1. Introduction

A requirement for a diurnally alternating temperature is a major factor in the germination ecophysiology of wild (non-domesticated) seeds (Probert, 1992). The subject has consequently become well-researched (Baskin and Baskin, 2001; Morinaga, 1926; Murdoch et al., 1989; Thompson and Grime, 1983). The effect of germination incubation regimes, which were chosen on the basis of temperature patterns found within the fynbos (Mediterranean fire-prone shrubland-type) habitat in the Cape Floristic Region during the autumn germinative period, was tested on seeds of 6 Leucospermum species over 5 taxonomic sections (L. cordifolium, L. cuneiforme, L. erubescens, L. glabrum, L. reflexum, L. vestitum). Seeds of each species were scarified, soaked in water and incubated at 15 combinations of diurnal low (16 h) and high (8 h) temperatures. The results indicated that Leucospermum seeds generally require alternating temperatures for germination. Regression analysis of germination percentage responses were used to estimate provisional optimum low [T_{L} (LOW)] and optimum high [T_{H} (HIGH)] temperature requirements for individual species. These requirements differed markedly among species, and across species they averaged 9.9 and 21.2 °C, respectively. Individual requirements correlated positively with mean late autumn air temperatures obtained from weather stations near the natural habitats of species. We conclude that a diurnal alternating temperature requirement is a character syndrome in Leucospermum in which the T_{L} (LOW) and T_{H} (HIGH) components are narrowly adaptive, independent and genetically stable characters relating to the known ecophysiological roles of low and high temperature requirements (Brits, Cutting, Brown and Van Staden, 1995). Ecological and adaptive roles of these requirements are compared with those in some persistent small-seeded soil-stored seed banks. © 2014 SAAB. Published by Elsevier B.V. All rights reserved.
appeared to be correlated with differences in the climatic temperature regimes associated with their mountainous habitats.

The natural Cape fynbos habitat of *Leucospermum* species is characterized by contrasting microclimates (Rourke, 1972) and the question arises whether, and how closely, species are adapted to their environmental temperature regimes.

*Leucospermum* seed germination involves the interaction of environmental and seed factors, including several forms of innate dormancy as well as natural variation in viability across seed lots (Brits et al., 1999; Kelly et al., 1992). To distinguish between poor viability and dormancy effects we employed viability testing of seed lots with tetrazolium in the present study (Brits and Van Niekerk, 1976; Brits, 1990; Brits et al., 1999).

In previous work, the six species chosen for this study (Table 4) germinated maximally when incubated under an alternating temperature regime, in combination with oxygenation related treatments (Brits, 1990). Assuming that natural scariification of *Leucospermum* seeds must occur in the soil-stored seed bank before oxygen dependent germination can take place (Brits, 1990; Brits et al., 1993, 1999) we optimized possible confounding effects of temperature with the dormancy effects of intact (oxygen impermeable) seed coat layers in our study, and also simulated natural scariification in fynbos, by applying concentrated H2SO4 acid scariification prior to incubation (Brits and Van Niekerk, 1976; Brits et al., 1999). However, the status of smoke as a ubiquitous germination stimulant is as yet inconclusive in *Leucospermum* (Brown Leucospermum, 1986) and encompasses the average minimum and maximum air temperatures recorded across the respective habitats of species during the autumn germination period (Table 4). The choice of a single 16 h low × 8 h high diurnal temperature cycle was based on the ambient temperature regimes prevailing in fynbos during autumn. This is in accordance with the need for relatively long periods at low temperature for optimal germination response within diurnally fluctuating temperature cycles (Thompson, 1974; Totterdell and Roberts, 1980).

Seeds in this, and previous studies were obtained from essentially non-domesticated sources, usually produced within fynbos areas close to their natural habitats, or collected directly from the wild (e.g. Brits, 1990 — except L. cordifolium, see the Materials and Methods section). Experience has shown that *Leucospermum* seed characters are highly heritable and that present-day seeds behave essentially as wild-type material.

