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1 **Abstract**

2 Germination rates and germination fractions of seeds can be predicted well by the
3 hydrothermal time (HTT) model. Its four parameters hydrothermal time, minimum soil
4 temperature, minimum soil moisture, and variation of minimum soil moisture, however,
5 must be determined by lengthy germination experiments at combinations of several levels
6 of soil temperature and moisture. For some applications of the HTT model it is more
7 important to have approximate estimates for many species rather than exact values for only
8 a few species. We suggest that minimum temperature and variation of minimum moisture
9 can be estimated from literature data and expert knowledge. This allows to derive
10 hydrothermal time and minimum moisture from existing data from germination
11 experiments with one level of temperature and moisture. We applied our approach to a
12 germination experiment comparing germination fractions of wild annual species along an
13 aridity gradient in Israel. Using this simplified approach we estimated hydrothermal time
14 and minimum moisture of 36 species. Comparison with exact data for three species shows
15 that our method is a simple but effective method for obtaining parameters for the HTT
16 model. Hydrothermal time and minimum moisture supposedly indicate climate related
17 germination strategies. We tested whether these two parameters varied with the climate at
18 the site where the seeds had been collected. We found no consistent variation with climate
19 across species, suggesting that variation is more strongly controlled by site-specific factors.

20 **Zusammenfassung**

21 Keimungsgeschwindigkeit und Anteil gekeimter Samen lassen sich gut mit dem
22 Hydrothermalzeit-Modell bestimmen. Dessen vier Parameter Hydrothermalzeit,
23 Mindesttemperatur, Mindestbodenfeuchte und Streuung der Mindestbodenfeuchte müssen
24 jedoch durch aufwendige Keimungsversuche bei Kombinationen von mehreren
25 Temperatur- und Feuchtigkeitsstufen bestimmt werden. Für manche Anwendungen des
26 Hydrothermalzeit-Modells sind aber ungefähre Werte für viele Arten wichtiger als genaue
27 Werte für wenige Arten. Wenn die Mindesttemperatur und die Streuung der
28 Mindestfeuchte aus Veröffentlichungen und Expertenwissen geschätzt würde, können die

29 Hydrothermalzeit und Mindestbodenfeuchte aus vorhandenen Daten von
30 Keimungsversuchen mit nur einer Temperatur- und Feuchtigkeitsstufe berechnet werden.
31 Wir haben unseren Ansatz auf einen Keimungsversuch zum Vergleich der Keimungsquote
32 wilder einjähriger Arten entlang eines Trockenheitsgradienten in Israel angewendet. Mit
33 diesem Ansatz bestimmten wir die Hydrothermalzeit und Mindestfeuchtigkeit von 36
34 Arten. Der Vergleich mit genauen Werten für drei Arten zeigt, dass mit unserem Ansatz
35 Hydrothermalzeit-Parameter einfach und effektiv bestimmt werden können.
36 Hydrothermalzeit und Mindestfeuchtigkeit sollten auch bestimmte klimabedingte
37 Keimungsstrategien anzeigen. Deshalb testeten wir, ob diese zwei Parameter mit dem
38 Klima am Ursprungsort der Samen zusammenhängen. Wir fanden jedoch keinen für alle
39 Arten übereinstimmenden Zusammenhang, so dass die Unterschiede vermutlich stärker
40 durch standörtliche als durch klimatische Ursachen hervorgerufen werden.

41

42 **Key words**

43 climatic gradient, germination rate, dormancy, hydrothermal time model, minimum soil
44 moisture, annual plant species, Mediterranean

45

46

46 **Introduction**

47 Seed germination is probably the most important life stage transition for annual plants in
48 arid and semi-arid climates (Goldberg, Turkington, Olsvig-Whittaker, & Dyer, 2001).
49 Namely, the high variability of rainfall frequency and amount must be matched by an
50 appropriate germination strategy (e.g., Cohen 1966, Clauss & Venable, 2000). For
51 example, seeds must germinate only when there is enough soil moisture for roots to grow
52 sufficiently fast to reach longer-lasting reservoirs of soil moisture. On the other hand, seeds
53 should germinate quickly to get a head start over others which often translates into
54 competitive dominance (Weiner, 1985). The cue for germination within the rainy season is
55 usually the moisture surrounding the seed at the onset of rains. These cues, however,
56 cannot indicate germination conditions exactly. Therefore, a plant should spread the risk of
57 early germination among its seeds or evolve mechanisms for predictive germination to
58 maximize fitness (Cohen, 1966, 1967; Philippi & Seger, 1989). Especially annual plant
59 species, which must rely on their seed bank to buffer inter-annual variability of growth
60 conditions, show a wide range of response to intra-annual rain patterns as cue for
61 germination (e.g., Brown, 2002; Volis, Mendlinger, & Brown, 2004).

62 The so-called hydrothermal time (HTT) model of germination (Gummerson, 1986;
63 Bradford, 1995, 2002) is a conceptual model appropriate for comparing germination
64 strategies and evaluating the signals necessary to indicate favorable conditions. The basic
65 HTT model assumes that there are upper and lower thresholds of moisture and temperature
66 that allow germination. Within these bounds, seeds generally germinate faster the moister
67 and the warmer their environment. According to this concept, a seed germinates when it
68 has ‘accumulated’ enough moisture and heat. The HTT model has been expanded to
69 include, for example, soil salinity, priming, and maximum germination temperature
70 (Bradford, 2002). Thus, the model is versatile and its parameters are easily explainable in
71 terms of ecological characteristics of a species. Practical applications of the HTT model
72 include prediction of the timing and germination fraction of crop seeds and weeds in

73 agricultural fields (Finch-Savage & Phelps, 1993) and the calculation of germination
74 fractions of wild species under conditions of global climate change.

75 The experiments necessary to determine the four parameters of the basic HTT model,
76 however, are very time- and resource-consuming because they require germination
77 experiments at several levels of soil moisture and temperatures in factorial combination.
78 Therefore, experiments are usually restricted to a single or few species at the expense of
79 generality (Roman, Thomas, Murphy, & Swanton, 1999; Grundy, Phelps, Reader, &
80 Burston, 2000; Rowse & Finch-Savage, 2002). We know of only one paper (Allen, Meyer,
81 & Khan, 2000) that reports HTT parameters for twenty-four wild species. For some
82 applications, however, exact knowledge of all four HTT parameters may not be required.
83 Relative or approximate values may be used for comparative studies, computer simulations
84 of climate change, long-term projections of the significance of germination strategies for
85 fitness, or prediction of germination time courses in the field. In these cases, parameters
86 that are less important or do not vary strongly among species may be estimated based on
87 expert knowledge, which reduces the number of experimental units. Alternatively, the
88 number of experimental units can be kept the same with the benefit of including more
89 species.

