-sq	0.9663
Tlow (-a/b)	11.67
DD req. (1/slope)	149

Data point highlighted in red was removed because temperature - development relationship became non-linear





Results:

- A jump in the percent of females laying non-viable eggs from 26 to 30C suggests temps are suboptimal above ca. 26C
- Devel - temp relationship for pupae becomes non-linear between 30 and 34C, consistent w/ data for larvae in other studies (Sidibe and Lauge 1977, Nasr and Nassif 1974)
- A large increase in pupal mortality from 20 to 16C is concordant w/ similar results for larvae (Bhatt 1976)
- With forcing through the x-intercept at 11.67C, the DD requirement for pupae was 149 DDC
- High pupal mortality at RH = 33% suggests sensitivity to desiccating soil conditions; RH = 76% is optimal

10. Salama, H.S., N.Z. Dimetry, and S.A. Salem. 1971. On the host preference and biology of the cotton leafworm *Spodoptera littoralis*. Z. Angew. Entomol. 67:261-266.

- Studied larval development and mortality on various plants, and measured whether plant was acceptable as a food source
- Quantified larval and pupal developmental duration of individuals raised on different host plants, raised at 25-26C
- They found differences in larval development, but not pupal development
- Average DD requirements for larval development are consistent with estimates for other studies (assumed Tlow = 11.67C)
- Similarly, Nasr et al. (1974, Bull. Soc. Ent. Egypt 57:27-32) documented variation in development rates across seven different host plants

Host	Mean larval duration (d)	DD req (Tlow = 11.67C)
Castor oil	11.4	157.7
Cotton	17.1	236.5
Pepper	16.4	226.8
Sesban	15.6	215.7
Sweet potato	19.7	272.5
Average	**16.0**	**221.8**

11. Sidibe, B. and G. Lauge. 1977. Effect of warm periods and of constant temperatures on some biological criteria in *Spodoptera littoralis* Boisduval (Lepidoptera Noctuidae). Ann. Soc. Entomol. Fr. 13:369-379. [In French]

- Reared larvae and pupae at 8 constant temperatures (5 to 40C) and 4 thermoperiods (fed an artifical diet)
- Optimal constant temp for larvae and pupae was 25C (est. larval and pupal duration as 221 and 108 DDs, respectively)
- Relationship between temp and larval development becomes nonlinear at 30C - this was also documented by Nasr and Nassif (1974)

Days development

Temp C	1st instar	2nd instar	3rd instar	4th instar	5th instar	6th instar	All instars
15	11.6	8.9	17.9	11.8	6	15.3	71.5
20	5	3	3.5	4.3	4.7	8.1	28.6
25	3.2	1.5	3.3	2.2	2.1	5.5	17.8
30	3.5	2.7	2.8	2.8	2.2	1.7	15.7
35	2.3	1.9	1.5	3.1	2.8	3.9	15.5

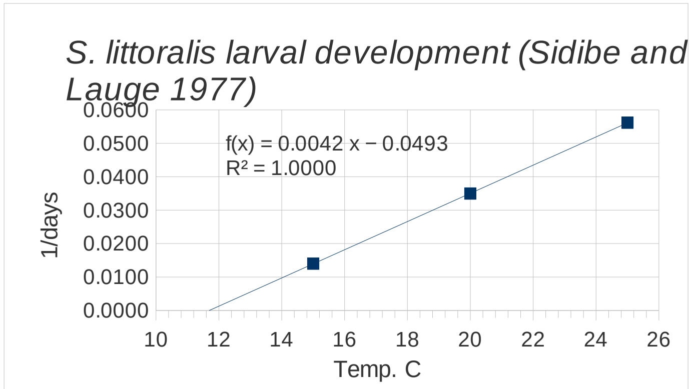
Larval development (no forcing)

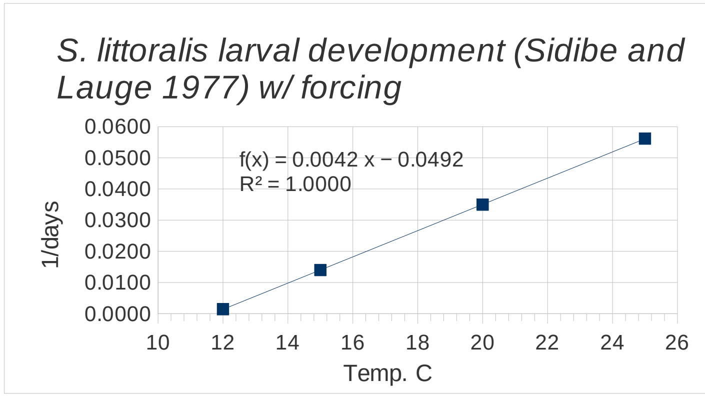
Data points for 30 and 35C were removed becaus relationship became non-linear

Temp C	Days	1/days
15	71.5	0.0140
20	28.6	0.0350
25	17.8	0.0562
30	15.7	
35	15.5	
	slope	0.0042
	y-intercept	-0.0493
	R-sq	1.0000
	Tlow (-a/b)	11.69
	DD req. (1/slope)	237

Larval development (w/ forcing)

Temp C	Days	1/days
12	700	0.0014
15	71.5	0.0140
20	28.6	0.0350
25	17.8	0.0562
	slope	0.0042
	y-intercept	-0.0492
	R-sq	1.0000
	Tlow (-a/b)	11.67
	DD req. (1/slope)	237





Results: Using a forced x-intercept of 11.67C resulted in a DD req of 237 DDC for larvae (identical to value derived without forcing).
The temperature - development relationship became non-linear at 30C, which is consistent with larvae data presented by Nasr and Nassif (1974).