The present study tests three hypotheses relating to germination temperature requirements in a group of 6 *Leucospermum* species with contrasting phylogeny (representing 5 of the 9 taxonomic sections in the genus — Table 4) and originating from varied climatic backgrounds: 1) that diurnally alternating temperatures are correlated requirements within the genus in fynbos (character syndromes sensu Angevine and Chabot, 1979); 2) that the temperature requirements of individual species differ; and 3) that specific differences are correlated with ecological determinants, i.e. they are a function of selective pressures.

### 2. Materials and methods

#### 2.1. Seed sources

*Leucospermum* seed was produced under cultivation at the Tygerhoek Experimental Farm at Riviersonderend, South Africa (34°9'S, 19°54'E) within a typically mesic mountain fynbos area. Fresh, dry, fully matured seeds were harvested under controlled conditions and hand sorted, and in a few instances of short supply they were supplemented by cultivated 1–2 yr-old seed obtained from commercial seed suppliers. All experimental seed plants had been cultivated for only one or two generations from seed following collection from the wild (Brits, 1990) excepting *L. cordifolium*, a partially domesticated species (“wild/crop species” sensu Watt and Bloomberg, 2012).

Seeds were thoroughly mixed and divided into lots of convenient size for acid scariification treatment. Seeds were treated for 7 min in (c) H2SO4 (based on previous tests with *L. cordifolium* — Brits and Van Niekerk, 1976), washed and soaked in distilled water for 24 h. Seeds were then air-dried and dusted with thiram wp fungicide (Brits, 1990). Petri dishes (9 cm) were divided into 6 segments and 25 seeds per species (except 22 for *L. cuneiforme* and *L. erubescens*) were transferred to each segment per petri dish onto one layer of Whatman no. 1 filter paper. Each petri dish constituted one replication and this was repeated 6 times within each of the temperature regimes.

#### 2.2. Temperature regimes

Seeds were dark-incubated at 15 different constant and alternating temperature regimes (Table 1). Where temperatures were alternated the lower and higher temperatures were maintained for 16 and 8 h respectively. Mean daily temperature was calculated as the time weighted mean of the two temperatures.

Alternating temperatures were obtained by transferring petri dishes with seeds from one to another of five incubators which were kept at constant temperatures, with a daily variation not exceeding ± 1°C. A seed was considered to have germinated when the radicle had emerged 1 mm; germinated seeds were counted and removed weekly for 14 weeks, giving both cumulative and final germination percentage responses.

A viability test with tetrazolium (Brits and Van Niekerk, 1976) was carried out on samples of all 6 species.

The relationship between mean daily temperature, temperature amplitude and germination percentage was determined by means of bivariate 2nd order polynomial regression analysis. From these the turning points (maxima) were estimated of X1 (mean daily temperature) and X2 (temperature amplitude) for untransformed percentage data. Using the estimated turning points X1 and X2, the optimum diurnal low [T0(Low)] and optimum high [T0(High)] germination temperatures (for eliciting maximal germination percentage responses) for the six species were calculated by transposition (Brits, 1986):

\[
T_{0}(\text{LOW}) = X_1 - 1/3X_2
\]

and

\[
T_{0}(\text{HIGH}) = X_1 + 2/3X_2
\]

### Table 1

Incubation temperature regimes (°C), their means and amplitudes, for six experimental *Leucospermum* species.

<table>
<thead>
<tr>
<th>Regime</th>
<th>Mean</th>
<th>Amplitude</th>
<th>Regime</th>
<th>Mean</th>
<th>Amplitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>4</td>
<td>4</td>
<td>9.</td>
<td>4 × 28</td>
<td>12</td>
</tr>
<tr>
<td>2.</td>
<td>10</td>
<td>0</td>
<td>10.</td>
<td>10 × 16</td>
<td>12</td>
</tr>
<tr>
<td>3.</td>
<td>16</td>
<td>0</td>
<td>11.</td>
<td>10 × 22</td>
<td>14</td>
</tr>
<tr>
<td>4.</td>
<td>22</td>
<td>0</td>
<td>12.</td>
<td>10 × 28</td>
<td>16</td>
</tr>
<tr>
<td>5.</td>
<td>28</td>
<td>0</td>
<td>13.</td>
<td>16 × 22</td>
<td>18</td>
</tr>
<tr>
<td>6.</td>
<td>4 × 10</td>
<td>6</td>
<td>14.</td>
<td>16 × 28</td>
<td>20</td>
</tr>
<tr>
<td>7.</td>
<td>4 × 16</td>
<td>8</td>
<td>15.</td>
<td>22 × 28</td>
<td>24</td>
</tr>
<tr>
<td>8.</td>
<td>4 × 22</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Germination rates (GR) for treatments and species were calculated 
(Brits, 1990) using the formula of Heydecker (1973) and Ranal 
and de Santana (2006) for calculating the coefficient of velocity of 
germination:

