Determination of a Relationship Between Soil Moisture and Screwworm Fly (Diptera: Calliphoridae) Activity

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ABSTRACT To model screwworm fly (Diptera: Calliphoridae) population dynamics, it is necessary to quantify the relationship between soil moisture and screwworm fly numbers. Climatic data from one case study of *Chrysomya bezziana* (Villeneuve) and five case studies of *Cochliomyia hominivorax* (Coquerel) from tropical and subtropical areas were statistically analysed to determine the effect of soil moisture (corrected for temperature) on screwworm fly incidence. Significant relationships occurred in three of the six cases; in two cases the relationship was humped, and in the other linear. Both prolonged dry conditions and soil saturation cause reduced screwworm fly emergence whereas intermediate soil moisture is adequate for pupal development and adult emergence. The relationship previously used in the CLIMEX package was found to be biased because it did not adequately penalise saturated soil conditions. An improved function was estimated to correct for this bias.

Introduction

The screwworm fly (SWF) is a serious parasite of warm blooded animals, particularly domestic livestock species. It inflicts considerable physical damage resulting in loss of condition, infertility or death (Spradbery 1994). Although not yet present in Australia, the SWF has been shown to be climatically suitable (Sutherst *et al.* 1989) and could cause extensive damage, particularly to the beef industry. The annual value of societal losses (measured by the reduction in both producer and consumer surplus) has been estimated at A$775 million (Anaman *et al.* 1994).

Both species of SWF, the Old World *Chrysomya bezziana* (Villeneuve) and the New World *Cochliomyia hominivorax* (Coquerel), are endemic in tropical and subtropical areas of the world (Spradbery 1994), expanding their ranges into temperate areas when climatic conditions are favourable. Being tropical species, their ranges are largely limited by temperature, although rainfall has also been proposed as an important contributing factor (Rahn and Barger 1973).

A number of studies have demonstrated that drought or extended dry conditions are detrimental to New World SWF activity (Rahn and Barger 1973; Spencer *et al.* 1981; Krafsur 1985; Mackley 1986). Periods with moderate rainfall and favourable temperatures lead to an increase in the incidence of New World SWF (Rahn and Barger 1973), whilst anecdotal information indicates depressed Old World SWF numbers during extended wet periods, such as the monsoonal season in Papua New Guinea (M. Nunn, pers. comm.). Previous studies attempting to quantify the effect of rainfall have been inconclusive, indicating only very weak lagged relationships (Rahn and Barger 1973; Spencer *et al.* 1981; Krafsur 1985; Mackley 1986).

Mature SWF larvae drop from the host animal and enter a prepupal phase during which they burrow into suitable soil and form a hard outer shell (puparium), a process lasting approximately 1d (Spradbery 1992). The puparium protects the pupae against a wider range of moisture and temperature conditions than what the prepupae can tolerate. The vulnerable prepupae are prone to desiccation where hot dry conditions prevail (Baumhover 1963; Spradbery 1992) and to drowning if the top soil layers are saturated (Thomas 1986; Spradbery 1992). Consequently, low SWF survival occurs at both ends of the soil moisture spectrum. This agrees with the Moisture Index relationship from CLIMEX, a computer model which predicts the potential distribution and abundance of animals or plants on a world-wide basis (Sutherst and Maywald 1985). A SWF population dynamics model has been developed that uses CLIMEX moisture and temperature indices to predict changes in the adult female population (Mayer *et al.* 1992; Atzeni *et al.* 1994).

High New World SWF numbers were obtained by Spencer *et al.* (1981) during periods when little rain fell, but while the soil moisture was still adequate for pupal development. Rather than rainfall, it appears that it is the resultant soil moisture conditions which directly influence survival. Variations in soil water holding capacity, initial moisture levels and evapotranspiration losses may well have confounded the influence of rainfall in previous studies.

By estimating soil moisture conditions in published SWF studies and adjusting for temperature, this paper investigates the relationship between soil moisture and SWF survival, as measured by subsequent SWF activity.

Materials and methods

From the literature, five data sets on *Cochliomyia hominivorax* contained adequate information for analysis (Table 1). Spencer *et al.* (1981) and Mackley (1986) published SWF and necessary climatic data, and Dr E. Krafsur kindly sent us data from Krafsur (1985). The sixth data set in Table 1 was an unpublished study on *Chrysomya bezziana* conducted by one of us (J.P.S.).