90 Here, we present an approach for determining two focal parameters from a single
91 experiment with only one level of soil temperature and moisture: (i) the hydrothermal time,
92 *i.e.*, the sum over time of suitable temperature and moisture conditions required for
93 germination of seeds of a specific species, and (ii) the soil moisture at or below which half
94 of the seeds will germinate if the temperature is above that required for germination. We
95 applied the approach to a germination experiment with annual Mediterranean species and
96 derived the two parameters for 36 species. We tested whether the two parameters are
97 correlated as this would further simplify parameter estimation. Since the HTT parameters
98 are supposed to reflect germination strategies, we also tested the hypothesis that the two
99 estimated parameters vary systematically with climatic conditions at the site of the seed
100 source.

101 **Materials and Methods**

102 *Hydrothermal time model of germination*

103 The HTT model (Gummerson, 1986) is an extension of the more familiar temperature
104 sum concept. According to this concept, an individual plant starts to germinate or flower
105 when the sum of differences between mean daily temperature T and a minimum
106 temperature T_{\min} , accumulated over several days, passes a threshold θ_T (measured in
107 degree-days), *i.e.*, $\sum(T - T_{\min}) > \theta_T$ or $(T - T_{\min}) \cdot t > \theta_T$ for constant T . The HTT model
108 expands the temperature sum with the accumulation of soil moisture potential per degree-
109 day. Thus, seeds are thought to germinate when they have been accumulatively exposed to
110 sufficient moisture and temperature, that is, when environmental conditions have persisted
111 for the required hydrothermal time θ_{HT} . Hydrothermal time is calculated by summing the
112 product of differences of daily moisture (Ψ_{soil} , measured as soil water potential), and
113 temperature (T_{soil}) to their respective base or minimum values (Ψ_{\min} , T_{\min}):

$$114 \theta_{HT} = \sum[(\Psi_{\text{soil}} - \Psi_{\min}) \cdot (T_{\text{soil}} - T_{\min})] \quad (\text{eq. 1a})$$

115 with $\Psi_{\text{soil}} > \Psi_{\min}$ and $T_{\text{soil}} > T_{\min}$.

116 For constant environments this simplifies to

$$117 \theta_{HT} = (\Psi_{\text{soil}} - \Psi_{\min}) \cdot (T_{\text{soil}} - T_{\min}) \cdot t \quad (\text{eq. 1b})$$

118 with t = number of suitable days.

119 Hydrothermal time θ_{HT} and minimum temperature T_{\min} are assumed constant for a
120 species, whereas minimum moisture Ψ_{\min} is assumed normally distributed within a
121 population of seeds (Meyer, Debaene-Gill & Allen, 2000) with a mean $\Psi_{\min 50}$ and its
122 standard deviation $\sigma(\Psi_{\min})$. Eq. 1b applied to a population of seeds can be transformed
123 (Bradford, 1995) to yield

$$124 \text{probit}(g_t) = \left[(\Psi_{\text{soil}} - \Psi_{\min 50}) - \frac{\theta_{HT}}{t \cdot (T_{\text{soil}} - T_{\min})} \right] / \sigma(\Psi_{\min}) \quad (\text{eq. 2a})$$

$$125 \text{or } \text{probit}(g_t) = \left(\frac{\sum \Psi_{\text{soil}} - \Psi_{\min 50}}{t} \frac{\theta_{HT}}{\sum T_{\text{soil}} - T_{\min}} \right) / \sigma(\Psi_{\min}) \quad (\text{eq. 2b})$$

126 for a variable environment, where g_t is the fraction of seeds germinated till day t and probit
127 is the inverse cumulative normal distribution function. Germination rate, the time until a

128 certain fraction of seeds has germinated, can be calculated by specifying g and the HTT
 129 parameters and solving eq. 2a for t . The mean minimum soil moisture $\Psi_{\min 50}$ has been
 130 found to vary more or less strongly with temperature in many species (Allen et al., 2000)
 131 and has also been shown to vary among seed lots (Bauer, Meyer, & Allen, 1998). The
 132 hydrothermal time model has been applied successfully to predict the germination of onion
 133 (*Allium cepa* L.) under field conditions (Finch-Savage & Phelps, 1993).

134 *Estimation of parameters*

135 The four HTT parameters θ_{HT} , $\Psi_{\min 50}$, T_{\min} , and $\sigma(\Psi_{\min})$ are usually determined by
 136 repeated probit regression or by non-linear regressions of data from germination
 137 experiments at factorial combinations of several levels of constant soil moisture and
 138 temperature (Bradford, 1995). This procedure is time consuming and requires large
 139 resources of space and experimental units. Therefore, these experiments are rarely
 140 conducted. In contrast, data on germination behaviour is often available from other
 141 experiments that typically use only one level of constant moisture and one level of constant
 142 temperature. These data, however, provide only two degrees of freedom to determine four
 143 parameters in non-linear regression. We suggest that given this simplified experimental
 144 setup, minimum temperature T_{\min} and minimum moisture variability $\sigma(\Psi_{\min})$ could be
 145 estimated based on expert knowledge or comparative considerations. This reduces the
 146 degrees of freedom to two and allows to obtain approximate values for the two focal
 147 parameters hydrothermal time threshold θ_{HT} and mean minimum moisture $\Psi_{\min 50}$ as slope
 148 and intercept of equation 2 in rearranged form

$$149 \quad \text{probit}(g_t) \cdot \sigma(\Psi_{\min}) = \frac{1}{(T_{\text{soil}} - T_{\min}) \cdot t} \cdot \theta_{HT} - (\Psi_{\min 50} - \Psi_{\text{soil}}). \quad (\text{eq. 3})$$

151 *Germination experiment*

152 We illustrate our approach using data from an experiment designed to compare
 153 germination fractions of seeds of annual species originating from four climates in Israel
 154 and placed in two neighbor treatments (K. Tielbörger, unpubl. data). Seeds of in total 74
 155 species of annual plants were collected at the end of the growing season (April–May 2002)

156 at four sites in Israel (En Ya'aqov, Matta, Lahav, Sede Boqer). The sites represent four
157 levels of aridity: mesic Mediterranean (800 mm mean annual precipitation), Mediterranean
158 (600 mm), semi-arid (300 mm), and arid (100 mm), respectively. Details on soil, climate,
159 and vegetation characteristics of the sites can be found in Holzapfel, Tielbörger, Parag,
160 Kigel, & Sternberg (2006). Most species occur in only one or two of the sites, fewer occur
161 in three or all four sites.

