Predicting climate compatibility of biological control agents in their region of introduction

M.J. Byrne, 1 J. Coetzee, 1 A.J. McConnachie, 1 W. Parasram 1 and M.P. Hill 2

Summary
Despite the presence of their host plants, many biological control agents of weeds fail to establish, apparently because of climatic incompatibility in the country of introduction. We examined the thermal physiology, in particular the lower development threshold (t), rate of development K, and CTMin and lower LT50, of four biological control agents. These parameters were used in degree–day, CLIMEX™, and minimum temperature models to compare the predicted distribution of the insects with their actual establishment. None of the models precisely accounted for all establishments or failures. However, incorporation of CTMin and LT50 thermal limits, in conjunction with the “Match Climates” module in CLIMEX may improve pre-release selection of agents or populations of agents, and thereby improve the probability of successful establishment.

Keywords: prediction, climate compatibility, biological control agents, introduction.

Introduction
Forty-four per-cent of weed biological control agents fail to establish because of climatic incompatibility of the agent, usually an insect, to its new area of introduction (McEvoy & Coombs 2001). This represents an enormous waste of time and money invested in foreign exploration and quarantine testing, which could be saved if some indication was available in advance of release of the physiological capabilities of the biocontrol agents. Here we examine methods that could contribute to improved forecasting of an agent’s likelihood of establishment.

Empirical field-testing of thermal physiology in the country of origin has been instructive (Papadopoulos et al. 1996), and successfully incorporated into models of both the potential and realized distribution of the Mediterranean fruit fly (Vera et al. 2002). Modelling the potential distribution of an organism in its country of introduction is also relatively successful, but is generally achieved by inferring the new geographical range based on locality records from the native range, or known range of establishment (Kriticos & Randall 2001). This works particularly well for weed species whose native or new range of establishment is well known (e.g. Robertson et al. 2001). One of the most widely used tools for this task is CLIMEX (Sutherst & Maywald 1985) which requires the user to create a template of physiological parameters for the species, which the program then uses in conjunction with meteorological data to infer the potential range of the species being introduced. The parameters in CLIMEX models are inferred from the distribution records. Confidence in CLIMEX models is gained through comparison of projected potential distribution with locality records that were not used in the model-fitting process. Locality records for the species from a fairly broad range of climates are required to test the model before it can be used with any assurance (Sutherst 2003). Nevertheless, meaningful models have been generated for many organisms (Sutherst et al. 1999).

Insect development (degree–day) models, using temperature and time to predict the number of generations that an insect can complete at a given locality, use only empirical data and are sometimes successful at predicting whether an insect can establish at a particular locality (e.g.
Africa. CTMin and CTMax, and LT50 were determined to assess the usefulness of these parameters in different insects species (marked * in Table 1) were insect’s habitat and its thermal physiology. Data on the thermal limits of 16 insect species were measured. The first is the critical temperature (CTMax or CTMin), being the temperature extremes at which the insect immediately loses locomotory function. Beyond these temperatures the insect cannot respond to any further change in temperature in the same direction, and therefore becomes vulnerable to predation, catastrophe or further temperature excess. Lethal temperatures (upper and lower LT50) define extreme temperature limits from which organisms cannot recover after a prolonged exposure (in this case two hours). These thermal limits can be determined in a few days of experimentation, by exposing small numbers of the insects to extreme temperatures in a controlled water bath. The data are analysed by probit analysis, and an LT50 is produced for the upper and lower limits of the lethal temperature, while the CTMin and CTMax are calculated from the mean values across the temperature range at which a response was recorded.

The aim of this paper is to compare methods that can be used to predict the probability of establishment of classical biological control agents prior to their release.

Methods

Data on the thermal limits of 16 insect species were collected from the literature and unpublished data, and were compared to detect any correlation between the insect’s habitat and its thermal physiology.

Different aspects of the thermal biology of four different insects species (marked * in Table 1) were used to assess the usefulness of these parameters in predicting the establishment of these insects in South Africa. CTMin and CTMax, and LT50 were determined using the methods of Mitchell et al. (1997). To generate an LT50 for the bud-galling wasp Trichilogaster acacielongifoliae, uneclosed pupae and adults that had not emerged from galls were exposed to the experimental temperature for two hours, then dissected out of the galls and examined for survival. Adults were scored as alive if they were able to self-right 24 hours after removal from the experimental temperature. Treated pupae were placed in separate wells of a 96-well enzyme-linked immunosorbent assay (ELISA) plate and kept at 25°C, 95% relative humidity (RH) until they emerged. A control sample received the same treatment but was never exposed to temperatures above 25°C. For all other species adult insects were used.

