THE

REGENERATION OF

Eucalyptus pauciflora Sieb. ex Spreng.

FROM SEED

by

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CHAPTER 7

DORMANCY, GERMINATION AND EMERGENCE IN THE FIELD

CHAPTER 7

Experiments in the previous chapters have considered the influence of some environmental factors on the dormancy and the timing of germination of Eucalyptus pauciflora seed under controlled conditions. The studies in this chapter examine changes in dormancy and germination of the seed and the emergence of seedlings in the field in order to test the importance of the responses noted in the laboratory under field conditions.

The responses noted in Chapters 4 and 5 suggest that the strength c dormancy of seed which becomes moist at high temperatures will be increased and as the temperature declines to temperatures below 9°C dormancy will be broken. "he first study in this chapter tests whether there are changes in the strength of dormancy or germination of seed planted in late summer and relates the changes to the physical environment.

Successful regeneration depends on seed germination and seedling emergence at a time when conditions are suitable for survival and growth of the seedling. Experiments in Chapters 3,4 and 6 have shown that differences in the germination behaviour of seed from different altitudes are not likely to result from variation in the temperature response of breaking dormancy or germination but are more likely to be associated with the strength of dormancy. The differences in the strength of innate dormancy in seed collected at higher altitudes suggests that this seed would be less likely to germinate in autumn than seed from lower altitudes (Section 3.2, Section 4.2.1). The second section of this chapter examines the emergence of seedlings from seed transplanted between altitudes with a view towards assessing the ability of the transplanted seed to produce emergent seedlings at altitudes other than those of its origin.

As soil temperatures decline during autumn, the conditions will be less likely to induce dormancy and will become increasingly favourable for germination of the seed and, in late autumn for the breaking of dormancy. The time of planting of seed could therefore be expected to have a critical influence on survival of the seed and the number of seedlings which emerge in spring. The final study in this chapter investigates the emergence of seedlings from seed planted at a range of times during autumn and in late winter.

7.1 Changes in dormancy and germination in the field

Methods:

Bags made of fine synthetic mesh (120 mm X 80 mm) were divided into 3 sections and 0.3 g (51.9 viable seeds) of cleaned seed, collected near Dicky Cooper Ck., was placed in each section.

A plot (1.5 m X 2.0 m) located on the southern edge of a clearing in a stand of E. pauciflora near Rennix Gap (1610 m) was cleared of vegetation and leveled in October 1982. On February 8 1983, forty-four bags of seed were buried at approximately 10 mm depth. The plot was fenced to minimize disturbance by animals.

Five bags of seed were randomly selected for retrieval at approximately fortnightly intervals during the period February 15 to May 5 and again on May 28 1983. Field germination during spring was assessed by retrieving one bag at weekly intervals, beginning on August 28. Bags were retrieved with the surrounding soil intact (to a depth of 15 mm) and were sealed in a plastic bag to minimize changes in the moisture content of the seed.

On the day following retrieval, the soil surrounding the mesh bags was brushed off and used for determination of gravimetric soil moisture content. The mesh bags containing the seed were rinsed to remove the remnants of soil. Seed was removed from each section of the bag and seeds which had germinated in the field were counted and discarded. The seed which remained was placed on filter paper in a 60 mm petri dish to which 2.0 ml of Benomyl*R fungicide in water (0.2 g/l) had been added. The seed from one section of each bag was stratified (5°C) for either

0, 4 or 8 weeks and then set to germinate at 15°C.

A CR21 data logger (Campbell Scientific Inc., Logan, UTAH), was used for continuous monitoring of the climatic environment in the field. The previous experiments had shown the importance of temperature and moisture availablility in determining the changes in dormancy of seed and it was decided to monitor these aspects of the environment closely. Screen temperature (1.5 m), and soil temperatures at 0.01 m, 0.1 m, 0.2 m depth were samnled every 30 minutes using matched, calibrated thermistors. Rainfall was measured with a tipping bucket rainguage and soil moisture was monitored by daily readings of gypsum soil mcisture blocks (Beckman Instruments Inc., Cedar Grove, NEW JERSEY) installed at 0.1 m and 0.2 m. Rainfall, gravimetric soil moisture content (core from the surface to 0.05 m), and soil temperatures at 0.5 m, 1.0 m were monitored weekly in addition to the continuous records from the data logger.

Results:

(i) Weather measurements

Rainfall, soil moisture and soil temperature (0.01 m) data are summarized in Figure 7.1. The soil moisture blocks were found to be unreliable and therefore the weekly gravimetric soil moisture measurements have been used as an indication of soil moisture status.

