A COMPARISON OF THE GERMINATION CHARACTER OF SPECIES OF CARYOPHYLLACEAE COLLECTED IN CENTRAL GERMANY

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INTRODUCTION

Earlier reports (Thompson 1968, 1970a, b), described experiments with seed of species of Caryophyllaceae obtained from the living plant collections at the Royal Botanic Gardens, Kew, or from wild populations growing in different parts of Europe. The results showed that certain parameters of the germination response—in particular the speed of germination at low temperatures, the maximum and minimum temperatures at which germination occurred, and the overall temperature span favouring germination—could be correlated with the geographical distribution of individual species. Thus, the temperature responses found for the germination of species distributed predominantly in deciduous woodland zones of Europe could be distinguished from those found for species growing around the Mediterranean, and, in turn, from those in steppeland areas of eastern and central Europe.

However, species which have quite different overall geographical distributions may be found in any locality. Their occurrence in one area may result from natural overlapping of their ranges, from localized variations in edaphic conditions, or from the activities of man which may support aliens under conditions which are naturally unfavourable to the long term survival of the population.

The observations reported here were made with a group of nine species all drawn from the sub-family Silenoideae of the Caryophyllaceae. The seed used had been collected during the summer and autumn of 1967 from wild populations growing around Halle in central Germany.

MATERIALS AND METHODS

The species used and the locations of the populations collected are listed in Fig. 1. Six of the species: *Silene dioica*, *S. alba*, *S. noctiflora*, *S. nutans*, *S. vulgaris* and *Lychnis viscaria* are widely distributed in deciduous woodland zones of Europe, characteristic of the area in which the collections were made. Of the other three: *Petrorhagia prolifera* and *Silene dichotoma* are steppeland species, possibly adventive from eastern Europe; and *Agrostemma githago* originated in the eastern Mediterranean, although it has been widely established as a weed of cultivation throughout Europe for several thousand years.

Tests were made either in incubators covering, at 5° C intervals, a temperature span from 6 to 31° C, or on thermo-gradient bars providing a complete temperature range from 0 to 40° C. Seeds tested in incubators were set up in fully randomized block/plot arrangements providing for each species five replicates of thirty seeds at each temperature condition. Daily germination counts were made during the first 8 days and then at longer intervals until the end of the experiment on the twenty-first day. Confidence limits at the 1% level, and '*F*' ratios were calculated by analysis of variance from the original data and are used to express significant differences in the tables of results below. The seeds, sown on a substrate composed of a weak mineral nutrient stabilized with agar at 0·75% and providing a pH of 5·8, were illuminated with low intensity light for 12 h each day from a 13 W Philips fluorescent tube set in the back of each incubator.

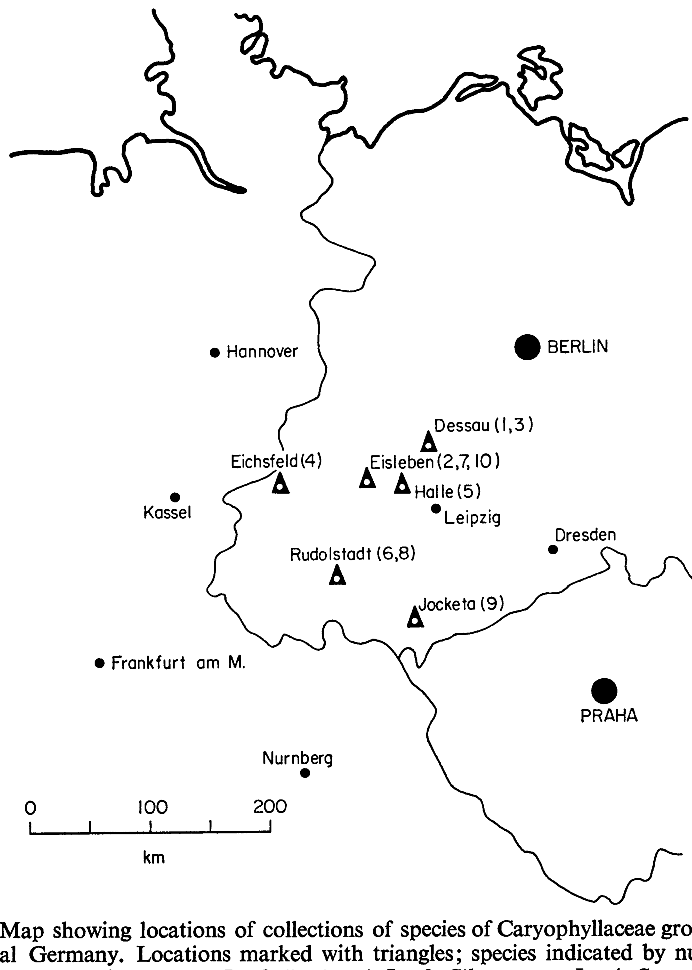


FIG. 1. Map showing locations of collections of species of Caryophyllaceae growing wild in central Germany. Locations marked with triangles; species indicated by numbers in parentheses. 1, *Lychnis viscaria* L.; 2, *L. viscaria* L.; 3, *Silene nutans* L.; 4, *S. noctiflora* L.; 5, *S. dioica* (L.) Clairv.; 6, *S. alba* (Miller) E. H. L. Krause; 7, *Agrostemma githago* L.; 8, *Silene dichotoma* Ehrh.; 9, *Petrorhagia prolifera* (L.) P. W. Ball & Heywood; 10, *Silene vulgaris* (Moench) Garcke.