12. Yones, M., S. Arafat, A. Abou Hadid, H.A. Abd Elrahman, and H.F. Dahi. 2012. Determination of the best timing for control application against cotton leaf worm using remote sensing and geographical information techniques. Egyptian Journal of Remote Sensing and Space Science 15:151-160.

- Analyzed thermograph and satellite image data to estimate DD requirements to complete a generation, in order to better time insecticide applications
- Study was conducted during 2006 in northern Egypt (Ezbet Shalaqan, Al-Qalyubiya Governate)
- Field experiment involved 4 replicates (cages) in which eggs were raised to the adult stage, and the timing (DDs) of each stage transition was documented
- Stages emerged slightly later than their predictions for all data types - perhaps because they used a low threshold (9.89C)? (Yones et al. 2008, MSc thesis)
- Their estimated generation durations were higher than DDs based on laboratory data (524.7 DDC, Yones et al. 2008)
- They suggest the best timing of control application for mature larvae is 174.85-197.59 DDs
- Tmax and tmin air temp data derived from satellite images were most accurate for predicting development

Developmental durations (corrected DDs) based on satellite-derived air temps (Tlow = 9.89C) [Table 3]

Stage	Days	DD req.
Egg	3	54.9
Larva	16	289.27
Pupa	8	157.05
Pre-oviposition	2	32.48

Generation time based on 3 methods (Tlow = 9.89C)

Method	Air temp	Soil temp
Satellite	599.6	640.63
Thermograph	544.98	

Comparison / synthesis of above temperature-development results

Comparison of Tlow (unforced)

Red values – consider as outliers

Source	Egg	Larvae	Pupae	PreOV	OV	Generation	Average:
1. Baker and Miller 1974	14.8	11.5	13.0				**13.1**
2. Bhatt 1976		12.2					**12.2**
3. Dahi 2005	11.9	7.7	12.3	10.7			**10.6**
4. El-Malki 2000	11.8	12.5	11.3	10.7	10.8	12.6	**11.6**
6. Nasr and Nassif 1974	12.0	8.3	12.0			11.2	**10.9**
8. Ocete Rubio 1984	10.5	12.3	11.8			10.8	**11.3**
9. Rivnay and Meisner 1966			12.6				**12.6**
11. Sidibe and Lauge 1977		11.7					**11.7**
Average:	**12.2**	**10.9**	**12.2**	**10.7**	**10.8**	**11.5**	**11.8**
Avg (excl. outliers)	**11.5**	**12.0**	**12.2**	**10.7**	**10.8**	**11.5**	**11.6**

Results: The overall average unforced lower threshold, with or without outliers, was very close to our selected threshold of 11.67C.

Duration in degree-days Celsius (using a Tlow of 11.67C)

determined through subtraction, addition, or average of other studies represented in table

Red values – consider as outliers

Source	Country	Egg	Larvae	Pupae	Egg-to-adult	Pre-OV	Female longevity	Approx. mid OV	Egg-to-Egg assume 1st OV	Full Gen. assume ca. mid OV
1. Baker and Miller 1974	England	44	222	179	446					
2. Bhatt 1976	India		249							
3. Dahi 2005	Egypt	53		156	209	28				
4. El-Malki 2000	Egypt	46	184	125		14		37	420	
6. Nasr and Nassif 1974	Egypt	46	235	129	410	33	66	40	443	483
8. Ocete Rubio 1984	Spain	58	237	176	472				494	
9. Rivnay and Meisner 1966	Israel			149						
11. Sidibe and Lauge 1977	France		237							
Average:		**49**	**236**	**152**	**437**	**25**	**66**	**38**	**462**	**476**
Avg (excl. outliers)		**49**	**227**	**152**	**384**	**25**	**66**	**38**	**454**	**467**

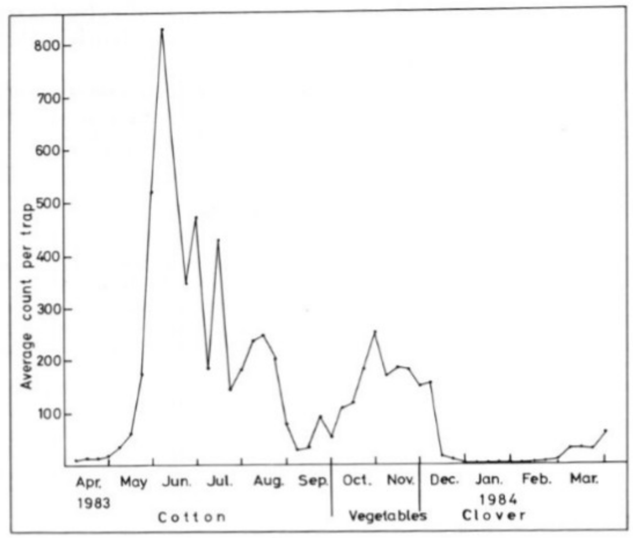
Results: using averages exluding outliers, egg, larval, pupal, pre-OV, and egg-to-egg generation times were 49, 236, 152, 25, and 462 DDC. Full generation time assuming ca. Mid-OV At 38 DD is 476 DDC.

B) Evidence for Springtime Flight Phenology

1. Salem, S. and H.S. Salama. 1985. Sex pheromones for mass trapping of *Spodoptera littoralis* (Boisd) in Egypt. Zeitschrift Fur Angewandte Entomologie – J. of Appl. Entomol. 100:316-319.

