RESEARCH INTO SEED DORMANCY AND GERMINATION

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INTRODUCTION

Stocks of seed of horticultural and agricultural crop plants must possess germination characteristics which result in rapid germination of a high proportion of the seed to produce evenly distributed, evenly developed stands of plants. Amongst crop plants particular restrictions in the range of conditions which result in germination may limit the geographical range of the plant or determine particular procedures for its cultivation; for example, high temperature sensitivity of leek seed prevents germination in low latitudes or during the summer in higher ones, and the requirements of celery seed demand greenhouse conditions for successful germination in the spring.

Since it is possible to find dormancy mechanisms still restricting germination in seeds of a crop plant as ancient as the leek it is not surprising that such mechanisms should be present in the seeds of plants taken more recently into cultivation, such as hardy ornamental nursery stock, both shrubby and herbaceous, which are the day to day concern of the nurseryman Indeed, in these plants, germination may be so restricted or so uncertain from one year to the next that use of seeds as a means of propagation may be reduced to the point where it is abandoned and replaced by some means of vegetative propagation. This is, of course, a necessary procedure for the multiplication of selected forms, but its use in other cases means that the nurseryman may forgo the advantages of raising stock from seed in favor of a form of multiplication which inherently increases the risk of virus dispersal and stereotypes plant variation in a way which may limit the range of interest within the species and increase the chance of epidemic disease.

Reluctance to depend on seed germination may stem, as implied in the previous paragraph, from poor results when this method has been attempted. Modern requirements tending to more and more precision in the growing of plants set a high standard for a satisfactory performance. Thus it may be, if some form of spaced sowing to obviate pricking-out is used, and if heated glasshouse accommodation is to be used fully, that the nurseryman's requirements fall not far short of those of the farmer or grower who, protected by the Seed Acts expects an assured minimum year-to-year germination within a short period of sowing Perhaps one could go so far as to state this aim in terms of a 75% germination within a fortnight of sowing; if one does so the statement serves well to exemplify how far short the performance of most nurserymen's seed samples falls.

This paper does not attempt to provide information for obtaining such a standard for even a small proportion of species, but is concerned first with a discussion of the part that dormancy plays in the natural distribution and survival of plants and, second, with a few of the techniques that may successfully be used to overcome seed dormancy and induce germination.

DORMANCY IN RELATION TO PLANT DISTRIBUTION

Apart from its main function as the means of propagation of a species from one generation to another the seed also serves other important natural functions. It provides a state of refuge by which plants may survive adverse conditions, such as intense drought or cold, and then ensures that a part, often the larger part, of a plant population in a given area exists in a protected condition most likely to survive the ordinary or even the extraordinary seasonal hazards of the locality. It provides a condition in which plants may easily be transported to extend the range of a species, and also one in which plants may remain present in the ground, sometimes over periods of many years being, therefore, the main agent by which plants are dispersed in time and space.

It can easily be understood that not only must the seed be capable of germination, but also that it must possess checks and controls which act to prevent germination at one time but to permit it at another. These controlling mechanisms, contained within the seed, are actuated or triggered by external conditions such as temperature, light, water tension or the gaseous content of the surrounding soil which provide physical or chemical stimuli to which the seed can respond. The seed's response to these external stimuli is very often modified as time passes by internal changes occurring within the seed itself. Thus germination is dependent on a combination of external stimuli and internal conditions and consequently can be precisely controlled to occur only in response to particular conditions occurring only at particular seasons of the year. Successful adaptation of a species to a geographical area depends on the triggers which promote germination being operated in such a way that when germination does occur it does so at a season which promises a high chance of survival and maturation for the resulting plant Therefore germination controls must be clearly correlated with climatic features of the geographical region in which the species occurs, not only reacting to the stimuli of the past, but also reflecting the conditions of the future.

It is reasonable to suppose that a better understanding of the seed germination behavior of a species in relation to the climate of its natural habitat would provide a valuable guide to the controls regulating dormancy and the conditions needed to promote germination. The discussion which follows draws examples from the European flora to illustrate, for a region in which both the flora and the main climatic features are generally well understood, some of the ways in which climate and germination responses may be linked. The main physical parameters limiting plant growth in the area are: the severity of winter cold (Fig. 1); the severity of summer drought (Fig. 2), and the overall length of the growing season (Fig. 3). There are

Fig. 1. Severity of winter cold. Temperature minima and duration of coldest period.

many ways in which Europe may be divided geo-botanically, but a very simple division is to distinguish five main regions, represented by shading in Figures 1, 2 and 3. The intention here is to consider the climate of these regions in relation to the conditions regulating seed germination of some of the plants which are found within them.

a. **The Mediterranean Basin.** The dominant feature of this area is the regular occurrence of drought during the summer broken, especially in the western parts, by occasional thunderstorms which provide short periods when moisture is readily available but separated

