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Dr. D. O. Chilcote

Field and growth chamber studies were conducted to ascertain the effects of some environmental factors on the persistence of viable buried seed of Agrostis tenuis, Avena fatua, Lolium multiflorum, Lolium perenne, and Poa annua.

Through the use of a population model, specific effects of environment on parameters of viability and nonviability were studied. The parameters of viability included seed quiescence and terminal dormancy. In situ germination and nonviability among ungerminated seed plus their composite, total nonviability, comprised the parameters of nonviability.

Of the five species studied, only buried seed of L. perenne was found to be nonpersistent. Variation in the degree of persistence was found among different seed lots of L. multiflorum.

Quiescence among buried seed of the persistent species was greater at deeper burial depths. Nonviability among buried seed was found to be less extensive at deeper burial depths.

Seed samples of persistent species recovered from burial under perennial ryegrass plant cover displayed higher levels of terminal dormancy than similar samples recovered from indigenous weed, wheat and alfalfa plots.

Low soil temperature and high soil moisture, characteristic of winter conditions in western Oregon, were effective in maintaining viability of buried seed. These conditions were also found to be conducive to the induction of secondary seed dormancy. The depletion of viable, buried seeds through in situ germination occurred at intermediate soil temperatures and soil moisture. Such conditions prevail in western Oregon during autumn and spring periods. High temperature and soil moisture percentage was found to increase nonviability among ungerminated seed.

Seed quiescence played an important role in persistence during the early stages of seed burial. With the progression of time, terminal dormancy played an increasingly important role as a mode of buried seed persistence.

In situ germination was the principle mode of buried viable seed depletion in A. fatua, L. multiflorum, L. perenne, and P. annua. Nonviability among ungerminated seed was found to be the principle mode of viable seed depletion in A. tenuis.

Factors Influencing Dormancy and Persistence in Buried Seed of Five Grass Species

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INTRODUCTION

The persistence of buried seed represents a survival mechanism to plant species. The highly effective persistence mechanism of certain species is undesirable from the agriculturists point of view, since persistence of seeds constitute a source of weed plants. The rigid requirements of crop seed certification accentuate this problem since contamination by certain weed species and other varieties are not tolerated. Thus, knowledge of seed persistence and dormancy would facilitate the construction of more adequate certification standards. Also, this knowledge would be of use in establishing weed control measures to deal with persistent species.

Few detailed studies on the influence of environment upon the persistence and depletion of buried seed have been reported. Adequate population models that permit evaluation of the mode of persistence and depletion of buried seed are not available. The present study was undertaken to explore these areas. The recent report of Rampton and Ching (43) established a foundation for the investigations reported in this thesis.

The species studied in the following investigations represent a variety of persistence types. Lolium perenne for example, has been

reported to be nonpersistent while its close relative, Lolium multiflorum displays a persistent behavior in the soil (43). Agrostis tenuis, like L. multiflorum can play a dual role, that of economic crop and that of a weed. The other two species investigated, Poa annua and Avena fatua are notorious for their weedy habit.

A population model, composed of parameters of viability and nonviability, was utilized to evaluate the status of buried seed populations. By subjecting seeds to various environmental variables in the field and growth chamber, changes in the aforementioned parameters were studied over a period of time. Such an approach permitted an evaluation of the mode of buried seed persistence and depletion among the plant species studied.

LITERATURE REVIEW

I. Introduction

Seed dormancy and persistence in higher plants has come under extensive study in recent years. The literature concerning seed dormancy and persistence is voluminous and attests to the diversity in dormancy types, mechanisms and causal factors encountered in this phase of seed physiology.

Several texts, (13, p. 114-139; 33, p. 115-169; 37, p. 304-325; 39, p. 61-100) contain sections on seed dormancy and a number of general reviews, (1, p. 408-424; 5, Vol. 15 (II), p. 699-717; 3, p. 174-182; 52, p. 265-288; 53, p. 185-224) are also available on this subject. The influence of seed characteristics and environmental factors on dormancy and persistence of seeds is described in several other reviews. These include the influence of seed coat, (2, Vol. 15 (II), p. 727-742); light, (18, Vol. 15 (II), p. 804-847); temperature (44, Vol. 15 (II), p. 746-803); and endogenous inhibitors (55, Vol. 15 (II), p. 909-924).

The literature presented in this review will be concerned primarily with the persistence and dormancy of seeds buried in the soil.

The study of buried seeds has proceeded along two lines. In one case, investigations have dealt with direct control and study of

buried seed populations. The second type of inquiry has involved the assessment of buried seed populations under a variety of soil types and cropping systems. Both lines of investigation have been helpful in the elucidation of factors involved in buried seed persistence and dormancy.

II. The Persistence of Buried Seeds

A. Controlled Experimentation

The prolonged viability of buried seed has been verified by a number of investigations in which seed of sundry species were buried in the soil and later recovered and tested for germination.

The results of a seed burial experiment initiated in 1879 by Beal, as reported by Darlington and Steinbauer (14), show that 11 of the 20 species investigated survived 20 years of burial. Nine species remained germinable after 40 years of burial. Germinable seed of Rumex crispus, Oenothera biennis and Verbascum blattaria were found after 80 years of burial. The longevity of seeds, Darlington and Steinbauer suggests, will depend upon the original vigor of the seeds, the depth of burial and the environmental conditions following burial.

In 1902, a burial experiment was initiated by Duval. Seed of 107 species were buried at depths of 8, 22 and 42 inches in the soil.

Toole and Brown (49), reporting on the final results of this study found germinable seed of 36 species after 39 years of burial. Earlier recoveries of buried seed samples yielded the following number of species with germinable seed.

1 year	71 species
6 years	68 "
10 "	68 "
20 "	51 "
30 "	44 "

Toole and Brown reported that buried seed of Avena fatua retained their germinability for one year.

The results of a seed burial study performed at the Danish State Seed Testing Station were reported by Kjaer (34, 35). While the buried seed of most crop species lost viability rapidly, the seed of a number of weed species were persistent. After ten years of burial, 20 of the original 37 species displayed some germination after recovery from burial. Seed of Lolium perenne germinated only one percent after one year of burial. Subsequent tests on the buried seed of L. perenne failed to disclose any germinability. These experiments did not include tests for seed dormancy.

Lewis (38) reported on a seed burial experiment conducted in Aberystwyth, Wales. Seed of various cereal, grass, legume and weed species were buried at depths of 5, 10 and 15 inches. The data revealed few differences in the retention of viability (laboratory germination plus subsequent germination in containers of soil) among

buried seed of L. perenne or Lolium italicum. Relatively high viability percentages were obtained from seed of these species recovered after one and two years of burial. The viability of these seeds, however, was nearly exhausted after four years of burial. Buried seed of A. fatua displayed some viability after one year of burial, with only a trace of viability after two and four years of burial. Buried seed of Agrostis tenuis showed a high degree of viability at each recovery period.

Recently, Rampton and Ching (43) reported on the longevity and dormancy of nine species of crop seeds buried at different depths. The seed of L. perenne 'Linn' rapidly declined in viability. Less than 0. 05 percent of the recovered L. perenne seed germinated after five months of burial under well-drained and poorly-drained sites. The percent dormant seed was 0. 1 and 0. 3 after the first five months of burial on well-drained and poorly-drained sites, respectively. L. multiflorum 'Oregon Annual', on the other hand, retained a relatively high percentage of germinability and dormancy during the first two years of burial. After the first five months of burial, L. multiflorum averaged 10. 8 percent germination and 19. 0 percent dormancy on the well-drained site; and 12. 2 percent germination and 16. 3 percent dormancy on the poorly-drained site. The germinability and dormancy of L. multiflorum seed was low during the third year of testing. Buried seed of A. tenuis displayed the

highest percentage dormancy of the grass species studied in this experiment. Seed of this species recovered after five months of burial on a well-drained site gave 1. 1 percent germination and 39. 3 percent dormancy. After two years of burial, recovered seed germinated 1. 2 percent with 18. 5 percent dormant seed. Seed recovered after three years of burial showed 5. 0 percent germination and 7. 8 percent dormancy, respectively.

The seedling emergence of a number of species including L. perenne, L. multiflorum, A. tenuis, and Poa annua was studied by Harris (24) in New Zealand. The total emergence expressed as percentage of viable seed sown was found to be 64 percent and 95 percent for L. perenne and L. multiflorum, respectively. In reference to seed persistence and dormancy, Harris stated, "the results of this experiment indicate that there may be more danger of contamination by perennial ryegrass than by Italian ryegrass since a higher percentage of perennial ryegrass seed was unaccounted for at the end of the first autumn". According to Harris, the emergence percentage of P. annua and A. tenuis, 60 percent and 24 percent respectively, indicated a relatively high degree of dormancy in these species. However, no viability tests were made on ungerminated seed during these experiments.

Thurston (47) has studied the germination and emergence of A. fatua sown in pots and under field conditions. The maximum

survival of A. fatua was three years in pots and slightly longer in the field. This worker found no evidence of induced dormancy in seeds of A. fatua buried at depths ranging to 20 inches. In a later report of field investigations, Thurston (48) concluded that maximum survival of viable seeds of A. fatua was 61 months. However, 20 percent or less of the seeds sown produced seedlings.

B. Buried Seed Populations Under Field Conditions

The buried seed populations of numerous species have been studied by a number of British workers. These investigations have dealt with the populations of buried viable seeds associated with various vegetative cover types, soil types and land forms.

These evaluations were made by removing soil samples from the experimental site, placing these under conditions favorable for seed germination, and determining the number and species of emerging seedlings. The nature of such studies precluded the quantitative determination of seed dormancy and persistence.

Brenchley (7) found germinable seed of L. perenne in soil samples taken from sites classified as old pasture, and pasture which was originally arable. Germinable seed was restricted to shallow depths in the former location while seed was found at depths ranging to 12 inches in the latter site. Large numbers of germinable seed of Agrostis spp. were also found in these two pasture types. In addition,

large numbers of buried seeds of this species were recovered from arable land. While the greatest number of buried germinable seeds were found in the upper two inches of soil, germinable seeds were recovered at soil depths ranging to 12 inches. Relatively few P. annua seedlings were observed in soil samples recovered from pastures which were originally arable. Arable land soil samples, however, gave rise to relatively large numbers of P. annua seedlings.

Milton (41) has reported on the buried seed populations of several land forms and cover types. The maximum germinable buried seed population of L. perenne under swards less than five years old was estimated to be 0. 2 million seeds per acre to a depth of seven inches. The actual buried germinable seed population of L. perenne was considered to be lower than expected from analysis of the cover composition. The buried germinable seed population of Agrostis spp. and P. annua were estimated to be 11. 2 and 27. 5 millions of seed per acre, respectively. Large buried germinable seed populations of Agrostis spp. and P. annua were also found under old pastures, hill land, marsh and woodlands. In these locations, the buried seed populations of Agrostis spp. exceeded those of P. annua.

Milton (40) also found relatively small numbers of germinable L. perenne, L. italicum and P. annua seed buried in calcareous clay soil. The number of germinable buried seeds on land of this soil

classification was relatively high.

Few germinable seeds of L. perenne were obtained from soil samples taken from numerous grassland sites sampled by Chippendale and Milton (12). Many germinable seeds of Agrostis spp. and P. annua were recovered. While the majority of viable seeds of these species were situated in the uppermost two inches of soil, viable seeds were recovered from depths ranging to ten inches. Generally, the buried germinable seed populations of Agrostis spp. and P. annua were greater than would be expected from analysis of cover composition. The opposite relationship was found for L. perenne.

The relationships among cover types, soil types and buried germinable seed populations were studied by Champness and Morris (9). The maximum germinable seed populations for the following species in millions per acre to a depth of seven inches for grassland and arable land were reported as:

	grassland	arable
A. tenuis	56.18	25.00
L. multiflorum	0.90	3.24
L. perenne	8.72	15.46
P. annua	12.27	25.42

These authors concluded that the number of buried seed of L. perenne was lower than would be expected from evaluations of sward composition. Very high buried seed populations of L. perenne were, however, found under certain lowland areas where this species

was not represented in the sward composition. Champness and Morris suggest that these high germinable buried seed populations were a result of the cold, poorly aerated, acid soils characteristic of these areas. Although several instances of buried viable seed of L. multiflorum were also reported, data concerning this species were variable. Both A. tenuis and P. annua contributed more to the buried seed population than would be expected from analysis of the sward composition.

III. Factors Influencing the Persistence of Buried Seed

The soil environment has a profound influence on the persistence and maintainance of viability of buried seeds. To be successful in this respect, buried seed must have the capacity to remain in a state of quiescence or enter secondary dormancy until favorable conditions prevail. A review of the literature implicated such factors as depth of burial, soil moisture, soil atmosphere, soil temperature and pH as influential in persistence of buried seeds.

A. Depth of Burial

The influence of depth of burial was discussed by Turner (51, p. 257-269). He suggested that seeds are better preserved at deeper soil depths because of:

(a) high, uniform soil moisture

(b) low, stable soil temperature
(c) low oxygen supply

Harris (25) also ascribed the preservation of deeply buried seeds to the high soil moisture and low temperature and oxygen supply characteristic of deeper depths.

Chepil (11) studied the influence of tillage treatments on the germination of weed seeds. For seeds having a relatively long period of dormancy, the highest percentage of emergence occurred from seeds lying on the soil surface. The deeper the seeds were buried, the lower was the emergence of seedlings and correspondingly higher was the number of seedlings surviving the burial period. Depth of burial, however, exerted very little influence on the longevity of seeds having a short period of dormancy.

Although the seed of Thlaspi arvense and Brassica arvensis remained highly germinable at lower soil depths, Bibbey (6) found greater seed survival at these depths. Bibbey concluded that quiescence rather than secondary dormancy was the major factor in the persistence of these seeds under the conditions of his experiments. Bibbey suggested that quiescence is of greater influence in the persistence of seeds than generally recognized.

Thurston (48) placed seeds of A. fatua at 5 and 15 cm depth in field plots subjected to periodic cultivation. It was found that seed of A. fatua survived longer at the 15 cm depth.