For each site a soil water-balance model, GRASP (McKeon *et al.* 1990), was used to estimate soil moisture levels over time for the top 10 cm of soil. Larvae generally burrow around 2.5-3.75 cm for New World SWF (Rahn and Barger 1973) and 7.4 cm for Old World SWF (Spradbery 1992), so the average moisture levels of the top 10 cm of soil were extracted to use as the independent (predictor) variable. The Moisture Index for CLIMEX, based on the top 1 m of soil, needed to be calibrated to this biologically more meaningful depth, so comparisons could be made.

The following information was collated for input: soil type; daily rainfall; and monthly averages for: maximum temperature; minimum temperature; solar radiation; evaporation; vapour pressure deficit.

Various data sources were used to compile a complete data set for each location, including (in order of preference) information published in each study, historical meteorological data for the nearest town from the World Weather Disc (Anon. 1990), and average data from the CLIMEX package (nearest town). To estimate the necessary daily rainfall patterns from listed monthly or fortnightly totals, the study areas were "matched" to a location with daily records using CLIMEX's "match climates" routine, and the proportionate daily patterns applied to the listed totals. Whilst only approximate, this method should be accurate enough, as daily soil moisture values were then averaged over fortnights, months or 3-months as required by the level of SWF data detail in the six case studies. Similarly the temperature values were averaged over the same time periods.

Actual SWF incidence figures were regressed against linear and quadratic terms of soil moisture and temperature. Due to heterogeneity of variances, the SWF counts from the vicinity of Port Moresby, Papua New Guinea and Southern Texas, USA were log transformed prior to analysis. Lagged regressions were also carried out for up to 3 months in fortnightly intervals, wherever the data permitted.

In general, the quadratic temperature term did not add to the degree of fit, so this term was omitted from all regressions for consistency. Where the quadratic soil moisture term was non-significant (egg mass data from Coastal Mexico, and low elevation data from Central Mexican highlands), it also was removed. Presentation of the relationship between incidence and soil moisture was adjusted for temperature to the predicted value at the average temperature. Within the data set from Southern Texas, the strains of the sterile flies released changed over the 15-year period of data collection. Analyses showed no significant differences between strains, so these data were pooled. The Mexican highlands data (low and high elevations) experienced different climatic conditions, so were analysed separately.

Results and discussion

The degrees of fit for various lag periods are listed in Table 2. In favourable conditions, the SWF emerge as adults after about 1 week as pupae, become mature adults after a further week, and then survive as adults for up to 3 weeks (Spradbery 1994). Hence, maximum observed changes in activity are expected to occur 2-4 weeks after critical soil moisture events. The best fits (as determined by R^2) were generally in this range, so for biological reasons and data presentation, we chose the lag periods as bolded in Table 2. In two cases the regressions were significant (capture data from Coastal Mexico and high elevation data from Central Mexican highlands) and in one case (egg mass data from Coastal Mexico) almost significant (P = .054). Lagged data from all six sets, along with these regression lines, are separately plotted in Figure 1.

Table 1. Summary of available SWF incidence data.

Source	Spencer *et al.* (1981)		Krafsur (1985)	Mackley (1986)		CSIRO (Unpubl.)
Location	Coastal Mexico		Southern Texas	Central Highlands of Mexico		Port Moresby PNG
				Low elevation	High elevation	
Measure of Activity	captures/trap	total egg mass	ln (strikes + 1)	captures/trap	captures/trap	ln (strikes + 1)
No. Observations	27	20	60	11	11	40
Sampling Frequency	Fortnightly	Fortnightly	3-Monthly	Monthly	Monthly	Monthly
Data Collection Period	March 1978-March 1979	June 1978-March 1979	1962-1976	1980	1980	Sep. 1975-Dec. 1978
Ranges of:						
— SWF Activity	0.5- 3.5	4 -35	0 - 8.9	0 - 0.170	0 - 0.150	1.8- 3.7
— Average Soil Moisture (%)	3.9-89.6	2.7-88.7	29.9-79.8	15.6-68.6	22.6-62.9	22.4-69.8
— Average Temperature (°C)	25.5-29.4	25.5-29.4	12.8-30.3	23.5-28.0	14.6-18.3	19.2-20.5

Table 2. Percentage variance accounted for (R^2) by multiple regression models for various lag periods.