162 Seeds collected in spring 2002 were stored in the field under natural climatic conditions
163 to ensure that seeds received the necessary environmental signals that break dormancy.
164 Batches of seeds were stored in ca. 10 cm × 10 cm flat cloth bags (organza, transparent and
165 aerated) that were fixed with stones at the corners to the ground in the field. Therefore,
166 storage conditions were very similar to the conditions experienced by seeds after dispersal.
167 Pre-sowing treatments are not necessary when seeds are stored in the field and we did not
168 want to artificially enhance germination. Viability was tested for selected species
169 (*Biscutella didyma*, *Bromus fasciculatus*, *Carrichtera annua*, *Hippocrepis unisiliquosa*,
170 *Hymenocarpus circinnatus*, *Reboudia pinnata*, *Stipa capensis*, *Valantia hispida*) that are
171 common across the sites and represent different dormancy groups: grasses (low
172 dormancy), crucifers (intermediate dormancy) and legumes (high dormancy). Seeds of
173 these species were germinated on constantly moist filter paper on Petri dishes at 23 °C in a
174 greenhouse. We added gibberilic acid to speed up the germination. Ungerminated seeds
175 were inspected by poking with a needle for the fleshy viable embryo (Pake & Venable,
176 1996). The tests indicated that the majority of seeds were viable and estimates of
177 germination fraction based on seed numbers sown were a good estimate of germination
178 fractions per viable seeds (M. Petrů, unpubl. data). The seeds in the bags were retrieved
179 from the field before the first rains in November 2002, bags were packed in individual
180 paper bags and air-mailed to Germany.

181 A few days later, in December 2002, seeds of each of species were sown in pots (Ø 7 –
182 10 cm) and placed in a greenhouse at Potsdam University, Germany. There were eight
183 replicate pots for each species per site. A 1:1 mix of garden humus and sand was used as
184 potting soil instead of local soil from each site to provide a common medium. Previous

185 trials have shown that germination does not differ between sand, garden soil, and
186 vermiculite when the seeds are watered such that the soil is always saturated. Pots of
187 almost all species contained 20 seeds. The pots of five species included in Tables 1 and 2
188 (*Crithopsis delileana*, *Filago contracta*, *Ononis squarrosa*, *Plantago cretica*, *Valantia*
189 *hispida*) had 27–54 seeds to account for known or presumed higher dormancy. The actual
190 seed density of these species was determined by seed availability. For the same reason the
191 pots of three species listed in the tables (*Alyssum strigosum*, *Geropogon hybridus*, *Stipa*
192 *capensis* [semi-arid]) were sown with only 10 seeds. Within each species–site combination
193 the seed density was the same in each pot.

194 The position of all pots was completely randomized across two greenhouse benches. All
195 pots were watered every 1 – 2 days to saturation so that soil moisture was \geq field capacity,
196 which by definition results in a soil water potential Ψ_{soil} of ≥ -0.036 MPa (Kuntze,
197 Roeschmann & Schwerdtfeger, 1988). Mean temperature in the unregulated greenhouse
198 ranged between 0 °C (night) and 20 °C (day) similar to January conditions in Israel.

199 Germinated seeds were counted almost daily from day 3 to day 29, and then every 3–8
200 days till day 55. Seedlings were removed after counting so they could not affect the
201 germination of remaining seeds. We combined germination data across pots for each site
202 and each species because we were mostly interested in gross estimates of hydrothermal
203 time parameters and their variation along a climatic gradient of aridity.

204 Under natural conditions, seeds are not only surrounded by conspecifics but also by
205 seeds of other species. Therefore, in addition to pots containing only one species, eight
206 replicate pots (25 – 35 cm diameter) per site were seeded with a species mixture (10 – 47
207 species) that is typical of the annual plant community at that site. This includes 32 rarer
208 species for which there were not enough seeds to use for both neighbor treatments. The
209 number of seeds per pot was 20 with the exceptions described for single-species pots.
210 Seedlings in mixed-species pots that could not be identified immediately were marked by a
211 toothpick and identified later by comparison with conspecifics in single-species pots.
212 Therefore, the parameters for species in mixed-species pots, especially those without
213 reference in single-species pots (*Geropogon hybridus*, *Plantago afra*, *Scabiosa palaestina*,

214 *Trisetaria macrochaeta*, *Valerianella vesicaria*), may be biased. We felt, however, that it
215 was more important to present approximate parameters than not to report any parameters
216 for these species.

217 *Calculation of HTT parameters*

218 Following our simplified approach for the experiment with annuals from an aridity
219 gradient, we estimated minimum temperature T_{\min} and minimum moisture variability
220 Ψ_{\min} from results by Allen et al. (2000) who determined the four HTT parameters in
221 experiments with factorial combinations of several levels of temperature and soil moisture
222 for 24 annuals from warm and cold deserts. Allen et al. (2000) found that fourteen out of
223 eighteen species growing on soils similar to ours had minimum temperatures $T_{\min} = 0$ °C,
224 the others had a T_{\min} of 1, 3, 8, and 10 °C. Based on these results we assumed for the
225 species in our experiment that $T_{\min} = 0$ °C. T_{\min} of species in other climates may be
226 estimated from experience or anecdotal evidence of the minimum temperature that species
227 require for germination. The median value of the minimum moisture variability $\sigma(\Psi_{\min})$ of
228 the eighteen species in Allen et al. (2000) was 0.345. We used this value in our
229 calculations.

230 Following Grundy et al. (2000) we based the cumulative germination fraction g_t on the
231 total number of germinated seeds at the end of the experiment instead of the number of
232 sown seeds to account for differences in dormancy. This implies that only those seeds that
233 germinated within 55 days were fully after-ripened. The maximum germination fractions
234 in Tables 1 and 2 can be used to recalculate the hydrothermal time parameters based on the
235 percentage of sown seeds. We added 1 to the total number of germinated seeds to avoid the
236 undefined value of probit (1.0).

237 Soil temperature in the experiment was variable, similar to field conditions. To derive
238 an average T_{soil} for use in the equations we compared the performance of two species that
239 our experiment had in common with Allen et al. (2000)'s experiment (*Bromus fasciculatus*
240 and *Stipa capensis*). We excluded *Carrichtera annua* that was also used in both
241 experiments because its mean minimum moisture for germination $\Psi_{\min 50}$ increases
242 strongly with temperature (0.24 MPa/K), whereas that of *Bromus* increases only slightly

243 (0.03 MPa/K), and that of *Stipa* is constant between 15 and 25 °C (Allen et al., 2000). We
 244 inserted in eq. 1b the time after which 50% of the seeds have germinated (median
 245 germination time), $t_{50} = 7$ d for *Bromus* and *Stipa* and soil moisture (field capacity: $\Psi_{\text{soil}} =$
 246 -0.036 MPa) from our experiment, and hydrothermal time θ_{HT} , mean minimum moisture
 247 $\Psi_{\text{min}50}$, and minimum temperature T_{min} for each species from Allen et al. (2000) (*Bromus*:
 248 30 MPa·K, -0.83 MPa, 0°C ; *Stipa*: 27 MPa·K, -0.73 MPa, 0°C). Then we solved eq. 1b for
 249 temperature T . The mean of the results ($T_{\text{Bromus}} = 5.4$ °C, $T_{\text{Stipa}} = 5.6$ °C) was 5.5 °C and
 250 used in our further calculations. Since $\Psi_{\text{min}50}$ of *Stipa* does not vary with T_{soil} , we are
 251 confident about the obtained value.