The results of seed burial projects concerning the influence of depth of burial on seed persistence and degree of viability are not in complete agreement. Data of the Duval burial project, as reported by Toole and Brown (49), show greater retention of germinability at deeper burial depths. Rampton and Ching (43) concluded that the retention of germinability and dormancy in buried seed was lowest at shallow depths and increased with depth of burial. However, according to Lewis (38), depth of burial did not influence seed viability.

B. Soil Moisture

The effect of soil water tables on seed viability and preservation was reported by Evans (19). Seed of most species had largely germinated after two months when held above the water table. Seed buried at the same depth, but below the water table remained dormant and were germinable in subsequent tests. In another report, Evans (20) stated that in situ germination was the primary factor in the depletion of seed numbers in loam, sand and peat soils to a depth of eight inches. Seed lying below the water table remained dormant and viable, while those above the water table germinated and perished. Lewis, as cited by Rampton and Ching (43), found that seed persisted for longer periods of time when buried below the soil water level.

Goss and Brown (21) noted that buried seed of red rice

remained viable longer under irrigated conditions. However, prolonged viability under high soil moisture does not appear to be characteristic of all species and conditions. Bruch (8) reported on the viability of buried seed of 12 weed species under irrigated and nonirrigated conditions. The results of this study revealed few differences in the viability of seed recovered from these burial sites. Chepil (10), found that irrigation in addition to natural precipitation had no appreciable effect on germination or longevity of seed in the soil.

Rampton and Ching (43) used well-drained and poorly-drained soils as a variable in evaluating dormancy and germinability of buried seeds of L. multiflorum and L. perenne. Dormancy and germinability, in most cases, were found to be higher in seed recovered from the poorly-drained site.

Since seeds buried in the soil are in the imbibed state, seed persistence may be dependent upon some mechanism to control metabolic activities. The absence of such a mechanism would lead to in situ germination or loss of viability. Barton (4) found a ten-fold reduction in respiration for seeds of Amaranthus retroflexus when held under moist storage at 20 C. Barton also found a progressive decrease in the respiratory rate of Impatiens balsamina seed held in moist storage at 20 C.

The storage of moist seed at high temperature was studied by

Toole and Toole (50). One lot of lettuce seed was held in the imbibed state at 30 C while other lots were stored under conditions of high humidity at 30 C. Subsequent tests revealed higher germination for those seeds held in the imbibed condition. These authors suggest that dormancy of the imbibed seeds suppressed those processes that lead to seed deterioration. It was also suggested that such a check may be responsible for survival of seeds in moist soil.

C. Soil Atmosphere

The oxygen supplying power of the soil environment has been studied by Hutchins (29). This worker measured the diffusion of oxygen from the soil into porous cups placed at different depths. The oxygen supplying power was found to diminish with soil depth. This index of oxygen availability, at a given soil depth, was greater for dry or less firmly packed soil and lesser for moist or more firmly packed soils. The oxygen supplying power was also found to fluctuate with wetting and subsequent drying, --being lesser when the soil above the depth in question was moist and greater when it was dry. Hutchins related these findings to the germination of seeds and found that the minimum oxygen level required for germination varied among species.

Bibbey (6) found that lower-than-normal oxygen or higher-than-normal CO_2 pressures were effective in depressing germination of seeds that show marked quiescence. Seed of species which are

relatively short lived in the soil did not show this sensitivity.

D. Soil Temperature

Turner (51, p. 257-269) has emphasized the importance of low, stable temperature, characteristic of deeper soil depths, in maintaining seed viability. He suggested that the decreased magnitude of temperature fluctuation found at deeper soil levels may be particularly important in maintaining viability of seed requiring temperature alternation for germination.

E. Soil pH

Champness and Morris (9) suggest that acid soil conditions may enhance seed preservation while inhibiting germination. This was considered to be particularly relevant when acid condition were associated with cold, poorly aerated soils. These workers suggest that acid soil conditions may retard the growth of soil bacteria and fungi responsible for seed deterioration. However, data from the seed burial experiment of Lewis (38) indicate that acid peat (pH 4. 18) was inferior to mineral soil as a medium for seed preservation.

IV. Factors Associated with the Induction of Secondary Seed Dormancy

Secondary dormancy has been associated with the prolonged survival of buried seed. A review of the literature revealed

considerable diversity in factors responsible for the onset of secondary seed dormancy. However interaction between or among factors such as gaseous exchange, alteration in atmospheric composition and extreme temperature or their singular effects appear to be associated with the induction of this type of seed dormancy.

A. Atmospheric Composition and Gaseous Exchange

Kidd (31) found that seed of Brassica alba could be induced to dormancy by high partial pressures of CO_2. Buried seed experiments were also utilized to support these findings. When vegetative material was placed at a level below buried seeds and allowed to decay, germination of these seeds was depressed while dormancy was induced. Kidd concluded that this response was due to CO_2 arising from the decaying vegetation. In another report, Kidd (32) observed that low temperature and low oxygen supply increased the inhibition of germination produced by a given partial pressure of CO_2.

The onset of secondary dormancy in embryos of Ambrosia trifida was studied by Davis (17). Secondary dormancy could be induced by subjecting the embryos to high temperature associated with limited oxygen supply. Davis concluded that secondary dormancy in embryos of A. trifida was caused by restricted respiration at high temperature.

Secondary dormancy in embryos of Xanthium was induced by

embedding the moist embryos in agar or clay (Davis, 16). This treatment, Davis suggested, placed a restriction upon the normal pattern of gaseous exchange. Davis also suggested that secondary dormancy was maximized when the embryos were subjected to high temperature associated with an oxygen supply just below that required for germination.

Secondary dormancy of Xanthium seed was also investigated by Thornton (45). It was found that dormancy could be induced in upper and lower Xanthium seeds by subjecting these to atmospheres lacking oxygen but containing N_2, H_2, CO_2 or various mixtures of N_2 and CO_2. Small concentrations of oxygen were effective in lowering the dormancy response produced by these atmospheres. Thornton considered these treatments to have their effect on the embryo since these seeds were unable to grow if the seed coats were removed.

The influence of oxygen supply on the induction of secondary dormancy in seeds was reviewed by Thornton (46, p. 487-500). Secondary dormancy, Thornton suggested, is induced by accumulation of intermediary products formed by partial anaerobic respiration. These intermediary products may act as inhibitors since the oxidation system has been temporarily impaired by insufficient oxygen supply.

Vegis (54, p. 94-99) supported this hypothesis when he stated, "the cause of secondary dormancy in embryos appears to be due to restricted aerobic respiration at high temperatures". An oxygen

supply just below that necessary for germination at high temperature was suggested to be optimum for the induction of secondary dormancy.

B. Submergence in Water

Kommedahl and associates (36) observed a reduction in germination of A. fatua seed after being soaked in water under partial vacuum for one hour. The germination of seed was also reduced by wetting followed by a drying period. Removal of the lemma and palea negated the effect of wetting and subsequent drying.

Hay (27) reported that dormancy could be induced in A. fatua by soaking the seed in boiled water at 25 C for 12 hours. This induced dormancy was thought to be similar to natural field dormancy since both types were broken by application of gibberellin, KNO_3 and H_2O_2. Hay also found that dormancy was not induced if aerated water was used in the soak or if high oxygen tension was administered during the germination phase. Similar results were reported in a later publication (26).

Hay and Cumming (28) found that immersion of A. fatua seed for two days preceding the germination period resulted in viable seed of which less than ten percent germinated. The germinability could also be depressed by soaking the seed in cool, boiled water prior to the germination period.

C. Temperature

Secondary dormancy in seed (of some species) may be induced by temperature alone. Popcov as cited by Barton (5, Vol. 15 (II), p. 699-717) found that secondary dormancy in Taraxacum megalorhizon could be induced by relatively high temperature (30 C) or by low temperature (0 - 1 C).

D. Other Factors

Other factors have been found to induce secondary seed dormancy. Nutile (42) used coumarin to induce dormancy in seed of Lactuca sativa. Kahn (30) found that dormancy in seed of L. sativa could be induced by prolonged soaking in organic and inorganic solutions which included saccharose, mannitol, NaCl, KCl and $CaCl_2$. Dormancy in L. sativa has also been found to be induced by gamma-radiation (23).

The need for additional studies concerning the influence of soil environment on buried seed persistence and dormancy appears obvious from this review of the literature. Disparity concerning the influence of burial depth, irrigation and vegetation cover types on buried seed behavior have been noted. Also, few detailed studies on the effects of soil moisture and temperature on the persistence and dormancy of buried seeds are available. This is also true for the

causes of depletion of buried seed populations. The actual importance of secondary seed dormancy under field conditions has not been extensively investigated.

METHODS AND MATERIALS

Seed used in these investigations represented lots of *Avena fatua* L., *Agrostis tenuis* Sibth., *Lolium multiflorum* Lam., *Lolium perenne* L., and *Poa annua* L.. Each seed lot was identified and stored at room temperature during these investigations. Information on these seed lots are given on Table 1.

A host of terms have been used to describe the chronology and mechanisms of dormancy and other states in which seeds exist. This extensive terminology inevitably leads to confusion. To overcome this problem, a standard set of terms was employed in this thesis to define the status of seed. Definitions of these terms are given in the Glossary.

I. Long Term Burial Experiment

This experiment was designed to test the influence of vegetation type and depth of burial on the persistence of buried seed over a three year period. Results from the first year are reported in this thesis.

Seed of *A. fatua*, *A. tenuis*, *L. multiflorum* (lot 1), *L. perenne* (lot 1), and *P. annua* were buried at two depths under four vegetation cover types.

Approximately 500 seeds were placed in 6.2 X 12.4 cm Saran mesh packets. The packets were then sewn shut with nylon thread.

Table 1. Information on species and seed lots used in studies on seed dormancy and persistence.

Species	lot no.	Accession no.	Source	Year of harvest	Germination %	Primary dormancy %
A. fatua	-	-	Weed seed collection Hyslop Agronomy Farm	1964	83.00	9.00
A. tenuis	-	-	Dr. John Thomas, Forage breeding project, Farm Crops Dept.	1964	91.50	0.50
P. annua	-	-	Weed seed collection, Hyslop Agronomy Farm	1964	94.50	0.75
L. multiflorum	1	32574	Cooperative seed testing laboratory, Corvallis, Oregon	1962	97.00	0.25
	2	80328	"	1966	95.00	0.75
	3	80158	"	1966	96.75	0.00
	4	79748	"	1966	95.50	1.00
L. perenne	1	69015	"	1965	88.00	1.00
('Linn')	2	81673	"	1966	96.50	0.75
	3	80671	"	1966	94.75	1.25

Each packet was identified by a coded pattern of metal staples placed on one end.

The burial plot was established on September 21, 1965 at Hyslop Agronomy Farm, on soil described as Woodburn silty clay loam (43). Prior to burial, the plot was prepared to a firm, level condition. Trenches, 10 cm wide and 5 and 10 cm deep were made by a power digger. The seed packets were agitated to disperse the contents, placed flat in the trenches, covered with soil and packed. To exclude rodents, a 90 cm wide sheet metal barrier was placed in a 60 cm deep trench dug around the plot area. Spaces remaining between the trench walls and the sheet metal were filled with soil.

After the packets were buried, respective main plots were broadcast seeded to Medicago sativa L. 'Du Puits', L. perenne and Triticum aestivum L. 'Druchamp.' An indigenous weed cover treatment was included in a fourth set of main plots. Dominant weeds in this treatment included Capsella bursa-pastoris (L.) Moench., Poa annua L., Trifolium incarnatum L., and Brassica, Bromus, Lupinus, Rumex, Senecio, and Vicia spp.

The experimental design was a split-split plot with two replications. Two seed packets (subsamples) were included in each replication. Main plots were cover types and burial depths. Species of buried seeds were sub plots. One replication was sprinkler irrigated for two hours on September 30, 1965 to determine the influence

of fall irrigation upon buried seed persistence.

The buried seed packets were recovered on September 30, 1966. One hundred seeds were randomly selected from each packet and placed in a 15 cm petrie dish containing three layers of filter paper and 20 ml of water. The petrie dishes were placed in a growth chamber and subjected to a regime of 25/15 ± 1 C which corresponded to eight hours fluorescent light (880 ft-c) and 16 hours dark, respectively. The duration of germination was ten days for A. fatua, 14 days for L. multiflorum and L. perenne, and 21 days for A. tenuis and P. annua. Germination counts were made at the end of these respective durations. The viability of ungerminated seed was ascertained by the tetrazolium test (22).

II. Short Term Burial Experiment

The status of A. fatua, A. tenuis, L. multiflorum (lots 2, 3, and 4), L. perenne (lots 2 and 3) and P. annua seed after short durations of burial was determined in this experiment. Seed of these species were buried at a depth of 10 cm and recovered at two, four, and six month intervals.

One hundred seeds, constituting one sample, were placed in a 5 X 5 cm Saran mesh packet. A coded plastic strip was placed in each packet to permit identification. The packets were sewn shut with nylon thread.

The experiment was initiated on October 14, 1966, near the site described in Experiment I. The plot area was worked to a firm level condition prior to burial. Trenches 7.5 cm wide and 10 cm deep were made with a power digger. The seed packets were agitated to distribute the seeds contained within, placed in the trench, covered with soil and packed.

The experimental area was broadcast seeded to L. perenne after the packets were buried. Soil temperature at 10 cm depth was recorded with Rustrak and Tempscribe thermal recorders. The soil moisture percentage was determined at weekly intervals.

The experimental design was a split plot with four replications. Durations of burial were main plots and species were sub plots.

The seed packets were recovered at the end of each duration. The in situ germinated seeds were counted and the remaining seeds were placed in 15 cm petrie dishes containing three layers of filter paper and 20 ml of water. These seeds were germinated at 25/15 ± 1 C which corresponded to eight hours fluorescent light (880 ft-c) and 16 hours dark, respectively. Germination counts were made at the end of ten days for A. fatua, 14 days for L. multiflorum and L. perenne and 21 days for A. tenuis and P. annua. To determine the relationship between terminal dormancy and capacity for subsequent germination, ungerminated seeds were treated as follows:

(i) One-half of the ungerminated seeds of each sample were evaluated for viability by the tetrazolium test (22).