Degree–day models were calculated for three insects using a variety of fixed rearing temperatures, depending on the species. The values of K and t for each species were derived from the reduced major axis regression method of Ikemoto & Takai (2000). These were then used to calculate accumulated degree–days according to the methods of Campbell et al. (1974) at each location in the CLIMEX meteorological database, which has monthly mean maximum and mean minimum temperatures for 128 South African localities. The number of generations per annum each species could theoretically complete was calculated and projected onto contour maps of South Africa created with ARCVIEW. These data were compared with the number of generations in the native range of the insect. Because the mirid Eccritotarsus catarinensis, a natural enemy of water hyacinth, failed to overwinter at a high altitude site in Johannesburg, the number of generations able to survive the highveld winter months from April to August was also calculated and presented as above.

Results and discussion

Insects generally have thermal limits that reflect the environments in which they have evolved (Table 1). However, this relationship does not yield any sensible correlation between estimates of environmental temperature and lower thermal limits (CTMin and LT50), primarily because we know so little about the microclimate in which the insects live (McConnachie 2004), and not least because of the multitude of methods and exposure times used by different workers to measure these limits.

Explicable correlations of thermal limits with environmental temperature

Trichilogaster acacielongifoliae is a bud-galling wasp of Acacia longifolia. Adult wasps were found to have an upper LT50 of 41.1°C ($Y = 109.067 - 2.651x$, $r^2 = 0.855$), while the pupae to have an upper LT50 of 41.3°C ($Y = 31.782 - 0.767x$, $r^2 = 0.396$) (Fig. 1), which is well above the January mean maximum of 26°C for Sydney, in its Australian native range, and satisfactorily explains why the wasp has been able to thrive on the South African highveld, and the KwaZulu Natal lowveld, despite the predictions of Dennill (1990), who used Walter and Leith’s (1960) climate diagrams to...
### Table 1. Thermal limits of insects, in relation to their native range.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Region of origin</th>
<th>Stage tested</th>
<th>Upper LT50</th>
<th>CTMax</th>
<th>Lower LT50</th>
<th>CTMin</th>
<th>Environmental low temp</th>
<th>Exposure time</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acyrthosiphon svalbardicum</td>
<td>Homoptera</td>
<td>High Arctic, Europe</td>
<td>Eggs</td>
<td>–33 SCP&lt;sup&gt;c&lt;/sup&gt;</td>
<td>–16.7</td>
<td>1 min</td>
<td>Strathdee et al. (1995)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhopalosiphum padi</td>
<td>Homoptera</td>
<td>N. temperate, Europe</td>
<td>Eggs</td>
<td>–36 SCP</td>
<td>1.7</td>
<td>1 min</td>
<td>Strathdee et al. (1995)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dendroides canadensis</td>
<td>Coleoptera</td>
<td>N. temperate, Canada</td>
<td>Larvae</td>
<td>–20 SCP</td>
<td>–32.8</td>
<td>?</td>
<td>Olsen et al. (1998)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pringleophaga marioni</td>
<td>Lepidoptera</td>
<td>Subantarctic islands</td>
<td>Caterpillars</td>
<td>38.7</td>
<td>–9</td>
<td>–0.6</td>
<td>0</td>
<td>1 hour</td>
<td>Klok &amp; Chown (1997)</td>
<td></td>
</tr>
<tr>
<td>Celatoblla quinquemaculata</td>
<td>Dictyoptera, Stalidiae</td>
<td>Alpine &gt;1300m New Zealand</td>
<td>Nymphs</td>
<td>–9.5</td>
<td>–7</td>
<td>5 mins</td>
<td>Block et al. (1998)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hodotermes mossambicus</td>
<td>Isoptera</td>
<td>Subtropical South Africa</td>
<td>Major workers</td>
<td>42.9</td>
<td>47.3</td>
<td>2.84</td>
<td>7.1</td>
<td>–1.8</td>
<td>2 hours</td>
<td>Mitchell et al. (1993)</td>
</tr>
<tr>
<td>Spodoptera exempta</td>
<td>Lepidoptera</td>
<td>Subtropical South Africa</td>
<td>Caterpillars</td>
<td>50</td>
<td>10</td>
<td>2.8</td>
<td>1 hour</td>
<td>Klok &amp; Chown (1997)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Imbrasia belina</td>
<td>Lepidoptera</td>
<td>Subtropical South Africa</td>
<td>Caterpillars</td>
<td>48</td>
<td>10</td>
<td>2.8</td>
<td>1 hour</td>
<td>Klok &amp; Chown (1997)</td>
<td></td>
<td></td>
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<tr>
<td>Cirina forda</td>
<td>Lepidoptera</td>
<td>Subtropical South Africa</td>
<td>Caterpillars</td>
<td>47</td>
<td>11</td>
<td>2.8</td>
<td>1 hour</td>
<td>Klok &amp; Chown (1997)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Desert tenebriions</td>
<td>Coleoptera</td>
<td>Subtropical Namibia</td>
<td>Adults</td>
<td>50</td>
<td>10</td>
<td>?</td>
<td>2 hours</td>
<td>Roberts et al. (1991)</td>
<td></td>
<td></td>
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<tr>
<td>Philonthus sananus</td>
<td>Coleoptera</td>
<td>Subtropical South Africa</td>
<td>Adults</td>
<td>42.82</td>
<td></td>
<td></td>
<td></td>
<td>2 hours</td>
<td>Byrne (1998)</td>
<td></td>
</tr>
<tr>
<td>Philonthus labdarius</td>
<td>Coleoptera</td>
<td>Subtropical South Africa</td>
<td>Adults</td>
<td>40.48</td>
<td></td>
<td></td>
<td></td>
<td>2 hours</td>
<td>Byrne (1998)</td>
<td></td>
</tr>
<tr>
<td>*Trichilogaster acaciaelongifolii</td>
<td>Hymenoptera</td>
<td>Mediterranean Australia</td>
<td>Adults, Pupae</td>
<td>41.1</td>
<td>41.3</td>
<td></td>
<td></td>
<td>2 hours</td>
<td>Byrne (unpublished data)</td>
<td></td>
</tr>
<tr>
<td>*Gratiana spadicea</td>
<td>Coleoptera</td>
<td>Subtropical Argentina</td>
<td>Adults</td>
<td>–7.1</td>
<td>4.9</td>
<td>5.0</td>
<td></td>
<td>2 hours</td>
<td>Byrne et al. (2002)</td>
<td></td>
</tr>
<tr>
<td>*Stenopelms rufinassus</td>
<td>Coleoptera</td>
<td>Tropical Florida</td>
<td>Adults</td>
<td>–12.1</td>
<td>1.3</td>
<td>1.6</td>
<td></td>
<td>2 hours</td>
<td>McConnachie (unpublished data)</td>
<td></td>
</tr>
<tr>
<td>*Eccritotarsus catarinensis</td>
<td>Hemiptera</td>
<td>Tropical Brazil</td>
<td>Adults</td>
<td>37</td>
<td>49.6</td>
<td>–3.5</td>
<td>1.2</td>
<td>13.9</td>
<td>2 hours</td>
<td>Coetzee (unpublished data)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Notes: CTMax and CTMin, upper and lower are defined in the text. <sup>b</sup>Insects marked with an asterisk are mentioned in the text. <sup>c</sup>Environmental low temp. is the lowest mean minimum temperature in the region of origin. 