Tests on thermo-gradient bars were done at pre-set temperature ranges. Each bar was divided into twenty-two sections of 2·5 cm and fifty seeds were sown in each section. Temperatures at the mid-point of successive sections differed from each other by about 1·5° C. Each section was manipulated as a unit for experimental purposes and germination counts were made from them in the same way as for experiments in incubators. The bars were lined with strips of 3 mm Whatman filter paper kept moist with water from reservoirs at the warm ends of the bar, and seeds were sown directly on the filter paper; for technical reasons it was not found possible to use agar in experiments on gradient bars.

RESULTS

Detailed results presented in Table 1 show the percentage germination rates of different species at different temperatures after incubation periods of 3, 5, 8, 14 and 21 days. The seed of any particular species germinated uniformly and rapidly over at least a part of the temperature range and, by the eighth day of the experiment, there were no significant differences between any of the species when tested at 21 and 26° C and only very small differences between them in tests made at 16° C. Consequently differences in germination behaviour between different species were largely confined either to the very early stages of the experiment, or to temperature conditions at either end of the range tested. Thus at 31° C, which was supra-optimal for most species, practically no germination occurred with *Agrostemma githago* and *Silene noctiflora*. However, a very high proportion of the seeds of *Petrorhagia prolifera* and *Silene dichotoma* germinated, and indeed for the first 7 days germination rates of these two species at 31° C were significantly better than those of any of the other species tested.

Similarly, at 6° C germination rates remained very low with *S. vulgaris*, *S. dioica*, both populations of *Lychnis viscaria*, and *Silene noctiflora*, were moderate with *S. dichotoma*, *S. nutans* and *Petrorhagia prolifera*, and very high with *Agrostemma githago*. The last was also notable for the rapidity of its germination both at 11 and 6° C. The germination behaviour of the two populations of *Lychnis viscaria* was very similar and differed significantly only at 31° C.

In Fig. 2 results, presented graphically for four species, illustrate the form of the germination curves obtained, and the nature of the differences between different species. The responses of *L. viscaria* and *Silene alba* were fairly similar in respect both to the speed of germination at different temperatures, and in reactions to temperatures at the upper and lower end of the scale tested. The pattern of germination of *S. dichotoma* was rather different in respect both to timing and temperature responses than those of the two former species, and that of *Agrostemma githago* appeared quite distinct from any of the other three. On the other hand expression of these apparent differences depends on quantitative distinctions which are difficult to render concisely, and which do not serve well as a vehicle for a comparative study of the differences in germination character between different species.

This problem arises from the difficulty of integrating a family of curves embodying the three dimensions of germination rate, time and temperature. The same problem is present to an even greater degree in the interpretation of results from thermo-gradient bars, and one method of resolving it used in other experiments (Thompson 1968, 1970a, b) is to plot, for a particular germination rate, the maximum and minimum temperatures at which germination occurs on successive days after sowing. The selection of a standard germination rate must be largely arbitrary, and in previous papers the curves presented have all been based on 50% of the maximum germination rate. In Fig. 3 curves are presented for the four species illustrated in Fig. 2 to show the results of plots made for germination percentages of 25, 50 and 75. The individual character of different species is much more readily apparent in these curves since the speed of germination over the optimal temperature range, and the positions of maxima and minima for germination, are clearly defined. The character of the curve is relatively stable irrespective of the standard

Table 1. *Percentage germination rates of species of Caryophyllaceae tested in incubators at different temperatures*