(ii) The remaining one-half of the ungerminated seeds were placed in 15 cm petrie dishes containing three layers of filter paper and 20 ml of 0.1 percent KNO_3 and subjected to a temperature of 5 ± 1 C for five days. Then the seeds were germinated for 30 days at 25/15 ± 1 C corresponding to eight hours fluorescent light and 16 hours dark, respectively. Additional germination was determined at the end of this time. Ungerminated seeds were then treated with tetrazolium chloride to determine the final dormant seed percentage.

In the case of odd numbered lots of ungerminated seeds, the smaller portion (n-1) was directed to treatment (i), while the larger portion (n) was tested by treatment (ii). The results of treatment (i) and (ii) were expanded to a 100 seed sample basis by the use of appropriate correction factors.

III. Controlled Environment Experiment

The effects of soil moisture and temperature on buried seeds were determined in this study. Seed of A. fatua, A. tenuis, L. multiflorum (lots 2, 3 and 4), L. perenne (lots 2 and 3) were buried

in greenhouse soil containing 4. 5, 22. 5 and 40. 5 percent moisture at 5, 10 and 15 ± 1C for a 30 day period.

One hundred seeds were placed in 5 X 5 cm open Saran mesh packets. A coded plastic strip was placed in each packet to permit identification. One packet of each seed lot was buried at a depth of 7. 5 cm in screened greenhouse soil contained in 33 X 23 X 11 cm plastic trays. The appropriate soil moisture percentage was established by the method outlined by Daubenmire (15, p. 115). After water had been added to the trays, the weight of the tray assembly was recorded. Evaporation losses were replenished at weekly intervals by adding sufficient water to equal the original tray assembly weight. Constant temperatures were maintained by placing the trays in growth chambers.

At the end of 30 days, the packets were recovered and in situ germinated seeds counted. Ungerminated seeds were placed in 15 cm petrie dishes containing three layers of filter paper and 20 ml of water. The germination regime was the same as that outlined in Experiment I. The viability of ungerminated seed was estimated by the tetrazolium test.

Three replications of each treatment were made. The experimental results were analyzed as a completely randomized design with factorial arrangement.

IV. Statistical Analysis

Statistical analyses of data from Experiments I and III were made via the Fortran 3300 computer. While Experiments I and II were established as a split-split plot and split plot design, respectively, the data from these experiments were analyzed as a completely randomized block design.

Missing data analysis was utilized in Experiment II to adjust for four missing observations.

Percentage data between 0 and 20 or 80 and 100 were converted via arcsin transformation prior to analysis. The original values are given for illustrative purposes.

RESULTS

The persistence of buried seed, recovered and tested in these experiments, was examined via parameters of viability and nonviability. The viable class of the buried seed populations included parameters of quiescence and terminal dormancy. The nonviable class included *in situ* germination and nonviability among ungerminated seed.

The rationale underlying the use of these parameters is given in the following expression which defines the status of seeds buried below the maximum depth of emergence.

$$BSP = V + NV$$

where:

BSP = buried seed population

V = total viable segment of buried seed population

NV = total nonviable segment of buried seed population.

The V component of the expression may be expanded:

$$V = Q + D_t$$

where:

Q = quiescence

D_t = terminal dormancy

Likewise the NV component of the expression may be expanded to:

$$NV = G_{is} + S$$

where:

G_{is} = in situ germination[1]

S = senescent seed or nonviability among ungerminated seed.

Thus, the complete expression describing the segments of the buried seed population is:

$$BSP = Q + D_t + G_{is} + S$$

These components will be used throughout the text of this thesis to describe persistence and depletion of buried seeds.

I. Long Term Burial Experiment

The persistence of buried seed recovered and tested in this experiment was examined via the parameters quiescence, terminal dormancy and total nonviability. The inclusion of a fourth parameter, in situ germination, was rendered impossible due to the advanced state of deterioration characteristic of seeds recovered from burial.

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[1] While certain in situ germinated seeds may be regarded as living, they are placed in this category since their longevity is short.

Hence, nonviability was a composite of the population components G_{is} and S.

The quantitative values of quiescence, terminal dormancy and nonviability are given in Tables 2 through 4 of the Appendix.

A. Parameters of Viability and Persistence

1. Quiescence (Q Component). The germination of seed recovered from burial differed among the five species studied. Of these, A. fatua gave the highest germination percentage. The germination of A. tenuis, L. multiflorum and P. annua were of intermediate magnitude. Germination was rarely observed among seed samples of L. perenne.

The germination of seed recovered from the 10 cm soil depth was greater than that of seed taken from the 5 cm depth. The germination of the five species at the two burial depths are shown on Figure 1.

The germination of seed recovered from the four cover types was not significantly different. However, germination tended to be lower among samples recovered from the wheat plots.

Replications were not significantly different, hence the fall irrigation had little influence on the germinability of seeds tested in this experiment.

2. Terminal Dormancy (D_t Component). The terminal

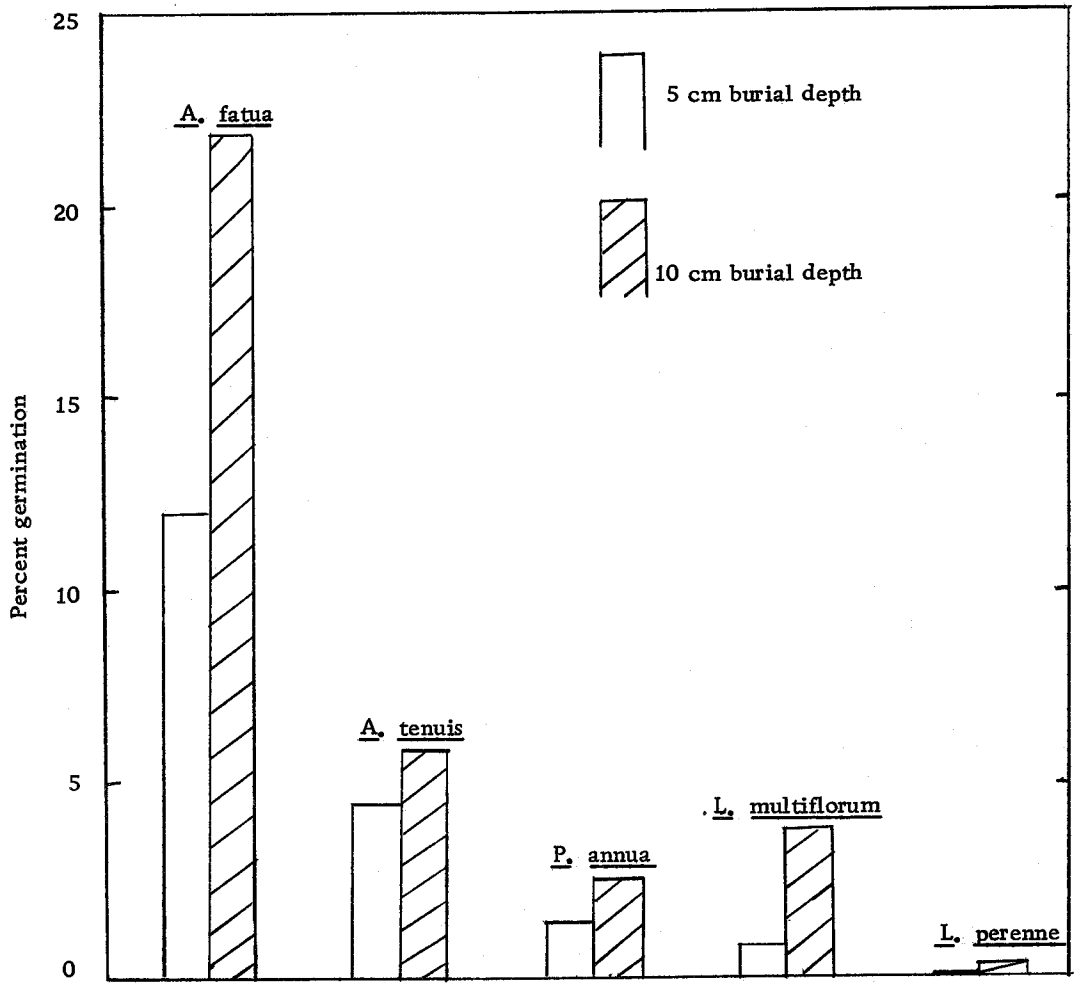

Figure 1. Quiescence of seed recovered after one year of burial at two depths.

dormancy percentage of ungerminated seed, estimated by the tetrazolium test, was relatively low for all of the species studied. This may, in part, be a result of the low staining potential of the 2, 3, 5-triphenyl tetrazolium chloride used in this experiment.[2] However, terminal dormancy did vary among the five species. A relatively high percentage of dormancy was found among ungerminated seed of A. fatua. Intermediate numbers of dormant seed were observed among ungerminated seed of A. tenuis, P. annua and L. multiflorum. Very few dormant seeds were found among samples of L. perenne.

The content of dormant seed among samples recovered from perennial ryegrass plots was greater than among similar samples taken from wheat, weed and alfalfa plots. Only slight differences in terminal dormancy percentage were noted among seed samples taken from the latter plots.

Terminal seed dormancy data of the five species taken from the four cover types is illustrated on Figure 2. Terminal dormancy of seed as contrasted with germinability, was not influenced by depth of burial. As with germination, fall irrigation had no influence upon the level of seed dormancy.

In order to define the dormancy type, the relationship between

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[2] The lot of triphenyl tetrazolium chloride used in this experiment possessed 94 percent of the staining potential of the lot used in Experiments II and III.

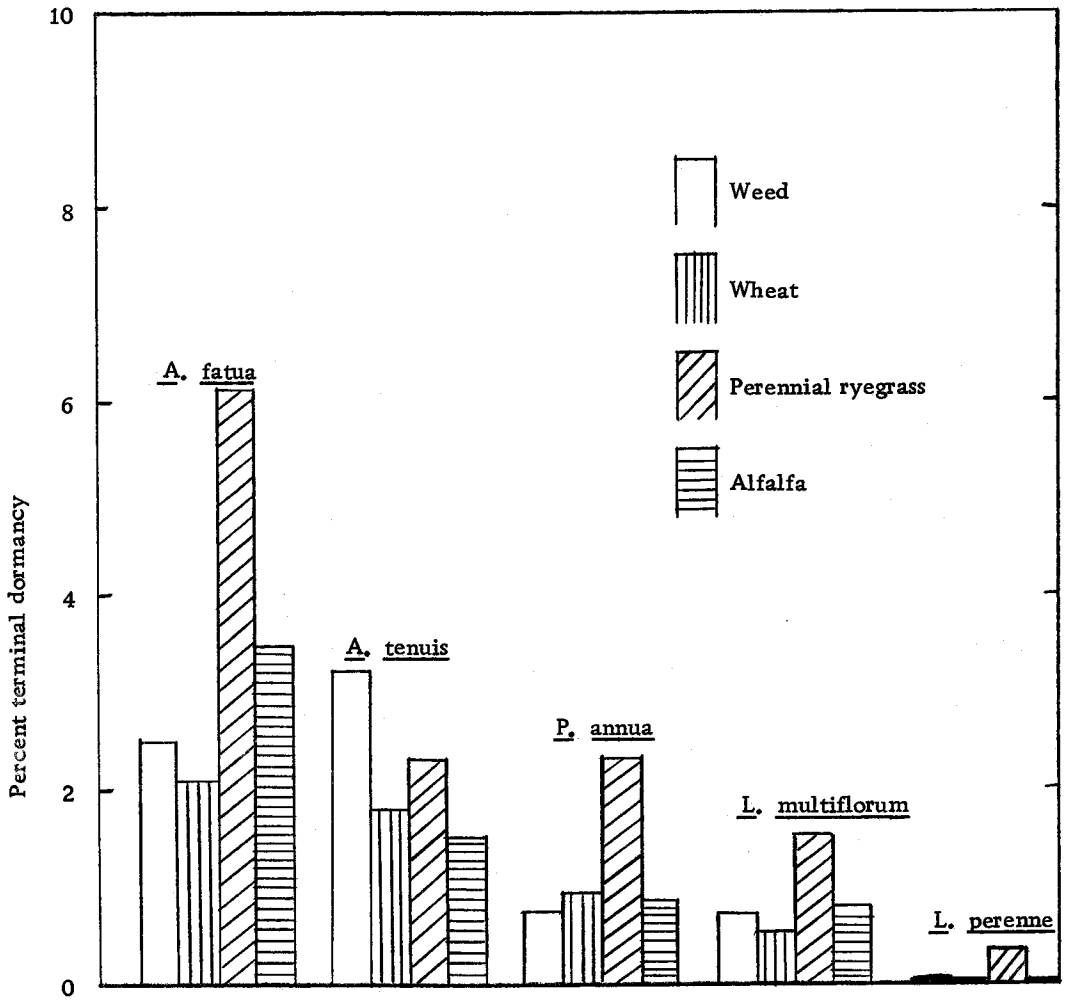

Figure 2. Terminal dormancy of seed recovered after one year of burial under four vegetation cover types.

primary dormancy and terminal dormancy was examined. The dormancy type was classified as indeterminate if primary dormancy exceeded, or was not significantly different from the terminal dormancy percentage. Terminal dormancy percentages that were significantly greater than primary dormancy were interpreted to indicate the presence of a secondary dormancy in addition to an indeterminate dormancy type. The results of this analysis are shown on Table 2. Relative secondary dormancy was found only in A. tenuis recovered from the weed cover treatment at 5 cm depth, and from perennial ryegrass and alfalfa cover treatments at 10 cm burial depth.

The mode of persistence may be examined by the relationship:

$$Mp = \frac{Q}{D_t}$$

where:

Mp = mode of persistence

Q = quiescence

D_t = terminal dormancy

These ratios, obtained from species means are shown on Table 3. These values may be somewhat enlarged as a result of the low staining potential of the tetrazolium chloride used in this experiment. However, these values show that quiescence constituted the largest component of the persistent, viable seed population.

Table 2. Test for the presence of secondary seed dormancy, made by computing F values for primary versus terminal seed dormancy of persistent species subsequent to recovery from two depths of burial under four vegetative cover types.