-does not undergo diapause in Egypt

-pupates in the ground 3-5cm deep



Numbers of male moths of *S. littoralis* captured by pheromone traps in 1983 and 1984

- From Fig. 1, it appears that adults can begin flying by early March in clover, perhaps later in cotton (due to later planting and emergence of cotton; authors report that cotton is planted from mid-March through mid-April).
- Estimated 6 generations at Beni-suef Governorate (ca. 80km S. of Cairo along the Nile river. (ca. 29N Latitude).

Based on this report, with no weather data from Egypt, select sites with matched climates and latitudes in N. America, and calculate average Dds Jan 1- Mar 2 over recent years

	Hermisillo MX		Patterson LA	Bay City LA	Orlando, FL	
	C9464	C2548	KPTN	KBYY	KMCO	Average
Latitude:	29N	29N	29.7N	28.9N	28.5N	
2009	446	427	232	290	310	341
2010	356	296	92	135	198	215
2012	373	463	322	328	419	381
2014	469	577	170	224	368	362
2015	495	525	144	156	318	328
2016	458	525	181	233	314	342
2017	387	457	378	414	482	424
2018	440	511	306	292	453	400
2019	332	384	256	247	443	332
2020	354	406	268	338	483	370
avg	411	457	235	266	379	350
range	332-469	296-577	92-378	135-414	198-483	215-424

Results: Jan 1 – Mar 2 cumulative Dds averaged 350 across five locations with similar climate and latitude to Cairo Egypt.
The minimum average, 235 for Patterson LA, might be close to the best conservative value to use in the model.

2. Yathom 2019. Distribution and flight period of Noctuidae species in Israel in 1959-1970 (annotated).

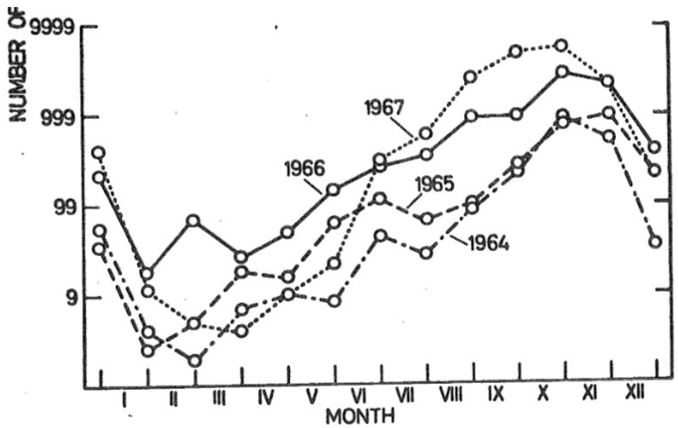


Fig. 2. Number of S. littoralis moths caught in a light trap in 'En Harod. (Averages per 10 nights for each month).

From Fig. 2 and from text, moths trapped during all months with lowest counts in Feb. This is evidence that while moths that emerged in the fall may fly even in January, it is likely that overwintering is primarily in the larval and perhaps pupal stage, producing new adults in March and April.

As Israel has a climate somewhat similar to Egypt and Cyprus, the estimation of Dds between Jan 1 and early March should be similar to other results arrived at above (#1) and below (#3 - #5).

3. Campion, D., B. Bettany, J. McGinnigle, and L.R. Taylor. 1977. The distribution and migration of *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae), in relation to meteorology on Cyprus, interpreted from maps of pheromone trap samples. Bull. Ent. Res. 67:501-522.
- Monitored moths across a network of 51 pheromone traps in Cyprus across 7 months in 1972 and recorded catches of males each day
- Moth catches fell sharply when Tmin reached 5C
- Peak catches were often associated with wind strength and direction, but also approximated the generation cycles
- Their estimations of generation cycles were imprecise but suggest five generations
- In SE Cyprus potato growing areas first emergence was in mid-March; first catches in traps March 6-20 in 1973

Based on this report, with no weather data from Cyprus available, select climatically similar sites in US and calculate average Dds Jan 1- Mar 8 over recent years
latitude of Cypress: 35N

		Mugu Naval Ai	Santa Monic	Brownsville TX	Laguna Vista TX	
		KNTD	KSMO	KBRO	D1996	AVG
Latitude		34N	34N	26N	26N	
	2013	198	193	478	439	327
	2014	311	290	364	324	322
	2015	357	345	294	na	332
	2016	259	286	441	430	354
	2017	162	168	661	643	409
	2018	241	255	524	441	365
	2019	129	198	483	453	316
	2020	183	218	530	518	362
avg		230	244	472	464	353

Results: Single sine Dds base 11.67 averaged from 230-244 DD for S. CA coastal locations with a similar latitude as Cyprus, whereas 2 S. Texas coastal locations at 26N (further south in latitude), averaged from 472-464 DD. The more conservative value to use would be the lower averages, 230-240 DD

Estimated Dds for first adult flight and egg-laying:	230

4. Ellis, S.E. 2004. New pest response guidelines: Spodoptera. USDA APHIS PPQ PDMP.

-The species overwinters best as late instar larvae. The larvae develop slowly during the winter and pupate in the spring.
-larval development requires from 12 days during hot summer months to 85 days in winter.
-females live for 2 days in summer to 22 days in winter.

Interpretation: this supports the other works that indicate that while adults may fly in Jan and Feb, it is unlikely that mating and oviposition will happen until larval and pupal development are complete. Assuming that late instar larvae need additional heat units, or that 50% of larval development occurs after Jan 1. That plus pupal development would make:

½ larval devel.	pupal devel.	Total before spring emergence:
118	152	270

Results: Based on this analysis spring activity would not be expected until about 270 Dds after Jan 1., in good accord with the other sources.