<sup>c</sup>SCP = super cooling point.
suggest that the wasp would fail to establish because of high summer temperatures in these areas.

The lower CTMin of *Gratiana spadicea* (4.9°C; Table 1) is close to the lower average winter temperatures recorded at Buenos Aires, its most southerly collection site and the lower LT50 of –7.1°C is close to the lower extreme temperatures at South African release sites, where the beetle has had a patchy establishment and overwinters in very low numbers (Byrne et al. 2002).

*Eccritotarsus catarinensis* has a CTMin of 1.2°C. Those locations in South Africa that experience mean minimum temperatures below this level include Johannes- burg, where there has been an establishment failure, and are to the south of successful establishment sites (Fig. 2). However, this parameter fails to explain the lack of establishment at some Western Cape sites.

### Inexplicable correlations of thermal limits with environmental temperature

*Stenopelmus rufinasus* is thought to originate from the Florida region of the United States of America and has successfully established throughout South Africa wherever *Azolla filiculoides*, the target weed, occurs (McConnachie et al. 2003). The CTMin of 1.3°C and lower LT50 of –12.1°C bear little relationship to the climate of the country of origin (Table 1). However, these extreme values did give us the confidence to predict that the weevil would survive the cold winters of the high altitude interior of South Africa. *Stenopelmus rufinasus* has also established in Britain (Richard Shaw, CABI, pers. comm.), which is not that surprising given its lower LT50.

### Degree–day model successes

The degree–day model predicted a minimum of 4, to a maximum of 20 generations of *S. rufinasus* per year at various localities around South Africa (Fig. 3). This has been confirmed by the widespread establishment of the beetle, and field sampling suggests that these figures may be slightly low (A.J. McConnachie, unpublished data).