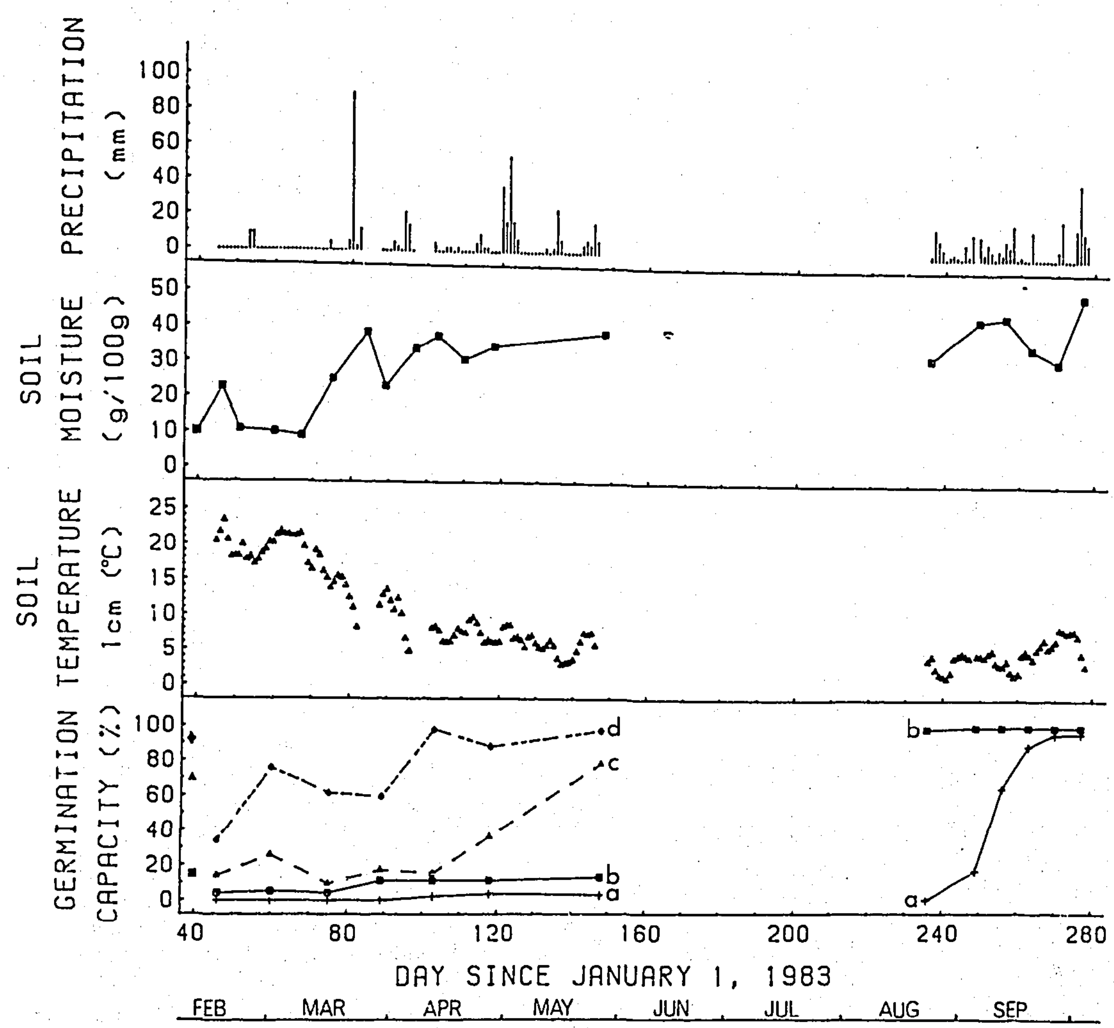

Figure 7.1 The changes in dormancy in relation to the climate during spring and autumn 1983 at Rennix Gap (1610 m).
a. % germinated seeds at retrieval
b. % germinated seeds at 15°C
c. % germinated seeds at 15°C after 4 weeks at 5°C
d. % germinated seeds at 15°C after 8 weeks at 5°C

(soil temperature is the mean temperature of 48, 30-minute samplings for each day)

(ii) Changes in dormancy during autumn

The analysis of the germination capacities of the seed retrieved and stratified prior to germination at 15°C confirms that there are significant differences in the response of seed, retrieved at different times to stratification (Table 7.1).

TABLE 7.1

Summary of analysis of deviance for germination capacities of seed retrieved from Rennix Gap in autumn and germinated in the laboratory.

Model terms	d.f.	Residual deviance	RMD	d.f.	Change deviance	CMD	F Ratio	P
Total	104	3492	33.58					
Retr +Strat	96	605.9	6.31	8	2886.1	360.76	79.37	0.005
Retr .Strat	84	381.8	4.55	12	224.1	18.68	4.11	0.005

Retr =Date of retrieval from Rennix Gap
Strat=Stratification treatment (0,4,8 weeks)

The germination capacity of seed samples after various periods of stratification permits an assessment of the strength of dormancy since seed with a lower germination capacity after a certain duration of stratification has a stronger dormancy. The trends in the germination capacity of the seed show that the seed became strongly dormant within a week of planting and that there was a progressive weakening of dormancy in late autumn as the soil temperatures fell and the soil moisture rose to high levels (Figure 7.1). Weakening of dormancy in late March and April was first apparent in the seed retrieved on April 13 which showed an increase in germination capacity after 8 weeks stratification but not after 4 weeks stratification. By April 28 the germination capacity of the seed stratified for 4 weeks was beginning to rise whilst the germination capacity of the seed stratified for 8 weeks remained at a high level. This trend continued until the final retrieval during autumn (May 28).

The refrigerator used for stratification had a mean temperature of 2°C in the first week of stratification of the seed retrieved on February 15, compared to 5°C for all other weeks in the experiment.

This occurrence would be expected to have reduced the rate at which dormancy was broken and may have resulted in the very low germination capacity of seed stratified for 8 weeks after retrieval on that day compared to seed retrieved in subsequent weeks. The contrasting lack of difference in the germination capacity of seed retrieved on February 15 compared to subsequent weeks after 4 weeks stratification is probably accounted for by the inability to break the dormancy of the seed.

(iii) Changes in dormancy and germination in spring

The weakening of dormancy due to low temperatures continued throughout winter. By August 28 the seed was non-dormant at 15°C, and in the ensuing weeks the seed germinated in the field. The daily mean temperatures during this period did not exceed 5°C (Figure 7.1).

(iv) Seed mortality

The number of viable seeds in the samples retrieved from the field were analysed in order to investigate mortality of seed due to storage in the field over the autumn period. The number of viable seeds was calculated as the sum of those seeds which germinated before and after retrieval from the field and the seeds judged to viable by squashing at the end of the laboratory germination period. Analysis of variance showed that the time of retrieval may have had a significant effect on the number of viable seeds ($p=0.048$), but there was no significant trend in the mean number of viable seeds with date of retrieval from Rennix Gap (linear regression $p=0.155$) during autumn.

TABLE 7.2

The mean number of viable seeds for each of the days of retrieval

Date (1983)	FEB 15	MAR 1	MAR 16	MAR 30	APR 13	APR 28	MAY 28
Day from Jan 1	46	60	75	89	103	118	148
Viable seeds	51.9	56.9	58.7	50.1	53.8	48.7	52.5

LSD_{005} = 7.58

Seed retrieved in spring also showed significant differences in the number of viable seeds (ANOVA, p=0.004); however, there was no trend in the number of viable seeds with time of retrieval between August 28 and October 4 (linear regression, p=0.58). The mean number of viable seeds in the autumn and spring retrievals were not significantly different indicating that there was little mortality of seeds due to storage in the soil during winter.

Discussion:

Changes in the dormancy of seed stored in the soil in the field have an important bearing on the chances for successful germination and seedling establishment. Seed planted in late summer became strongly dormant as a result of the exposure of moist seed to high soil temperatures; this behaviour is consistent with the induction of dormancy noted in Chapter 5. Rainfall caused an increase in soil moisture during early April when temperatures were too hot for dormancy to be broken. At this time a low proportion of the seeds germinated but no further strengthening of dormancy was observed. As the soil temperatures declined during April, with soil moisture at a high level, the dormancy of the seed became progressively weaker.

Dormancy was broken at temperatures below 9°C in the laboratory (Chapter 4). Figure 7.2 shows that the increase in the germination capacity after 4 weeks stratification of seed retrieved from the field was associated with the duration of exposure (number of 30-minute periods) to temperatures below 9°C in the field.

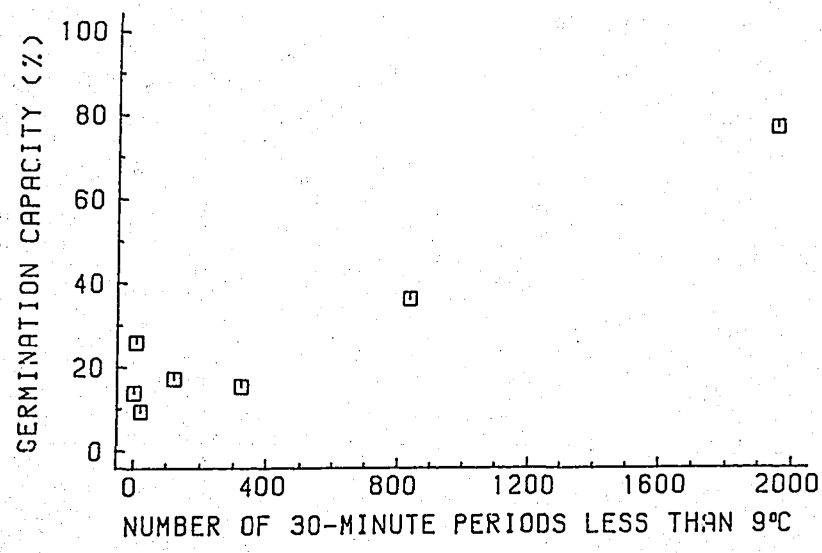

Figure 7.2 The germination capacity of seed stratified for 4 weeks plotted against the number of 30-minute periods below 9°C.