5. Etmany. A.A.M. 1989. On some factors influencing the population dynamics of Spodoptera littoralis (Boisd.), Sp. Exigua (Hbn.), Syngrapha circumflexa (L.), Autographa gamma L Heliothis armigera (Hbn.)(Lep., Noctuidae) in Egypt. J. Appl. Ent. 108:182-190.

- For female S. littoralis moths captured in Fayoum, Egypt, no moths caught until March; of one moth caught in March, had one spermatophore. For 123 moths caught in April, 75% were mated a spermatophores.
-This provides evidence that spring activity does not normally occur until March at the earliest (at least in Egypt, which is at ca. 29N Latitude (Fayoum is just South of Cairo)

We conclude that, as CONUS except for S. Texas and Florida, is at more northerly and cooler locations than this study (Egypt), that adult flight and mating before March is rather unlikely for most all regions.

5. Symmons, P.M., and L.J. Rosenberg. 1978. A model simulating mating behavior of *Spodoptera littoralis.* J. Appl. Ecol. 15:423-437.

- Developed a computer model for simulating the mating behavior and population increase of ECW adults on a site in Cyrpus
- One parameter they estimated was the rate of emergence of the overwintering population
- In Cyprus it overwinters as a late instar larva, probably only in localized habitats, and then pupate in the spring
- During the summer and autumn there are clear peaks in moth catches which are probably different generations
- The location of the site is not specified, but Cyprus is a fairly small island

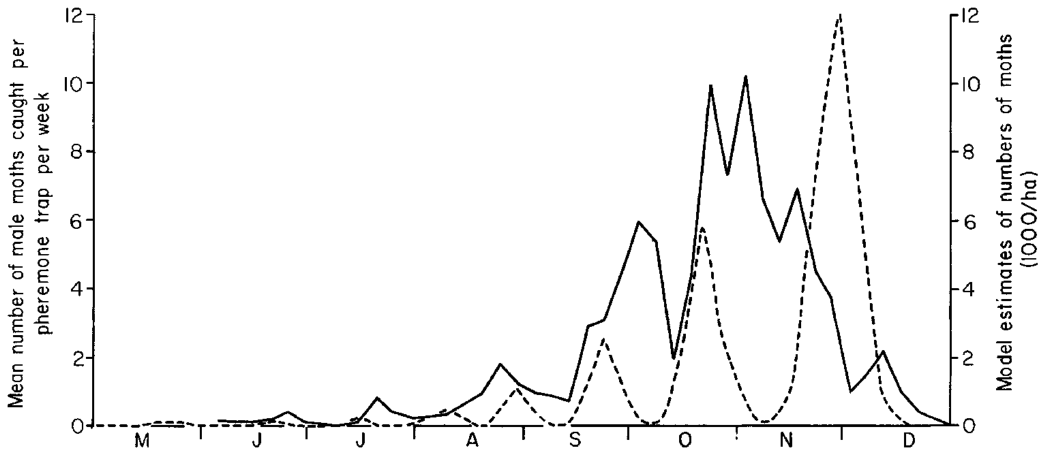


FIG. 2. Mean number of moths caught by pheromone traps in Cyprus in 1972 (solid line) and numbers of moths emerging on a site predicted by the model (dashed line) (D. G. Campion, unpublished data).

The above estimates for earliest first spring flight of 230,235, and 272 DDC, which assumes that while lingering fall adults may be flying even in January, that the primary overwintering is by larvae. The conservative approach is to use a rounded average of ca. 240 DDC as first adult filght and egg-laying. While peak flight is also difficult to determine, adding an additional 33% of the egg to first egg time (462 DD) or 154 DD, provides an initial estimate for this species.

Estimated first flight and oviposition:	**240**
Estimated peak flight and oviposiiton:	**394**

Phenology Model Summary:

Model for uspest.org/dd/model_app (single sine method, start date Jan. 1)

	Deg. C	Deg. F	
Lower devel. threshold	11.67	53	
Upper devel. threshold	35	95	
Event	**DDC**	**DDF**	**Notes**
First moths OW gen.	240	432	
Peak flight OW gen.	394	709	
Peak egghatch 1st gen.	443	798	
First moths 1st gen.	702	1,264	
Peak flight 1st gen.	870	1,565	
Peak egghatch 2nd gen.	919	1,654	
Peak flight 2nd gen.	1,345	2,422	
Peak flight 3rd gen.	1,821	3,278	
Peak flight 4th gen.	2,297	4,135	
Peak flight 5th gen.	2,773	4,991	

Event Ranges for Degree-Day lookup table Maps (same thresholds)

	DDC		DDF	
Event	**(begin)**	**(end)**	**(begin)**	**(end)**
OW gen. Flight activity	240	701	432	1,263
1st gen. Larval activity	337	798	606	1,436
1st gen. Flight activity	702	1,164	1,264	2,095
2nd gen. Flight activity	1,165	1,626	2,097	2,928
3rd gen. Flight activity	1,627	2,089	2,929	3,760
4th gen. Flight activity	2,090	2,551	3,762	4,592
5th gen. Flight activity	2,552	3,014	4,594	5,425

DDRP OW Parameters:		**DDC**	Notes
distro_mean	average DDs to OW larvae first pupation	242	
distro_var	variation in DDs to OW larvae first pupation	5000	
xdist1	minimum DDs (°C) to OW larvae first pupation	88	
xidst2	maximum DDs (°C) to OW larvae first pupation	396	
distro_shape	shape of the distribution	normal	

CLIMATE SUITABILITY MODEL

1. Venette, R.C., E.E. Davis, H. Heisler, and M. Larson. 2003. Mini risk assessment, Egyptian cotton leafworm, *Spodoptera littoralis* (Lepidoptera: Noctuidae). Cooperative Agricultural Pest Survey, Animal and Plant Health Inspection Service, USDA.