\[ GR = \frac{\sum_{i=1}^{k} \frac{n_i}{D_i \times n_i}}{\sum_{i=1}^{k} D_i \times n_i} \times 100 \]

where  
- \( k \) = final week of germination
- \( D_i \) = number of weeks from sowing
- \( n_i \) = number of seeds newly germinated in week \( D_i \)
- \( i \) = week 1 to week \( k \)

2.3. Statistical methods

A 6 × 15 factorial experiment was carried out within a completely 
randomized design with 6 replicates. The factors were 6 species and 
15 temperature regimes. Each experimental unit consisted of 25 or 22 
seeds. The appropriate analyses of variance were performed on the per-
temperature regimes. Each experimental unit consisted of 25 or 22 
seeds. The appropriate analyses of variance were performed on the per-
temperature series. Within the six 4 °C lower-temperature 
series, for example, realized total germination percentages tended to 
follow a parabolic trend, in five species, i.e. a clear maximum is discern-
able within each temperature series – as in \( L. cordifolium \) (Fig. 1). Para-
bo\( lic \) trends (with clear turning points) are required within most 
temperature series of a species data set to be able to calculate 
\( T_{0}(LOW) \) and \( T_{0}(HIGH) \), using regression. However parabolism was 
not evident in \( L. glabrum \) realized germination percentages in all series were ascending 
throughout the temperature test ranges used and turning points clearly 
could not be estimated. We therefore postulated a series of 10 extreme 
values at which germination is expected to be very low or not to occur at 
al (Table 2). We propose that these values, based on our experimental 
experience with \( Leucospermum \), are \( T_{MIN} \) or \( T_{MAX} \); and that they be used 
here to calculate provisional estimates of \( X_{1}/T_{0}(LOW) \) and \( X_{2}/T_{0}(HIGH) \).

For example, a \( T_{0}(LOW) \) temperature of below 0 °C will conceivably 
lead to a zero response in most \( Leucospermum \) species, since prolonged 
sub-zero temperatures do not occur in the generally temperate fynbos 
montane climate during the germination period (Rourke, 1972). In ad-
dition the sensitive seedlings could be frost damaged during emergence 
(personal observation). On the other extreme an average supra-optimal 
temperature of 34 or 40 °C could be severely inhibitive since such high 
high temperatures tend to suppress germination strongly (Brits, 
1986; Brits and Van Niekerk, 1986; Brown and Van Staden, 1971); aver-
age maximal temperatures of this order also do not occur during the 
temperate autumn germinative period in nature (Table 4). The set of 
chosen artificial temperatures and responses was standardized over 
the experimental species.

The resulting bivariate 2nd order polynomial functions (Fig. 3) 
allowed calculation of \( T_{0}(LOW) \) and \( T_{0}(HIGH) \) estimates and these 
corresponded reasonably well to the trends evident in the bar diagrams. 
\( L. glabrum \), for example, appears to need a high \( T_{0}(HIGH) \) both from in-
spection of the bar diagrams and from the regression estimates (Fig. 1, 
Table 4) and, by contrast, \( L. reflexum \) requires a low \( T_{0}(LOW) \) tempera-
ture. The regressions yielding these estimates in three cases gave very 
similar Rd values to those of regressions based only on experimental 
data (Table 3), the other values deviating where experimental 
data did not show sufficient parabolism. Considering the limitations of 
our data we propose that the \( T_{0}(LOW) \) and \( T_{0}(HIGH) \) calculated here 
from additional, artificial values be viewed as provisional, working 
estimates.