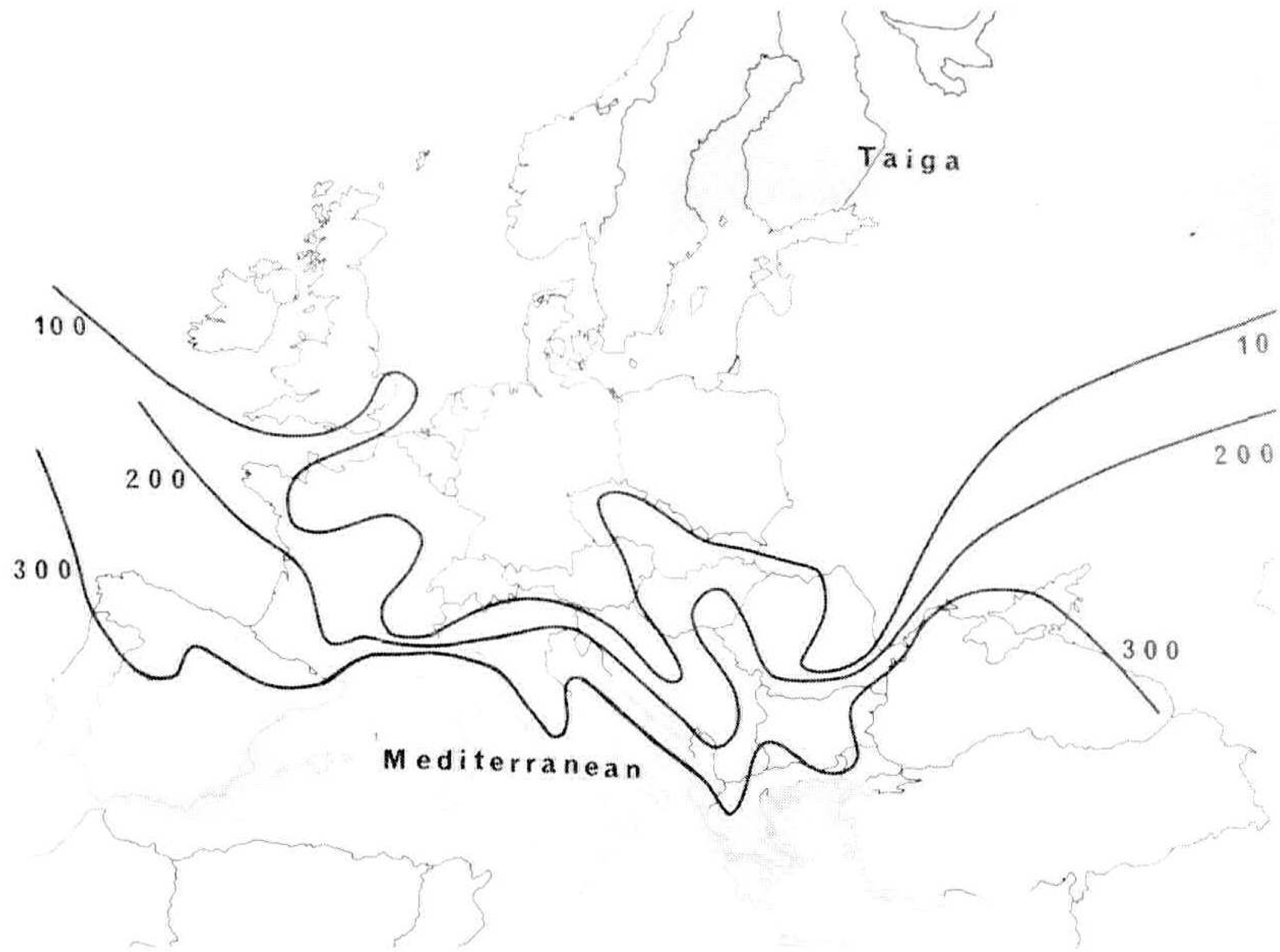

Fig. 2. Severity of summer drought. Average precipitation deficits (mm) — June, July, August.