Species of buried seed	Depth of burial (cm)	Vegetative cover type: Weed F[1]	Weed Symbol[2]	Wheat F	Wheat Symbol	Perennial Ryegrass F	Perennial Ryegrass Symbol	Alfalfa F	Alfalfa Symbol
A. fatua	5	--	Di	--	Di	--	Di	--	Di
	10	--	Di	--	Di	--	Di	--	Di
A. tenuis	5	17.3*	Ds	1.2	Di	1.0	Di	0.3	Di
	10	2.7	Di	3.0	Di	6.0*	Ds	27.1*	Ds
P. annua	5	--	Di	--	Di	2.4	Di	0.5	Di
	10	--	Di	0.1	Di	2.9	Di	--	Di
L. multiflorum	5	--	Di	2.0	Di	0.9	Di	--	Di
	10	1.0	Di	--	Di	5.1	Di	3.4*	Di

[1] F values computed with 1 and 6 degrees of freedom. Dashes indicate that primary dormancy exceeded or was equal to terminal dormancy. *-F values significant at the five percent level of probability.

[2] Di = indeterminate dormancy, Ds = secondary dormancy.

Table 3. Mode of persistence calculated as quiescence/terminal dormancy among seed of four persistent species recovered after one year of burial. [1]

Species	quiescence / terminal dormancy
A. fatua	4.81
A. tenuis	2.18
P. annua	1.67
L. multiflorum	2.31

[1] Ratios calculated from species means of seed quiescence and terminal dormancy.

B. Parameter of Seed Depletion and Nonviability

1. Total Nonviability (NV Component). Nonviability was affected by those factors--but in an opposite sense-- that influenced germination of the recovered seed samples.

Among the five species, L. perenne had the highest percent nonviability. In order of descending magnitudes of nonviability, the other species were P. annua, L. multiflorum, A. tenuis and A. fatua.

Depth of burial had a significant effect upon seed nonviability. Samples taken from the 5 cm depth were higher in nonviable seed than samples taken from the deeper burial level (Figure 3).

While cover types did not have a statistically significant effect upon the percentage of nonviability, samples taken from wheat plots tended to be higher in nonviable seed content.

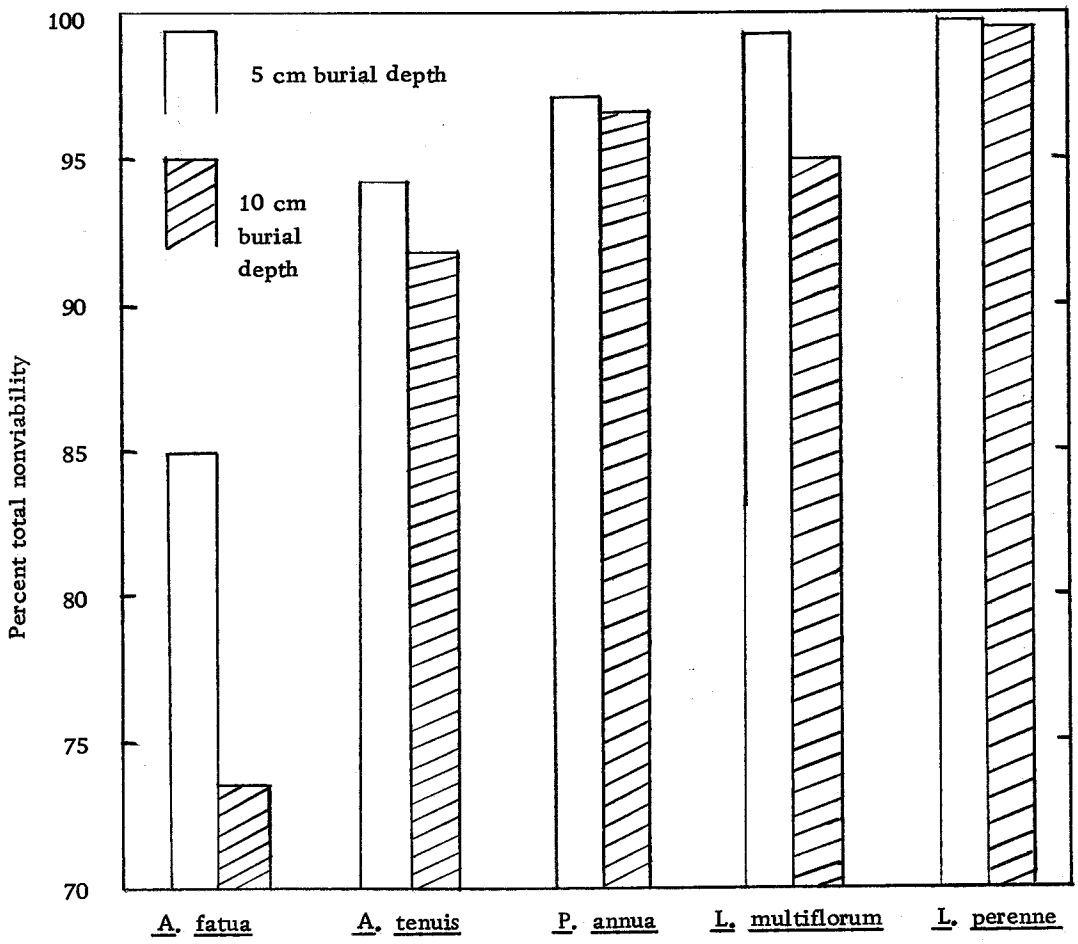

Figure 3. Total nonviable seed recovered after one year of burial at two depths.

Since replications were not different, it may be concluded that the single fall irrigation had little influence on loss of seed viability.

II. Short Term Seed Burial Study

Parameters of seed viability studied in this experiment included quiescence and terminal dormancy. Parameters of seed nonviability were in situ germination and nonviability among ungerminated seeds after 60 days of burial, and total nonviability over the duration of the study.

Weekly determinations of soil moisture and continuous records of soil temperature were made to permit correlation of these environmental factors with the parameters of viability and nonviability. Soil moisture and temperature for the duration of this experiment are illustrated on Figure 4. Quantitative values for the viable and nonviable parameters are given on Tables 7 through 12 of the Appendix.

A. Parameters of Viability and Persistence

1. Quiescence (Q Component). High levels of readily germinable seed were found among recovered samples of L. multiflorum. A low percentage of quiescence was found among A. tenuis seed after recovery from burial. Readily germinable seeds were rarely encountered among samples of A. fatua, P. annua, and L. perenne.

Figure 5 shows that quiescence decreased rapidly during the

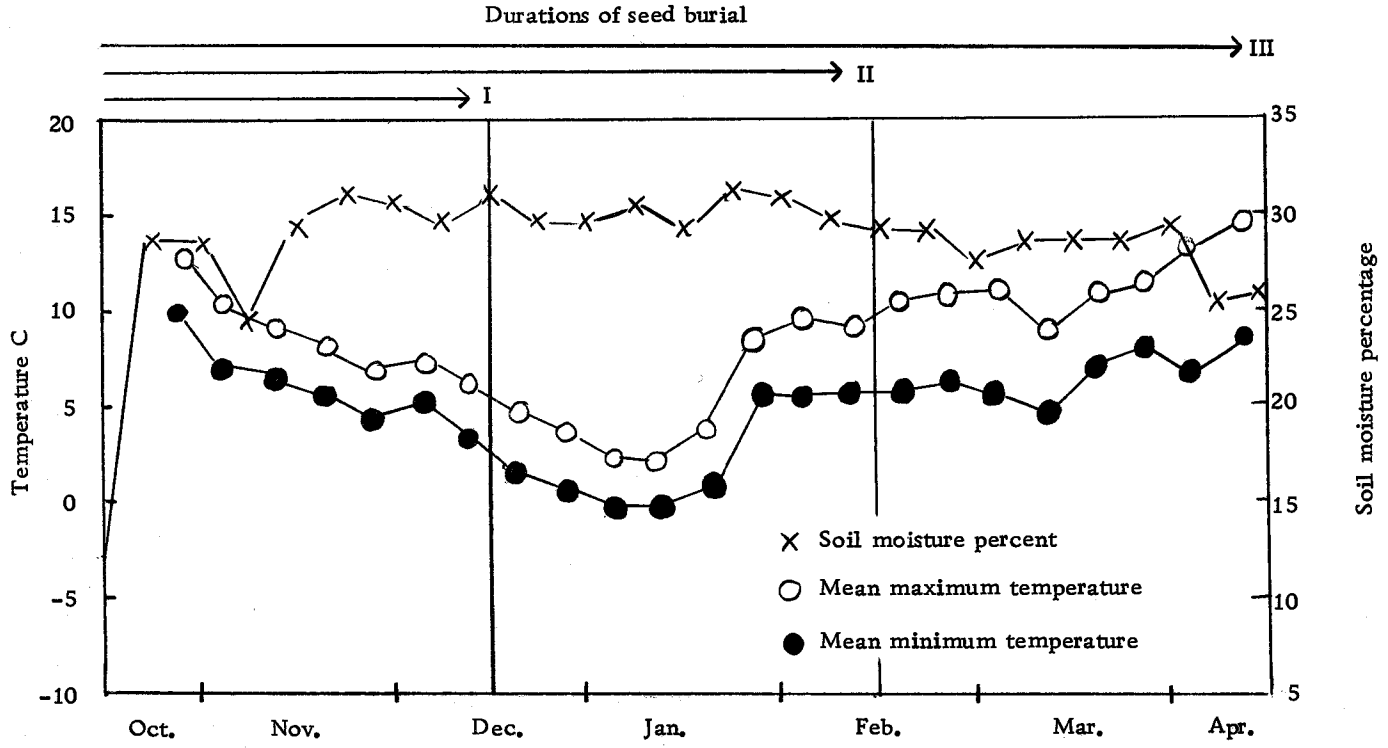

Figure 4. Soil moisture percentages and weekly mean maximum and minimum temperatures at 10 cm soil depth during the period of October 14, 1966 through April 14, 1967.

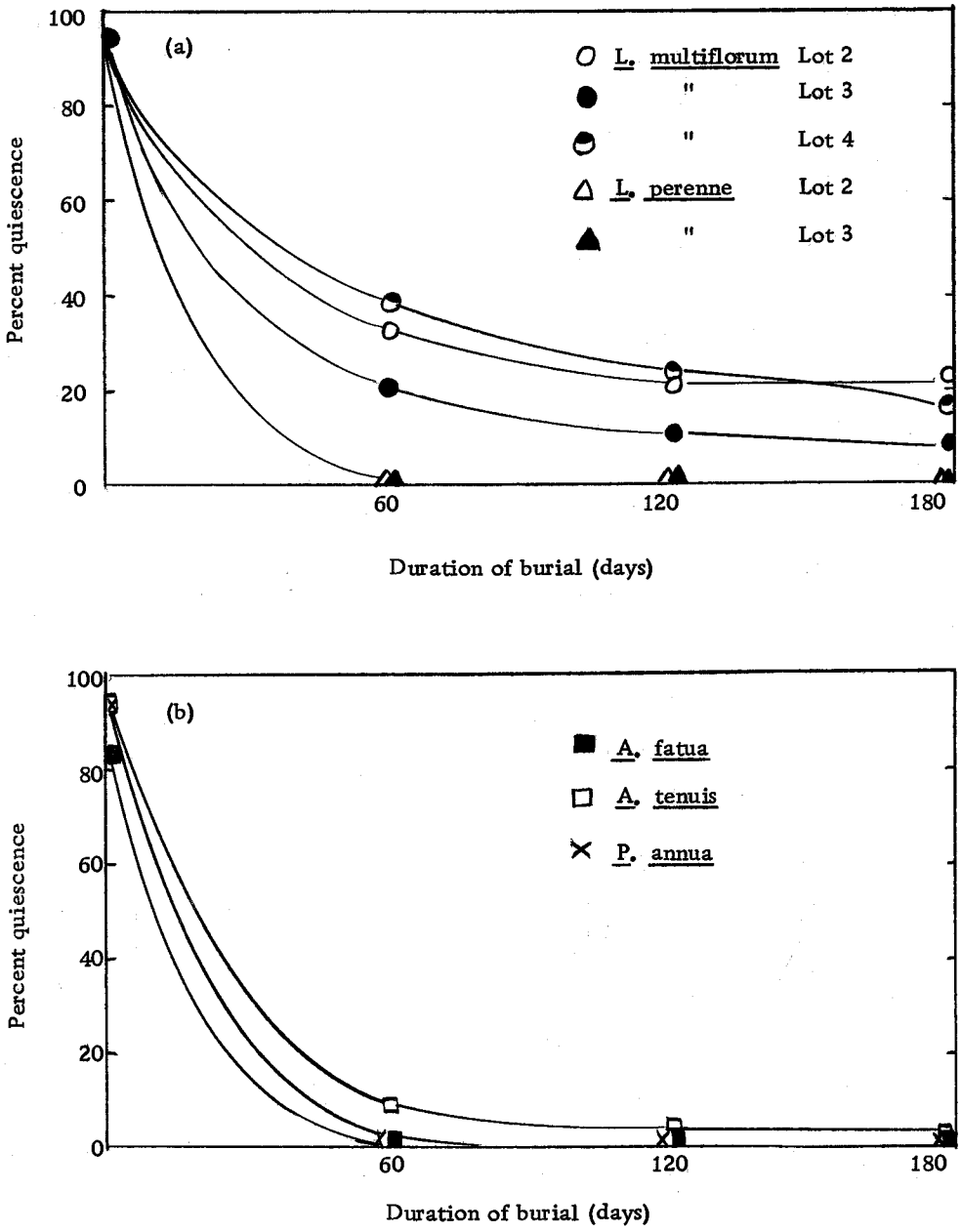

Figure 5. Quiescence among seed of L. multiflorum and L. perenne (a) and A. fatua, A. tenuis, and P. annua (b) after three durations of burial.

first two months of burial. Climatological data on Figure 4 indicates that this period was characterized by soil temperature generally in excess of 5 C and soil moisture percentages ranging from intermediate to high. The rate of quiescence loss diminished during the period of February 14 through April 14, 1967 when prevailing conditions were those of low soil temperature and high soil moisture.