3. Results and discussion

Final, maximal, germination percentages for species and treatments 
differed statistically highly significantly (P < 0.001) and the 
interaction found for species × treatments was likewise highly significant 
(P < 0.001). For this reason the values for species and treatment means 
are presented individually (Fig. 1).

Maximal germination percentage response of species correlated 
strongly with tetrazolium viability estimates (\( r = 0.81; P = 0.05 \), 
\( L. erubescens \) being an outlier – Table 4), indicating that in most seed 
lots an optimum combination of treatments released seeds from dor-
mancy. Tetrazolium viability scores over-estimated realized germin-
ations so strongly with tetrazolium viability estimates (\( r = 0.81; P = 0.05 
\), P = 0.05, 1987). These temperature parameter values would be preferred when fitting the bi-
variate 2nd order regression on total germination percentage responses 
within each temperature series. Within the six 4 °C lower-temperature 
series, for example, realized total germination percentages tended to 
follow a parabolic trend, in five species, i.e. a clear maximum is discern-
able within each temperature series – as in \( L. cordifolium \) (Fig. 1). Para-
bo\( lic \) trends (with clear turning points) are required within most 
temperature series of a species data set to be able to calculate 
\( T_{0}(LOW) \) and \( T_{0}(HIGH) \), using regression. However parabolism was 
not evident in \( L. glabrum \) realized germination percentages in all series were ascending 
throughout the temperature test ranges used and turning points clearly 
could not be estimated. We therefore postulated a series of 10 extreme 
values at which germination is expected to be very low or not to occur at 
al (Table 2). We propose that these values, based on our experimental 
experience with \( Leucospermum \), are \( T_{MIN} \) or \( T_{MAX} \); and that they be used 
here to calculate provisional estimates of \( X_{1}/T_{0}(LOW) \) and \( X_{2}/T_{0}(HIGH) \).

For example, a \( T_{0}(LOW) \) temperature of below 0 °C will conceivably 
lead to a zero response in most \( Leucospermum \) species, since prolonged 
sub-zero temperatures do not occur in the generally temperate fynbos 
montane climate during the germination period (Rourke, 1972). In ad-
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(personal observation). On the other extreme an average supra-optimal 
temperature of 34 or 40 °C could be severely inhibitive since such high 
high temperatures tend to suppress germination strongly (Brits, 
1986; Brits and Van Niekerk, 1986; Brown and Van Staden, 1971); aver-
age maximal temperatures of this order also do not occur during the 
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The resulting bivariate 2nd order polynomial functions (Fig. 3) 
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corresponded reasonably well to the trends evident in the bar diagrams. 
\( L. glabrum \), for example, appears to need a high \( T_{0}(HIGH) \) both from in-
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Table 4) and, by contrast, \( L. reflexum \) requires a low \( T_{0}(LOW) \) tempera-
ture. The regressions yielding these estimates in three cases gave very 
similar Rd values to those of regressions based only on experimental 
data (Table 3), the other values deviating where experimental 
data did not show sufficient parabolism. Considering the limitations of 
our data we propose that the \( T_{0}(LOW) \) and \( T_{0}(HIGH) \) calculated here 
from additional, artificial values be viewed as provisional, working 
estimates.

3.2. Relationship of estimates with natural temperature regimes

The relationship between the \( T_{0}(LOW)/T_{0}(HIGH) \) estimates for 
\( Leucospermum \) species and climatic determinants was investigated 
(Table 4). Estimated temperature requirements correlated positively 
with mean air temperature during May, at nearby weather stations. 
This was strong in the case of \( T_{0}(LOW) \) and minimum air temperature 
(\( r = 0.82; P = 0.04 \), Fig. 4A); between \( T_{0}(HIGH) \) and maximum air 
temperature the correlation was weaker and not statistically significant
(r = 0.65; P = 0.16 — Fig. 4B). Low temperature is the most important environmental requirement and May (mid-autumn) was shown to be the month of maximum emergence in seed bed germinated *L. cordifolium* seed (Brits and Van Niekerk, 1986).