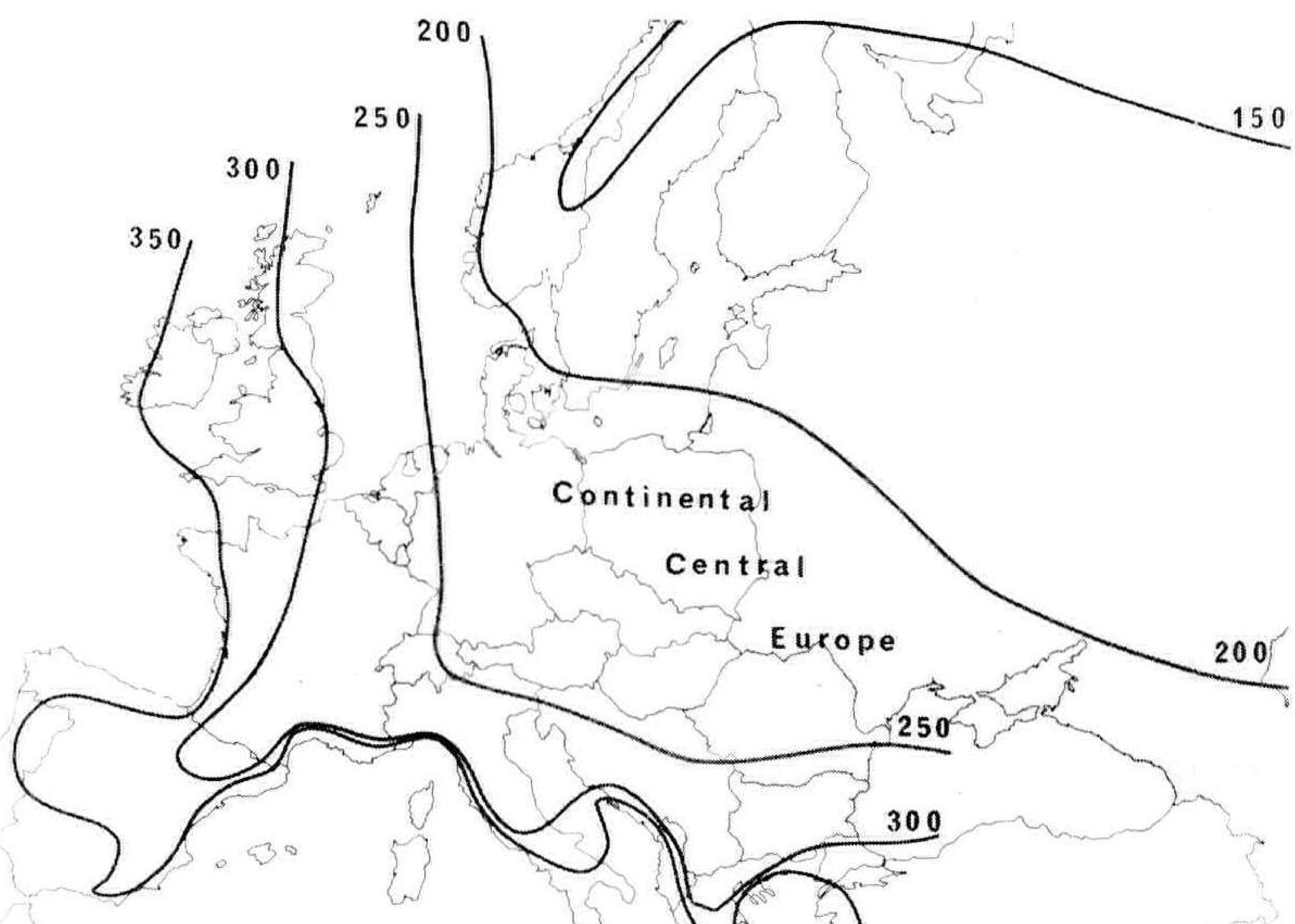

Fig. 3. Length of growing season. Mean days each year with average air temperature above 5° C (41° F) in Europe.

by long periods of intensely arid conditions. In the true mediterranean region winters are mild with a mean minimum for the coldest month around 3-5° C. (37-41° F.). However many areas which are generally mediterranean in character have colder winters than this due either to exposure to cold winds or to altitude Dry summers and mild or cool winters result in a situation where the main season for growth of herbaceous plants lasts from September to April, broken in the colder areas by low temperatures in mid-winter, and where annuals, in particular, survive the summer as seeds. Germination normally occurs as temperatures start to fall in early autumn coincident with the start of the winter rainfall Survival of species within this area depends on their seeds remaining dormant immediately after they are shed in the late spring and during short periods of intermittent moisture in summer, to germinate later under cooler conditions in September or October. The results of germination tests made with seeds of three species from the Mediterranean area are shown in Table 1. An overall view shows that in each case the seeds germinate best at the lower temperatures, though not necessarily at the lowest. They

Table 1.Germination (percentage) of seed of three species of Mediterranean origin comparing responses at a range of temperatures using freshly gathered seed compared to stored dry in the laboratory for six months.