Species	Temperature (°C)					
(a) Incubation period: 3 days						
	6	11	16	21	26	31
Petrorhagia prolifera	0	1	94a	96ab	98a	97a
Silene dichotoma	0	5	94a	95abc	97a	90a
S. vulgaris	0	0	72b	92abc	96a	63b
S. dioica	0	0	8cd	68f	79b	57b
Lychnis viscaria (a)	0	0	1d	91bcd	94a	38c
L. viscaria (b)	0	0	4d	87cd	92a	21d
Silene alba	0	0	13c	71ef	67c	18de
S. nutans	0	0	7d	76e	79b	7ef
S. noctiflora	0	0	1d	84d	92a	0
Agrostemma githago	11	97	98a	97ab	97a	6f
(b) Incubation period: 5 days						
Petrorhagia prolifera	0	73	97ab	97	98a	97a
Silene dichotoma	0	88	96ab	95	97a	91a
S. vulgaris	0	20	90c	96	98a	72b
S. dioica	0	2	63e	88	88b	77b
Lychnis viscaria (a)	0	0	90c	98	95a	53c
L. viscaria (b)	0	0	93bc	92	96a	29d
Silene alba	0	15	76d	93	94a	41cd
S. nutans	0	14	88c	94	94a	42c
S. noctiflora	0	0	34f	98	97a	0e
Agrostemma githago	96	97	100a	97	97a	6e
				NSD		
(c) Incubation period: 8 days						
Petrorhagia prolifera	40	94a	97a	98	98	97a
Silene dichotoma	46	93a	97a	95	97	93a
S. vulgaris	0	36c	92bc	96	98	75bc
S. dioica	0	24c	82d	94	91	84ab
Lychnis viscaria (a)	0	63b	95ab	98	95	57d
L. viscaria (b)	0	57b	97a	93	96	30e
Silene alba	3	66b	89c	97	97	53d
S. nutans	5	94a	94ab	96	95	63cd
S. noctiflora	0	1d	79d	98	98	1f
Agrostemma githago	97	97a	100a	97	97	6f
				NSD	NSD	
(d) Incubation period: 14 days						
Petrorhagia prolifera	69b	96a	98a	98	98	97a
Silene dichotoma	56c	94a	97ab	95	97	94ab
S. vulgaris	4f	39d	92b	96	98	86abc
S. dioica	1f	89ab	86c	96	92	84bc
Lychnis viscaria (a)	2f	83bc	95ab	98	96	73d
L. viscaria (b)	0f	83bc	98a	93	96	38e
Silene alba	29e	79c	92b	98	98	84bc
S. nutans	48d	95a	95ab	97	95	79cd
S. noctiflora	1f	81bc	79d	98	98	1f
Agrostemma githago	97a	97a	100a	97	97	6f
				NSD	NSD	
(e) Incubation period: 21 days						
Petrorhagia prolifera	69b	96a	98a	98	98	97a
Silene dichotoma	56c	94ab	98a	95	97	94ab
S. vulgaris	4e	42e	92b	96	98	87abc
S. dioica	2e	92ab	87c	96	93	84bcd
Lychnis viscaria (a)	8e	86bcd	95ab	98	96	75d
L. viscaria (b)	2e	84cd	98a	93	96	40e
Silene alba	37d	81d	92b	98	98	87abc
S. nutans	51c	95a	96ab	97	95	81cd
S. noctiflora	3e	89abc	82d	98	98	1f
Agrostemma githago	97a	97a	100a	97	97	6f
				NSD	NSD	

(a) *Lychnis viscaria* from Dessau; (b) *L. viscaria* from Eisleben.

A common suffix (within a single column) indicates no significant difference between the results at the 1% confidence level. NSD at the bottom of a column indicates no overall significant differences between the figures based on '*F*' ratios obtained by analysis of variance.

germination rate selected, but, as in *Silene alba*, the positions of maxima and minima may shift appreciably depending on which rate is chosen, and, in the absence of obvious criteria on which to base a reasoned selection, the standard germination rate adopted here and elsewhere has been the 50% level.