### Degree–day model failures

The moth *Parachaetes insulata* released against *Chromoalaena odorata* in South Africa is predicted to complete four to six generations per year at subtropical release sites in Kwazulu Natal (Fig. 4). The moth has so far failed to establish a viable permanent population, but this might be because of severe larval predation (Kluge 1994) or low humidity levels (W. Parasram, unpublished data).

*Eccritotarsus catarinensis* was predicted to complete from 3 to 14 generations per year at different

![Figure 1](image.png)

**Figure 1.** Upper LT50 of pupal (A) and adult (B) *Trichilogaster acaciaelongifoliiae*, in relation to mean maximum January temperatures at sites where the wasp has been introduced and was predicted to establish or fail (C). Numbers at the tops of histogram bars refer to the sample size tested at that temperature.
localities in South Africa, and five generations at the Johannesburg site where it failed to overwinter. Extremes of temperature at this site exceed the lower thermal limits measured for the mirid. However, small populations have established on the Vaal River, which experiences similar low winter temperatures. The inability to develop sufficiently during the winter months may hinder overwintering of this insect, which survives as an adult for only 50 days (Fig. 5). The mirid can only develop through one generation during the winter months of April to August at the Johannesburg site, but can complete 1.3 generations at a site 80 km away near Pretoria where the insect has established (Fig. 5). Such bottlenecks probably force the population into non-overlapping generations, which makes them even more vulnerable to extremes of weather. However, the lack of establishment in the Western Cape where 1.7 generations are predicted does not yield to this explanation where winter rainfall and exposure to wind may also play a role.

**Conclusion**

Unfortunately none of the methods reviewed above has been revealed as an ideal technique for identifying an agent’s thermal shortcomings at an early stage of laboratory testing. Upper thermal limits are generally well above average environmental temperatures, but may be below microhabitat extremes which active insects would be expected to avoid. However, the lower thermal limits, and in particular the LT₅₀, show some utility for estimating an insect’s chances of surviving extreme winter conditions. The present weakness of the measure, which prevents cross species comparisons

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**Figure 2.** Areas in South Africa that experience temperatures above or below 1.2°C, the CTMin of Eccritotarsus catarinensis. Note the boundary between the Pretoria establishment and the Johannesburg failure sites.

**Figure 3.** Map of South Africa indicating the number of generations that Stenopelmae rufinasus is expected to complete within a year.
and detection of large-scale patterns, is that low temper-
atures may have a cumulative effect, causing insects to
die of cold stress, before the LT50 is reached. Lack of
standardization with regard to exposure and recovery
times over which the LT50 is measured has also contrib-
uted to its vague value. We propose that an exposure
time of two hours, with 24 hours for recovery, meas-
ured by the ability to self-right, should be used for
measurements of LT50. Two hours at an extreme
temperature represents a reasonable approximation of
an overnight “cold snap” that could decimate a local
insect population.

At this stage, the CTMin appears to be a weak
measure of cold tolerance because most insects, what-
ever their geographical origin, go into torpor close to
2°C. A series of days where the temperature drops
below the CTMin will presumably produce physiolog-
ical stress. It may be instructive to compare patterns of
sequential days below the CTMin at establishment and
failure sites to estimate the effects of accumulated cold
stress on the insects (Vera et al. 2000).

Figure 4. Map of South Africa indicating the number of generations that Parachaetes
insulata is expected to complete within a year.

Figure 5. Map of South Africa indicating the number of generations that Eccrito-
tarsus catarinensis is expected to complete within five winter months of
April to August.
The degree–day model is most satisfying because
the results appear sensible, and are useful for different
geographical areas. However, in this review it has only
worked well for one of the three examples given,
largely because S. rufinasus is extremely cold tolerant.
Comparing species reveals a pattern that reflects the
underlying isotherms of the local climate, expressed as
the number of potential generations. Our modification
of this model to account for longevity and replacement
of the parental generation adds a new dimension to
prediction of the number of favourable months available
to a species at a particular locality. This could be
improved by including a pre-oviposition period, combined with an oviposition threshold and population
structure. Nevertheless, the number of insects required
and the time involved in gathering data for a degree–day model remains daunting.

Two recommendations emerge for steps to reduce
climate-incompatibility failures-to-establish in clas-
sical biological control. Firstly, before any foreign
exploration is undertaken, a climatic characterization
of the native and introduced geographical range of the
weed is prepared, followed by a comparison using
CLIMEX “match climates”, to identify areas in which suitable control agents should be sought. Secondly, a
prompt experimental determination of the CTMin and
LT50 values of the candidate agents should be carried
out while they are still in quarantine, followed by a
general comparison of these data with the extremes of
climate in the proposed area of introduction, to estimate
the chances of survival of the potential agents.

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