252 We determined hydrothermal time θ_{HT} and minimum moisture $\Psi_{\text{min}50}$ as slope and
 253 intercept of equation 3 with a constant T_{soil} of 5.5 °C (see above), $T_{\text{min}} = 0$ °C (value of 14
 254 species in Allen et al. [2000], see above), constant $\Psi_{\text{soil}} = -0.036$ MPa (watering to field
 255 capacity), and $\sigma(\Psi_{\text{min}}) = 0.345$ MPa (median value of 18 species in Allen et al. [2000], see
 256 above). The ratio $\theta_{\text{HT}}/t_{50}$ can serve as a test for our assumed value for minimum moisture
 257 variability. This ratio is independent of minimum moisture variation $\sigma(\Psi_{\text{min}})$ because
 258 $\text{probit}(50\%) = 0$ (eq. 2a rearranged: $\theta_{\text{HT}}/t_{50} = [\text{probit}(50\%) \cdot \sigma(\Psi_{\text{min}}) + (\Psi_{\text{min}50} - \Psi_{\text{soil}})] \cdot$
 259 $(T_{\text{soil}} - T_{\text{min}})$). Since the estimate of hydrothermal time θ_{HT} is contingent on minimum
 260 moisture variation $\sigma(\Psi_{\text{min}})$, outliers in a quantile boxplot of $\theta_{\text{HT}}/t_{50}$ values identify species
 261 whose true minimum moisture variation $\sigma(\Psi_{\text{min}})$ deviates strongly from the assumed value
 262 of 0.345 . For these outliers we calculated a new hydrothermal time threshold using the
 263 average $\theta_{\text{HT}}/t_{50}$ ratio (excluding the outliers), assuming that for outlier species this ratio is
 264 more similar to other species than minimum moisture variation $\sigma(\Psi_{\text{min}})$. The relative
 265 change of hydrothermal time θ_{HT} was then used to calculate an adjusted minimum
 266 moisture variability: $\sigma_{\text{adjusted}} = \theta_{\text{new}}/\theta_{\text{old}} \cdot \sigma_{\text{old}}$. The adjusted value was then used in eq. 3
 267 for deriving a new value of the minimum moisture $\Psi_{\text{min}50}$.

268 We tested the sensitivity of the determination of minimum temperature T_{min} , soil
 269 temperature T_{soil} , soil potential Ψ_{soil} and minimum moisture variability $\sigma(\Psi_{\text{min}})$ on the
 270 hydrothermal time threshold θ_{HT} and minimum moisture $\Psi_{\text{min}50}$. The sensitivity of T_{min}
 271 and T_{soil} depends on their difference (eq. 3). Therefore, we report the sensitivity for the

272 temperature difference $\Delta T = T_{\min} - T_{\text{soil}}$. Changing the temperature difference ΔT by
273 $\pm 10\%$ changes hydrothermal time θ_{HT} by the same proportion and leaves $\Psi_{\min 50}$
274 unaffected. Changing minimum moisture variability $\sigma(\Psi_{\min})$ by $\pm 10\%$ changes θ_{HT} by the
275 same proportion *and* changes $\Psi_{\min 50}$ by $\pm 9.6\%$. Changes of $\pm 10\%$ to both temperature
276 difference and minimum moisture variability have a multiplicative effect on hydrothermal
277 time threshold θ_{HT} but affect minimum moisture $\Psi_{\min 50}$ only via the change to minimum
278 moisture variability. A $\pm 10\%$ change to soil potential Ψ_{soil} affects minimum moisture
279 $\Psi_{\min 50}$ by less than 0.4% and has no effect on hydrothermal time θ_{HT} . The observed
280 temporal germination pattern is within the plotted time course for a $\pm 10\%$ change to the
281 values chosen for temperature difference and minimum moisture variability (Fig. 1),
282 indicating that the values are well founded.

283 *Statistical analyses*

284 Species with ≤ 20 germinated seeds in all pots of one site were excluded from the analysis
285 (20 species \times site combinations in single-species and 48 in mixed-species pots). For
286 deriving the two focal HTT parameters we determined for each species slope (θ_{HT}) and
287 intercept ($\Psi_{\min 50} - \Psi_{\text{soil}}$) in eq. 3 using an analysis of covariance (ANCOVA) of the data
288 from all sites where the species occurred. This was possible for twelve species in single-
289 species pots and eight species in mixed-species pots. When the ANCOVA indicated that
290 slopes did not differ significantly ($P > 0.1$) among sites, hydrothermal time θ_{HT} was
291 calculated across sites. When the ANCOVA further indicated that the intercept did not
292 vary among sites either, both parameters were calculated across sites. Else the HTT
293 parameters were calculated for each site. Statistics were calculated with JMP 5.1 (SAS
294 Institute, Cary, North Carolina, U.S.A.).

295 HTT parameters are thought to represent different germination strategies. Therefore, we
296 examined whether hydrothermal time and minimum moisture requirements differ among
297 species or sites along the climatic gradient using ANCOVA. This analysis was restricted to
298 species occurring in two or more sites. Further, we examined whether hydrothermal time
299 θ_{HT} was correlated with minimum moisture requirement $\Psi_{\min 50}$ because such a correlation
300 would further simplify the estimation of HTT parameters. The two parameters

301 hydrothermal time θ_{HT} and moisture requirement Ψ_{min50} , however, are calculated from the
302 same data set for each species \times site combination so that the true covariance between the
303 two parameters is inflated by an additional artifactual covariance (Mauricio, Rausher, &
304 Burdick, 1997). We used Mauricio, Rausher, & al.'s (1997) method to estimate artifactual
305 covariance.

306 **Results**

307 Using our simplified approach we determined two focal parameters of the hydrothermal
308 time model from a germination experiment and estimated the other two parameters from
309 literature data (Tables 1, 2). The goodness of fit (R^2) for all regressions for determining
310 HTT parameters was very high. Outlier inspection indicated six species whose minimum
311 moisture variation $\sigma(\Psi_{min})$ at some sites presumably deviates strongly from the assumed
312 0.345, resulting in extreme values for hydrothermal time θ_{HT} and minimum moisture
313 Ψ_{min50} : *Bupleurum lancifolium*, *Catapodium rigidum*, *Chaetosciadium trichospermum*,
314 *Coronilla scorpioides*, *Onobrychis squarrosa*, and *Plantago afra* (Tables 1, 2). The
315 following analyses are based on recalculated parameters (see Methods) for the
316 aforementioned species.