Seed quiescence was absent or negligible among samples of A. fatua and L. perenne recovered after each of the three durations of burial. This response was very different from those of the other three species, and accounted for a significant species X burial duration interaction.

2. Terminal Dormancy (D_t Component). In addition to positive tetrazolium reaction, terminal dormancy was also estimated by delayed germination response. The latter estimate permitted evaluation of those seeds in a deep state of dormancy, since seeds remaining ungerminated after the prolonged germination period were analyzed via the tetrazolium test. The following results pertain to positive tetrazolium tests and delayed germination response.

Relatively high levels of terminal dormancy were found among samples of A. tenuis and L. multiflorum lots 2 and 4. L. multiflorum lot 3 and P. annua were characterized by intermediate levels of dormancy. Very low terminal dormancy percentages were recorded for A. fatua and the two lots of L. perenne (Figure 6).

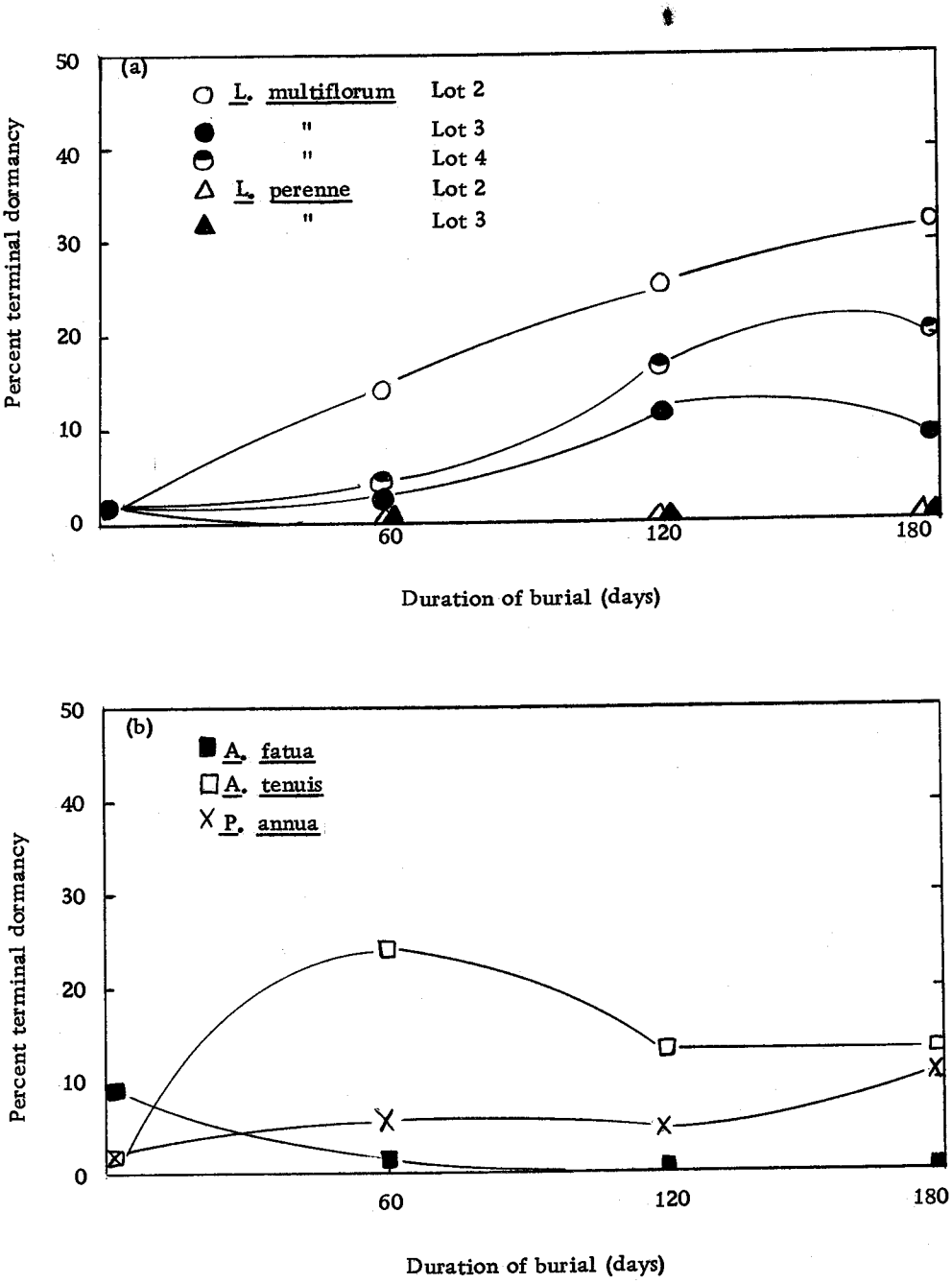

Figure 6. Terminal dormant seed of L. multiflorum and L. perenne (a) and A. fatua, A. tenuis, and P. annua (b) estimated by delayed germination response, after three durations of burial.

The degree of terminal dormancy, estimated by both tetrazolium reaction and delayed germination response, generally increased with duration of burial. Figure 4 shows that these initial changes occurred when soil temperature was decreasing and soil moisture was at a high level. The latter portion of the six month burial duration was characterized by increasing soil temperature. Several differences were noted between data of the tetrazolium analysis and that of the delayed germination test. In the tetrazolium analysis, no significant differences were found between terminal dormancy of seed recovered at 60 and 120 day intervals (Appendix Table 8). In the delayed germination test, no differences were observed between the 120 and 180 day recovery intervals (Appendix Table 9). Close inspection of the tetrazolium test data shows only limited staining of A. tenuis and P. annua ungerminated seed at the 120 day recovery period. These terminal dormancy percentages are much less than those of the same samples tested by delayed germination response. Also, this is in sharp contrast to the high percentage of tetrazolium reaction observed among seed after 60 and 180 days of burial. These factors account for the disparity between data of the 120 day recovery period as obtained from the two analyses.

While terminal dormancy among seed of P. annua and L. multiflorum tended to increase with duration of burial, no significant

differences were found among terminal dormancies of A. fatua at the three recovery dates. Also, limited terminal seed dormancy of L. perenne was found at each recovery date. In addition, terminal dormancy among seed of A. tenuis declined after two months of burial. These factors account for a significant species X burial duration interaction.

The essential point brought out by these analyses is the fact that normal seedlings can be obtained from terminal dormant seed of these species. Also, stratification associated with dilute KNO_3 is an effective combination for breaking dormancy. The extent of its effectiveness could not be ascertained, however, since parallel delayed germination tests without stratification were not conducted.

The relationship between positive tetrazolium tests and capacity for delayed germination was studied via correlation analysis. A correlation coefficient of .84 indicated that the degree of positive tetrazolium staining was significantly and directly related to the subsequent germination of the seeds. The regression coefficient of delayed germination on positive tetrazolium staining was .89. The relationship between tetrazolium staining and capacity for delayed germination is shown on Figure 7.

Positive tetrazolium reaction of seeds remaining ungerminated subsequent to the delayed germination test was an estimate of the percentage of seeds in a deep state of dormancy (Figure 8).

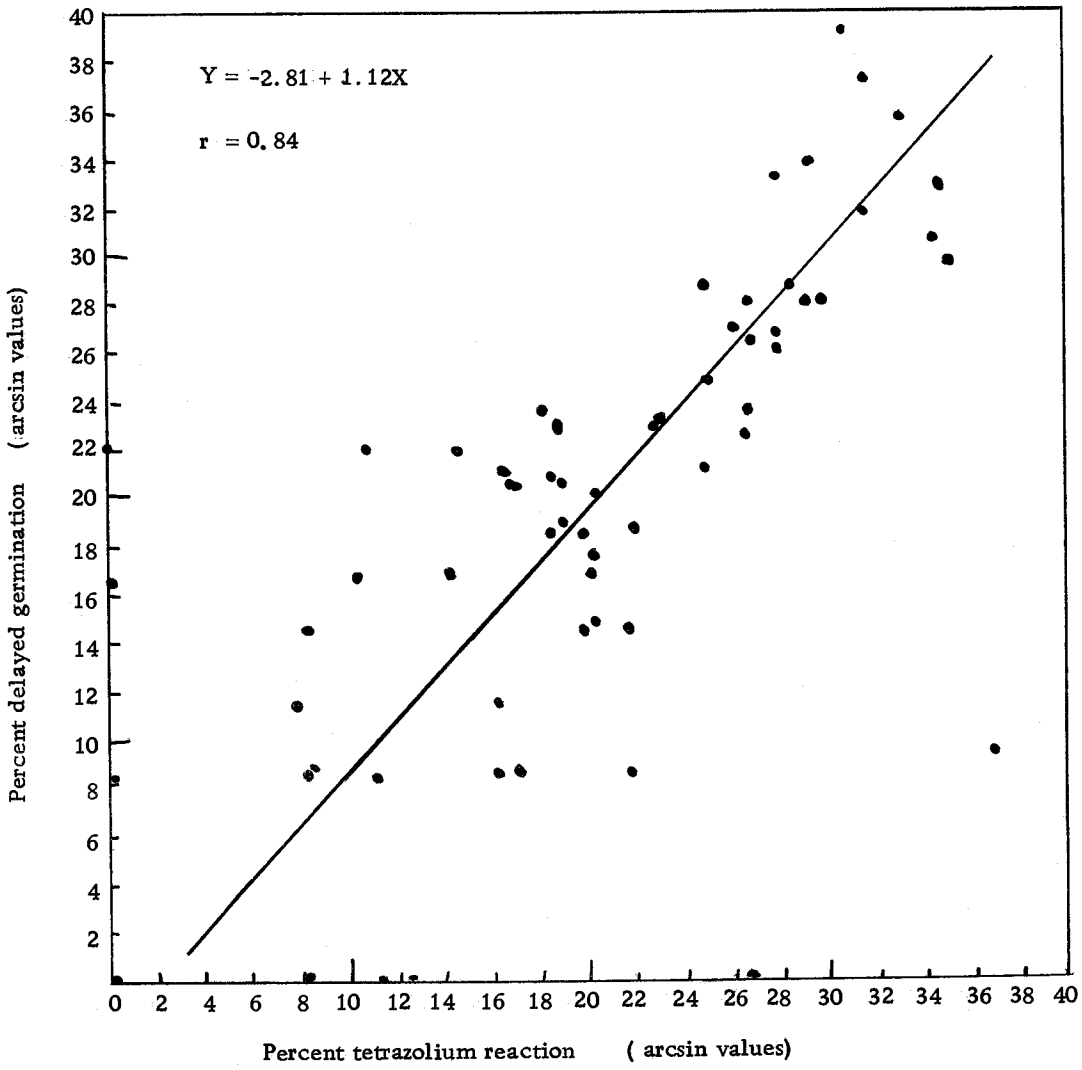

Figure 7. Relationship between tetrazolium reaction and capacity for delayed germination among seed of five grass species.

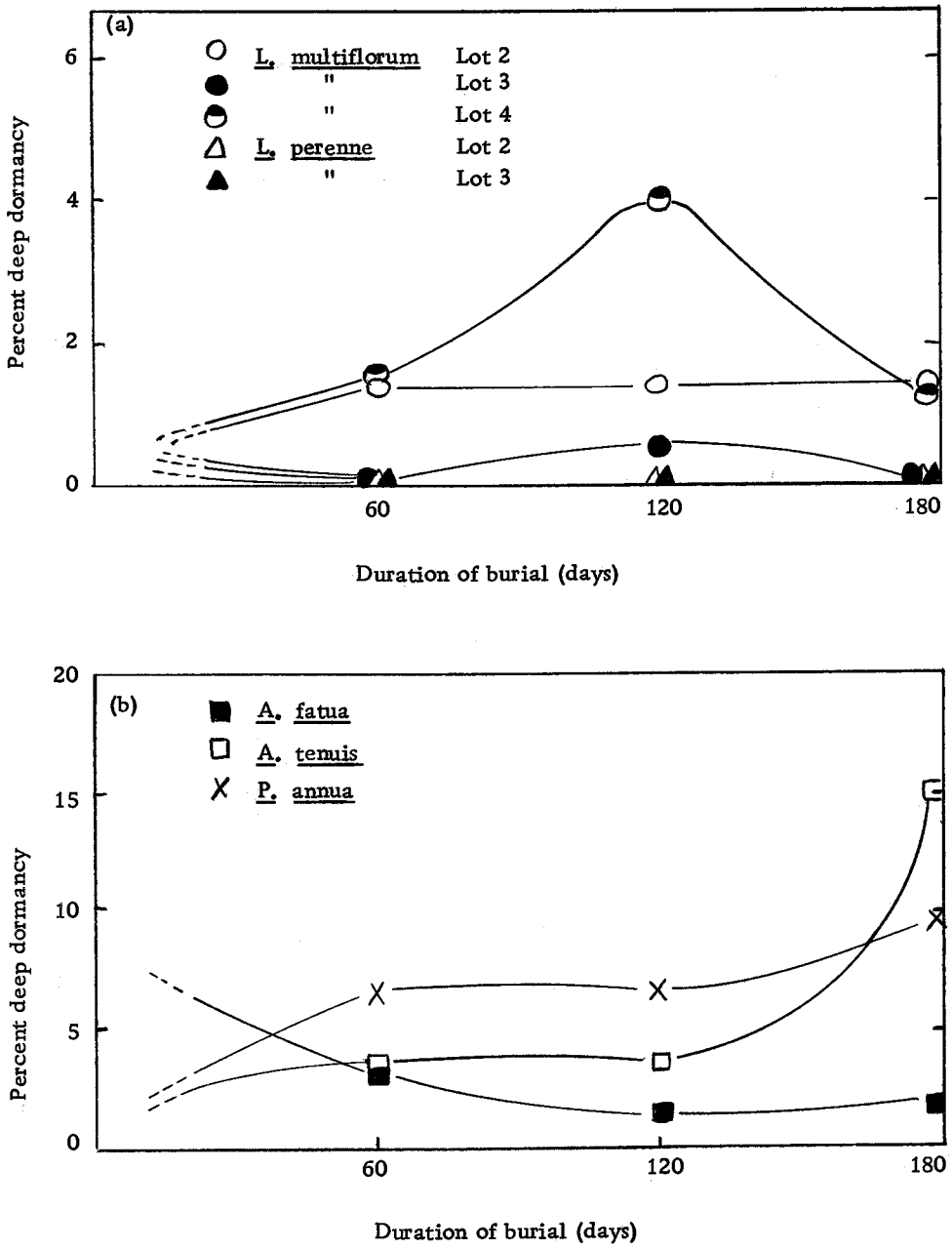

Figure 8. Deep dormancy among seed of L. multiflorum and L. perenne (a) and A. fatua, A. tenuis, and P. annua (b) after three durations of burial.