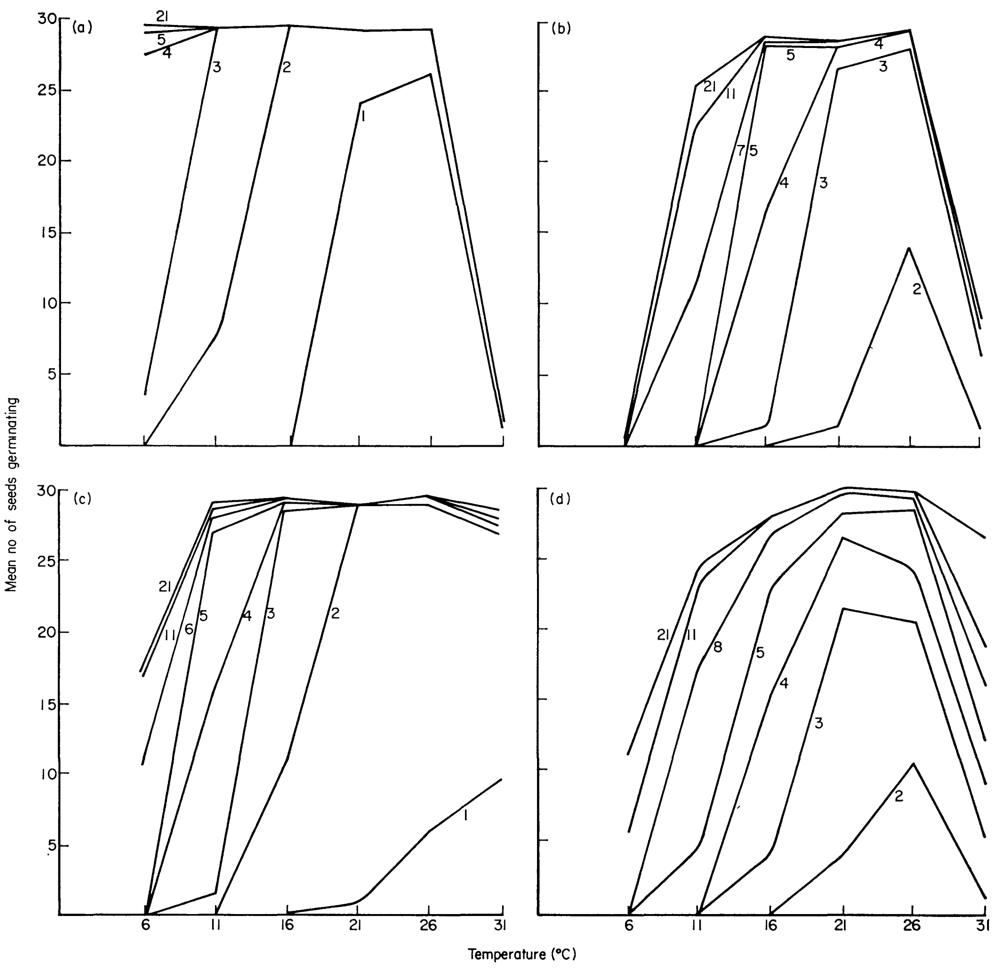


FIG. 2. Germination responses on successive days of four species tested in incubators at temperatures set at 5° C from 6 to 31° C. Numerals on graphs indicate incubation period in days prior to counting. (a) *Agrostemma githago*; (b) *Lychnis viscaria*; (c) *Silene dichotoma*; (d) *S. alba.*

Germination curves for all nine species plotted for a standard 50% germination rate are shown in Fig. 4. Comparison of the curves in this figure with the detailed germination data presented in Table 1 shows that although the germination curves present a greatly simplified synthesis of the original data, and are based on an arbitrarily standardized proportion, yet in general they represent the situation found in the detailed analysis very accurately. Thus the curves for *S. dichotoma* and *Petrorhagia prolifera* in Fig. 4(a) are closely similar throughout their length; in Table 1 it was shown that no significant differences were found between these two except at 6° C towards the end of the experiment. Of the four species tested in Fig. 4(b) each appears, with the possible exception of *Silene vulgaris*, to be closely similar in respect to its maximum temperature for germination. In Table 1 it was shown that the germination rates of these species at 31° C did not differ significantly after the fourteenth day, although there were differences within the group on the fifth and eighth day, corresponding to the variations in form of the graphs in Fig. 4(b) after short incubation periods. At low temperatures a much more complicated pattern of difference is apparent in Table 1 and this is also reflected in the form of the curves; for instance at 11° C *S. vulgaris* germinated significantly less well than any of the other three species (in Fig. 4b) and both it and *S. dioica* scarcely germinated at all at

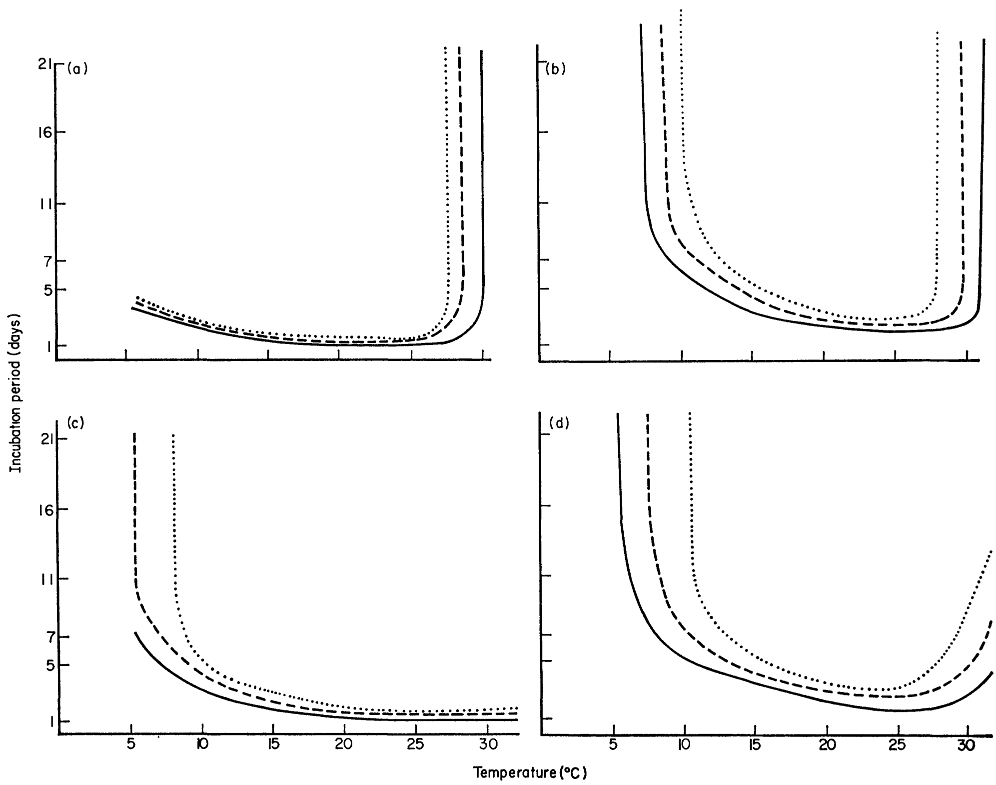


FIG. 3. Graphs obtained from those illustrated in Fig. 2 by plotting, for successive days, the maximum and minimum temperatures at which particular percentage germination levels were reached. Values were plotted for 25% (——), 50% (- - -) and 75% (· · ·). (a) *Agrostemma githago;* (b) *Lychnis viscaria;* (c) *Silene dichotoma;* (d) *S. alba.*