Table 1

Table 2 *Single-species pots*

318 The values for hydrothermal time θ_{HT} were strongly skewed among species \times site
319 combinations with a median of 36 (10-percentile: 23, 90-percentile: 76) (Table 1). The
320 values for Ψ_{min50} were normally distributed with a mean of -0.93 MPa (± 0.17 , SD, $n =$
321 53).

322 Hydrothermal time θ_{HT} decreased significantly with increasing mean minimum
323 moisture Ψ_{min50} (Fig. 3A). The artifactual covariance (-0.0002) was much smaller than
324 observed covariance (-1.5199) indicating that it is negligible in the correlation. Neither
325 hydrothermal time θ_{HT} nor minimum moisture Ψ_{min50} varied with mean annual
326 precipitation within or across species. The average coefficient of variation of hydrothermal
327 time among species (25%) was much smaller than the average CV among sites (45%).
328 Similarly, the average CV of minimum moisture was smaller among species (13%) than

329 among sites (18%).

330 *Mixed-species pots*

331 The values for hydrothermal time θ_{HT} were strongly skewed among species \times site
332 combinations with a median of 28 (10-percentile: 22, 90-percentile: 75) (Table 2). The
333 values for minimum moisture Ψ_{min50} were normally distributed with a mean of -0.95 MPa
334 (± 0.18 , SD, $n = 35$).

335 Hydrothermal time θ_{HT} did not vary significantly with minimum moisture Ψ_{min50} (Fig.
336 3B). Neither θ_{HT} nor Ψ_{min50} varied with precipitation within or across species. The
337 average CV of θ_{HT} among sites (34%) was smaller than the CV among species (41%). The
338 average CV of Ψ_{min50} was similar among sites (18%) and species (20%).

339 **Discussion**

340 We used literature-based estimates of minimum temperature T_{min} and minimum moisture
341 variability $\sigma(\Psi_{min})$ to derive hydrothermal time θ_{HT} and minimum moisture Ψ_{min50} for
342 germination of 36 wild species from a germination experiment with one level of soil
343 moisture and unregulated temperature.

344 Our findings suggest that our method is a simple but effective method for obtaining
345 parameters for the HTT model. Using our parameters, the HTT model predicted well the
346 time course of germination (Fig. 4). The values for hydrothermal germination threshold
347 θ_{HT} and minimum soil moisture Ψ_{min50} (Tables 1, 2) were in the range of those obtained
348 by Allen et al. (2000). Furthermore, the goodness of fit in our study was high, similar to
349 the results of Allen et al. (2000), although our regressions had only two degrees of
350 freedom.

351 Our parameters are based on two simplifying assumptions. First, we assumed that
Fig. 4 $\sigma(\Psi_{min})$
352 variation of minimum moisture $\sigma(\Psi_{min})$ does not differ among species. Based on the
353 interquartile range of $\sigma(\Psi_{min})$ observed by Allen et al. (2000), the actual values of θ_{HT}
354 and Ψ_{min50} could differ from our estimates by $\pm 37\%$. Furthermore, we identified only six
355 out of 94 species \times site combinations where extreme values of θ_{HT} and Ψ_{min50} suggested
356 that our assumption was severely violated. Second, we assumed that minimum temperature

357 T_{\min} equals 0 °C. It seems unlikely that the Mediterranean species in our experiment could
358 experience lower minimum temperatures, i.e. that they could germinate at subzero
359 temperatures. On the other hand, six species, *Bupleurum lancifolium*, *Catapodium rigidum*,
360 *Coronilla scorpioides*, *Onobrychis squarrosa*, *Plantago cretica*, and *Trisetaria*
361 *macrochaeta* had median germination times > 15 d, possibly indicating higher minimum
362 temperatures than we have assumed. A higher minimum temperature would decrease
363 hydrothermal time threshold θ_{HT} (eq. 3) but would not affect the calculation of minimum
364 moisture $\Psi_{\min 50}$.

365 The minimum moisture $\Psi_{\min 50}$ derived with our approach strictly refers only to the
366 (mean) soil temperature T_{soil} at which the experiment was conducted. For many of the
367 species studied by Allen et al. (2000), the relationship between minimum moisture and soil
368 temperature seems to be U-shaped and bounded between T_{\min} and an upper threshold
369 around 25 – 30 °C (Allen et al. 2000). Our T_{soil} was close to T_{\min} , so the minimum
370 moisture $\Psi_{\min 50}$ at intermediate temperatures could be lower for many species. This would
371 have to be taken into account if parameters derived with our approach are applied to
372 situations with higher temperatures.

373 We found a weak negative correlation between hydrothermal time θ_{HT} and minimum
374 moisture $\Psi_{\min 50}$ in single-species but not in mixed-species pots, suggesting that both our
375 correlations may be spurious. Allen et al. (2000) also observed a negative correlation
376 between these two parameters, but it was caused by high values of hydrothermal time θ_{HT}
377 combined with low minimum soil moisture $\Psi_{\min 50}$ for halophytes that were not included
378 in our study. Thus, our study corroborates Allen et al.'s (2000) interpretation that the two
379 parameters are not correlated in non-specialized species.

380 If ecotypes of species are adapted to climate, seeds from more arid sites may be
381 expected to have lower minimum moisture requirements ($\Psi_{\min 50}$) to ensure that they
382 germinate in sufficiently wet soil, and low hydrothermal time thresholds (θ_{HT}) so that
383 germination is fast (Cohen 1967). However, we found no evidence that θ_{HT} or $\Psi_{\min 50}$, i.e.,
384 indicators of germination strategies, varied consistently with mean annual precipitation
385 along the climate gradient for all species combined. Nonetheless, both parameters,

386 especially θ_{HT} , differed among sites even within species. The variation could be correlated
387 with microclimate and other habitat characteristics that differ among sites, but the cause of
388 the variation could not be detected with our experiment. Similarly, Bauer et al. (1998)
389 studying *Bromus tectorum* also found variation of hydrothermal time θ_{HT} or minimum
390 moisture Ψ_{min50} among seeds of different sites. The site effect suggests that the difference
391 was already caused at the site of origin, maybe as a maternal effect (Andersson & Milberg,
392 1998). The lack of consistent variation of hydrothermal time and minimum moisture with
393 precipitation or climate does not mean that climate change could not have an effect on the
394 order of emergence among species. Less precipitation would reduce the germination
395 fraction according to eq. 3 even if the two parameters were constant.