Location	Coastal Mexico		Southern Texas	Central Highlands of Mexico		Port Moresby PNG
	Capture data	Egg mass data		Low elevation	High elevation	
Model Terms#	sm, t, sm²	sm, t	sm, t, sm²	sm, t	sm, t, sm²	sm, t, sm²
Lag (months)						
0	51.9**	25.4	**6.1**	.1	64.3+	**3.3**
0.5	**56.2****	**29.0+**	—	—	—	—
1	48.8**	18.8	—	**17.6**	**71.7***	1.4
1.5	42.7**	10.1	—	—	—	—
2	20.6	9.2	—	.7	57.1	3.7
2.5	22.1	11.4	—	—	—	—
3	22.8	5.8	12.2+	20.1	52.7	2.0
3.5	21.1	6.1	—	—	—	—

sm = soil moisture; t = temperature
+ $P < 0.10$; * $P < 0.05$; ** $P < 0.01$

Dashes indicate no analysis possible due to data frequency.
Bolded values indicate best-fit model.

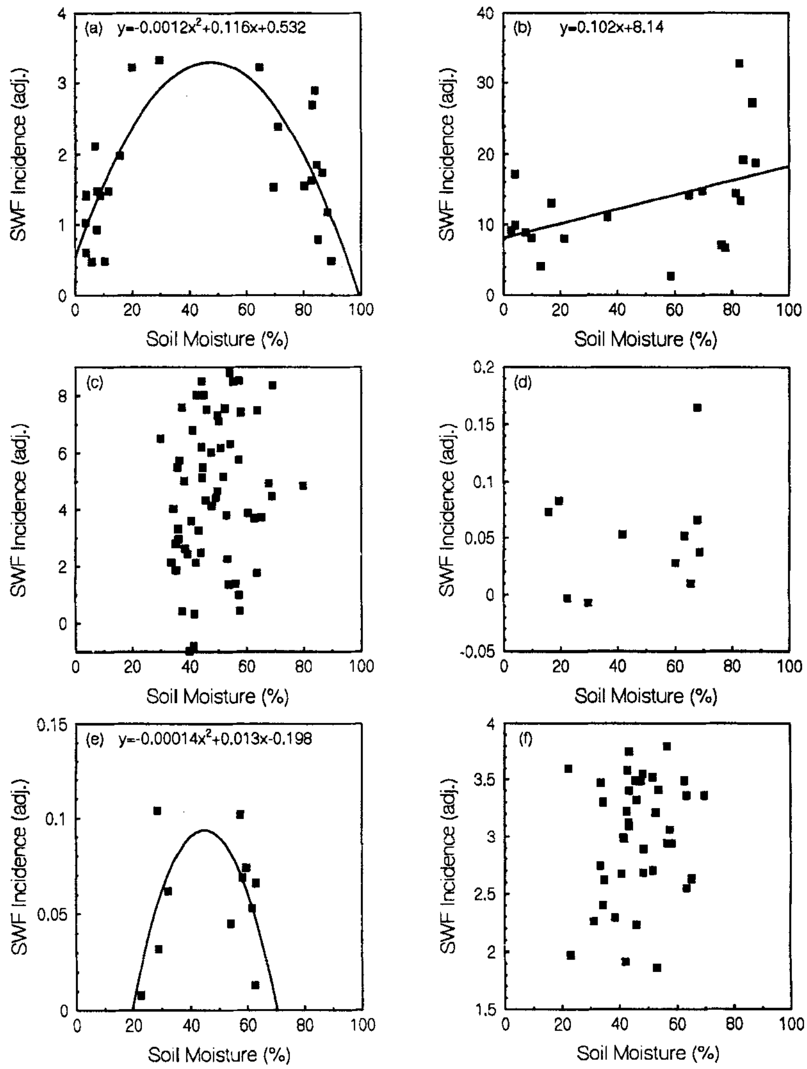

Fig. 1. SWF incidence data adjusted for temperature, and fitted regressions (see Table 2). (a) Coastal Mexico (.5 mth lag)—capture data; (b) Coastal Mexico (.5 mth lag)—egg mass data; (c) Southern Texas (no lag); (d) Central Mexico (1 mth lag)—low elevation; (e) Central Mexico (1 mth lag)—high elevation; and (f) Port Moresby (no lag).

Although the resultant soil moisture effect varied over the three significant case studies, all displayed an initial increase in SWF numbers (with increased soil moisture) which is in general agreement with the moisture relationship in CLIMEX. The two quadratic relationships show predicted maximum incidence of SWF occurring at 46% and 48% soil moisture respectively, but the relationship in Figure 1(b) indicates maximum incidence at a higher soil moisture level.