6° C. Germination rates of *S. nutans* on the fourteenth and twenty-first day were higher than those of *S. alba* and the differences at 11° C on the eighth day also favoured *S. nutans*. In Fig. 4(c) the similarity in the position of the minimum temperature for germination reflects the absence of significant differences in the behaviour of the three species in counts on the twenty-first day at 6 and 11° C. At the upper end of the temperature scale no significant differences were measured between these three batches of seed at 26° C but there were differences throughout the experiment at 31° C suggesting that the apparent small differences in temperature maxima shown in Fig. 4(c) probably reflect real differences. Thus the order and positioning of the species in Fig. 4 accurately reflect

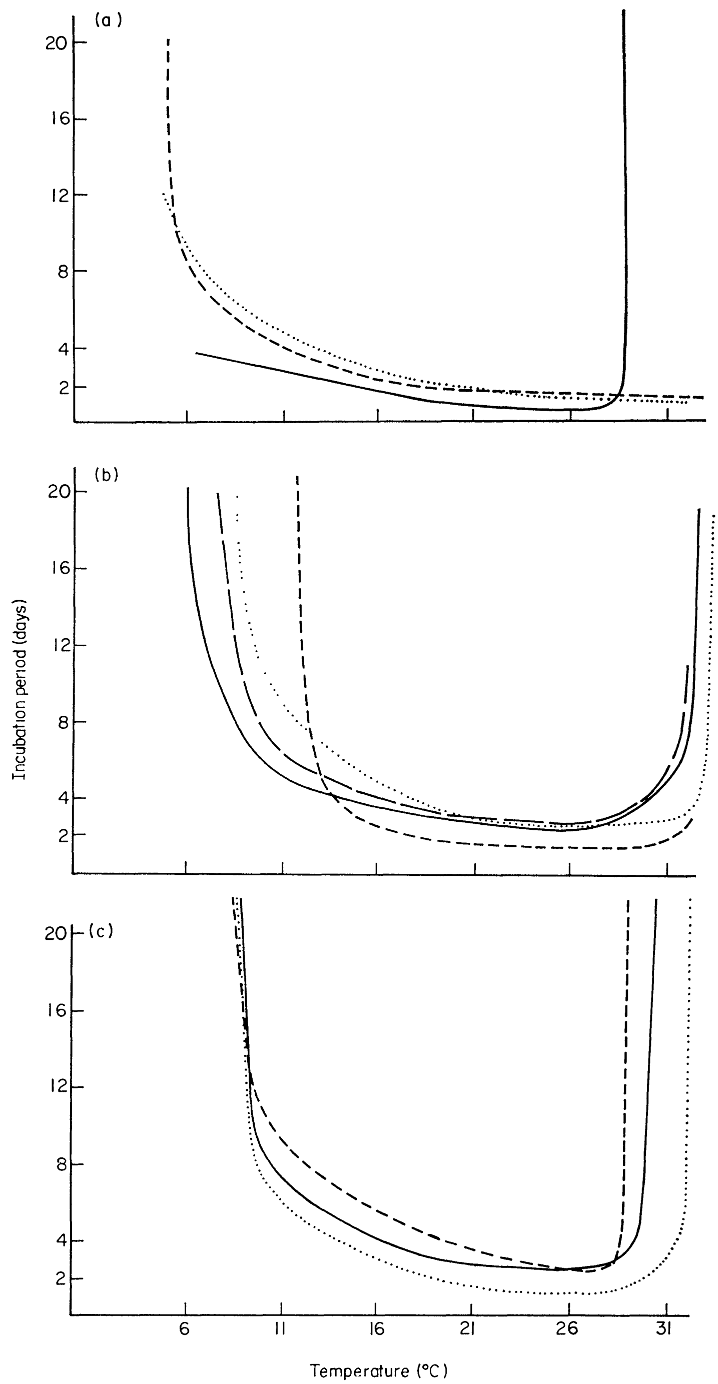


FIG. 4. Germination response curves plotted as the maximum and minimum temperatures providing a 50% germination rate on successive days after sowing seeds of nine species of Caryophyllaceae. (a) *Silene dichotoma* (– – –), *Petrorhagia prolifera* (· · ·), *Agrostemma githago* (——); (b) *Silene nutans* (——), *S. alba* (— —), *S. dioica* (· · ·), *S. vulgaris* (– – –); (c) *S. noctiflora* (– – –), *Lychnis viscaria* 'a' (· · ·), *L. viscaria* 'b' (——).

specific variations presented in a much more complicated and less readily comparable form in Table 1.