Ranunculus chius. (Southern Greece):

	Day / Night temp. (° C)					
	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Fresh seed	77	49	67	0	0	0
Stored seed	87	96	87	85	72	0

Anemone coronaria. (Israel):

	Temperature of test (° C)					
	6	11	16	21	26	31
Fresh seed	9	68	72	0	0	0
Stored seed	2	91	87	39	0	0

Mandragora officianalis. (Cyprus):

	Temperature of test (° C)					
	6	11	16	21	26	31
Fresh seed	1	4	12	18	0	0
Stored seed	7	79	100	96	81	0

also show that the germination responses change during storage so that six months after harvest a higher proportion of the seeds germinate over a wider temperature range than was the case when they were freshly shed. Thus at the time the seeds are shed they are in a partially dormant condition so that few or none will germinate at the prevailing soil temperatures During the summer high soil temperatures prevent germination, even if moisture is present, but after-ripening processes occurring within the seed steadily increase the maximum temperature at which germination occurs so that once soil temperatures start to fall in the autumn the first significant rainfall will create conditions in which a very high proportion of the seeds will germinate. Seed dormancy in species occurring in this area is most commonly of this type, induced by exposure to high temperatures and absent at lower ones. In some species high temperatures induce a condition known as secondary dormancy, after which the seed will germinate only if first exposed to temperatures close to freezing point but, in general, chilling treatments of this kind do not appear to be necessary for securing germination of typically mediterranean plants.

b **Continental Central Europe.** This large and complex area contains a variety of distinctively different floristic regions, but is characterized by the occurrence of a continental climate in which winters are cold and summers warm to hot. The length of the growing season decreases and the severity of winter cold increases as one goes east and north from the Atlantic Ocean. Summer drought is a regular feature in the southern parts of the region and particularly in the eastern parts where it is responsible for the development of steppe-like regions in which grassland is the dominant component. Elsewhere the climax vegetation is usually deciduous forest and summer droughts, although sometimes occurring, are neither regular nor severe. Over most of the region the growing season is moderately long. Plant establishment in the area depends, therefore, on adaptations which enable survival through the winter and short periods of drought in the summer The effects of winter cold are tempered by the presence, for long periods, of snow cover which shelter the plants from dessication by wind and protect them from the attacks of mammals, insects, molluscs and fungi by reducing the activity or growth rate of these predators and pathogens. This produces a situation in which many plants survive the winter as seedlings to grow away rapidly as soon as warmer weather comes in the spring to produce flowers and fruits relatively early in the summer. As a result fruit and seed production in annuals and other herbaceous plants, particularly, tends to occur during short periods of summer drought; seeds germinating in late summer and early autumn have time to grow large enough to build up resources of storage reserves to last them through the winter.

The germination behavior of four species that occur in parts of Europe with a continental climate are shown in Tables 2 and 3.

Table 2. **Germination (percentage) of *Delphinium orientale* seed. Fresh seed and seed stored dry in the laboratory for various periods were tested at a range of constant or fluctuating temperatures.**

Temperatures (fluctuating cycles):

	Day / night temperatures (° C)					
	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Fresh seed	36	16	44	39	0	0
Stored seed	68	36	65	53	11	1

Temperatures held constant throughout experiment:

	Temperature of test (° C)					
	6	11	16	21	26	31
One-year-old seed	89	88	12	0	0	0
Three-year-old seed	82	93	30	3	0	0

Delphinium orientale, (Table 2), is found throughout all parts of the Balkan Peninsula extending north into Hungary on arable ground, usually in areas subject to summer drought. Germination tests gave responses rather similar to those already described for mediterranean species, with marked inhibition at high temperatures and some improvement in germination rates after six months of laboratory storage.

Each of the other three species showed high germination rates immediately after harvest, and after a period of storage at most of the temperatures tested, although germination of freshly shed *Lychnis coronaria* seed was restricted or prevented when tested at day temperatures of 25° C. (77° F.). Germination responses of this kind imply that seed shed in mid to late summer would either be capable of immediate germination, given sufficient soil moisture, or would lie in the soil for a short time during the hottest part of the year to germinate in early autumn. In either case it would appear that dormancy plays little part in controlling the season of seed germination and that the species would overwinter as young plants rather than as dormant seed

c. **The North-Western Oceanic Region.** This area extends along the Atlantic coasts of Europe from northern Spain to Norway, and includes the whole of the British Isles. Most of the area is practically free from summer drought except for parts of southwestern France and for occasional isolated short periods in eastern England and western France The growing season is long especially in the extreme west where winter temperatures equivalent to those of the mediterranean result in almost frost-free conditions throughout the year. Winter temperatures in other parts of the area are relatively high with no month where mean monthly temperatures fall below 0° C. (32° F.). Mean values for winter cold, rainfall, or other meteorological parameters are misleading since the area is characteristically highly variable in its weather patterns. Winters vary both in their overall character from relatively severe to mild and in the monthly pattern which is made up of variable periods of cold, or mild or wet weather. Prolonged periods of frost or snow are unusual. It has already been noted that snow cover may not only mitigate the effects of cold, but may also assist plant survival by reducing losses from pathogens and predators. Thus the physically severe climate of continental Europe may be relatively innocuous to plants hardy enough to withstand a period of low temperatures but paradoxically, the milder conditions prevalent in oceanic areas may pose much greater hazards to the winter survival of young plants.