396 We have estimated HTT parameters for 36 wild annual species from the eastern
397 Mediterranean. Although we have presented a quick way for calculating HTT parameters
398 from germination experiments, this does not replace specific experiments that investigate
399 whether and how HTT parameters vary systematically with environment of the seed, its
400 mother plant, taxonomy, or functional group. Nonetheless, our parameters can be used to
401 predict germination time courses (Fig. 4) and to calculate germination fractions depending
402 on available moisture. This may be applied, e.g., in succession models to predict changes
403 of vegetation due to changes in climate. HTT models may need modifications to meet the
404 purpose of the vegetation model (e.g., Rowse & Finch-Savage, 2002; Allen, 2003). This,
405 however, is often easier than obtaining estimates for HTT parameters. We conclude that
406 our parameters are useful for qualitative or comparative studies or for ecological models of
407 germination where the emphasis is on the order of germination and less on the
408 physiological mechanism of germination.

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479 **Tables**

480 Table 1. Germination parameters for annual plants in single-species pots. Seeds have been
 481 collected at four sites along a climatic gradient of aridity in Israel. Climate — mM: mesic
 482 Mediterranean (800 mm mean annual precipitation), M: Mediterranean (600 mm), s-a:
 483 semi arid (300 mm), a: arid (100 mm). Parameters – $\Psi_{\min 50}$: mean minimum soil moisture,
 484 θ_{HT} : hydrothermal time, t_{50} : median germination time, g_{\max} : maximum germination
 485 percentage. θ_{HT} and $\Psi_{\min 50}$ have been calculated for 5.5 °C, $T_{\min} = 0$ °C, and $\sigma(\Psi_{\min}) =$
 486 0.345 except where indicated. R^2 values are reported for linear regressions for each site
 487 within a species, if ANCOVA indicated that slope and intercept of the covariate (θ_{HT})
 488 differed among sites. Else, R^2 values refer to ANCOVAs constrained to parallel slopes
 489 (θ_{HT}) and variable intercepts ($\Psi_{\min 50}$) or to regressions across sites if intercepts did not
 490 differ either among sites.

491

492

Species in single-species pots	Climate	θ_{HT} (MPa·K·d)	$\Psi_{\min 50}$ (MPa)	t_{50} (d)	g_{\max} (%)	R^2
<i>Aegilops ovata</i>	mM	34	-0.98	7	61	0.98
<i>Aegilops peregrina</i>	M	40	-1.15	6	62	0.96
<i>Alyssum strigosum</i>	mM	26	-0.56	10.5	66	0.92
	M	26	-0.82	7	78	
<i>Atractylis cancellata</i>	s-a, M	36	-0.81	10	47	0.93
<i>Biscutella didyma</i>	mM	22	-0.82	7	72	0.90
	M	22	-0.97	5	46	
	a	22	-0.93	6	54	
<i>Brachypodium distachyon</i>	mM	38	-0.89	7	82	0.97
	M	38	-0.95	7	88	
	s-a	38	-0.96	10	90	
<i>Bromus fasciculatus</i>	M	40	-0.98	7	98	0.98
	s-a	40	-1.00	10	62	
	a	26	-0.87	6	88	
<i>Calendula arvensis</i>	s-a	35	-0.86	9	26	0.99
<i>Carrichtera annua</i>	s-a	25	-1.11	5	32	0.99
	a	25	-1.05	5	53	
<i>Catapodium rigidum</i>	mM	63	-1.03	11.5	35	0.95
	M	44 ^a	-0.74 ^a	10	57	
<i>Chaetosciadium trichospermum</i>	s-a	59 ^b	-0.92 ^b	14	45	0.98
<i>Crepis sancta</i>	M	24	-0.86	8	90	0.94
<i>Crithopsis delineana</i>	s-a	53	-1.20	10	50	0.99
<i>Filago contracta</i>	s-a	22	-0.88	6	47	0.95

<i>Gymnarrhena micrantha</i>	a	34	-0.85	7	66	0.96
<i>Hedypnois rhagadioloides</i> ^A	mM	36	-0.78	10	33	0.95
	M	36	-0.80	10	56	
	s-a	36	-0.67	12	25	
<i>Hedypnois rhagadioloides</i> ^B	mM	33	-0.94	6.5	38	0.98
	M	48	-0.94	12	41	0.94
	s-a	32	-0.82	8	41	0.98
<i>Lagoecia cuminoides</i>	mM	76	-1.15	12	40	0.82
	M	76	-1.39	10	47	
<i>Lolium rigidum</i>	M	47	-1.15	7	71	0.96
<i>Onobrychis squarrosa</i>	s-a	48	-0.80	12	16	0.97
<i>Plantago cretica</i>	mM	139	-1.00	33	50	0.85
	M	45	-0.59	22	29	0.81
	s-a	104	-0.89	27	17	0.82
<i>Plantago ovata</i>	a	38	-1.25	6	68	0.99
<i>Reboudia pinnata</i>	a	23	-0.87	6	55	0.96
<i>Reichardia tingitana</i>	s-a	32	-1.04	6	67	0.99
<i>Rhagadiolus stellatus</i> ^A	M	22	-0.94	5	91	0.98
	s-a	24	-1.03	5	82	0.99
<i>Rhagadiolus stellatus</i> ^B	mM	28	-0.64	11	37	0.91
	M	28	-0.89	6	50	
	s-a	28	-0.80	7	58	
<i>Stipa capensis</i>	M	26	-0.72	8	53	0.97
	s-a	24	-0.84	6	79	
	a	33	-0.81	10	40	
<i>Torilis tenella</i>	M	65	-1.18	10	42	0.98
<i>Urospermum picroides</i>	mM	35	-0.98	6	39	0.96
<i>Valantia hispida</i>	M	80	-1.20	14	76	0.95

493

494

495 ^A inner achene, ^B outer achene

496 adjusted $\sigma(\Psi_b)$: ^a 0.174, ^b 0.178

497

498

498 Table 2. Germination parameters for annual plants in mixed-species pots. Seeds have been
 499 collected at four sites along a climatic gradient of aridity in Israel. Symbols — see Table 1.
 500