The results presented so far were obtained from experiments in incubators covering a limited range of temperatures, and providing information only at intervals of 5° C. The positions of temperature maxima and minima for several species were beyond the range of temperatures set and could not be determined. It could also be argued that the wide intervals between successive temperatures resulted in too great a reliance on extrapolated values for the calculation of the germination character curves in Figs. 3 and 4. A better way of measuring temperature responses is to use thermo-gradient bars covering

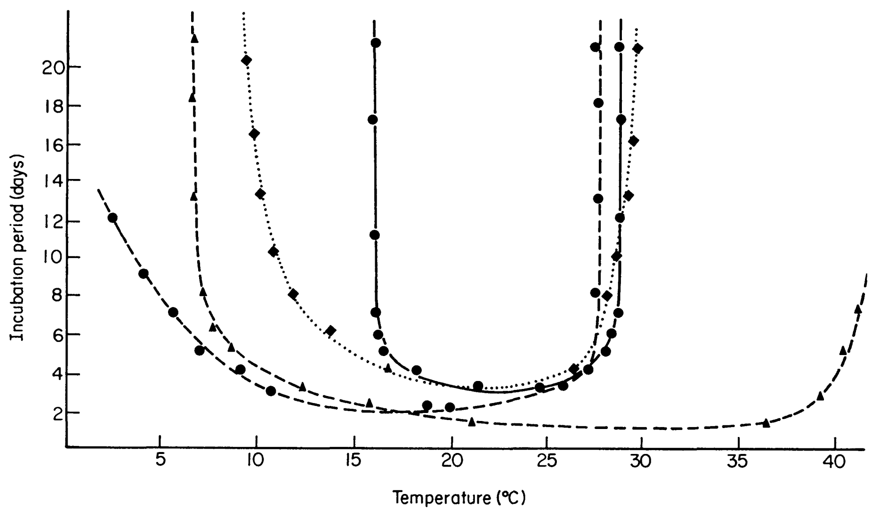


FIG. 5. Germination response curves for maximum and minimum temperatures providing a 50% germination rate on successive days. Tests were made, for four species, on thermo-gradient bars set to cover the range 2–42°C. *Agrostemma githago* (– – ● – –); *Silene dichotoma* (▲); *Lychnis viscaria* (◆); *Silene noctiflora* (— ● —).

a wide range of temperatures on which measurements of germination may be made at many more points along the temperature range covered. In Fig. 5 results are presented for four species tested in this way with germination counts made on successive days after sowing over the range 2–42° C at *c.* 1·5° C intervals. Comparisons of these germination curves with those in Fig. 4 show almost identical maxima in both experiments for *Agrostemma githago*, *Silene noctiflora* and *Lychnis viscaria*, and closely similar minima for *L. viscaria* and *Silene dichotoma* although the minimum for *S. noctiflora* varied between the two experiments by more than 5° C. Borriss (1952) has demonstrated that germination rates in this species are sensitive to the nature of the substrate and this could be the cause of the differences found here. Fig. 5 also provides a complete expression of the

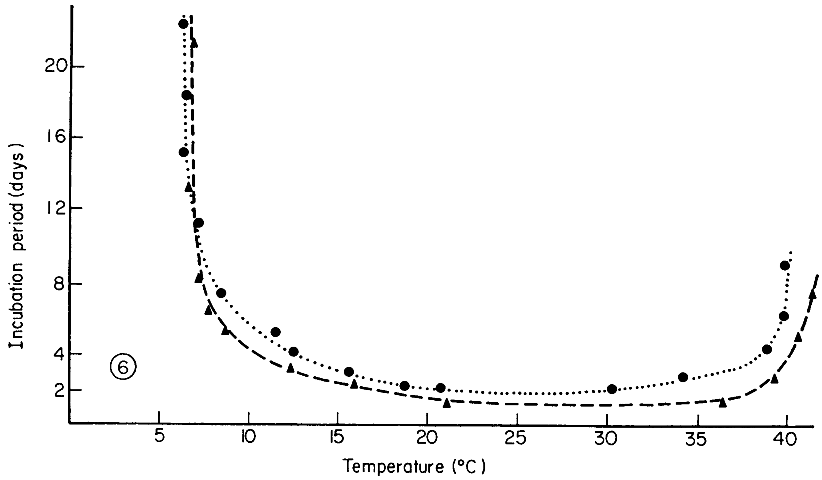
FIG. 6. Germination response curves obtained from plots at the 50% level for populations of *Silene dichotoma* from (a) Eisleben, central Germany (▲); (b) Valais, Switzerland, 1300 m.s.m. (●).