Relatively high percentages of deep dormant seed of A. tenuis and P. annua were recorded. A limited number of deep dormant seeds were found among samples of A. fatua and L. multiflorum. No deep dormancy was found among ungerminated seed of L. perenne.

While the level of deep dormancy tended to increase with time of burial, the burial duration F test was not significant.

Clarification of terminal dormancy in relation to primary and secondary dormancy was made by the analysis outlined in part I of Results. Table 4 shows that relative secondary dormancy was induced in seed of A. tenuis, P. annua and L. multiflorum under field conditions. The terminal dormancy of A. fatua was of an indeterminate type. Terminal dormancy of ungerminated seed was rarely encountered among lots of L. perenne.

The mode of seed persistence during the six months of burial, shown on Table 5, was determined by comparing species means for quiescence/terminal dormancy. These ratios indicate that terminal dormancy was the principle mode of persistence of A. fatua, A. tenuis and P. annua during the period of October, 1966 through April, 1967. With L. multiflorum, however, seed quiescence was equal to or exceeded terminal dormancy as a mode of persistence.

Table 4. Test for the presence of secondary dormancy, made by computing F values for primary versus terminal dormancy among seed lots of four persistent species recovered after two, four and six months of burial. [1]

Species	Lot no.	Days of burial: 60 F [2]	60 Symbol [3]	120 F	120 Symbol	180 F	180 Symbol
A. fatua		--	Di	--	Di	--	Di
A. tenuis		115.7*	Ds	252.1*	Ds	27.7*	Ds
P. annua		26.8*	Ds	16.8*	Ds	24.1*	Ds
L. multiflorum	-2	96.0*	Ds	53.5*	Ds	137.0*	Ds
	-3	9.0*	Ds	30.9*	Ds	98.6*	Ds
	-4	8.7*	Ds	50.3*	Ds	50.9*	Ds

[1] Terminal dormancy in this case was a composite of delayed germination and deep dormancy for each treatment.

[2] F values computed with 1 and 6 degrees of freedom. Dashes indicate that primary dormancy exceeded or was equal to terminal dormancy. *F values significant at the five percent level of probability.

[3] Di = terminal dormancy was of an indeterminate type, Ds = presence of relative secondary dormancy.

Table 5. Mode of persistence, calculated as seed quiescence/ terminal dormancy at each of four durations of burial for four species possessing seed persistence. [1]

Species	Lot no.	Days of burial 0	60	120	180
A. fatua		9.22	0.00	0.00	0.00
A. tenuis		183.00	0.32	0.04	0.01
P. annua		126.00	0.06	0.00	0.00
L. multiflorum	-2	126.66	2.08	0.78	0.67
	-3	∞	14.33	0.92	1.00
	-4	95.50	7.75	1.15	0.79

[1] The ratios were calculated from treatment means for quiescence and terminal dormancy. Terminal dormancy was a composite of delayed germination response and deep dormancy among seed of each treatment.

B. Parameters of Seed Depletion and Nonviability

1. In Situ Germination (G_{is} Component). In situ germination counts were made after the 60 day burial period only. Accurate estimates of in situ germination at 120 and 180 day recovery periods were impossible due to deterioration of radicles and shoots of the buried seeds. In situ germination of seed of the eight seed accessions is shown on Figure 9.

Low levels of in situ germination were found among samples of A. tenuis. Lots 2 and 4 of L. multiflorum were also relatively low in in situ germination. Recovered seed samples of A. fatua, P. annua

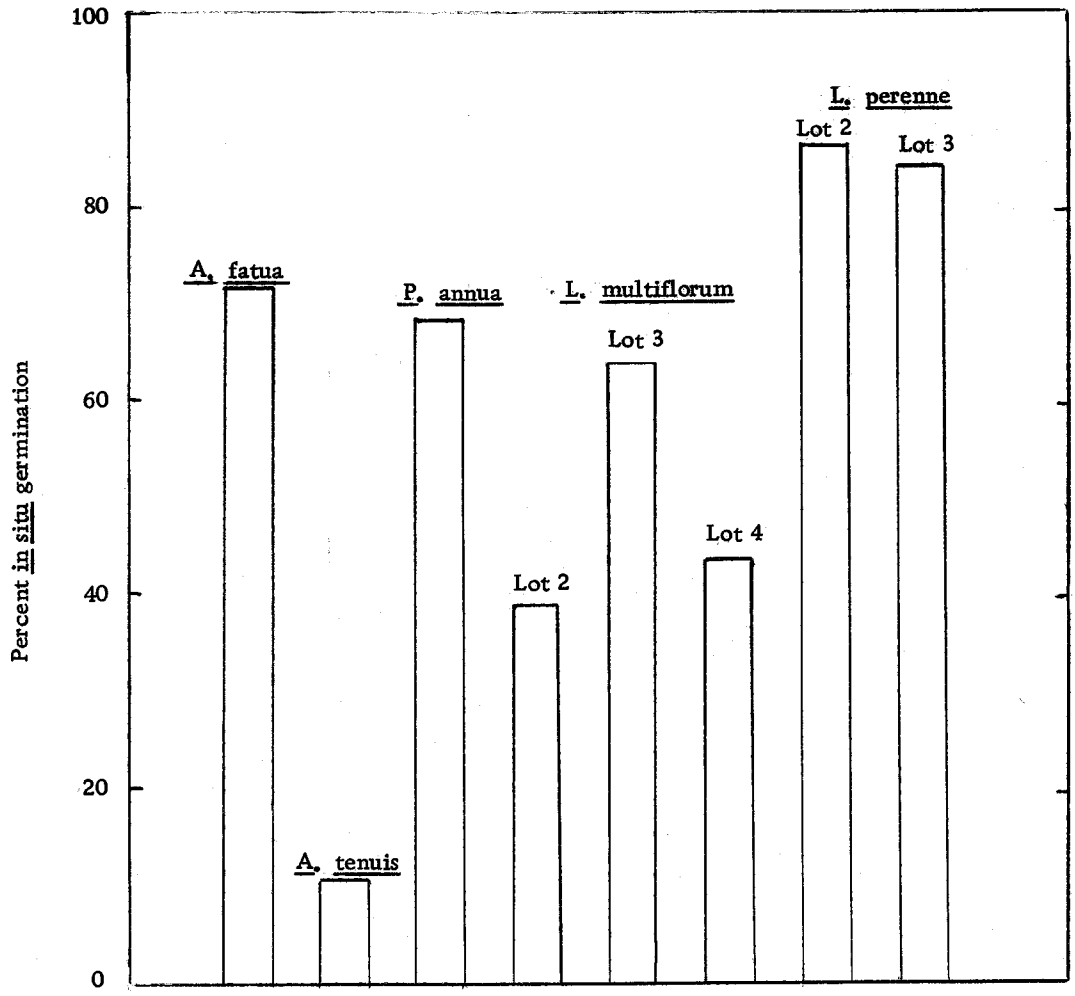

Figure 9. In situ germination among seed samples of five grass species recovered after 60 days of burial.

and lot 3 of L. multiflorum showed intermediate percentages of in situ germination. Very high in situ germination percentages were recorded for lots 2 and 3 of L. perenne. These effects were noted after a period characterized by intermediate soil temperature and moisture. The same also applies to the following S component parameter.

2. Nonviability Among Ungerminated Seed (S Component). Since in situ germination was considered only for the 60 day burial period, a valid estimate of nonviability among ungerminated seeds could only be made for the first duration of burial. The levels of nonviability among ungerminated seed in each of the eight populations is shown on Figure 10.

After 60 days of burial, ungerminated seed of A. tenuis had the highest percentage of nonviable seed of the eight populations. The remainder of the species were similar in nonviable seed percentages. However, the percent nonviable seed of A. fatua was significantly greater than that of L. multiflorum lot 2.

3. Total Nonviability (NV Component). Statistical analysis revealed significant differences among the species in regard to total nonviability (Figure 11). Lots 2 and 3, L. perenne and A. fatua lost viability rapidly. Recovered seed samples of A. tenuis, P. annua and lot 3 L. multiflorum, while being significantly different, were also relatively high in nonviability. Lots 2 and 3 of L. multiflorum

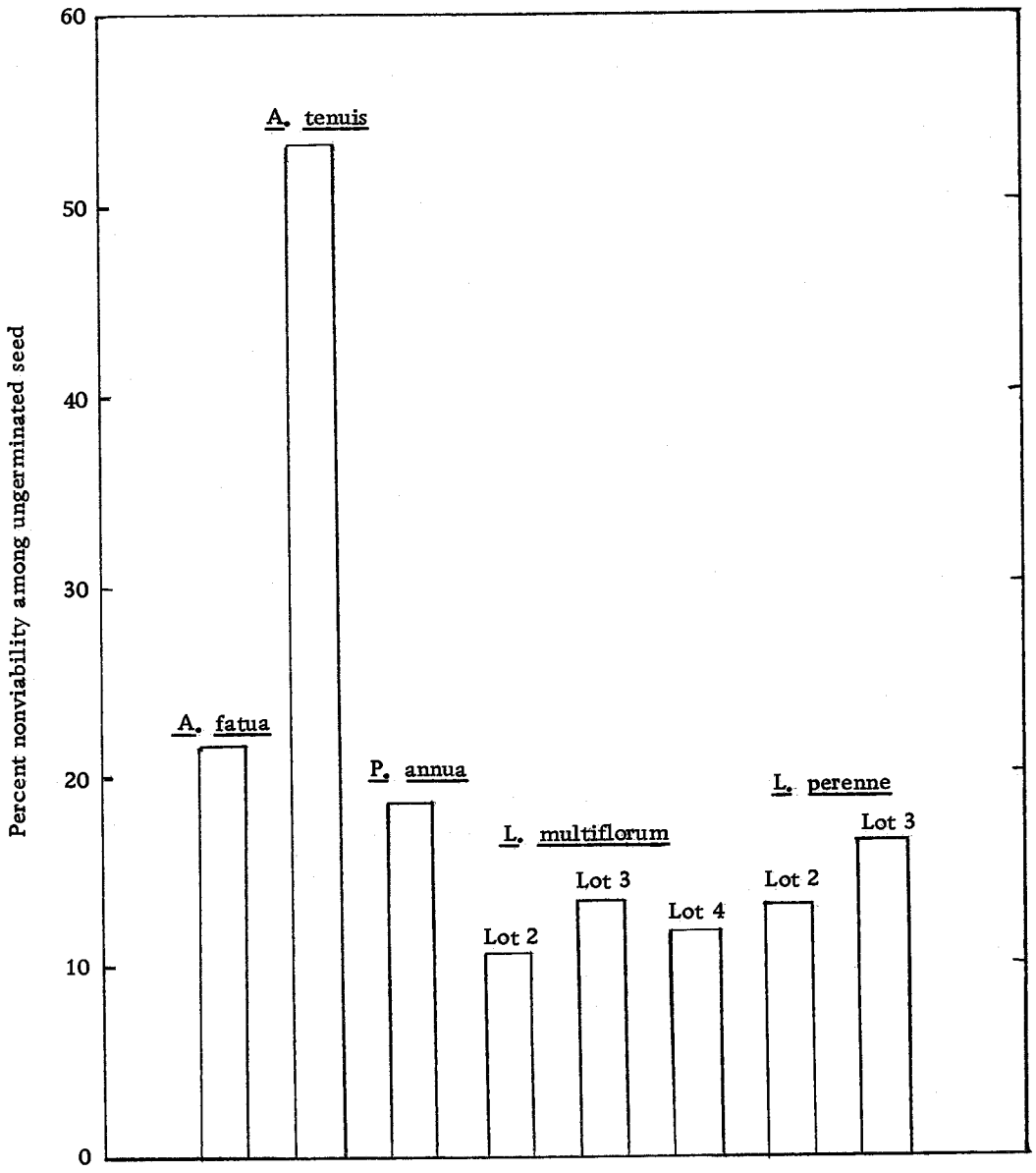

Figure 10. Nonviability among ungerminated seed of five grass species.