Species in mixed-species pots	Climate	θ_{HT} (MPa·K·d)	Ψ_{min50} (MPa)	t_{50} (d)	g_{max} (%)	R^2
<i>Aegilops ovata</i>	mM	26	-1.03	6	62	0.90
<i>Aegilops peregrina</i>	M	34	-1.39	5	63	0.91
<i>Alyssum strigosum</i>	mM	23	-1.08	5	59	0.78
	M	23	-1.08	5	75	
<i>Atractylis cancellata</i>	M	31	-1.06	6	52	0.88
	s-a	31	-1.06	6	26	
<i>Bromus fasciculatus</i>	s-a, a	30	-0.96	7	73	0.92
<i>Bupleurum lancifolium</i>	s-a	88 ^a	-1.11 ^a	23	29	0.67
<i>Calendula arvensis</i>	s-a	24	-0.96	6	18	0.88
<i>Catapodium rigidum</i>	mM	47	-0.84	10	18	0.92
	M	81 ^b	-0.68 ^b	21	32	0.94
<i>Chaetosciadium trichospermum</i>	s-a	18 ^c	-0.52 ^c	3	56	0.90
<i>Coronilla scorpioides</i>	mM	73 ^d	-0.77 ^d	21	36	0.92
<i>Crepis sancta</i>	M	21	-1.14	4	91	0.96
<i>Crithopsis delileana</i>	s-a	28	-1.07	7	50	0.84
<i>Filago contracta</i>	s-a	35	-1.06	7.5	39	0.98
<i>Filago desertorum</i>	s-a	44	-0.99	8	42	0.81
<i>Geropogon hybridus</i>	M	25	-1.21	5	82	0.80
<i>Gymnarrhena micrantha</i>	a	40	-1.22	7	58	0.84
<i>Lolium rigidum</i>	M	27	-0.84	7	58	0.98
<i>Onobrychis squarrosa</i>	M	63 ^e	-1.21 ^e	16	19	0.87
	s-a	22	-0.68	7.5	15	
<i>Plantago afra</i>	M	14 ^f	-0.68 ^f	2	69	0.93
<i>Plantago cretica</i>	mM	75	-0.73	27	66	0.77
	M	75	-1.07	16	37	
	s-a	75	-0.67	27	15	
<i>Plantago ovata</i>	a	26	-1.04	6	61	0.94
<i>Reboudia pinnata</i>	a	22	-1.14	4	51	0.91
<i>Reichardia tingitana</i>	s-a	27	-1.07	6	76	0.74
<i>Rhagadiolus stellatus</i> ^A	mM	25	-0.69	7	41	0.91
	M	25	-0.80	10	59	
	s-a	25	-0.83	8	59	
<i>Scabiosa palaestina</i>	M	22	-0.75	5	21	0.95
<i>Stipa capensis</i>	M	26	-0.84	7	59	0.91
	s-a	26	-0.85	7	78	
	a	26	-1.03	5	44	
<i>Torilis tenella</i>	M	42	-0.94	8	22	0.84
<i>Trisetaria macrochaeta</i>	s-a	154	-1.51	21	20	0.82
<i>Urospermum picroides</i>	mM	34	-1.20	7	43	0.95
<i>Valerianella vesicaria</i>	s-a	41	-0.89	8	28	0.90

501
 502 ^A inner and outer achenes mixed
 503 adjusted $\sigma(\Psi_b)$: ^a 0.861, ^b 0.096, ^c 0.186, ^d 0.153, ^e 1.003, ^f 0.231

504 **Figures**

505 Fig. 1. Sensitivity of predicted cumulative germination of *Brachypodium distachyon* to an
506 increase (lower dashed line) and a decrease (upper dashed line) of 10% to both temperature
507 difference ΔT and minimum moisture variability $\sigma(\Psi_{\min})$. The continuous line indicates
508 the predicted cumulative germination derived in this paper. Circles connected with a
509 stippled line indicate observed values (recalculated for 100 sown seeds).

510

511 Fig. 2. Regression of hydrothermal time on median germination time of species from each
512 site germinated in A) single-species pots and B) mixed-species pots. Open circles represent
513 species with extreme combinations excluded from the regressions. Single-species: $\theta_{HT} = 7$
514 $+ 3.6 \cdot t_{50}$, $R^2 = 0.70$, mixed-species: $\theta_{HT} = 7 + 3.5 \cdot t_{50}$, $R^2 = 0.62$. Broken lines indicate
515 the 95% confidence interval.

516

517 Fig. 3. Correlation of hydrothermal time on minimum moisture requirement of species
518 from each site germinated in A) single-species pots (Pearson correlation coefficient $\rho = -$
519 0.40 , $P = 0.003$), and B) mixed-species pots (correlation not significant). The ellipses
520 indicate the 95% bivariate normal density: the more circular the ellipse the lower the
521 correlation. Points outside the ellipses are *Plantago cretica* from the mesic Mediterranean
522 and semi-arid sites and *Lagoecia cuminoides* from the Mediterranean site in A) and
523 *Trisetaria macrochaeta* in B).

524

525 Fig. 4. Observed and predicted cumulative number of newly germinated seeds
526 (recalculated for 100 sown seeds) of selected species. Predictions are for seeds in single-
527 species pots from Mediterranean climate, except *Carrichtera* (semi-arid).