Field germination of seed would be very unlikely in early winter since seed retrieved from the field on May 28 required a further 4 weeks stratification at 5°C in the laboratory for germination to occur at 15°C. Stratification of seed in the field is likely to take considerably longer because the soil temperatures will be lower than 5°C, and will result in a much slower breaking of dormancy (Section 4.3.1). The duration of stratification required would be further increased because germination at the low soil temperatures occurring during autumn and winter would necessitate a much longer period of stratification than is required at 15°C (Section 6.1).

The absence of significant mortality of seed in the field during the autumn and winter period is not consistent with the results of laboratory experiments which showed that mortality was associated with the induction of dormancy in moist conditions at 15°C. Grose (1963) also observed mortality of E. delegatensis seed during the autumn and winter period. The large variation in the number of viable seeds per replicate in the present experiment may have masked a low level of mortality during autumn and winter.

7.2 Seedling emergence from seed planted at four altitudes.

Seasonal changes in dormancy and germination of E. *pauciflora* seed tend to delay the germination of most of the seed in the soil until spring. Seed from higher altitudes has a stronger innate dormancy than seed from lower altitudes. The soil temperatures in autumn become more favourable for stratification at high altitudes and it is possible that seed with weaker dormancy would have an increased risk of germination during winter at higher altitudes. On the other hand, at low altitudes, the strong dormancy of the seed from higher altitudes may delay the germination of seed beyond the period of favourable conditions during spring. This section examines the extent and timing of seedling emergence from seed planted at four altitudes.

Methods:

Seed from four altitudes, Waste Point (960 m), Sawpit Ck. (1240 m), Dicky Cooper Ck. (1740 m) and Baker's Ck. (1910 m) was divided into units (1.0 g Waste Point, the rest 0.5 g). The approximate number of viable seeds in a unit of each seed source is shown in Table 7.3.

Four sites in clearings with northerly aspects, and a slope not greater than 5%, were selected near Waste Point (960 m), Sawpit Ck. Ranger Station (1215 m), Rennix Gap (1610 m) and Pipers Gap (1740 m). At each site, four plots (0.7 m X 0.7 m) were cleared of vegetation and the soil was dug over to a depth of 0.2 m, and rocks and roots were removed to provide an homogenous seed bed. Soil collected at Dicky Cooper Ck., which had been dried and sieved, was spread on the plots to a depth of 10 mm, to provide a uniform substrate for seed germination.

TABLE 7.3

The numbers of viable seeds in units of the seed collected near Waste Point, Sawpit Ck., Dicky Cooper Ck. and Baker's Ck..

SEED SOURCE SITE	ALTITUDE	SAMPLE WEIGHT	MEAN NUMBER OF OF VIABLE SEEDS[1]
Waste Point	960 m	1.0 g	24.9 ± 6.0
Sawpit Ck.	1240 m	0.5 g	27.5 ± 8.8
Dicky Cooper Ck.	1740 m	0.5 g	32.0 ± 5.6
Baker's Ck.	1910 m	0.5 g	43.0 ± 5.4

[1] Means of 8 replicates ± standard deviation

The sites of planting were not identical to the sources of the seed because of difficulties in collecting the amount of seed required from trees at sites which could be easily accessed during spring. An attempt was made to collect seed from populations of E. pauciflora from a wide altitudinal range (960 m to 1910 m).

On February 8 and April 13 1983, two of the plots at each altitude were planted with four replicates of the seed from each of the seed sources, using a latin square design. This design was used to permit an analysis of the effect of slope (rows) on the emergence of seedlings since some soil and water movement across the plot was expected. Each replicate of seed was confined to an area within the plot by a section of PVC waste water pipe (75 mm diameter) pushed into the soil to a depth of 90 mm to form a ring; the rings prevented the mixing of seed from different sources due to disturbance by needle-ice and runoff water.

Each replicate of seed was mixed with about 50 ml of sieved soil collected near Dicky Cooper Ck. which was then placed in a ring. The seed was planted in this way to ensure a range of planting depths for the seed ranging from 0 mm to 10 mm in an attempt to remove any differential effect of depth of planting on the germination response of the seed.

After planting, each plot was covered with a fine white gauze to minimize any effects due to raindrop splash; the whole plot was then covered with a chicken wire cage (10 mm mesh), to prevent disturbance by animals. The gauze was removed from plots at low altitudes in early August, and after snow melt at higher altitudes.

Measurements of soil temperature at 0, 0.1, 0.2, 0.5, 1.0 m depth, grass minimum temperature and rainfall were made at each site on a weekly basis. The temperature environments at the various sites were compared using temperature recorded at 0.5 m, because this was the shallowest depth at which the fluctuations in temperature observed over the 6 hours taken to visit all sites were negligible.

Eucalyptus pauciflora seedlings emerge from the soil with the cotyledons folded and often partially enclosed in the seed coat (personal observation). The seed coat falls off as the cotyledons expand. A seedling was classified as having emerged when the cotyledons were fully expanded. The numbers of emergent seedlings in each ring and the number of dead seedlings were recorded at approximately weekly intervals, and the tops of dead seedlings were removed.

The study reported in this section was first attempted in 1982. October and November were very dry in that year, and drought resulted in heavy mortality of seedlings at all altitudes of planting. The results presented in this section were obtained in the spring of 1983 in which soil moisture remained high throughout the period of emergence.

Results:

(i) The emergence of seedlings in autumn.

Seedlings began to emerge in early April at Waste Point and the timing of the first emergence was progressively delayed at higher altitudes. The emergence of seedlings in autumn is reflected in the number of emergent seedlings observed on May 28, 1983 (Table 7.4).

TABLE 7.4

The total number[1] of seedlings which had emerged by May 28 from seed collected at four altitudes and reciprocally transplanted on two occasions.

ALTITUDE	960 m		1215 m		1610 m		1740 m	
OCCASION	FEB	APR	FEB	APR	FEB	APR	FEB	APR
SEED SOURCE								
960 m	3	4	7	1	2	0	3	0
1240 m	6	10	2	0	4	0	1	0
1740 m	3	10	3	5	1	0	4	0
1910 m	3	3	0	0	0	0	0	0

[1] Sum of seedlings emerging in 8 replicates at each planting time at each altitude. The approximate number of seeds per replicate is given in Table 7.3

The number of seedlings which emerged in autumn was small in relation to the amount of viable seed planted and declined with increasing altitude of planting. The number of seedlings which emerged from seed planted on April 13 was generally less than from the later planting, although this trend was reversed at Waste Point (960 m) where more seedlings emerged from seed planted in April than February.