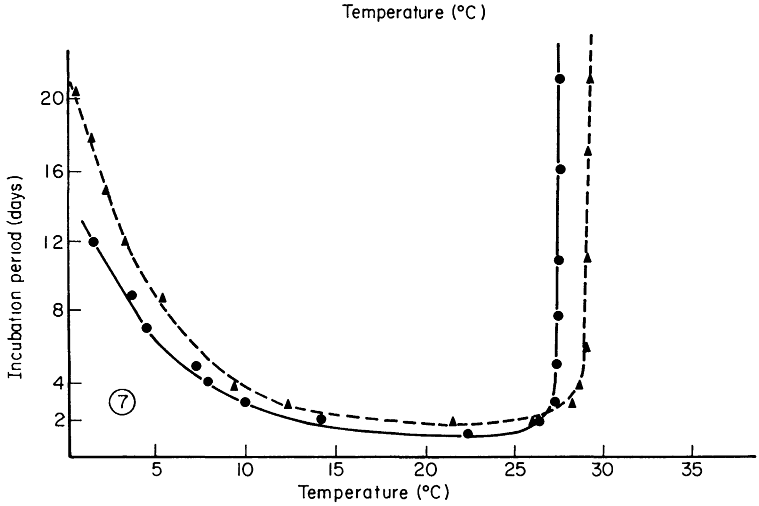
FIG. 7. Germination response curves obtained from plots at the 50% level for populations of *Agrostemma githago* from (a) Strykowo, Poland (●); (b) Jezainville, France (▲).

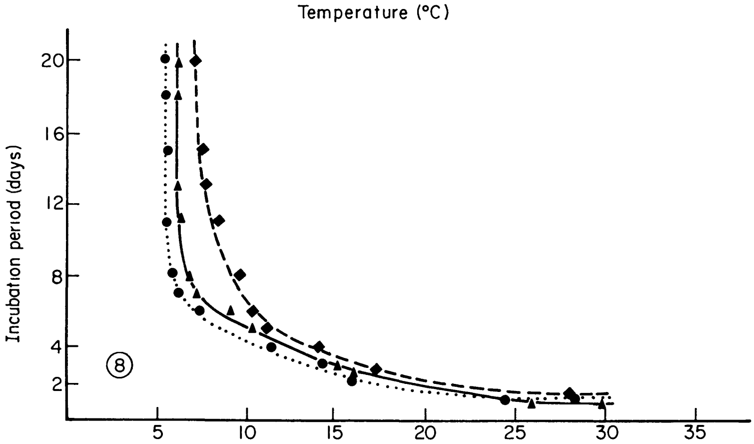
FIG. 8. Germination response curves obtained from plots at the 50% level for populations of *Petrorhagia prolifera* from (a) Art-sur-Meurthe, France (●); (b) Ain, France, 600 m.s.m. (▲); (c) Budapest, Hungary (◆).

germination responses of *Agrostemma githago* and *Silene dichotoma* for which minimum and maximum values respectively were unobtainable in the experiments in incubators.

The results of these experiments suggested broad similarities, overlying varying degrees







of differences, between the six species characteristic of deciduous woodland zones of Europe. Thus the temperature minima for a 50% germination rate in the group never fell below 6° C and, with the exception of *S. noctiflora* in Fig. 5, never rose above 11° C, and temperature maxima consistently fell between 28 and *c.* 32° C. Of the other three species, *Agrostemma githago* possessed a much lower temperature minimum than any other tested, and its maximum was also lower than any of the other species, though by only about 1° C in relation to *Silene noctiflora. S. dichotoma* and *Petrorhagia prolifera* were closely similar to each other, and temperature maxima were higher than those of any of the other species, and minima lower than any apart from *Agrostemma githago*. It could be argued that these three species, which have already been identified as possible adventives within the region, each possessed germination characters which were outside the normal range found for those species considered to be typical of deciduous woodland zones of Europe. More information on the correlations existing between geographical distribution and germination character is presented elsewhere (Thompson 1970a, b).

The preservation within a species of an alien character, as implied here, suggests that the germination responses of adventives, in this case well established as weeds, may not necessarily show obvious signs of adaptation in response to a changed environment. This point was examined in more detail for these three species by comparing the germination responses of populations of seed obtained from different parts of Europe. Two populations of *Silene dichotoma* were compared (Fig. 6), one from Eisleben in central Germany, the other collected in the Valais in Switzerland at *c.* 1300 m.s.m. Two populations of *Agrostemma githago* (Fig. 7) were compared, from Strykowo in Poland and from Jezainville in eastern France, and three populations of *Petrorhagia prolifera* (Fig. 8), from Art-sur-Meurthe in eastern France, from Budapest and from 600 m.s.m. in the Juras in eastern France. Only small differences were found, for any particular species, between the germination character of populations from different localities or altitudes, and in each case the characteristics of all the populations were closely similar to those already determined for the same species growing in central Germany.

DISCUSSION

The interpretation of the results of experiments in incubators or on thermo-gradient bars is frequently complicated by the quantity of data that must be scanned, and the changing emphases produced when differing incubation periods are compared. Simplification of the data to the point where the germination behaviour over a wide range of temperature and time may be expressed in the form of a single curve can be achieved by the method described in this paper. Curves obtained in this way have been used here or elsewhere to compare the responses of different species: of different populations of a species (Thompson 1970a); to assess the effects of the application of germination promoters and inhibitors; and to measure responses of seeds to preliminary after-ripening or chilling treatments prior to the start of incubation (Thompson 1970b).