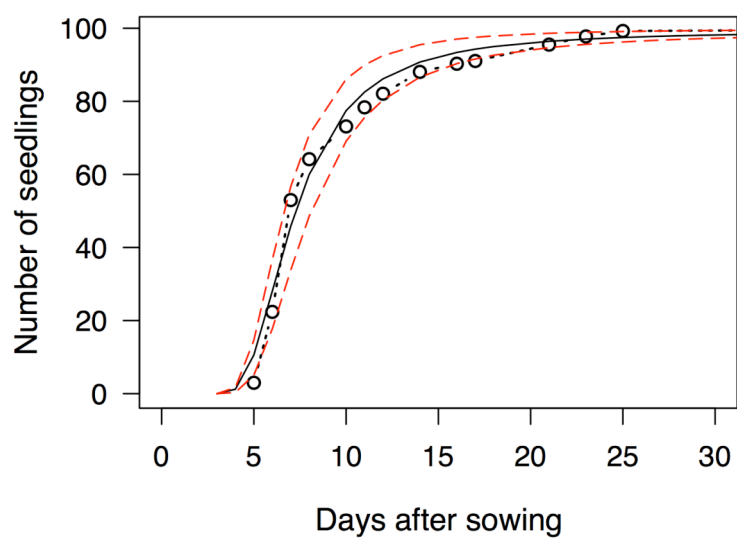


Fig. 1 Köchy & Tielbörger

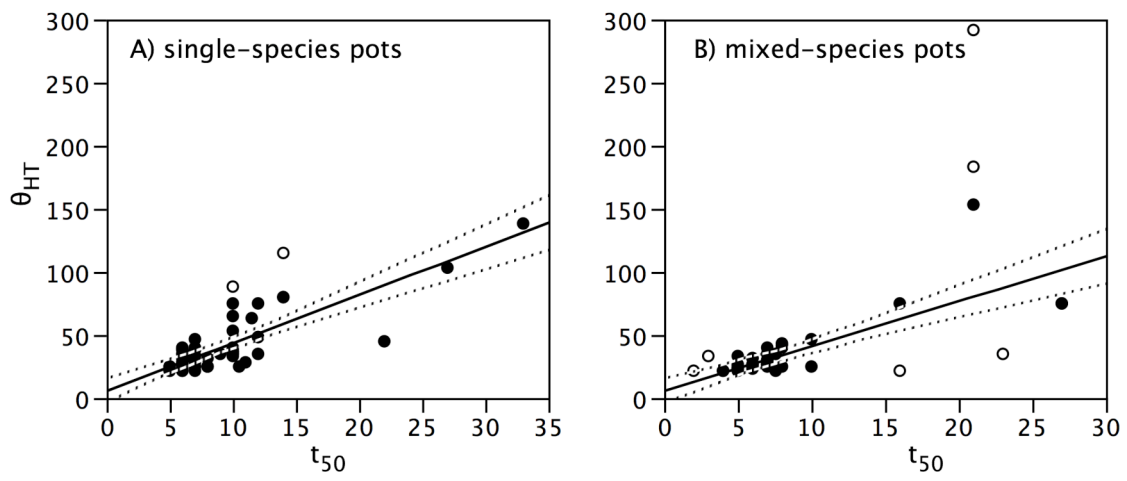


Fig. 2. Köchy & Tielbörger

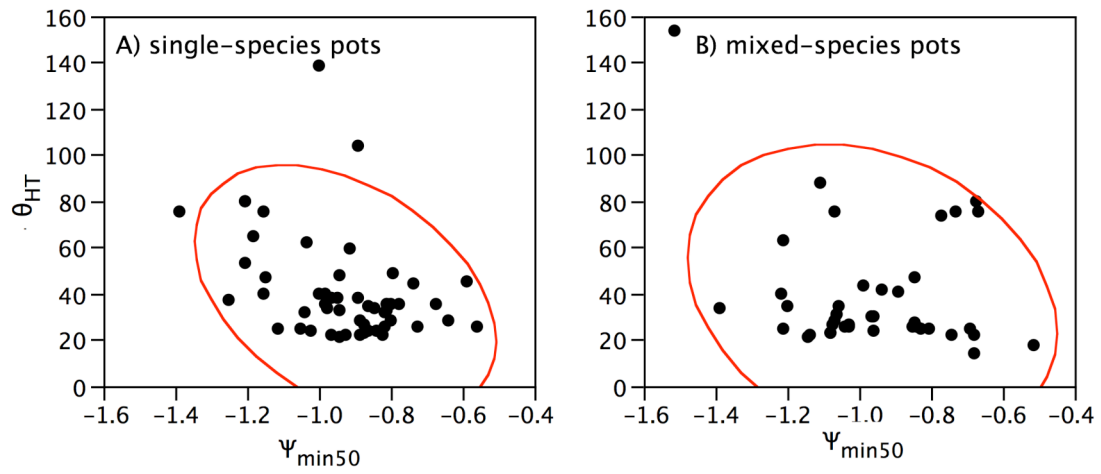


Fig. 3. Köchy & Tielbörger

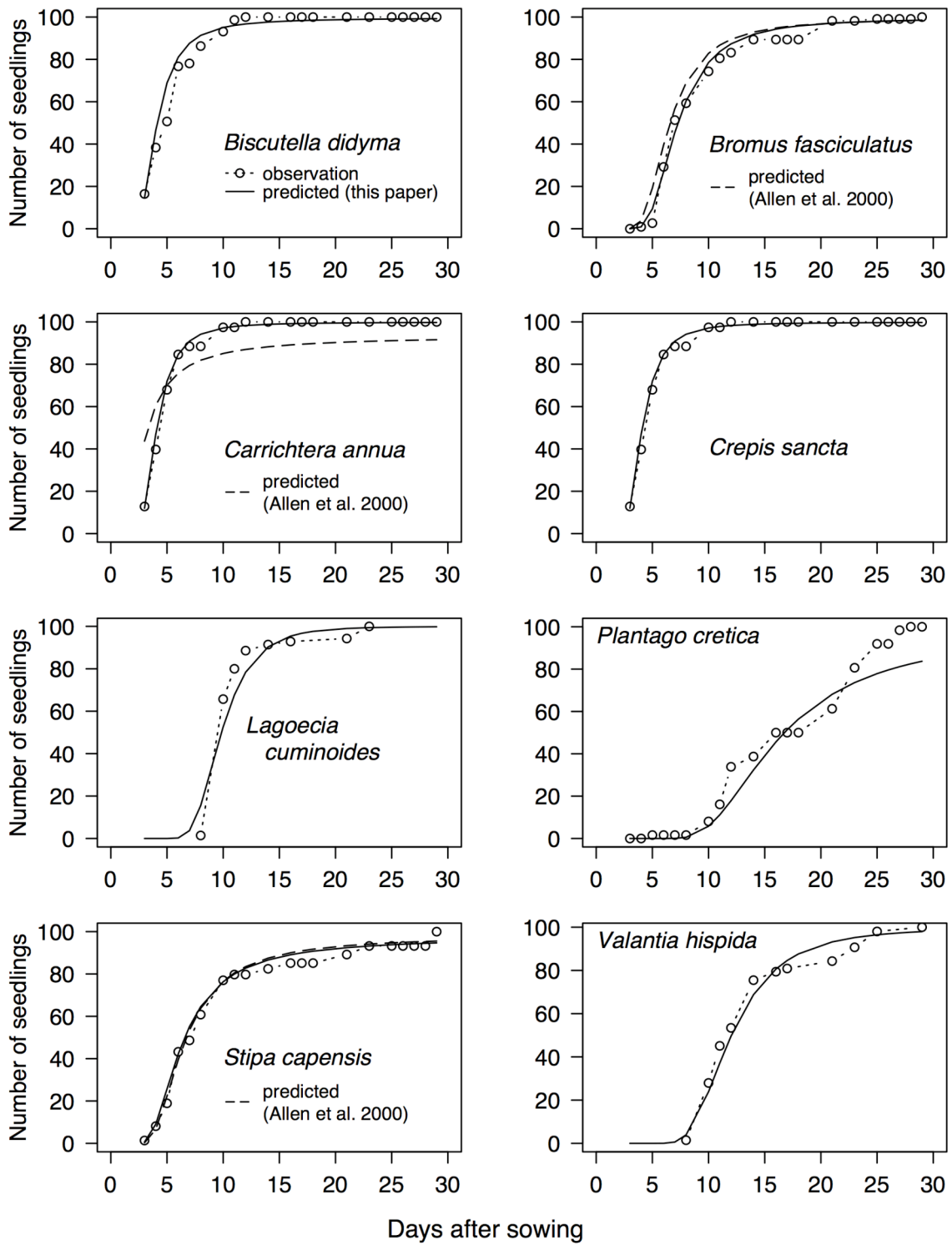


Fig. 4. Köchy & Tielbörger