Although mean minimum air temperatures reflect the altitude of weather stations (Table 4) habitat microclimates are also influenced by local topography and proximity to the coast. Coastal species (*L. cordifolium, L. glabrum*) showed more temperate requirements as opposed to inland species (*L. erubescens, L. vestitum*) and the "subalpine" species (sensu George, 1981) *L. reflexum* had both the lowest $T_0$(LOW) and $T_0$(HIGH) requirements. This correspondence of environmental and species attributes are not uncommon, e.g. pronounced low-temperature requirements were also found for the subalpine Banksia L.f. (Proteaceae) species *B. cane* J.H. Willis (750–1500 m), *B. saxicola* A.S. George (>600 m) and some forms of *B. marginata* Cavanilles (up to 1400 m) which required stratification at 5 °C, for germination. This was in contrast to species of lower altitudes which responded to higher germination temperatures (Salkin and Hallam, 1978). Trends in germination temperature requirements were also studied in 28 non-proteaceous perennial native Australian species (Bell and Bellairs, 1992). Generally the conditions yielding the highest germination percentages tended to coincide with those habitat temperature conditions most suitable for seedling establishment.

The relatively close experimental correlations of $T_0$(LOW)/$T_0$(HIGH) requirements with environmental temperature regimes (Table 4) are remarkable, considering the potential sources of experimental error. Weather station data used for *Leucospermum* in this study are at best approximations of the microsite regimes of species, the precise location of the original populations being unknown. In particular the air temperature data of weather stations would differ from the respective soil

---

Fig. 1. Mean seed germination percentages for six species of *Leucospermum* incubated under 15 regimes of constant and alternating temperatures: A — *L. cordifolium*; B — *L. cuneiforme*; C — *L. erubescens*; D — *L. glabrum*; E — *L. reflexum*; F — *L. vestitum*. LSDs = 9.6% (P = 0.05) and 12.7% (P = 0.01). — Tetrazolium viability estimates.
temperature regimes in localities. We therefore propose that the good correlations found here point to narrow adaptedness between germination attributes of species and their environments.

3.3. Ecological roles of Leucospermum temperature requirements in fynbos

Despite marked differences, germination temperature requirements in Leucospermum species are clearly all of a diurnally alternating nature. These indicate character syndromes in Leucospermum which synchronize seed germination of the long-living underground seed bank with only the first post-fire, ephemeral, (early) winter condition in fynbos, its obligate germination period (or germination window - Brits, 1986, 1987). During this period adequate moisture levels are available for

---

**Table 2**

Series of 10 extreme incubation temperature regimes (°C) at which germination was postulated not to occur in Leucospermum, daily experimental temperatures being either too low (≤Tb) or too high (≥Tc) for germination to occur: daily low (16 h) and high (8 h) temperatures, mean daily temperature X1 and temperature amplitude X2. Each regime was given an arbitrary germination value of 1% and used for calculating bivariate 2nd order regressions for six species.

<table>
<thead>
<tr>
<th>Regime</th>
<th>X1</th>
<th>X2</th>
<th>Regime</th>
<th>X1</th>
<th>X2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>High</td>
<td></td>
<td>Low</td>
<td>High</td>
<td></td>
</tr>
<tr>
<td>−2</td>
<td>4</td>
<td>6</td>
<td>−2</td>
<td>34</td>
<td>10</td>
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<tr>
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<td>16</td>
<td>18</td>
<td>16</td>
<td>40</td>
<td>24</td>
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<tr>
<td>−2</td>
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</tr>
<tr>
<td>−2</td>
<td>28</td>
<td>30</td>
<td>22</td>
<td>40</td>
<td>28</td>
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</tbody>
</table>

---

Fig. 2. 3-D bar diagrams of mean seed germination rates (GR) for six species of Leucospermum incubated under 15 regimes of constant and alternating temperatures: A — L. cordifolium; B — L. cuneiforme; C — L. erubescens; D — L. glabrum; E — L. reflexum; F — L. vestitum.
seedling establishment, following the dry summer (drought/desiccation avoidance), when concurrently the suppressive shrubland canopy has been removed by fire (canopy-competition avoidance). A competitive shrub canopy re-establishes within one season following fire (Brits, 1986).