- This publication does not appear to be available online anymore - the below map was presented in Ellis (2005)
- Venette's risk assessments are based on matching biomes between the native range and CONUS

The potential U.S. range of most spodoptera may be limited to the west coas through the lower southwestern and southeastern U.S., reaching as far north Maryland (Figures 2.1, 2.2). Migratory species may be capable of periodic spread into northern states and even Canada by late summer or early fall.

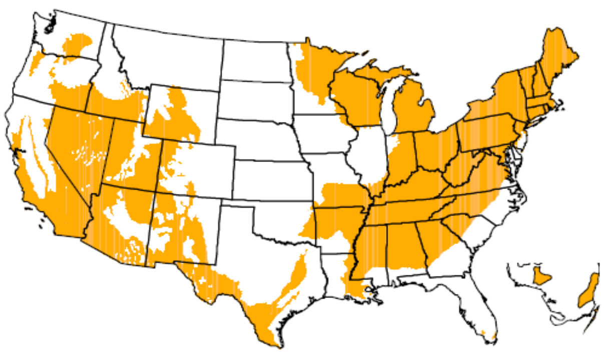


Figure 2.1. Predicted distribution of *Spodoptera littoralis* in the continental U.S. Southern Florida is enlarged for detail. Images courtesy of Venette and Davis (2003).

2. Hussey, N.W. and K.G. Gostick. 1964. Effects of low-temperature storage on the eggs of *Spodoptera littoralis* (Boisd.). Nature 203:323-342.

- Tested cold tolerance of eggs; controls were kept at 75F; treatments kept at constant 30-35F and then returned to 75F for 1 wk to test viability
- Reported that exposure to 30-35F (-1.1-1.6C) for longer than 5 days reduced viability and that after 10 days none were viable
- 18% hatched after 7 days exposure

3. Miller, G.W. 1977. Mortality of *Spodoptera littoralis* (Boisduval) (Lepidoptera: Noctuidae) at non-freezing temperatures. Bull. Entom. Res. 67:143-152.

- Eggs, larvae and pupae were exposed to 5 non-freezing constant temps (13, 10, 7, 4 and 1C)
- Species could not complete development at temps <14C
- Estimates of LD 99 showed that at all temps except 1C resistance to cold was pupae > larvae > eggs
- The egg was found to be the least cold-resistant stage at each temp, except at 1C, but this could be an artifact
- Mortality at 10C and 13C was significantly different to the other temps
- Different strains of *S. littoralis* may respond slightly differently
- Pupae exposed to 13C (±0.5C) for 70 days resulted in emergence of few adults, all of which were deformed and none mated or had fertile eggs
- Based on these data authors analyzed regions that experience these conditions, and found that they do occur in N. Italy and France (no OW there)
- Authors analyzed daily tmin and tmax of Mediterranean localities and concluded the reason the species can overwinter in southern Spain and Greece,

but not in Northern Italy or France, is because these areas do not have periods in excess of 70 days below 13.5C (see table below)
- Used these data to infer the northern range limit for overwintering (got coordinate data) in CLIMEX model fitting

Data from Table III (Months w/ tmax < 13.5C related to OW survival)

Locality	Country	Lat	Long	Mnths w/ tmax <13.5C	Days w/ tmax <13.5C	Overwinters
San Javier	Spain	37.8	-0.83	0	0	Yes
Alicante	Spain	38.45	-0.74	0	0	Yes
Valencia	Spain	39.46	-0.36	1	30	Yes
Barcelona	Spain	41.4	2.15	1	30	Yes
Cap Bear	France	42.51	3.13	3	90	No
Marseille	France	43.29	5.4	3	90	No
Le Luc	France	43.39	6.31	3	90	No
San Remo	Italy	43.81	7.76	3	90	No
Pisa	Italy	43.49	10.66	3	90	No
Roma	Italy	41.87	12.52	3	90	No
Napoli	Italy	40.86	14.23	2	60	Yes
Valentia	Italy	38.67	16.09	0	0	Yes
Licata	Sicily	37.1	13.94	0	0	Yes
Capo Carbonara	Sardinia	39.09	9.52	0	0	Yes
Alghero	Sardinia	40.55	8.32	3	90	Maybe
Ajaccio	Corsica	41.92	8.73	1	30	Maybe

4. Powell, D.F. and K.G. Gostick. 1971. Control of *Spodoptera littoralis* (Boisd.), *Myzus persicae* (Sulz.) and *Tetranychus urticae* (Koch) by cold storage and fumigation. Bull. Entom. Res. 61:235-240.
- Similar experiment as Hussey and Gostick (1964) but included all life stages
- Insects were cold stored at 0-1C and 1-2C
- After cold treatment the eggs, larvae, and pupae were kept at 22C
- Found that eggs more susceptible to cold than experiment of Hussey & Gostick (1964)
- Post-egg stages had similar resistance to cold as eggs; all individuals exposed at 1-2C for 10 days were killed

Table 1. Exposure of *S. littoralis* eggs to 0-1C and 1-2C

	Corrected % kill (average)			
Exposure (d)	0-1C	Rate (wk)	1-2C	Rate
1	21	0.048	8	10
2	29	0.034	34	11.6
4	96	0.010	94	9
7	100	0.010	100	14.2
10	100	0.010	100	14.2

Table 2. Exposure of *S. littoralis* larvae, pupae and adults to 1-2C

	Corrected % kill & SE		
Exposure (d)	Larvae	Pupae	Adults
3	17 (± 6.7)	21 (± 6.0)	67 (± 2.3)
5	37	42	96
10	100	100	100

5. Miller, GW. 1976. Cold storage as a quarantine treatment to prevent the introduction of *Spodoptera littoralis* (Boisd.) into glasshouses in the U.K. Plant Path. 25:193-196.
- Exposed eggs and young larvae to cold treatments of varying temps and duration to find quarantine treatment
- Previous method of 10 days storage at 1-2C kills all stages, but it also kills chrysanthemum cuttings

6. Miller, G.W. 1982. Reduced fecundity of females of *Spodoptera littoralis* emerging from pupae exposed to 16°, a temperature within the range for complete development. Ent. Exp. & Appl. 32:33-37.