(ii) The emergence of seedlings in spring

There are two aspects of the emergence of seedlings to be considered. The first is the general relationship between emergence of the seedlings and climate, and the second is variation in the emergence of the seedlings due to seed source at the different altitudes of planting.

The emergence curves generally show a gradual rise to a plateau (corresponding to the maximum number of emergent seedlings) then a decline as seedlings begin to die (Figure 7.3). The number of seedlings dying was negligible during the time when the number of seedlings emerging was increasing. There were, however, two notable departures from this trend. Severe needle-ice activity at Waste Point (960 m) during the week ending September 7 (day 250) resulted in the deaths of most of the seedlings which had emerged by that time. The marked reduction in the numbers of seedlings at Sawpit Ck. (1215 m) after September 27 (day 270) was due to flooding of the plots which caused death of most of the seedlings in the plots planted on April 13 and substantial mortality in the plots planted on February 8. The differences in the mortality of seedlings emerging from seed planted at different times appeared to be due to the position of the plots and not to differences in the characteristics of seedlings. The data from Sawpit Ck. site were excluded from further analyses.

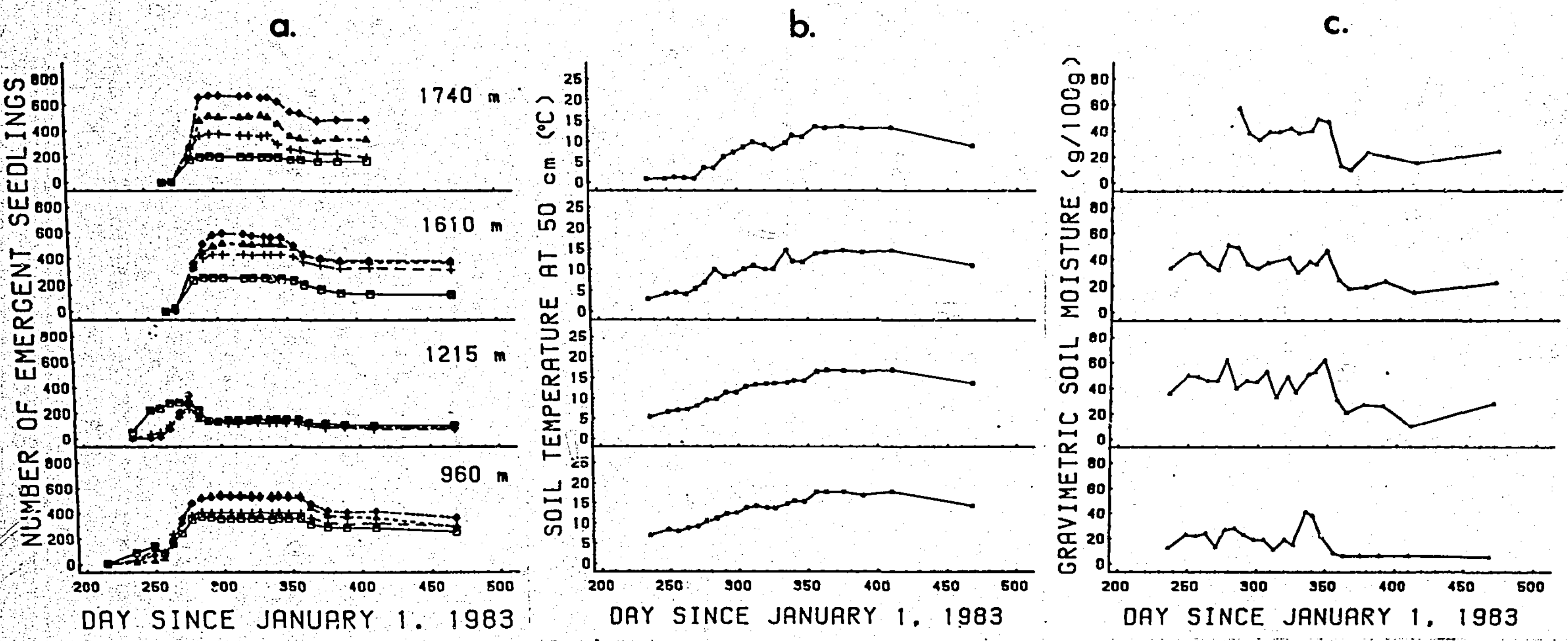

Figure 7.3 (a) The total number of seedlings emerging during spring 1983 from seed collected at 4 altitudes [◆ Baker's Ck. (1910 m); ▲ Dicky Cooper Ck. (1740 m); + Sawpit Ck. (1240 m); □ Waste Point (960 m)] and then planted at 4 altitudes [PG (1740 m); RX (1610 m); SC (1215 m); WP (960 m); see Figure 1.1 for site locations) during autumn 1983.
(b) The soil temperature at 50 cm over time at the 4 sites of planting during spring 1983
(c) The soil moisture (0-5 cm) over time at the 4 sites of planting during spring 1983

Spring emergence of seedlings predominated at all altitudes of planting, with differences in the timing of emergence shown in Figure 7.3. Seedlings from seed collected at 960 m emerged rapidly at 960 m and 1215 m compared to those from seed collected at higher altitudes. The difference in emergence of seed from 960 m compared with the other sources amounted to 20 days at 1215 m. The period from the emergence of the first seedling until the maximum number of seedlings had emerged decreased with altitude of planting. Conditions were suitable for germination over a long period at Waste Point; the higher soil temperatures may have permitted a fuller expression of the strength of dormancy of the seed both within and between the seed sources. The emergence of seedlings at higher altitudes was probably delayed by low temperatures under snow. When the soil temperatures began to rise following the snow melt, a greater proportion of the seed germinated and the seedlings emerged and established rapidly.

Seedling mortality increased in late December at the same time as soil moisture levels began to decline rapidly (Figure 7.3) and it is assumed that the mortality was related to drought. The onset of mortality was delayed at lower altitudes even though the decline in soil moisture showed a similar pattern at all altitudes. This is probably because the seedlings at lower altitudes were larger (personal observation) and presumably had deeper root systems, and therefore better access to water than those at higher altitudes. This interpretation may be further complicated by differences in root to shoot ratios of seedlings growing at different altitudes which were not investigated.

As the number of viable seeds planted in each ring was not known the comparison of the seed sources could not be based on the proportion of the seed emerging. Neither could the comparison of the seed sources be based on absolute differences in the number of emergent seedlings because differences in the processes which lead to emergence would be confounded with differences in the initial numbers of viable seeds (Table 7.3). However, comparisons of the behaviour of seed from each source planted at a range of altitudes will indicate whether there was any difference in emergence due to altitude of planting. The plateau region of the emergence curves of Figure 7.3 was used to investigate the differences due to seed source; the sampling was not intense enough to investigate the rising part of the curves, and the curves of the different seed sources show little variation after they reach the plateau. The variation in the number of emergent seedlings on November 16 will now be considered in detail.