Assuming narrow adaptedness in *Leucospermum* seed attributes, the advantages within a particular niche could be increased accuracy of response of a seed population to environmental constraints. This includes avoidance of seed bank loss to spurious germination cues during unfavorable conditions (Probert, 1992) for example short wet spells that occur sporadically during the dry season (Thompson and Grime, 1983; Watt and Bloomberg, 2012) as regularly occur during summer in fynbos (Le Maitre and Midgley, 1992). Such spells in fynbos are associated with relatively high ambient temperature and in *Leucospermum* the requirement for a continuous “background” of low temperature prevents seed germination during these moist interludes. Conversely, accurate and

![Fig. 3](image-url) Bivariate polynomial regressions of the data presented in Fig. 1, supplemented with artificial, extreme values (see Table 2). A – L. cordifolium; B – L. cuneiforme; C – L. erubescens; D – L. glabrum; E – L. reflexum; F – L. vestitum. For regression equations see Table 3.

<table>
<thead>
<tr>
<th>Species</th>
<th>Equation</th>
<th>SL</th>
<th>X1'</th>
<th>X2'</th>
<th>R²</th>
<th>%R²</th>
<th>Exp. only R²</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>cordifolium</em></td>
<td>$Y = -14.1 + 10.2X_1 + 1.14X_2 - 0.377X_1^2 - 0.093X_2^2 + 0.045X_1X_2$</td>
<td>0.001</td>
<td>14.26</td>
<td>9.53</td>
<td>68</td>
<td>68</td>
<td></td>
</tr>
<tr>
<td><em>cuneiforme</em></td>
<td>$Y = -12.2 + 2.64X_1 + 1.04X_2 - 0.077X_1^2 - 0.029X_2^2 - 0.018X_1X_2$</td>
<td>0.002</td>
<td>15.71</td>
<td>12.95</td>
<td>48</td>
<td>63</td>
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<tr>
<td><em>erubescens</em></td>
<td>$Y = -2.74 + 1.45X_1 + 0.47X_2 - 0.054X_1^2 - 0.021X_2^2 + 0.006X_1X_2$</td>
<td>0.015</td>
<td>14.24</td>
<td>13.24</td>
<td>36</td>
<td>39</td>
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<tr>
<td><em>glabrum</em></td>
<td>$Y = -19.1 + 3.31X_1 + 1.54X_2 - 0.102X_1^2 - 0.046X_2^2 - 0.002X_1X_2$</td>
<td>0.073</td>
<td>16.03</td>
<td>16.39</td>
<td>22</td>
<td>78</td>
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<tr>
<td><em>reflexum</em></td>
<td>$Y = +5.19 + 0.32X_1 + 0.101X_2 - 0.022X_1^2 - 0.013X_2^2 + 0.001X_1X_2$</td>
<td>0.518</td>
<td>8.81</td>
<td>8.49</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td><em>vestitum</em></td>
<td>$Y = +2.95 + 2.68X_1 - 0.006X_2 - 0.113X_1^2 - 0.024X_2^2 + 0.027X_1X_2$</td>
<td>0.022</td>
<td>12.75</td>
<td>7.04</td>
<td>35</td>
<td>39</td>
<td></td>
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</tbody>
</table>
early timing of germination and establishment during the fynbos germination period proper, could maximize interspecific seedling competitive success, through the pre-empting of available growth space (interspecies competition avoidance — Fenner, 1985; Stebbins, 1950). Thus our model of narrow germination temperature attributes predicts effective responses to various environmental constraints in Leucospermum species recruitment.

3.4. Comparative systems in alternative vegetation types

Some plants with persistent seed banks, e.g. many small-seeded weed and tropical forest-gap pioneer species, require increased fluctuation of daily temperature per se, around an optimum mean temperature, for germination. The seeds of these species respond to fluctuating temperatures in a relatively wide latitude (Murdoch et al., 1989; Pearson et al., 2002; Probert, 1992; Totterdell and Roberts, 1980) and research objectives often center on the characterization of an effective latitude for germination of a species. A fraction only of such seed banks are typically released from dormancy, often in conjunction with a light requirement (Baskin and Baskin, 2001; Pearson et al., 2002; Totterdell and Roberts, 1980). The effect of temperature here is eliciting, in recently disturbed soil, germination of only those seeds deposited close to or on the soil surface (hence also responsiveness to light) whereas the balance of the long-living soil-stored seed bank persists ungerminated at deeper soil levels, where temperatures fluctuate less, thus simultaneously avoiding 1) canopy-competition (Pearson et al., 2002) and 2) the loss of deeper-buried seed reserves (Baskin and Baskin, 2001).