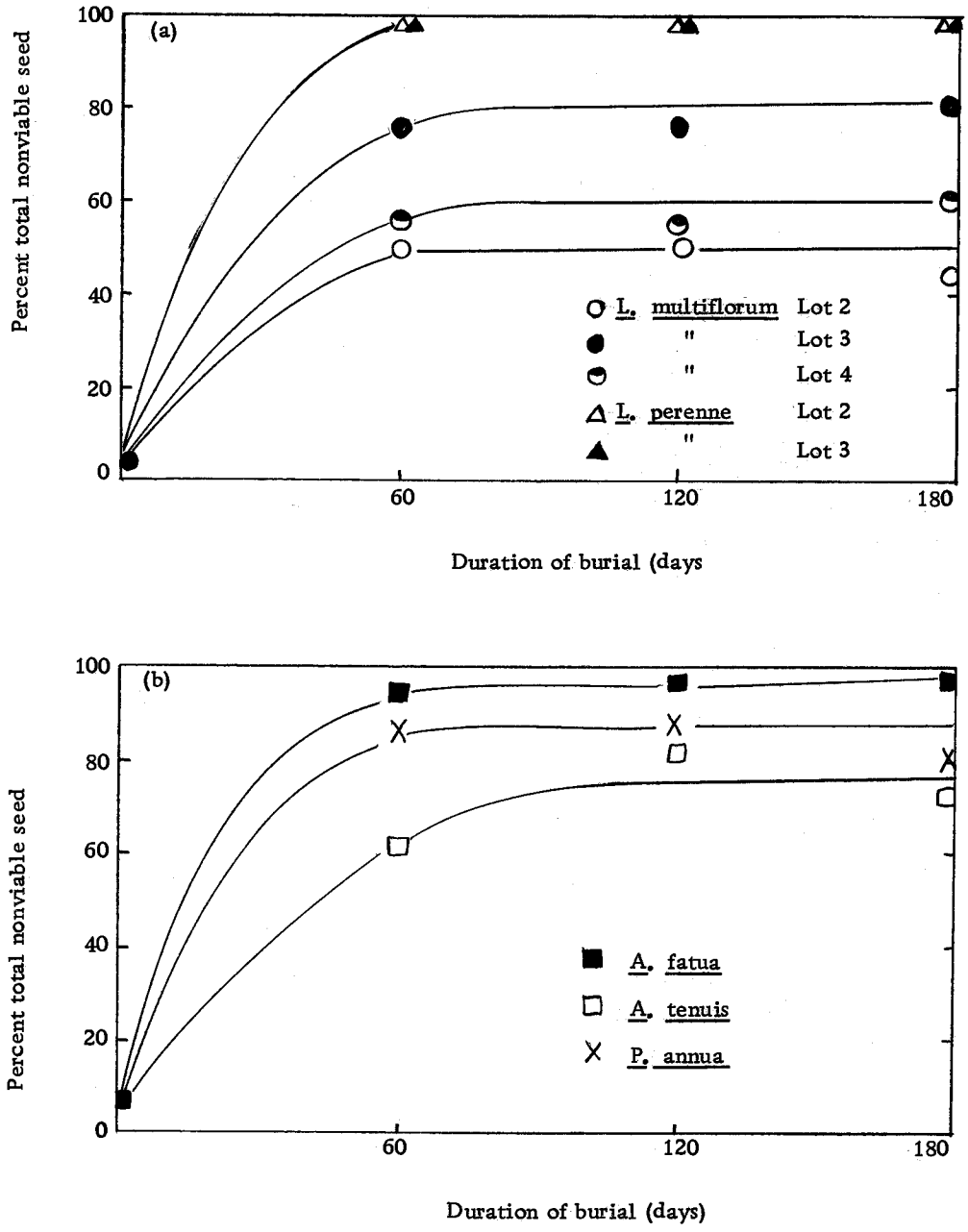

Figure 11. Total nonviability among seed of L. multiflorum and L. perenne (a) and A. fatua, A. tenuis, and P. annua (b) after three durations of burial.

had relatively low percentages of nonviable seed.

All seed samples showed considerable loss of viability after 60 days of burial, but did not increase in total nonviability up to 180 days. The mode of viable seed depletion during 60 days of burial can be defined by the expression:

$$Md = \frac{G_{is}}{S}$$

where:

Md = mode of depletion

G_{is} = in situ germination

S = nonviability among ungerminated seed.

These ratios are shown on Table 6. With the exception of A. tenuis, the primary mode of viable seed depletion during 60 days of burial (October through December, 1966) was in situ germination. This was particularly true for L. perenne.

Table 6. Mode of viable seed depletion calculated as a ratio of in situ germination/nonviability among ungerminated seed, after 60 days of burial. [1]

Species	Lot no.	in situ germination / nonviability among ungerminated seed
A. fatua		3.35
A. tenuis		0.20
P. annua		3.78
L. multiflorum	-2	3.76
	-3	4.80
	-4	3.79
L. perenne	-2	6.69
	-3	5.25

[1]Ratios constructed from species means for in situ germination and nonviability among ungerminated seed.

III. Controlled Environment Experiment

The short duration of this experiment permitted a complete study of the parameters of viability and nonviability of the buried seed populations.

A. Parameters of Viability and Persistence

1. Quiescence (Q Component). Seed quiescence, estimated by laboratory germination, was markedly influenced by soil temperature and moisture. Significant species differences were also observed. The quiescence of seeds, recorded in this experiment, are shown on Table 7. The level of quiescence was highest at 5 C and lowest at 15 C. The intermediate soil moisture regimes (22. 5 percent) had an adverse effect upon maintainance of quiescence, primarily due to depletion of viable seeds by in situ germination. Maintainance of the seed in dry soil (4. 5 percent) or saturated soil (40. 5 percent) resulted in a high level of readily germinable seed.

Recovered seed of A. tenuis was observed to have the highest percent quiescence of the species studied in this experiment. Relatively high levels of quiescent seed were also noted with P. annua and lots 2, 3, and 4 of L. multiflorum. Relatively low quiescent percentages were noted in lots 2 and 3 of L. perenne and A. fatua.

Temperature variables associated with 4. 5 percent soil

Table 7. Percentage quiescent seed of five species, estimated by standard germination test, after 30 days of burial at nine combinations of temperature and soil moisture. [1]

Species	Lot no.	Temperature 5 C, Soil moisture percent 4.5	5 C, 22.5	5 C, 40.5	10 C, 4.5	10 C, 22.5	10 C, 40.5	15 C, 4.5	15 C, 22.5	15 C, 40.5	Species $\bar{x}$
A. fatua		83.3 ijk	2.7 v	65.0 lm	83.7 ijk	0.0 w	41.3 op	75.0 kl	0.0 w	3.0 v	39.3 e
A. tenuis		94.3 a-h	74.7 kl	93.3 a-h	94.7 a-h	31.0 p-s	91.3 c-i	93.7 a-h	27.3 q-t	69.0 lm	74.3 a
P. annua		95.0 a-g	48.7 no	87.3 g-j	95.0 a-g	13.3 u	88.3 f-i	96.0 a-f	21.3 stu	70.3 l	68.3 b
L. multiflorum	-2	98.0 ab	56.7 mn	77.0 jkl	94.3 a-h	47.7 no	66.0 lm	97.3 abc	35.3 o-r	56.0 mn	69.8 b
	-3	96.0 a-f	25.7 rst	92.0 b-i	97.0 a-d	19.0 tu	89.7 e-i	98.3 a	16.3 tu	12.7 u	60.7 c
	-4	97.7 abc	48.3 no	90.0 d-i	95.7 a-f	37.0 o-r	75.0 kl	98.3 a	39.0 opq	46.0 no	69.6 b
L. perenne	-2	97.0 a-d	3.7 v	91.3 c-i	97.0 a-d	0.0 w	75.0 kl	97.0 a-d	0.3 w	0.0 w	51.2 d
	-3	96.3 a-e	2.7 v	86.3 hij	92.0 b-i	0.0 w	83.7 ijk	94.0 a-h	0.0 w	1.3 vw	50.7 d
Temperature means			70.9 a			62.8 b			47.8 c		
Soil moisture means					4.5 percent		94.0 a				
					22.5 percent		22.9 c				
					40.5 percent		64.6 b				

[1] Duncan's Multiple Range Test was applied independently to species, temperature, soil moisture and treatment means. Means having a common letter do not differ at the five percent level of probability. Continuity among long sequences of letters is indicated by a dash.

moisture during burial exerted very little influence upon subsequent laboratory germination of seed. Seed quiescence at 22. 5 and 40. 5 percent soil moisture, on the other hand, decreased with successively higher temperature regimes. These factors account for a significant temperature X soil moisture interaction.

A significant temperature X species interaction is, in part, the result of wide differences in species response at the 5 and 15 C regimes. In particular, lot 3 of L. multiflorum and lots 2 and 3 of L. perenne were observed to undergo considerable decrease in quiescence from the 10 to 15 C environments.

Very low percentages of readily germinable seed of A. fatua and L. perenne lots 2 and 3 were recorded at 22. 5 percent soil moisture. As contrasted to the 4. 5 percent soil moisture regime, pronounced dissimilarities in species germination response were noted at the 22. 5 and 40. 5 percent soil moisture levels. These factors largely account for the significant soil moisture X species interaction.

2. Terminal Dormancy (D_t Component). Terminal dormancy of ungerminated seed, estimated by the tetrazolium test, was relatively low for most of the treatments assessed in this experiment.

The terminal dormancy recorded for the various treatments included in this experiment are shown on Table 8. Dormancy was significantly influenced by temperature - being highest at 5 C and lowest at 15 C. Soil moisture also had an influence upon terminal

Table 8. Percentage terminal dormancy of five species, estimated by tetrazolium chloride reaction, after 30 days of burial at nine combinations of temperature and soil moisture. [1]

Species	Lot no.	Temperature 5 C, Soil moisture percent 4.5	5 C, 22.5	5 C, 40.5	10 C, 4.5	10 C, 22.5	10 C, 40.5	15 C, 4.5	15 C, 22.5	15 C, 40.5	Species $\bar{x}$
A. fatua		5.3 b-g	13.3 a	7.3 a-d	6.0 b-f	1.7 f-j	5.0 b-g	6.7 b-e	2.0 e-j	1.3 g-j	5.38 a
A. tenuis		0.3 jk	4.7 b-h	0.3 jk	0.3 jk	5.0 b-g	1.0 h-k	0.3 jk	0.3 jk	0.0 k	1.34 c
P. annua		1.7 f-j	1.7 f-j	8.7 abc	0.7 ijk	2.0 e-j	4.0 b-i	1.3 g-j	0.3 jk	3.0 d-j	2.56 b
L. multiflorum	-2	0.7 ijk	9.3 ab	6.7 b-e	1.3 g-j	3.7 c-i	5.3 b-g	0.7 ijk	1.0 h-k	2.3 e-j	3.40 b
	-3	0.0 k	1.0 h-k	1.7 f-j	0.0 k	1.0 h-k	1.0 h-k	0.3 jk	0.0 k	1.7 f-j	0.72 cd
	-4	0.0 k	4.0 b-i	2.3 e-j	1.0 h-k	0.7 ijk	2.3 e-j	0.3 jk	0.3 jk	1.3 g-j	1.34 c
L. perenne	-2	0.7 ijk	0.3 jk	2.0 e-j	0.3 jk	0.0 k	2.3 e-j	0.0 k	0.3 jk	0.0 k	0.63 d
	-3	0.7 ijk	0.3 jk	1.7 f-j	0.3 jk	0.0 k	2.7 d-j	0.7 ijk	0.0 k	2.0 e-j	0.89 cd
Temperature means			3.07 a			1.96 b			1.07 c		
Soil moisture means					4.5 percent		1.20 b				
					22.5 percent		2.18 a				
					40.5 percent		2.72 a				

[1] Duncan's Multiple Range Test was applied independently to species, temperature, soil moisture and treatment means. Those means having a common letter do not differ at the five percent level of probability. Continuity among long sequences of letters is indicated by a dash.

dormancy. Generally, the lowest percentages of terminal dormancy were found at 4. 5 percent soil moisture. While dormancy of seed recovered from 40. 5 percent soil moisture environment was somewhat higher than that of seed taken from 22. 5 percent soil moisture, the grand means of these treatments were not appreciably different.

A. fatua was observed to have the highest terminal dormancy percentage of the species studied in this experiment. Relatively high dormancy percentages were recorded among ungerminated seed of L. multiflorum lot 2 and P. annua. A. tenuis and L. multiflorum lot 4 were intermediate in terminal dormancy levels. Relatively low percentage dormancy was recorded among ungerminated seed of L. multiflorum lot 3 and L. perenne lots 2 and 3. Hence, a variable dormancy pattern was evident among the three lots of L. multiflorum.

No differences in dormancy could be detected at 4. 5 percent soil moisture at 5, 10 and 15 C. While terminal dormancy at 22. 5 percent soil moisture exceeded that of 40. 5 percent soil moisture at 5 C, the former soil moisture level was characterized by very low terminal dormancies at 10 and 15 C.

Statistical analysis revealed a significant soil moisture X species interaction. A. fatua was observed to have a higher level of dormancy at 4. 5 percent than at 22. 5 or 40. 5 percent soil moisture. Ungerminated seed of A. tenuis had a relatively high terminal dormancy percentage at 22. 5 percent soil moisture in contrast to the

low and high moisture regimes. P. annua, on the other hand, was observed to have its highest dormancy percentage at 40. 5 percent soil moisture. L. multiflorum lot 2 had high terminal dormancy levels at both 22. 5 and 40. 5 percent soil moisture.

Induction of secondary dormancy was tested via the analysis described in part I of the Results section (Table 9). These analyses show that relative secondary dormancy was induced in seed of A. tenuis, P. annua, L. multiflorum and L. perenne under specific treatments of intermediate and high soil moisture at 5 and 10 C. No induction of secondary dormancy was found at 15 C.

The mode of persistence, described by the relationship, quiescence/terminal dormancy was evaluated for the five species. These ratios are shown on Table 10. The magnitude of these ratios indicate that quiescence was by far the most important mode of persistence of seeds buried for 30 days.

B. Parameters of Seed Depletion and Nonviability

1. In Situ Germination (G_{is} Component).

In situ germination of buried seed was influenced by soil moisture and temperature. In situ germination was high at 22. 5 percent soil moisture, occurred to a limited extent at 40. 5 percent and was nonexistent at 4. 5 percent soil moisture. In situ germination was lowest at 5 C, and highest at 15 C. These data are shown on Table 14 of the Appendix.

Table 9. Test for induction of secondary dormancy, made by computing F values for primary versus terminal dormancy among seed lots after 30 days of burial at nine combinations of temperature and soil moisture.

		5 C temperature						10 C temperature						15 C temperature					
		Soil moisture percent						Soil moisture percent						Soil moisture percent					
	Lot	4.5		22.5		40.5		4.5		22.5		40.5		4.5		22.5		40.5	
Species	no.	F[1]	S[2]	F	S	F	S	F	S	F	S	F	S	F	S	F	S	F	S
A. fatua		--	Di	2.4	Di	--	Di	--	Di	--	Di	--	Di	--	Di	--	Di	--	Di
A. tenuis		--	Di	2.9	Di	--	Di	--	Di.	13.0*	Ds	0.2	Di	--	Di	--	Di	--	Di
P. annua		4.4	Di	4.7	Di	71.1*	Ds	--	Di	4.0	Di	10.0*	Ds	0.8	Ds	--	Di	3.8	Di
L. multiflorum	-2	--	Di	10.4*	Ds	29.5*	Ds	--	Di	7.4	Di	11.5*	Ds	--	Di	0.1	Di	0.7	Di
	-3	--	Di	3.0	Di	3.5	Di	--	Di	∞ *	Ds	∞ *	Ds	0.2	Di	--	Di	3.6	Di
	-4	--	Di	7.7	Di	12.4*	Ds	0.3	Di	--	Di	12.6*	Ds	--	Di	--	Di	2.0	Di
L. perenne	-2	--	Di	--	Di	∞ *	Ds	--	Di	--	Di	2.3	Di	--	Di	--	Di	--	Di
	-3	--	Di	--	Di	1.0	Di	--	Di	--	Di	1.9	Di	--	Di	--	Di	0.3	Di

[1] F values determined at 1 and 4 degrees of freedom. Dashes indicate that primary dormancy was equal to or exceeded terminal dormancy. *F value significant at the five percent level of probability.