The analysis summarized in Table 7.5 shows that the number of seedlings emerging from seed from different seed sources was significantly different (Source, $p<0.001$). Comparison of the mean number of viable seeds for each source (Table 7.6) with the estimated number of seeds planted (Table 7.3) shows that a high proportion of the seed emerged as seedlings (960 m, 71%; 1240 m, 91%; 1740 m, 93%; 1910 m, 83%).

The altitude of the seed source had a significant effect on the number of emergent seedlings. This could be expected from the differences in the numbers of viable seeds which were planted (Table 7.3). The results which are of particular importance are the significant interactions between planting time and seed source (Time*Source, $p=0.031$) and the altitude of planting and seed source (Altitude*Source, $p=0.002$): they show that the number of emergent seedlings differed within a seed source depending on the altitude and time of planting.

TABLE 7.5

Summary of analysis of variance[1] for the number of seedlings on November 16, 1983 which emerged from seed, from four altitudes, planted on February 9 and April 13 at four altitudes.

Source of Variation	d.f	Sum of Squares	Mean Square	Variance Ratio	Significance level
Altitude.Plot Stratum					
Altitude	2	176.3	88.1	0.18	0.843
Time	1	656.4	656.4	1.31	0.296
Altitude*Time	2	1408.8	704.4	1.41	0.316
Residual	6	3000.5	500.1	3.67	
Total	11	5241.9	476.5	3.49	<0.001
Altitude.Plot.Row Stratum	36	5478.8	152.2	1.12	0.327
Altitude.Plot.Column Stratum	36	4410.8	122.5	0.90	0.634
Altitude.Plot.Row.Column Stratum					
Source	3	8397.1	2799.0	20.52	<0.001
Altitude*Source	6	3196.5	532.7	3.91	0.002
Time*Source	3	1260.3	420.1	3.08	0.031
Altitude*Time*Source	6	764.5	127.4	0.934	0.524
Residual	90	12279.0	136.4		
Total	108	25897.4	239.8		
Grand Total	191	41029.0			

[1] Split plot with a Latin Square design in the sub-plot

Altitude :Altitude of planting (960, 1215, 1610, 1740 m)
Time :Time of planting (February 9, April 13)
Source :Source of seed (960, 1240, 1740, 1910 m)
Row, Column :Rows and Columns in the latin square
Plot :A full latin square (2 replicate plots /time /altitude

The number of emergent seedlings associated with the significant interaction between altitude of planting and seed source show that seed from 960 m produced less emergent seedlings as the altitude of planting was increased whereas seed from 1740 m and 1910 m both showed increases in the numbers of emergent seedlings with altitude. The seed collected near Sawpit Ck. (1240 m) had a similar number of emergent seedlings at all altitudes (Table 7.6).

Although the time of planting did not have a significant effect overall, the interaction between time of planting and seed source was significant (Time*Source, p=0.031 Table 7.5)). When the emergence of seedlings at each of the altitudes of planting was considered separately, the interaction between planting time and seed source was found to be significant only for seed planted at Piper's Gap (p=0.002). The means for this site show that the tendency for the later planting to produce fewer seedlings from seed collected at high altitudes was not apparent in the emergence of seed from low altitudes (Table 7.7). The main source of this interaction is the large effect of planting time on emergence of seed from Dicky Cooper Ck. (1740 m) and Baker's Ck. (1910 m) compared to the small differences in seed from lower altitudes.

TABLE 7.6

The mean number of emergent se...ngs at 960 m, 1610 m and 1740 m from seed collected at 1000 m, 1230 m, 1610 m, 1740 m.

PLANTING Location Altitude	ALTITUDE OF SEED SOURCE 960 m	1240 m	1740 m	1910 m	Mean for Location[1]
Waste Point 960 m	24.6	24.5	25.6	28.1	25.7
Rennix Gap 1610 m	15.6	27.1	32.2	36.9	27.9
Piper's Gap 1740 m	12.5	23.7	31.4	41.9	27.4
Mean for source[2]	17.6	25.1	29.7	35.7	

For comparison between:
Seed sources within an altitude of planting (rows) $LSD_{0.05}$ = 10.6
Altitudes of planting within a seed source (columns) $LSD_{0.05}$ = 8.2
Means for altitude of planting (1) $LSD_{0.05}$ = 7.9
Means for seed source (2) $LSD_{0.05}$ = 4.7

Sawpit Ck. (1215 m) data omitted due to flood damage

TABLE 7.7

The mean number of emergent seedlings from seed collected at four altitudes and planted either on February 8 or April 13 1983 at Piper's Gap (1740 m).

TIME OF PLANTING	ALTITUDE OF SEED SOURCE 960 m	1240 m	1740 m	1910 m	MEAN FOR PLANTING
February 8, 1983	10.3	26.0	41.9	49.8	32.0
April 13, 1983	14.8	21.4	21.0	34.1	22.8

For comparison between:
Seed sources within a time of planting $LSD_{0.05}$ = 9.2
Time of planting within a seed source $LSD_{0.05}$ = 8.9

Discussion:

The differences observed in seedling emergence may be attributed to an increase in the strength of dormancy of the seed with altitude of seed source (Section 4.2.1) since seed from different altitudes showed no differences in the temperature response of either stratification (Section 4.3) or germination (Section 6.2). Differences in the number of seedlings which emerge could be expected to reflect differences in the proportion of seed from each source which has a strength of dormancy which is appropriate for the environment of planting.

The reduction in the number of seedlings which emerged from seed from Waste Point planted at altitudes above 1215 m is consistent with the earlier germination and death of seedlings, as a result of the weaker dormancy of that seed compared to seed from higher altitudes. The reduction in the number of seedlings emerging from seed from Dicky Cooper Ck. and Baker's Ck. planted at 960 m could be explained by a reduction in the number of seeds germinating as a result of an incomplete breaking of dormancy at 960 m compared to seed planted at 1610 m and 1740 m. A high proportion (91%) of the seed from Sawpit Ck. emerged as seedlings at all altitudes of planting.

Differences in the strength of dormancy may explain differences observed in the response of seed collected at various altitudes to the time of planting at the highest altitude (1740 m) (Table 7.2). The reduction in the number of seedlings emerging from seed from Dicky Cooper Ck. and Baker's Ck. planted on April 13 compared to February 9 is unlikely to be due to the inability of the conditions at Piper's Gap to break the dormancy of the seed from higher altitudes: the experiment reported in the next section shows that a high proportion of seed from

Dicky Cooper Ck. planted on August 28 at 1610 m was able to break dormancy and emerge as seedlings. It is possible that the lower number of emerged seedlings in the later planting was due to premature germination of the seed during winter.

Conditions which were suitable for the breaking of dormancy must have occurred at Rennix Gap (1610 m) prior to April 13 because the strength of dormancy of the seed had begun to decline by that date (Figure 7.1). It could be expected that the onset of these conditions would have been earlier at Piper's Gap because of generally lower temperatures at the higher altitude. Seed planted on April 13 at Piper's Gap would therefore have been exposed to conditions which were suitable for the breaking of dormancy from the time it was planted. In contrast, the dormancy induced in the seed planted on February 8 would be far stronger on April 13 than the innate dormancy of the seed which was planted on that day. The germination of seed planted in late summer would thus be expected to occur at a later time than seed planted later in autumn.