- 1-day old female pupae incubated at 16C for 7, 14, and 21 days
- Authors wanted to know if development w/ little mortality would occur at temps slightly higher than 14C (the limit for development)
- 60 female pupae per treatment; 87 pupae for control
- Found that exposure to 16C for up to 21 days did not affect quality of emerging adults, but slightly reduced total % emergence at 21 days
- Also, treatments resulted in a delay in the start of oviposition, and had fewer eggs the longer they were exposed to 16C
- The decrease in total number of eggs was due to a reduction in ovariole length

7. CLIMEX model (this study)

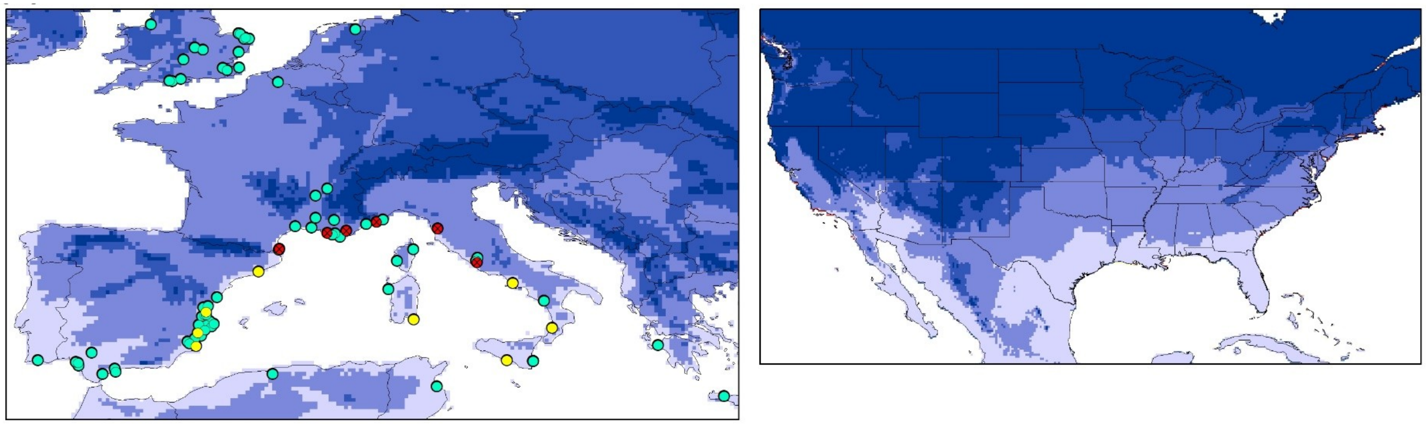
- Used locality data from GBIF (4 November 2020; GBIF Occurrence Download https://doi.org/10.15468/dl.avwfk5) and the literature to help with model fitting (see below)
- Applied a top-up irrigation rate of 2.5 mm day−1 for the winter and summer season
- Final parameters are shown below, with notes about the sources of data for the parameter values, followed by more discussion and results for cold and heat stress parameterization

Parameter	Value	Rationale
DV0	11.7	Lower developmental threshold (this study)
DV1	17	Lowest pupal mortality at 20C; egg viability highest after immatures exposed to this temp (Rivnay and Meisner 1967)
		Larval survival declines below 20C (Bhatt and Bhattacharya 1976)
DV2	30	Egg viability declines when immature stages exposed to higher temps than this (Rivnay and Meisner 1966)
		A temp of 25C is optimal for oviposition, number of eggs laid, and egg viability (Nasr and Nassif 1974)
		Survival to adulthood was highest at 20-25C (Ocete Rubio 1984)
		Larvae developed better at 25C than 30C (Khafagi et al. 2016)
DV3	35	Egg viability nearly 0 when larvae exposed to 34C, but some eggs still viable when pupae exposed to 34C (Rivnay and Meisner 1966)
		Average upper development threshold across stages was 36.5 according to El-Malky (2000)
		However two other studies (Nasir and Nassif 1974, Sidibe and Lauge 1977) documented non-linear development of larvae >= 30C
TTCS	10	Pupal mortality was 100% at 10C (Rivnay and Meisner 1966)
THCS	-0.0007	Resulted in the exclusion (EI=0) of most localities where overwintering is not known to occur (Miller 1977)
TTHS	37	Mortality is high at 37.5C (Rivnay and Meisner 1966)
THHS	0.0002	Results in the inclusion of locality records from hot parts of the species distribution
SMDS	0.05	No info on dry stress limits - origin of value here unknown (probably from a CLIMEX model of another CAPS species)
HDS	-0.00005	
SMWS	2.5	Used wet stress threshold rate reported by Zheng et al. 2012 (J. Ins. Sci 12:13) and Jung et al. 2019 (Entomol. Res. 49:519-528)
HWS	0.002	for Spodoptera exigua and S. litura, respectively
PDD	476	This study