The situation is a complex one in that seed germination in late summer or autumn to produce seedlings that overwinter as young plants provides an inbuilt advantage to the established plants which develop early and are well placed to survive competition from seedlings germinating in the spring. On the other hand, overwintering

Table 3.Germination (percentage) of seeds of three species distributed in parts of Europe having a continental climate.

Salvia sclarea:

	Day / night temperatures (° C)					
	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Fresh seed	83	59	81	80	94	76
Stored seed	89	91	83	87	84	76

Lychnis chalcedonica:

	Day / night temperatures (° C)					
	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Fresh seed	82	93	93	95	96	96
Stored seed	98	87	95	98	91	97

Lychnis coronaria:

	Day / night temperatures (° C)					
	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Fresh seed	85	80	95	72	43	0
Stored seed	77	89	93	90	85	88

as plants rather than seed greatly increases the exposure of the population to unpredictable degrees of varying risk from year to year. There is no single season or period of the year which can be said to be uniquely favorable for seed germination and plant survival, but each poses a balance of advantages and disadvantages.

It is not surprising to find, therefore, a complex of germination responses from the plants growing in the area so that some germinate predominantly in summer and autumn, others predominantly in the spring and, in others, some seed germinates immediately it is shed, while some remains dormant through the winter till the following spring Species from the area frequently display a diversity of germination responses which result in no more than a proportion of the seed population germinating under any given environment, and in this way some of the seeds remain dormant year by year to build up in the soil a reservoir of seed, some of which may not germinate for many years after they are shed.

In Table 4 results are shown of tests done with seed of four species collected in the British Isles, which exemplify some of the problems that may arise, and the variability in response that can be found from one test condition to another. Constant temperatures were unfavorable for germination of *Ballota nigra* and *Stachys silvatica* seed but high temperatures, including fluctuations from night to day, were very favorable (*vide* the comparison between responses at 25/25°, 15/15°, and 25/15°). There were few benefits from storing the seed prior to sowing, or in giving it a chilling treatment. Freshly picked seed of *Meconopsis cambrica* and *Scilla non-scripta (Endymion non-scripta)* failed to germinate, and no improvement was found with the latter when stored or given a chilling treatment. *M. cambrica* seed did germinate a little better after storage, particularly at 15/5°, which corresponds to natural cool days and cold nights. The welsh poppy and the bluebell are both species whose seed germinates freely under natural conditions and, in particular, developing bluebell seedlings may be quite conspicuous in early spring in any bluebell woodland. A much more extensive series of laboratory tests than those shown here, however, failed to achieve any better results than the ones shown and it seems likely that seeds of both these species require a succession of alternating leaching and chilling treatments, equivalent to the variable conditions of our winters, before they are able to respond to warmer conditions with the coming of spring. It is often not easy to establish artificial treatments which will produce results equivalent to those found under natural conditions for seed of species from oceanic areas of Europe, but as the first two species in Table 4 show, this is not always so, and frequently quite small variations in ambient conditions may make the difference between success and failure. Similarly preliminary chilling treatments may increase germination, as in *Ballota nigra*, or be disappointingly ineffectual, as in the bluebell.

Table 4. **Germination (percentage) of seed of four species collected in the British Isles.**

Ballota nigra:	Day / night temp. (° C)					
	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Fresh seed	2	1	12	47	50	1
Stored seed	4	4	8	56	40	3
Chilled seed[a]	66	40	68	75	47	16
Stachys silvatica:	Day / night temp. (° C)					
	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Fresh seed	32	0	3	88	78	0
Stored seed	6	5	40	90	70	2
Meconopsis cambrica:	Day / night temp. (° C)					
	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Fresh seed	0	0	0	0	0	0
Stored seed b	36	0	8	14	5	0
Endymion non-scripta:	Day / night temp. (° C)					
	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Fresh seed	0	0	0	0	0	0
Stored seed	0	0	0	0	0	0
Chilled seed c	0	0	0	0	0	0

[a]stored seed chilled at 2° C for 9 weeks after sowing before transfer to test temperatures.

[b]stored for 13 months.

[c]chilled for 6 weeks at 2° C.

d. **The Taiga.** This area, as defined in Fig. 2, is the name given to the coniferous forests of Scandinavia and Russia. In North America the corresponding forest zone is called the boreal forest. Areas of coniferous forest, characteristic of high altitudes, in mountain and alpine areas of Europe have broadly similar characteristics, and since the flora of these regions is of much greater horticultural interest than that of the true Taiga the examples considered here are mainly from such areas. The climate is characterized by a virtual absence of summer drought, even of short duration, and by long and severe winters during which the ground may be continually covered by snow for many months The summers are short and though day temperatures may be quite high the nights are normally cool, or even cold, which emphasizes the natural shortness of the growing season. In some seasons prolonged periods of rain and low temperatures in summer, or the early onset of winter may greatly curtail fruit set and seed production, resulting effectively in intermittent crop failures.