There are two possible explanations for the absence of significant differences in the number of seedlings emerging from seed planted in February and April at lower altitudes: the warmer conditions at lower altitudes after April 13 may have permitted the induction of dormancy in the seed, thereby delaying germination; or the shorter duration of winter at lower altitudes may have reduced the critical nature of the delay in germination (caused by the induction of dormancy) for the survival of the seedling. The breaking of dormancy observed in seed planted at 1610 m after April 13 (Section 7.1) renders the first possibility unlikely. However, in the absence of further information on the changes in dormancy at lower altitudes during autumn, it was not possible to determine the actual cause.

Interpretion of the results of the present experiment in terms of the adaptation of E. pauciflora to variation in environmental conditions with altitude requires an assessment of the characteristics of the season in which the study was carried out compared to the mean climatic conditions. The temperature conditions during the spring of 1983 were similar to the average (Figure 7.4) and the monthly precipitation was very high during September, October and November of that year. The consistently high soil moisture levels during the spring of 1983 provided an ideal opportunity to examine the effects of altitude, independent of soil moisture constraints. The dry conditions during October and November of 1982, which resulted in the mortality of almost all of the seedlings which emerged, shows the critical importance of soil moisture conditions in the spring following dispersal for the successful establishment of newly-germinated seedlings.

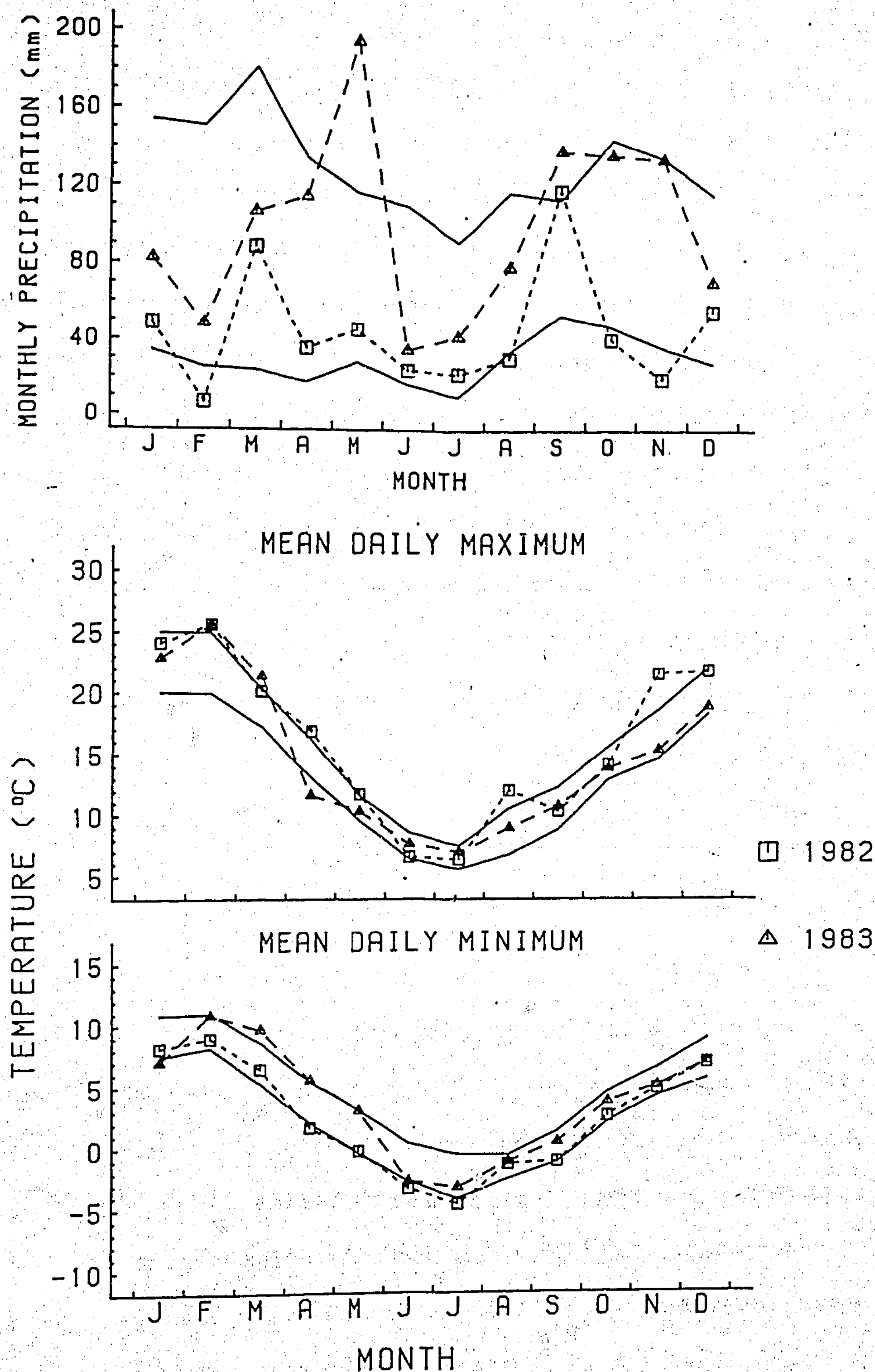

Figure 7.4 The climatic conditions during 1982 and 1983 at Sawpit Ck. (1215 m) in relation to the mean conditions over the period 1968-1983. Solid lines are 1 standard deviation above and below the mean.

7.3 The influence of time of planting on emergence of seedlings.

The previous experiment showed that the emergence of seed collected at a range of altitudes depended on the altitudinal difference in the seed source and the site of planting. Changes in the dormancy of seed planted in early autumn suggests that seed planted at later times might be expected to have a different dormancy compared with seed planted in early February (Section 7.1). Although replicate studies of the changes in dormancy of seed for different times of planting were not possible, some indication of the differences was obtained by examining the emergence of the seedlings from seed planted at different times. This study describes a study in which the emergence of seedlings from seed planted at a range of times in autumn and spring was monitored.

Methods:

A plot (0.8 m X 0.8 m) at the southern edge of a clearing in an E. pauciflora stand near Rennix Gap (1610 m) was prepared in a similar manner to the plots described in Section 7.2. Replicates of seed (0.5 g, 32 viable seeds), collected near Dicky Cooper Ck. (1740 m) were planted in five randomly selected rings each fortnight from February 15 to May 5 and then on May 28. All of the seed for the autumn plantings was weighed on the same occasion and was stored in dry conditions in a refrigerator until it was required for planting. A further planting on August 28 was undertaken in order to examine the breaking of dormancy in spring. The seed for the spring planting was from the same source but was collected a year later than the seed used for the autumn planting, and a larger amount of seed was planted in spring (0.7 g, 58 viable seeds). Seed was planted at a depth of between 7 mm and 10 mm.