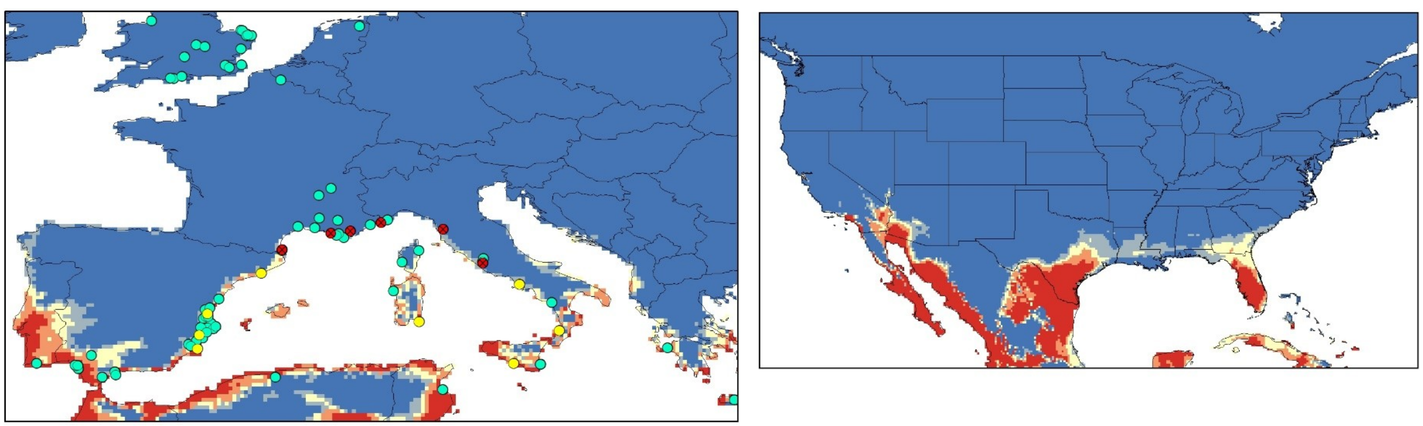
Cold stress parameters

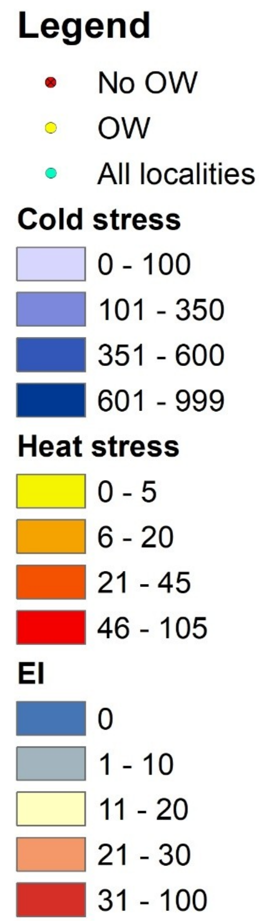
- Used localities from Miller (1977) to define northern range limits - i.e. to calibrate cold stress parameters so that localities where OW occurs were inc. in distribution (EI > 0)
- Conversely, areas where establishment is temporary (e.g. northern Europe) have EI = 0, and cold annual cold stress accumulation exceeds 100 units
- In below figures, red circles are sites where OW does not occur, yellow circles are sites where Miller (1977) documented overwintering; teal circles are all other localities
- Based on results for Europe, only very southern portions of CONUS are suitable for long-term establishment, but temporary populations could establish up to ca. 39 N

CLIMEX Cold Stress (Europe vs. CONUS)



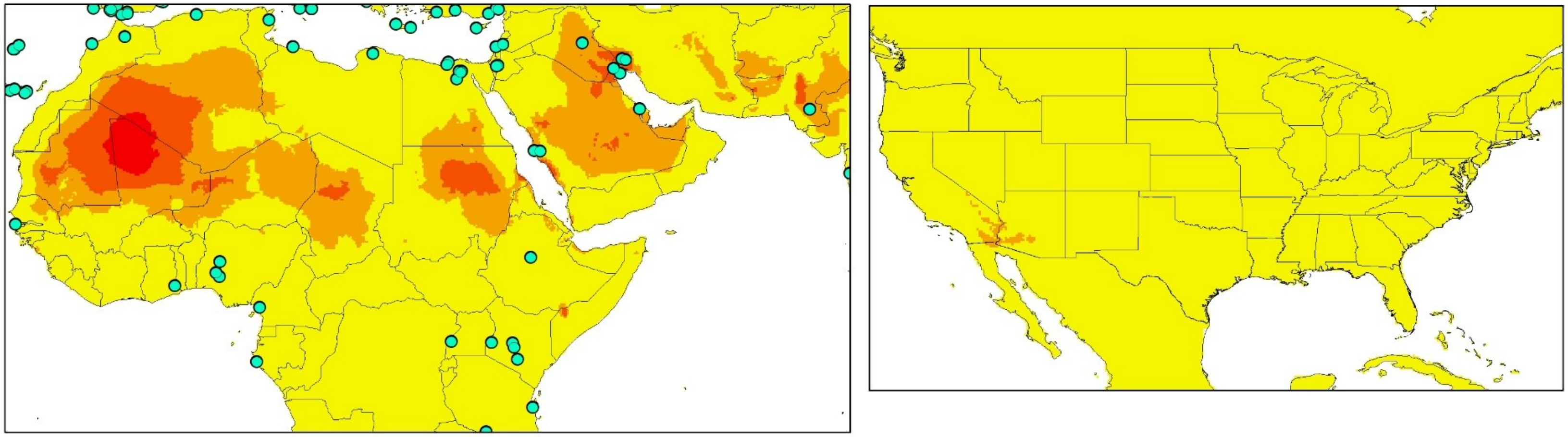
CLIMEX Ecoclimatic Index (Europe vs. CONUS)