In CLIMEX, four parameters describe the step-wise linear relationship between population size and soil moisture, which is averaged over the top 1 m of the soil profile. The population survival is zero when the soil moisture is below a critical threshold (SM0 = 9%) and when it is above an excessive moisture level (SM3 = 400%). The population's response is "ideal" between two intermediate moisture levels (SM1 = 80% and SM2 = 200%) with linear interpolation between the four levels (n.b. field capacity is considered to be 100% soil moisture, hence any moisture levels over 100 indicate saturated or flooded soils). These soil moisture parameters were fitted in CLIMEX to equate estimated world range of SWF with actual (in those countries where it is endemic). Whilst appropriate at the lower end of soil moisture ("too dry"), the "artificial" upper limits are never observed in practice, so these parameters never penalise predicted SWF populations in the "too wet" range.

To equate these CLIMEX parameters (measured over the top 1 m) to our area of interest (the top 10 cm, where the SWF pupate), a calibration relationship between the top 10 cm and the full 1 m profile was developed using the GRASP soil moisture predictions for these studies (n.b. the "full profile" modelled by GRASP is averaged over the top 85 cm, which we assume to be similar to values averaged over the top 1 m). There were no significant differences in this relationship between locations ($P>0.05$), so data for all sites were pooled, giving 257 monthly observations. These are plotted in Figure 2, along with the bent- stick relationship fitted statistically via general non-linear regression (R^2 = 0.50; $P<0.01$). The considerable scatter reflects the variability of moisture in the top layer, compared with the more stable levels in the whole profile. Similar R^2 values were obtained when log and power models were fitted, but these models did not extrapolate reasonably for high levels of soil moisture.

Using this bent-stick relationship which provides biologically realistic values across the whole range of soil moisture levels, the first two parameters from CLIMEX's Moisture Index, SM0 and SM1, correspond to 10 cm values of 26% and 63%, respectively. There is a change of slope at 37% soil moisture corresponding to the point of intersection of the two fitted straight lines from Figure 2. Using these recalibrated values, CLIMEX predictions of SWF activity are given as the solid line in Figure 3 along with standardised actual curves (dashed), plotted within their observed data range, from Figure 1. To standardise the incidence measures which vary considerably over the data sets, the top 10% of data points were taken as "highly suitable conditions". For each location, all data and the regressions were scaled by these to produce a relative (%) measure of activity.

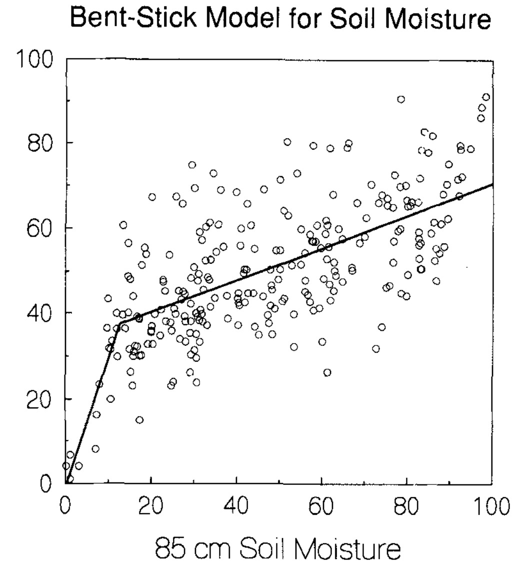

Fig. 2. Calibration of soil moisture in top 10 cm against top 85 cm, pooled for all experimental sites.

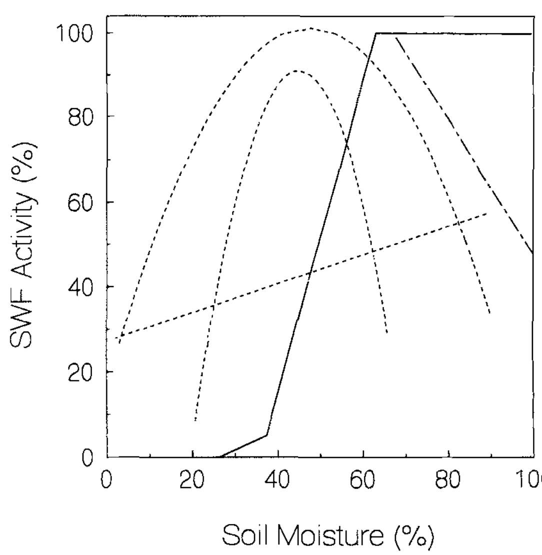

Fig. 3. Fitted standardised SWF activity against soil moisture for range of data observed at each location (----) (Coastal Mexico—capture and egg mass data, and Central Mexico—high elevation), the relationship from CLIMEX model (———), and the revised CLIMEX line for "saturated" conditions. (—·—·—)