Under these conditions there is usually insufficient time both for seed to ripen and be shed and for seedlings to germinate and build up sufficient resources to survive the winter. Seedlings starting growth in late summer or early autumn are still very small when the growing season ends and are very vulnerable to inclement conditions. There is little of the weather variability found from year to year and from week to week as in the oceanic regions and, in many ways, climatic features of the Taiga region are comparable in their regularity to those of the Mediterranean area—though directly opposite in their nature. The situation is one in which the seed of most species requires protection from germination before the winter starts, but requires the ability to germinate and grow rapidly as soon as the spring thaw is under way. The most characteristic dormancy pattern is one which responds easily and satisfactorily to chilling treatments as shown for three species in Table 5 Usually few changes in germination behavior occur in response to storage, nor are temperature combinations involving fluctuating day/night cycles effective ways of promoting germination

e. **The Tundra.** Tundra, or areas with similar conditions in Europe, occur along the northern fringe of the continent from Northern Norway eastwards, and at high altitudes on most of the main mountain chains. These areas are characterized by extremely short, cool or cold, growing seasons and very long periods of snow cover and winter cold. Usually only the surface layer of the soil thaws each spring, and the sub-soil remains frozen to create a condition known as perma-frost Such areas, especially on mountain tops are frequently

Table 5. Germination (percentage) of seed of species occurring at the altitudes of the coniferous forest in mountainous areas of Europe.

Gentiana verna	Temperature (° C)					
	6	11	16	21	26	31
Fresh seed	0	0	0	0	0	0
Stored seed	0	0	0	0	0	0
Chilled seed[a]	0	43	68	82	80	24

continued

Primula auricula

	Temperature (° C)					
	6	11	16	21	26	31
Fresh seed	0	0	0	0	0	0
Stored seed	0	0	0	0	0	0
Chilled seed[b]	0	73	62	30	0	0

Trollius europaeus

	Temperature (° C)					
	6	11	16	21	26	31
Fresh seed	0	0	0	0	0	0
Stored seed	0	0	0	0	0	0
Chilled seed[c]	6	43	56	72	14	0

[a]Chilled at 2° C for 8 weeks.

[b]Chilled at 2° C for 8 weeks

[c]Chilled at 2° C for 8 weeks

very exposed, and snow cover in the winter may be almost entirely removed by high winds, consequently plant exposure to winter cold and dessication may be very severe. Seed of plants from these regions probably normally germinates in early spring and the annuals found here are remarkable for the short time they require to complete their life-cycle. Perennial species may take several seasons to attain sufficient maturity to produce flowers. Many of the species found in such areas respond to chilling treatments in the same way as the mountain flora just described, but seeds of others, for example *Silene acaulis* and *Lychnis sibirica*, shown in Table 6, may require no special treatment, but germinate rapidly at a range of temperatures. Low temperatures are often unfavorable for germination, as exemplified here by *S. acaulis* and this would appear to be sufficient protection to prevent seed shed late in the autumn from germinating before the onset of winter. In a sense, therefore, it could be argued that in these circumstances the climate itself is so stringent that it practically predetermines the possible season for germination and only minimal adaptation is required by the plant to ensure correct timing of the process.

Table 6. Germination (percentage) of seeds of two species from Tundra regions of Northern Europe.

Silene acaulis

	Temperature (° C)									
	4	8	12	16	20	24	28	32	36	40
Stored seed	0	0	0	3	37	73	76	52	28	0

Lychnis sibirica

	Temperature (° C)									
	4	8	12	16	20	24	28	32	36	40
Stored seed	6	18	80	96	85	100	80	58	4	0

TECHNIQUES FOR OVERCOMING DORMANCY MECHANISMS

Seed germination occurs in response to the interaction of processes occurring within the seed and the environment in which it is placed. The preceding section, limited in scope though it may be, has outlined some of the significant factors determining whether a seed germinates or remains dormant and has described ways in which these factors can be related to the natural adaptations required by different species for survival in particular parts of Europe. In this section those factors which control germination are considered in relation to ways in which their identification may be used as an aid to increased efficiency when seeds are employed as propagating material for horticultural purposes. For this purpose the factors are most conveniently categorized, and the categories examined in turn to establish the significance of each in terms of its horticultural interest and applicability.