The plot was inspected at approximately weekly intervals for emergent seedlings during autumn and spring. The number of seedlings with fully expanded cotyledons and the number of dead seedlings were recorded, and the dead seedlings were removed.

Results:

(i) Climatic conditions

The climatic conditions during the period of planting and seedling emergence are shown in Figure 7.5. This figure also summarizes the relevant findings of Section 7.1 and shows that there was a progressive breaking of dormancy during the late autumn but that the proportion of seeds which germinated during autumn was low. Dormancy was broken during the winter, and a large proportion of the seed germinated in September; the emergence of the seedlings was, however, delayed by more than a month. The emergence of seedlings will now be considered in more detail for seed planted at different times during autumn.

(ii) Emergence of seedlings in autumn and winter

Some of the seed planted in autumn emerged before winter; however, the seedlings which did emerge were associated with particular planting times (Table 7.8) and all of these seedlings had died by August 3. The lower number of emergent seedlings associated with the earlier plantings reflects the induction of dormancy noted for seed planted on February 8 (which was discussed in Section 7.1). The lower number of emergent seedlings from seed planted later than March 30 could have resulted from conditions which were not suitable for immediate germination or from the shorter time available in which emergence may occur as winter approaches.

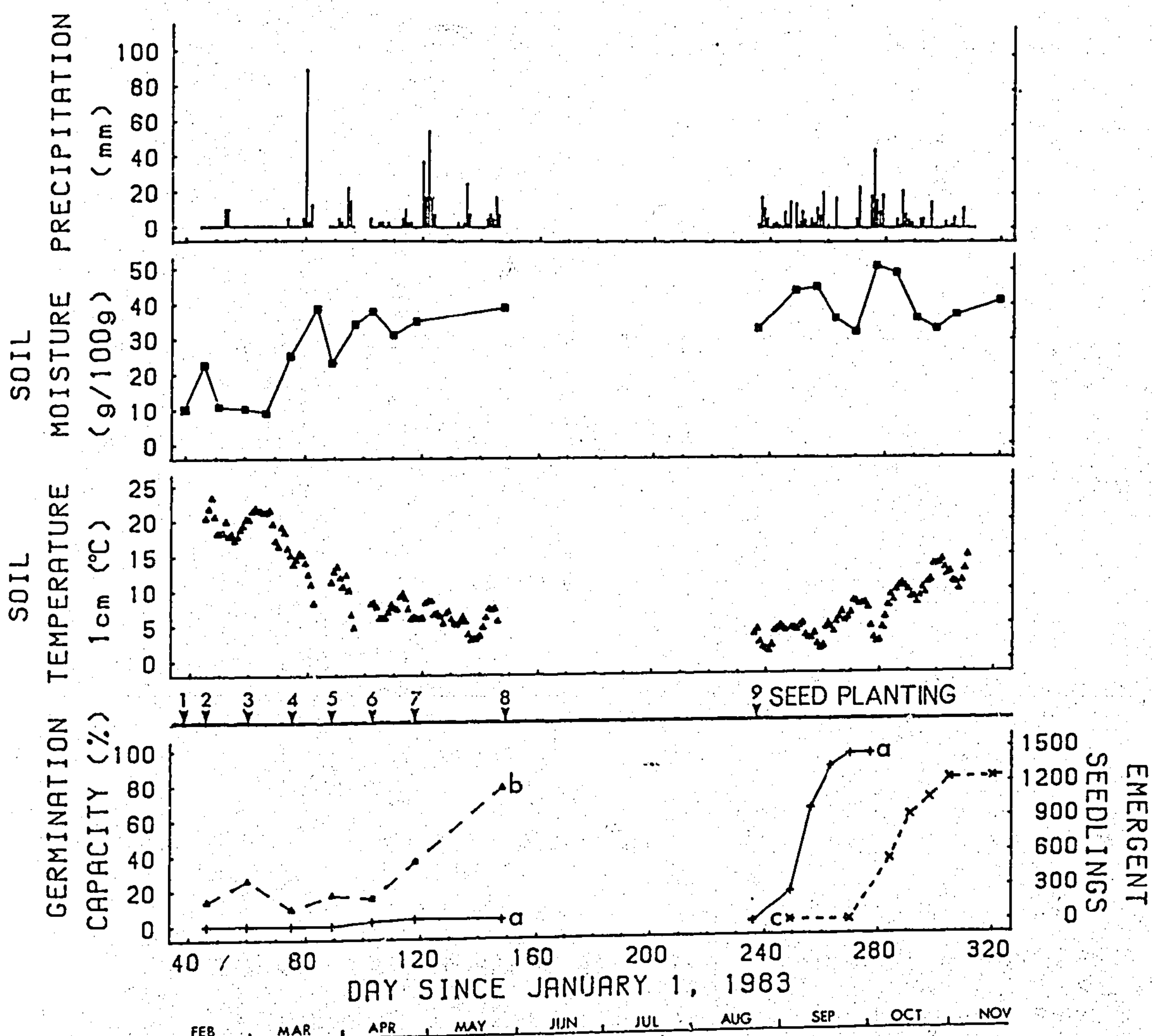

Figure 7.5 The dormancy and germination of seed and emergence of seedlings in relation to the climate during autumn and spring.
a. % germinated seeds at retrieval
b. % germinated seeds at 15°C after 4 weeks at 5°C
c. number of emergent seedlings

(soil temperatures are based on the mean of 48, 30-minute samples of temperature per day)

The site was visited at monthly intervals during winter and no emergence of seedlings was observed, probably as a result of the low temperatures and action of needle ice which frequently stirred the surface of the soil to a depth of 2 mm to 5 mm.

TABLE 7.8

The total number of seedlings which had emerged by various dates during autumn.

SEED PLANTING		NUMBER[1] OF EMERGENT SEEDLINGS DATE OF OBSERVATION			
Date	Occasion[2]	13 APR	28 APR	5 MAY	28 MAY
8 FEB	1	0	0	0	1 (1)
15 FEB	2	0	0	0	2
1 MAR	3	0	1	1	2
16 MAR	4	0	5	7	7 (5)
30 MAR	5	0	0	0	4 (4)
13 APR	6	0	0	0	0 (1)

[1] Total number of seedlings in 5 replicates
[2] from Figure 7.3
( ) indicate the number of additional seedlings which had emerged but did not have expanded cotyledons.

(iii) Emergence of seedlings in spring

The counts of emergent seedlings at successive times represent repeated measures which are not independent of each other and therefore the counts at each time were analysed separately. The spring planting of seed (August 28, [9]) was not included in the analysis because the number of seeds which were planted was different and therefore this treatment would be expected to show a significant difference in the numbers of seedlings which emerged. The soil in 4 rings was disturbed prior to emergence of the seedlings; two of these rings included seed planted on May 28 [8] and these plots were included as missing values in the analysis.