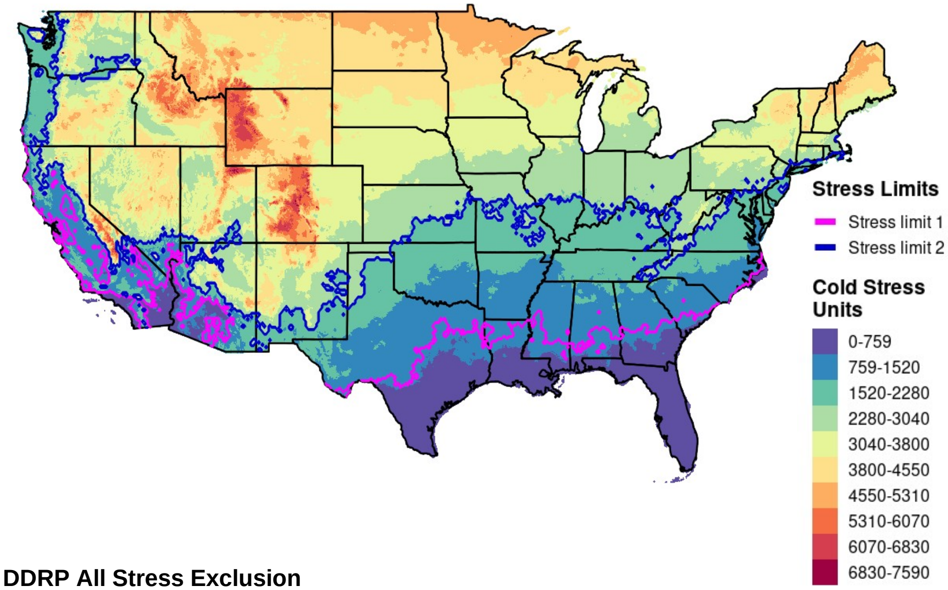
Heat stress parameters
- Little info on the upper heat tolerances of the species, which made calibration of heat stress parameters difficult
- Ensured that localities from hottest parts of the range were included in suitable areas (EI > 0) (e.g. SW Iran, Algeria)
- Figure below shows heat stress (red indicates higher stress) and all locality records (teal circles)
- Results for CONUS suggest that heat stress would not prevent establishment, even in the hottest areas (SW AZ & SE CA)

CLIMEX heat stress (Africa/Asia vs. CONUS)

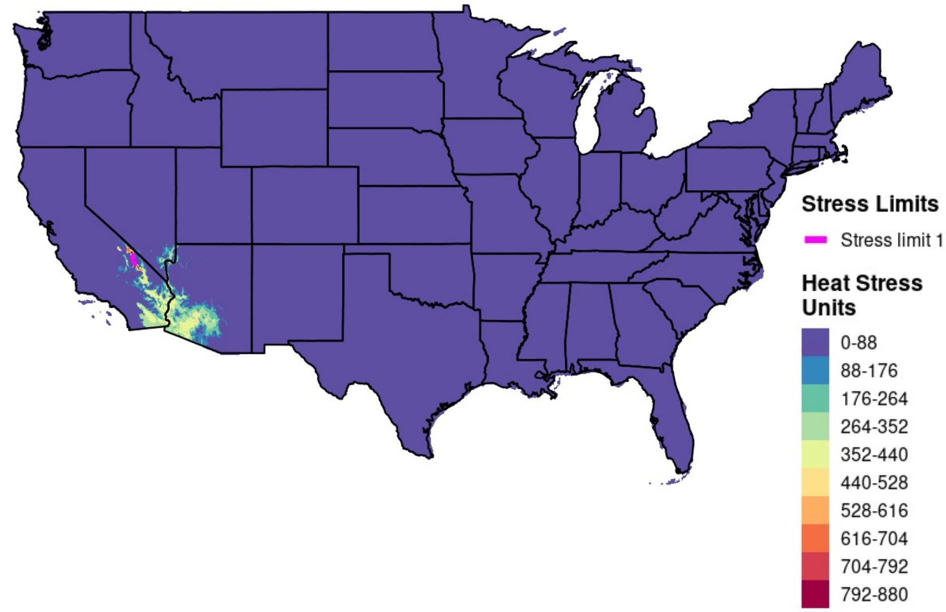


8. DDRP climate suitability model (this study)
- Analysis used daily downscaled 1961-1990 normals to match time scale of CLIMEX
- Applied the same cold and heat stress thresholds as CLIMEX (10C and 37C, respectively)
- For DDRP, calibrated cold stress limits as follows:
    1) areas in CLIMEX where annual cold stress accumulation is < 100 units are suitable for establishment (not excluded)
    2) areas between 100 and 350 units may be suitable for short-term establishment - i.e. migratory events (moderate stress)
    3) areas where stress exceeds 350 units are unsuitable for even short-term establishment (severe stress)
- Calibration resulted in moderate and severe cold stress limits of 950 and 2250 units, respectively
- Heat stress is not predicted to prevent establishment in CONUS according to CLIMEX, so set heat stress limits in DDRP very high (limit 1 = 800, limit 2 = 1100)
- Thus only potentially the hottest part of CONUS (vicinity of Death Valley) may temporarily exclude the species

DDRP Cold Stress	Value	Units
cold stress threshold	10	C
limit 1 (mod. cold stress)	950	DDC
limit 2 (sev. cold stress)	2250	DDC



DDRP Heat Stress	Value	Units
heat stress threshold	37	C
limit 1 (mod. heat stress)	800	DDC
limit 2 (sev. heat stress)	1100	DDC



DDRP All Stress Exclusion