The interpretation of these curves, especially in relation to the ecology of different species, requires great caution. Laboratory tests may not reflect accurately results occurring under natural conditions; thus Morley (1958) has shown that seed germination of subterranean clover is restricted in laboratory tests relative to field conditions, and Wesson & Wareing (1969) have shown that germination responses to light may be quite different when compared under field and laboratory conditions. Germination is not a stable character but may vary greatly at different times after the seed matures or in response to external conditions such as light or pre-conditioning treatments, and Salisbury (1965) has shown that the progressive reduction in dormancy effects associated with after-ripening may proceed at quite different rates in the soil and under dry storage conditions in the laboratory. Finally there may be differences in germination requirements occurring within the sample of seed used. These may reflect visible differences in seed morphology as shown by New (1958) in populations of *Spergula arvensis* collected in different parts of Britain. Or there may be differences between individual plants within a population, or between seeds obtained from different parts of the same plant as found in a study by Cavers & Harper (1966) on species of *Rumex*.

The effects of some of these factors on species used in this study have been examined in parallel experiments and are published elsewhere (Thompson 1970a, b). Many of the species show a restricted temperature response for germination in the first months after harvest, similar to that described by Borriss (1940) for *Agrostemma githago*, but within 1 year in dry storage a stabilized condition is attained (i.e. the seed is fully after-ripened) after which few, if any, further changes occur. The seed used in these experiments had completed post harvest after-ripening processes, and was also exposed to light for long periods each day during incubation. Certain variables were therefore eliminated but other important factors such as the effects of pre-conditioning treatments at high or low temperatures, the effects of variations in moisture stress or the gaseous atmosphere, were untested and it is not suggested that conditions of the tests simulated natural conditions.

It has been shown (Thompson 1968, 1970a, b) that correlations may exist between the germination character of a species, determined in the way described here, and its geographical distribution. All these species are characterized by a strong tendency towards simultaneous germination, following the definition of Salisbury (1929), over a moderately wide span of temperatures. The main differences between species were found in the temperature maxima and minima for germination and hence the position of the temperature range favouring germination, and it is on these characters that correlations with geographical distributions are determined. Thus the main factor influencing the timing of germination in this group appears to be the germination response to temperature modulated according to the progress of after-ripening. The situation is rather similar to that found for desert annuals by Went (1949) in which he showed that the representation of species within a population of seedlings was closely correlated with temperature, resulting in substantially distinct winter and summer annual floras.

The experiments reported here were done with a group of quite closely related species collected from a restricted geographical locality. Some of the species are distributed throughout the greater part of the deciduous forest zone of Europe typical of the area in which collections were made, and some species, which may be adventive in the area, have natural geographical distributions in steppeland or Mediterranean areas of Europe and Asia Minor. The results showed that the adventive species possessed germination characteristics which could be distinguished from those of the other six species, and also that germination responses of populations of the adventive species were markedly similar when comparisons were made between collections from different parts of Europe.

This implies that the fundamental germination character of a species may not necessarily change on transposition by man, even when the species has been maintained for a lengthy period in an alien environment, as is the case with *A. githago*. This interpretation must be accepted with reservation in view of a conflict of evidence on the point arising from the results of other workers. Thus Stearns & Olson (1958), McNaughton (1966), McWilliams, Landers & Mahlstede (1968) working with *Tsuga canadensis*, *Typha* species and *Amaranthus retroflexus* respectively have reported differences in the germination responses of populations from different parts of North America, and Harper (1965) notes that the germination requirement of a species may differ markedly over its geographical range, although Lauer (1953) found few differences in the responses of *Agrostemma githago* and *Datura stramonium* collected in various parts of Europe.

However, ecotypic variations in the physiological responses of European species are well authenticated with respect to plant height and flowering time (e.g. Turesson 1930) and a recent review by Hiesey & Milner (1965) has spotlighted the wide range of adaptive responses found in natural populations to variations in nutrient status, photoperiod, temperature and rates of photosynthesis and respiration. These examples of physiological adaptations to environment prevent an easy acceptance of the suggestion that the physiological responses involved in germination may be relatively non-plastic. But it is suggested that the examination of this problem depends largely on a concise, simple method of making comparisons of germination responses to different conditions such as the one described in this paper.

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SUMMARY

Germination behaviour of seed collected from natural populations of nine species was compared to establish the pattern of responses to temperature. Tests in incubators and on thermo-gradient bars were compared and the results used to provide curves integrating effects of temperature and time to provide simple comparisons of the germination character of different species.

It was found that six species naturally distributed in the locality all shared common features in their response to temperature, and varied in detail only, with respect to the positions of temperature maxima and minima. Three adventive species, maintained as weeds of cultivation, possessed distinctive germination characters, which appeared to be correlated with conditions in their area of origin. Populations of each of the three species collected in other parts of Europe showed similar responses, suggesting that the germination character of these species does not change on transposition by man to an alien environment.

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