After-ripening responses. Tables 1 to 6 repeatedly present data for freshly harvested and stored seed. In many cases they also show that the stored seed germinated better than the freshly shed, sometimes over a wide temperature range, but sometimes at only one or two particular temperatures. This reflects a condition frequently found in seeds in which germination immediately after harvest is restricted and remains so for a period during which physiological or morphological changes, known collectively as "after-ripening", occur and result eventually in the reduction of the dormant condition. The time taken for the completion of such "after-ripening" changes varies from a few days to several years and the effect may be to remove almost entirely barriers to germination, or to produce no more than a very slight effect over a restricted temperature range. The majority of seeds after-ripen satisfactorily in dry storage at room temperature and the process may be retarded or prevented by storage at low temperatures, particularly below 0° C. (32° F.). After-ripening requirements of this sort mean that, in general, it is preferable to store seed for a short period rather than to sow it immediately after gathering, but care must be taken to provide good storage conditions. Not surprisingly, dead seed germinates less well than living, and there can be little doubt that many reports purporting to compare the performance of freshly sown seed with old seed simply establish the advantage of the quick over the dead. Seeds of most species having small dry seeds are best stored in paper bags preferably over anhydrous calcium chloride; above all, seed storage in damp places with continuously changing temperatures should be avoided.

A minority of seeds complete their after-ripening processes only when they are fully imbibed with water; most of these are species in which the embryo is morphologically immature when the seed is shed. These species mainly require warm conditions for the completion of embryo development before treatments leading to germination are started.

Chilling treatments. This includes techniques often referred to by the gardener as "freezing" or "stratification". However, the three terms are not, in fact, synonymous and the actions covered by them should be distinguished from each other. Examples of seeds responding to chilling treatment have already been presented and it is very common indeed to find that the seeds of species distributed in the temperate regions of the world respond by enhanced germination to a preliminary cold treatment. In practice it is important to separate the two processes of chilling and germination, if both are to be understood and used most effectively. Chilling treatments must be applied to moist seed; low temperature storage of dry seed is ineffective. One of the best methods is to mix the seed with a quantity of moist sand, seal the mixture in a polythene bag, and to put the bag in an ordinary domestic refrigerator. These operate over the range 2-4° C. (36-39° F.) which is suitable for most species; temperatures below 0° C. are not only unnecessary but very often ineffective. This low temperature treatment should be maintained for some weeks, but the minimum effective period varies from species to species. Between one and three months is usually adequate but, generally speaking, the response increases as the chilling period is prolonged so that it is safer to increase rather than to decrease the period.

At the end of the chilling treatment the mixture of seed and sand should be spread out in a thin layer over compost and placed in a suitable temperature for germination. It is not usually necessary to use low temperatures for this phase; about 20° C. (68° F.) provides satisfactory conditions for seeds of many species. In principle, once the chilling treatment is complete the seed should be germinated and the young plants grown on as quickly as possible.

Temperature Treatments. The expression of dormancy frequently varies widely from one temperature to another and several examples of this are recorded in the data presented in Tables 1 to 6. When this occurs seeds that appear to be completely dormant when tested at one temperature germinate well at another higher or lower temperature without the need for any special treatment involving chilling or storage treatments. Some generalizations on the nature of these temperature responses are possible in relation to the natural origin of the seed and these have already been made. In practice the simplest way to guard against restricted germination resulting from particular temperature requirements is to ensure that seed is exposed to a range of temperatures after sowing. Constant temperature sowing boxes or accurately maintained glasshouse temperatures are undesirable and should be replaced deliberately by diurnal fluctuations between day and night temperatures. The difference between maxima and minima should be at least 10° C. (18° F.) and temperatures approximating 20/10° C. to 25/15° C. (day/night) have usually given good results. Apart from its value with species whose seeds possess particular specific temperature responses, a fluctuating temperature regime is an essential requirement for seeds of a fairly small group of species which respond only to fluctuating temperatures and fail to germinate at all under constant conditions.

Light. Many seeds require light for germination; many more germinate equally well in light or dark, and a small minority germinate only in the dark. Light requirements seem to follow taxonomic relationships but there is no evidence that they are associated with particular geographical patterns of distribution. Consequently, no mention has been made of them up till now, but Table 7 illustrates results obtained with seeds of six species chosen to exemplify ways in which the presence or absence of light may modify the germination response to temperature. *Gentiana asclepiadea* seed, which was highly dependent on particular temperatures for germination in the presence of light, failed entirely to germinate in the dark, and rates for dark-grown seed of *G. cruciata* and *Meconopsis regia* were extremely low. *Meconopsis napaulensis* seed germinated moderately at all temperatures in the light, but in the dark certain temperatures were much more favorable than others, and this same pattern shows up much more clearly in *Salvia sclarea*. On the other hand, *Gypsophila elegans* seed germinated equally well in light or dark at all the temperatures tested. The results demonstrate ways in which dark-grown seed frequently is more restricted in germination and less predictable in its responses to temperature than seed exposed each day to light. In practice it is not usually necessary to have detailed knowledge of the light requirements of a seed, except in the rare examples of seeds which germinate only in darkness. For all others it is sufficient simply to ensure that they are exposed to light each day by not covering them with light-proof material nor putting them in any kind of lightproof box. The light intensity required to promote germination is very low and may be supplied at any time, even in mid-winter by natural light, or alternatively, by low intensity fluorescent or incandescent lamps.