Analysis of variance showed that the numbers of seedlings emerging in spring from seed planted at different times in autumn was not significant (Table 7.9). The lack of significance of the effect of planting time on the number of emerged seedlings for all of the days of observation except October 18 may be due to the large amount of variation between the replicates (shown by the large value of the Least Significant Differences LSD). The major differences in the types of response resulted from variation in the maximum number of emergent seedlings and the rate at which the seedlings emerged (Figure 7.6). The mean number of seedlings for each planting date and day of observation are shown in Table 7.10 to permit the comparison of each of the planting dates. They show that, generally, the number of emergent seedlings from seed planted on occasions 3 (March 1), 4 (March 16), 5 (March 30) and 8 (May 28) was lower than seed planted at the other times.

TABLE 7.9

The summary of analyses of variance of the number of emergent seedlings from seed planted at various times for each observation occasion in spring.

Day[1] of Observation	Source of Variation	Variance ratio	p
284	Planting Date	2.10	0.075
291	"	2.62	0.031
298	"	2.17	0.067
305	"	2.27	0.056
320	"	2.25	0.058

[1] Day from January 1, 1983

TABLE 7.10

The mean number of seedlings from each planting date which had emerged on each day of observation.

DATE OF OBSERVATION	DATE OF PLANTING								
	8 FEB	15 FEB	1 MAR	16 MAR	30 MAR	13 APR	27 APR	28 MAY	LSD[1]
11 OCT	16.4	10.2	5.3	13.6	9.0	15.6	20.4	11.0	9.6
18 OCT	30.6	19.8	13.8	18.6	14.6	26.4	32.0	17.7	12.6
25 OCT	31.6	24.6	18.8	20.0	16.2	27.4	33.2	18.4	12.6
1 NOV	32.4	25.8	18.5	19.6	16.2	28.2	32.0	18.0	12.6
16 NOV	31.8	25.4	18.0	19.4	14.0	29.6	31.4	18.1	13.4

[1] value for significant difference between means within a day of observation at p=0.05.

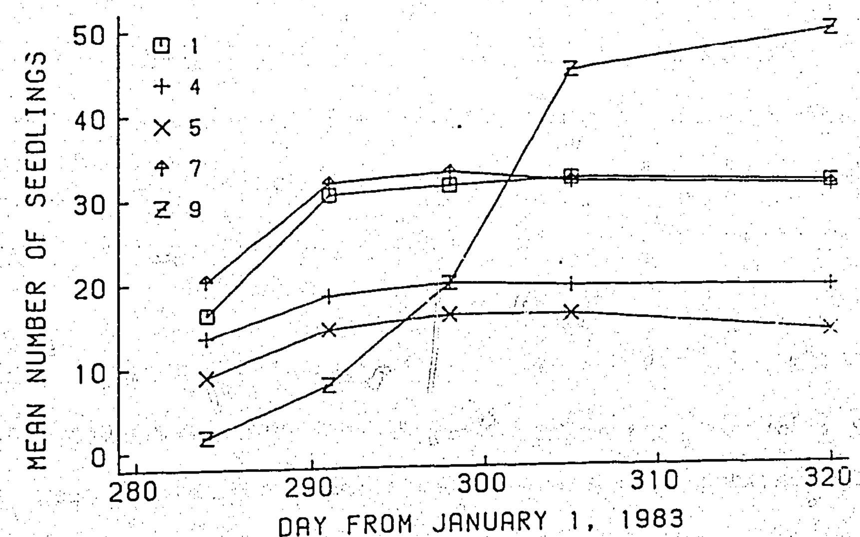

Figure 7.6 The mean number of seedlings which emerged from 5 replicates of seed planted at a range of times.

1: February 8
4: March 16
5: March 30
7: April 27
9: August 28

Discussion:

Although the variation between replicates means that the effect is not statistically significant, the trend in seedling emergence shows that the time of planting can affect the number of seedlings which emerge. This trend is consistent with the response predicted from earlier studies in this thesis.

Seed planted on February 8, at the same time and at the same site as the seed used in the experiments investigating changes in dormancy during autumn (Section 7.1), produced a large number of seedlings in spring. Section 7.1 showed that the temperature and moisture conditions were conducive to the induction of dormancy, following planting on February 8, and that only a small proportion of the seeds germinated (ca. 2%) and few seedlings emerged during autumn (Table 7.8). Seed planted on February 15 produced a similar number of seedlings to that planted on February 8.

The dry conditions following planting on March 1 probably meant that the seed planted on that occasion would have responded similarly to the seed planted on March 16 because changes in dormancy occurring at low seed moisture content occur very slowly (Section 4.1.1) and the seed would not have become moist until March 16 when it rained. The lower number of seedlings emerging in spring from seed planted on March 1, March 16, March 30 were all associated with higher numbers of seedlings emerging in autumn as a result of favourable moisture and temperature conditions for germination following planting. However, the number of seedlings which emerged in autumn from the latter plantings cannot account for the differences in the numbers of emerged seedlings in spring. Therefore, it was assumed that more seedlings germinated than emerged and that all of these seedlings died before spring.

Soil temperature and moisture conditions were apparently suitable for the breaking of dormancy from about March 30 onwards since the germination capacity of seed planted on February 9 began to weaken from that time (see Figure 7.1, curve d.). The seed planted on April 13 and April 27 was therefore exposed to conditions which consistently broke dormancy and produced higher numbers of seedlings in spring than the seed planted between March 1 and March 30.

The low number of seedlings originating from seed planted on May 28 is not consistent with the other observations in this chapter. The low numbers are unlikely to be due to the premature germination of the seed because seed planted on April 13 and April 27 would be expected to be more severely affected through exposure to even longer periods of conditions suitable for breaking dormancy. The low numbers are also unlikely to be due to incomplete breaking of the dormancy of the seed because a high proportion of the seed planted on August 28, at the beginning of spring, produced emergent seedlings. In addition, the studies in Section 7.1 showed that seed planted on February 9 and retrieved on May 28 had about the same strength of dormancy as fresh seed from the same source (the same seed used for the studies in this section), yet a high proportion of the former seed germinated. The low numbers are also unlikely to be due to a failure of seed planted on February 9 to emerge since seed planted on February 9 in the present experiment produced a large number of emergent seedlings. The reason for the low number of seedlings in seed planted on May 28 remains unresolved.

Planting seed in spring (August 28) resulted in a different germination behaviour compared to seed planted in autumn. Although the absolute numbers of seed cannot be compared, the pattern of emergence shows that the seed planted in spring broke dormancy and then emerged at a later time than the seed which had over-wintered in the soil.

7.4 Conclusions

1. The changes in dormancy in autumn are consistent with the results of the laboratory experiments since moist conditions and temperatures above 9°C resulted in the induction of dormancy in seed planted in late summer.

2. The induction of dormancy is important in limiting the germination of seed during autumn and in preventing germination during winter.

3. Seed germination in the field occurs when the soil temperatures are low at the end of winter (temperature at 10 mm did not exceed 9°C).

4. Seedling emergence occurred about 30 days after seed germination.

5. The proportion of seed which emerges as seedlings depends on the altitude of seed source and the altitude of planting. The reduction in the proportion of emergent seedlings was most marked when seed from high altitudes was planted at low altitudes and vice versa.

6. Drought may result in 100% mortality of seedlings at all altitudes.