In contrast, Leucospermum soil-stored seeds (large-sized, typically 100 mg in weight) germinate en masse during the (main) germinative period, from relatively even burial depths (Brits, 1987; Rourke, 1972); i.e. although the seeds are long-lived they do not seem to persist over successive germination periods (mass germination events). In this they clearly follow different recruitment strategies from those of the above-mentioned small-seeded persistent species, and which involve different patterns of avoidance mechanisms (compare Thompson et al., 1977).

Separate ecological roles are proposed in Leucospermum for the requirements of background low temperature (drought avoidance) and daily high temperature pulse (canopy-competition avoidance), suggesting independence of these characters. Leucospermum seeds are thermoinhibited (sensu Hills and Van Staden, 2003) at even moderately high temperature. This suggests a strong primary physiological role for a moderately low temperature background (Brits et al., 1995). In a separate physiological role for daily high temperature pulse, Leucospermum germination is induced through a rise in embryonic axis GA levels (Brits et al., 1995). Thus the ecophysiology of Leucospermum alternating germination temperature requirements suggests a model of specific temperature cue(s) acting on distinct seed physiological processes and enabling separate ecological functions.

We therefore propose that an optimum temperature amplitude requirement ("optimum temperature difference" sensu Totterdell and Roberts, 1980) should more accurately be characterized as a diurnal bi-temperature requirement in Leucospermum in fynbos. The physiology of alternating temperature requirement in seed germination is still not well explained (da Silva et al., 2007) and the above Leucospermum ecophysiological model does not appear to feature elsewhere in the literature.

Acknowledgments

We thank the Department of Agriculture, Forestry and Fisheries for provision of climatic data from weather stations. The valuable suggestions of two anonymous reviewers are gratefully acknowledged.

Table 4

<table>
<thead>
<tr>
<th>Species</th>
<th>Taxonomic</th>
<th>Performance</th>
<th>Habitat data</th>
<th>Weather station data</th>
<th>Regression estimates</th>
</tr>
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<tbody>
<tr>
<td>L. cuneiforme (Burn. f.) Rourke</td>
<td>Crassicladex</td>
<td>37</td>
<td>23</td>
<td>Southern foothills of Cape</td>
<td>0–1000</td>
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<tr>
<td>L. cordifolium (Salisb. ex Knight) Fourcade</td>
<td>Brevifilamentum</td>
<td>85</td>
<td>77</td>
<td>South Coast mountains</td>
<td>30–450</td>
</tr>
<tr>
<td>L. glutinum Phillips</td>
<td>Conocarpodendron</td>
<td>78</td>
<td>51</td>
<td>Coastal areas–Strand-veld</td>
<td>150–450</td>
</tr>
<tr>
<td>L. vestitum (Lam.), Rourke</td>
<td>Brevifilamentum</td>
<td>66</td>
<td>36</td>
<td>Inland, north/west facing slopes</td>
<td>60–1200</td>
</tr>
<tr>
<td>L. erubescens Rourke</td>
<td>Tumiditubus</td>
<td>63</td>
<td>17</td>
<td>Langeberg northern foothills</td>
<td>450–600</td>
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<tr>
<td>L. reflexum Buek ex Meisn.</td>
<td>Cardinistylys</td>
<td>54</td>
<td>25</td>
<td>Eastern Cedarberg (subalpine)</td>
<td>900–2000</td>
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<tr>
<td>Average</td>
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Fig. 4. Scatter diagrams and correlations for Leucospermum: A: Correlation between estimated optimum low incubation temperature \( T_{O(Low)} \) and average minimum air temperature during May (1983–1992) at weather stations close to the natural habitat of six Leucospermum species, as in A. B: Correlation between estimated optimum high incubation temperature \( T_{O(High)} \) and average maximum air temperature, for six Leucospermum species, as in A.
References