Table 7. Comparative effects of light and darkness on the percentage germination of seed of six species at different temperatures.

Meconopsis regia

	Temperature (° C) Day / Night					
	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Light	43	55	39	18	27	15
Dark	11	0	2	0	6	0

M. napaulensis

	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Light	44	41	39	29	44	28
Dark	6	5	13	11	31	0

Gentiana cruciata

	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Light	68	59	71	72	75	75
Dark	0	2	0	1	0	6

G. asclepiadea

	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Light	5	0	9	60	24	5
Dark	0	0	0	0	0	0

Gypsophila elegans

	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Light	99	100	98	89	98	99
Dark	97	94	98	98	97	98

Salvia sclarea

	15 / 5	15 / 15	20 / 10	25 / 5	25 / 15	25 / 25
Light	89	91	83	87	84	76
Dark	6	9	39	63	81	18

There is some danger of abnormal effects due to the spectral composition of artificial light sources but for most species this is very slight indeed. A further source of failure with seeds which require light for germination may be caused by unnecessarily deep sowing; light exclusion from this cause is particularly likely to result from the use of opaque, light-absorbing, soilless composts based predominantly on peat moss.

Chemicals. A large number of chemicals, including mineral salts and organic compounds, affect germination and may promote the growth of dormant seeds. The most widely used and effective compounds are found amongst the gibberellins including, particularly, gibberellin A4 and A7, and A3 (gibberellic acid). Although the latter is usually much less effective than A4 it is the only gibberellin readily available commercially and, therefore, Hobson's choice dictates that normally it is the one that is used.

The best results from gibberellin treatments occur when seeds are sown on pads of tissue, filter paper, or agar containing a gibberellin solution and left in contact with the chemical throughout the germination period. This technique is not well adapted to the potting shed and depends on some concessions to laboratory practice. Gibberellic acid must be formulated in a water soluble form and made up in a concentration appropriate to the seed being germinated. Table 8 illustrates the effect of gibberellic acid, formulated as the ammonium salt, on germination responses of a number of species, and, as may be seen, effective concentrations vary over a wide range. In general, it

Table 8. The effect of gibberellic acid (GA) treatments at various concentrations on seed germination responses of different species.

Species	Germination without GA	Germination with GA at — (mg / 1) 1	10	100	1000
Primula auricula	0	0	32	75	82
Primula reidii	33	48	63	75	74
Lycopus europaeus	0	0	0	10	89
Meconopsis cambrica	0	0	0	38	
Gentiana cruciata	26	23	22	74	68
Trollius europaeus	0	0	17	22	44

seems likely that this compound is most useful in specific situations for seeds of species known to be difficult to germinate by other methods, and for which techniques employing gibberellic acid have been specially developed.

SUMMARY

One conclusion that may be drawn from the experimental results and descriptions presented above is that the mechanisms controlling the germination and dormancy of seeds cannot be summarized in a series of simplified generalizations. However, there also seems to be some reason to believe that attention to the natural conditions of the areas in which species grow may indicate conditions most likely to give successful seed germination. Sometimes this approach will lead to the paradox that seed of species from the areas noted for high temperatures, like the Mediterranean region, germinate best when sown at low temperatures, whereas seed of species from areas noted for their freezing winters—like Poland—germinate best when sown at high temperatures. This paradox can be logically resolved, and it is hoped that the results presented in this paper will act in some way as a guide to interpretations of climatic factors in relation to seed dormancy and germination.

SEED COLLECTION AND EXTRACTION

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There has over the last few years been a great demand for trees and shrubs in large quantities, and as a result a much larger and improved seed sowing programme has been built up.

HARVESTING

Determining the correct time for harvesting seeds is of vital importance if good germination is to follow. The collector must know the criteria which indicate the optimum conditions for the particular kind of seed he is collecting. These will include size, color and moisture content of the seed.

Before harvesting large quantities of seeds it is advisable to make a cutting test to determine quality and ripeness of the seed sample. It is well known that many seeds will germinate the first year quite freely if the seeds are harvested before completely ripe. With seeds of some species, once the seed coat has hardened germination will not take place until the *second* spring after collection unless special treatments are given.

We have found that seeds which benefit from early harvesting include the following:

Acer campestre, Acer miyabei, Acer tegmentosum, some species of *Viburnum, Cotoneaster* and *Carpinus.*