It is obvious from actual data that "saturated" conditions show declining SWF activity, not reflected by the original CLIMEX relationship. After pooling and weighting (by number of observations) the standardised data, an overall quadratic fit indicated the relative SWF activities are reduced to zero at 130% soil moisture, which we have assigned as our new value for SM3. A biological interpretation of all data sets, considering also the quadratic fit to all pooled data, determined 67% (corresponding to SM2) to be an appropriate soil moisture level for maximum SWF activity. Converting back using the relationship shown in Figure 2, the revised CLIMEX values for SM2 and SM3 would be 90 and 250 respectively.

Conclusion

The original CLIMEX model, whilst accurately describing limits on the SWF range due to dry conditions, did not effectively model saturated conditions. Our analyses of lagged SWF activity (corrected for temperature) against soil moisture conditions qualitatively confirmed the rise in SWF incidence once conditions are beyond being too dry, and also demonstrated the decline in SWF activity when soil moisture levels were high. Hence we re-estimated the CLIMEX parameters, obtaining more realistic values for our own SWF modelling purposes.

References

Anaman, K. A., Atzeni, M. G., Mayer, D. G. and Walthall, J. C. (1994). Economic assessment of preparedness strategies to prevent the introduction or the permanent establishment of screwworm fly in Australia. Prev. Vet. Med. 20: 99-111.

Anon. (1990). World Weather Disc User Manual. Weather Disc Assoc. Inc.: Seattle.

Atzeni, M. G., Mayer, D. G., Spradbery, J. P., Anaman, K. A. and Butler, D. G. (1994). Comparison of the predicted impact of a screwworm fly outbreak in Australia using a growth index model and a life cycle model. Med. Vet. Ent. 8.

Baumhover, A. H. (1963). Susceptibility of screw-worm larvae and prepupae to desiccation. J. econ. Ent. 56: 473-475.

Krafsur, E. S. (1985). Screwworm, *Cochliomyia hominivorax*, eradication in Texas: effects of climate and strains of sterile flies. Entomol. exp. appl. 37: 297-305.

Mackley, J. W. (1986). Incidence of the Screwworm, *Cochliomyia hominivorax*, and the secondary screwworm *C. macellaria* (Diptera: Calliphoridae), in the Central Highlands of Chapas, Mexico. J. Med. Ent. 23: 76-82.

Mayer, D. G., Atzeni, M. G. and Butler, D. G. (1992). Adaptation of CLIMEX for spatial screwworm fly population dynamics. Math. Comput. Simulation 33: 439-444.

McKeon, G. M., Day, K. A., Howden, S. M., Mott, J. J., Orr, D. M., Scattini, W. J. and Weston, E. J. (1990). Northern Australian savannas: management for pastoral production. J. Biogeogr. 17: 355-372.

Rahn, J. J. and Barger, G. L. (1973). Weather conditions and screwworm activity. Agric. Meteorol. 11: 197-211.

Spencer, J. P., Snow, J. W., Coppedge, J. R. and Whitten, C. J. (1981). Seasonal occurrence of the primary and secondary screwworm (Diptera: Calliphoridae) in the pacific coastal area of Chiapas, Mexico during 1978-1979. J.Med.Ent. 18: 240-243.

Spradbery, J. P. (1992). Studies on the prepupal and puparial stages of the Old World screw-worm fly, *Chrysomya bezziana* Villeneuve (Diptera: Calliphoridae). CSIRO, Division of Entomology Technical Paper No. 29.

Spradbery, J. P. (1994). Screwworm fly: A tale of two species. Agric. Zool. Rev. 6.

Sutherst, R. W. and Maywald, G. F. (1985). A computerised system for matching climates in ecology. Agric. Ecosyst. Environ. 13: 281-299.

Sutherst, R. W., Spradbery, J. P. and Maywald, G. F. (1989). The potential geographical distribution of the Old World screw-worm fly, *Chrysomya bezziana*. Med. Vet. Ent. 3: 273-280.

Thomas, D. B. (1986). Age dependent susceptibility to drowning in pharate screwworms, *Cochliomyia hominivorax* (Coquerel). Southwest. Ent. 11: 161-164.

(Accepted 4 July 1994)