[2] S = symbol; Di = indeterminate dormancy; Ds = secondary dormancy.

Table 10. Mode of persistence, calculated as the ratio of seed quiescence/ terminal dormancy, among five species after 30 days of burial. [1]

Species	Lot no.	Quiescence / Terminal dormancy
A. fatua		7.28
A. tenuis		55.44
P. annua		26.68
L. multiflorum	-2	20.52
	-3	84.30
	-4	51.94
L. perenne	-2	80.00
	-3	56.96

[1] Ratios were calculated from species means for seed quiescence and terminal dormancy.

The depletion of viable seed of L. perenne via in situ germination was the highest of the species studied. A variable response among the three lots of L. multiflorum was evident. In situ germination of L. multiflorum lot 2 was similar to that of A. tenuis. The level of in situ germination of L. multiflorum lots 2 and 3 were similar to those of A. fatua and P. annua.

A significant temperature X soil moisture interaction represents a differential in situ germination, primarily at 22.5 percent soil moisture, at each of the three soil temperatures. At 22.5 percent soil moisture, the rate of increase of in situ germination decreased at each successively higher temperature.

In situ germination of buried seed of A. fatua, A. tenuis and L. multiflorum increased with temperature. The response curve of A. tenuis was particularly steep, originating from a very low level at 5 C. In situ germination of L. perenne remained relatively constant over the range of temperature studied. A nearly linear response curve for L. multiflorum and L. perenne across the three temperatures was noted. In situ germination of P. annua increased from the 5 C to the 10 C regime, but was recorded at an intermediate level at 15 C. These temperature X species interactions are shown on Figure 12.

The variable response of these species and lots, primarily at 22.5 percent soil moisture, account for the significant soil moisture

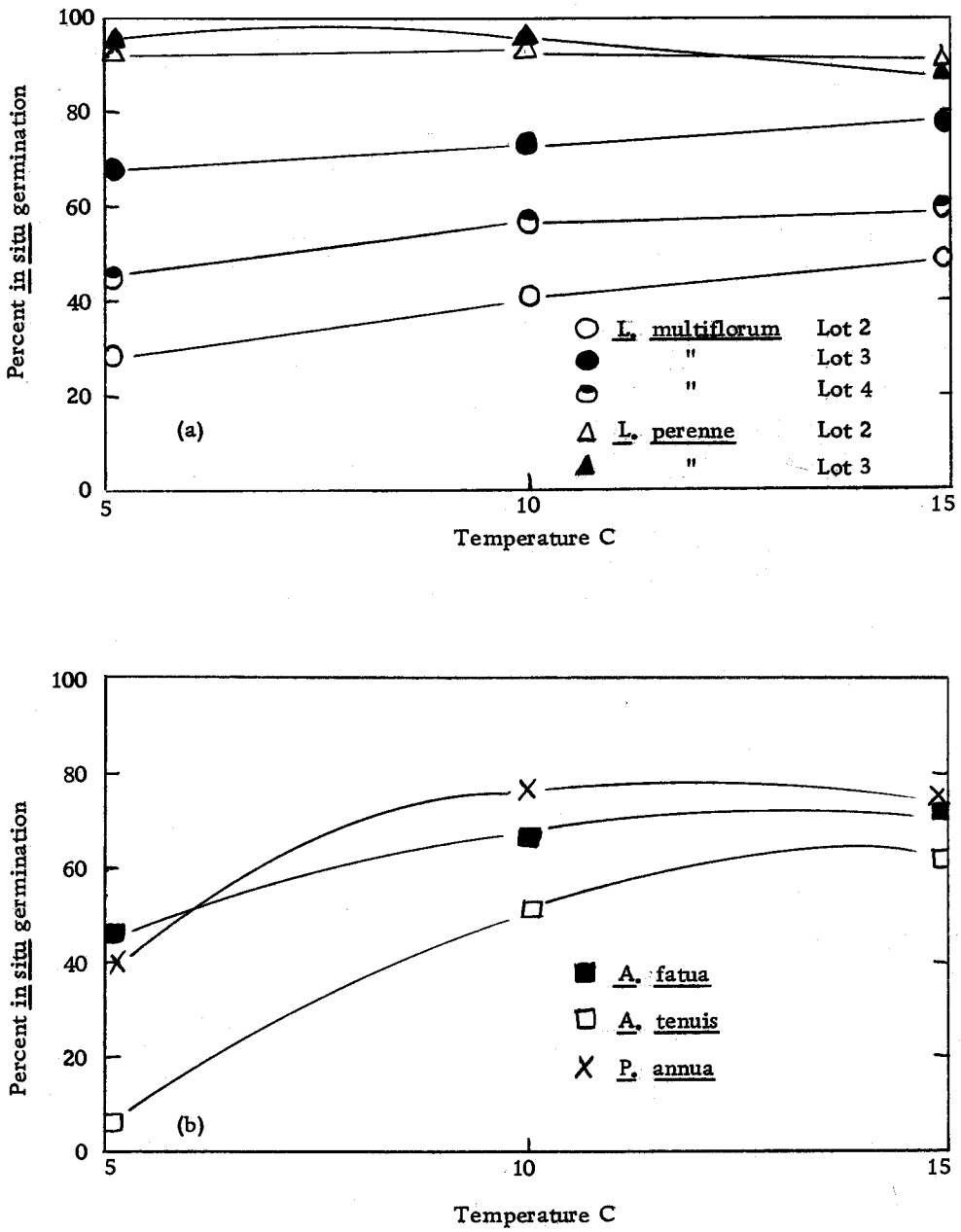

Figure 12. In situ germination among seed of L. multiflorum and L. perenne (a) and A. fatua, A. tenuis, and P. annua (b) during 30 days of burial at 22.5 percent soil moisture at three temperatures.

X species interaction.

2. Nonviability Among Ungerminated Seed (S Component). The percentage of nonviable, ungerminated seed among the treatments evaluated in this experiment are shown on Table 11. Nonviability was influenced by soil temperature - increasing with temperature increments from 5 to 15 C. The parameter was also influenced by soil moisture. In this case, nonviability was lowest at 4. 5 percent soil moisture and was highest at 40. 5 percent soil moisture.

Nonviability among ungerminated seed of A. fatua was the highest of the species studied. The two accessions of L. perenne were also relatively high in nonviability. Intermediate levels of nonviable seed of A. tenuis and the three accessions of L. multiflorum were observed. P. annua, on the other hand, was characterized by a relatively low level of nonviability.

Exceptionally high percentages of nonviability at the 15 C X 40. 5 percent soil moisture regime account for the significant temperature X soil moisture interaction.

A significant temperature X species interaction can be accounted for by pronounced differences in the magnitude of nonviability for the species at 15 C temperature environments. Particularly noticeable was the high nonviable percentage of L. perenne as contrast to the low levels recorded for P. annua and A. tenuis at this temperature. Generally, these species were characterized by

Table 11. Percentage nonviability among ungerminated seed of five species after 30 days of burial at nine combinations of temperature and soil moisture.[1]

Species	Lot no.	Temperature: 5 C; Soil moisture percent 4.5	5 C; 22.5	5 C; 40.5	10 C; 4.5	10 C; 22.5	10 C; 40.5	15 C; 4.5	15 C; 22.5	15 C; 40.5	Species $\bar{x}$
A. fatua		11.3 l-s	37.3 fg	27.7 ghi	10.3 st	30.7 f-h	53.7 d	18.3 i-l	28.0 ghi	94.7 b	34.6 a
A. tenuis		5.3 p-x	14.3 k-o	6.3 n-x	5.0 q-x	13.0 k-q	7.7 m-w	6.0 n-x	11.0 l-s	31.0 fgh	11.1 d
P. annua		3.3 t-x	9.7 stu	4.0 s-x	4.3 r-x	6.3 n-x	7.7 m-w	2.7 vwx	7.0 m-w	26.7 g-j	7.9 e
L. multiflorum	-2	1.3 x	4.7 r-x	16.3 j-m	4.3 r-x	8.0 m-w	28.7 f-i	2.0 wx	14.7 k-n	41.0 ef	13.4 cd
	-3	4.0 s-x	5.3 p-x	6.3 n-x	3.0 u-x	5.7 o-x	9.3 s-v	1.3 x	5.3 p-x	85.7 c	14.0 c
	-4	2.3 wx	3.3 t-x	7.7 s-w	3.3 t-x	5.7 o-x	22.7 h-k	1.3 x	2.7 vwx	52.7 de	11.2 cd
L. perenne	-2	2.3 wx	2.0 wx	6.7 s-x	2.7 vwx	5.0 q-x	22.7 h-k	3.0 u-x	11.0 l-s	99.3 a	17.2 b
	-3	3.0 u-x	4.0 s-x	12.0 l-r	7.7 m-w	8.0 m-w	13.7 k-p	5.3 p-x	10.0 l-u	96.7 ab	17.8 b
Temperature means			8.3 c			12.0 b			27.4 a		
Soil moisture means					4.5 percent		4.7 c				
					22.5 percent		10.5 b				
					40.5 percent		32.5 a				

[1]Duncan's Multiple Range Test was independently applied to species, temperature, soil moisture and treatment means. Means having a common letter do not differ at the five percent probability level. Continuity among long sequences of letters is indicated by a dash.

similar percentages of nonviability at 5 and 10 C, respectively.

A highly variable level of nonviability among species at 40. 5 percent soil moisture was noted, and largely accounts for the significant soil moisture X species interaction. This interaction was exemplified by the high percentage nonviability of the L. perenne accessions at this moisture level.

3. Total Nonviability (NV Component). Table 12 shows the total nonviable seed for the treatments employed in this study. Total nonviability was greatest at 22. 5 percent soil moisture due to extensive in situ germination. Extensive loss of seed viability did occur at 40. 5 percent soil moisture but was low at the 4. 5 percent level. Total nonviability increased with temperature. The lowest percentages were recorded at 5 C and the highest percentage total nonviability was found at 15 C.

Differences in total nonviability among species were noted. Recovered seed populations of A. fatua and L. perenne were characterized by relatively high levels of total nonviability. The variation among accessions of L. multiflorum noted in other parameters was also evident in their degree of total nonviability. Lot 3 of L. multiflorum had a high level of total nonviability while lots 2 and 4 were similar to A. tenuis and P. annua in this respect.

Extensive loss of buried seed viability at 15 C X 40. 5 percent soil moisture was a major factor in the significant temperature X soil

Table 12. Percentage total nonviability among seed of five species after 30 days of burial at nine combinations of temperature and soil moisture.[1]

Species	Lot no.	Temperature: 5 C, Soil moisture percent: 4.5	5 C: 22.5	5 C: 40.5	10 C: 4.5	10 C: 22.5	10 C: 40.5	15 C: 4.5	15 C: 22.5	15 C: 40.5	Species $\bar{x}$
A. fatua		11.3 q-v	84.0 cd	27.7 l-o	10.3 r-w	98.3 ab	53.7 g-j	18.3 n-r	98.0 b	95.7 b	55.2 a
A. tenuis		5.3 t-z	20.7 m-q	6.3 t-z	5.0 u-z	64.0 fg	7.7 s-y	6.0 t-z	72.3 ef	31.0 klm	24.2 e
P. annua		3.3 w-z	49.7 hij	4.0 v-z	4.3 u-z	84.7 c	7.7 s-y	2.7 xyz	78.3 cde	26.7 l-o	29.0 d
L. multiflorum	-2	1.3 z	34.0 kl	16.3 o-s	4.3 u-z	48.7 hij	28.7 lmn	2.0 yz	63.7 fg	41.7 jk	26.7 de
	-3	4.0 v-z	73.3 def	6.3 t-z	3.0 xyz	80.0 cde	9.3 r-x	1.3 z	83.7 cd	85.7 c	38.5 c
	-4	2.3 yz	47.7 ij	7.7 s-y	3.3 w-z	62.3 fgh	22.7 l-p	1.3 z	60.7 f-i	52.7 g-j	28.9 d
L. perenne	-2	2.3 yz	96.0 b	6.7 t-z	2.7 xyz	100.0 a	22.7 l-p	3.0 xyz	99.3 ab	100.0 a	48.0 b
	-3	3.0 xyz	97.0 b	12.0 p-u	7.7 s-y	100.0 a	13.7 p-t	5.3 t-z	100.0 a	96.7 b	48.3 b
Temperature means			25.9 c			35.2 b			51.0 a		
Soil moisture means					4.5 percent		4.7 c				
					22.5 percent		74.8 a				
					40.5 percent		32.6 b				

[1]Duncan's Multiple Range Test was applied independently to species, temperature, soil moisture and treatment means. Means having a common letter do not differ at the five percent level of probability. Continuity among long sequences of letters is indicated by a dash.

moisture interaction.

Disparity among total nonviability of P. annua, A. tenuis and L. multiflorum lots 2 and 4 at 5 C tended to be alleviated at 10 and 15 C. In addition, the rate of loss of total nonviability of both accessions of L. perenne and lot 3 L. multiflorum decreased with increasing temperature. These relationships account for a significant temperature X species interaction.

Differences among the species in regard to total nonviability were not pronounced at 4. 5 percent soil moisture, but became evident at the 22. 5 percent and 40. 5 percent soil moisture regimes. Hence, a significant soil moisture X species interaction was found.

The mode of viable seed depletion after 30 days of burial can be described by the ratio in situ germination/nonviability. Table 13 shows these ratios for the eight populations. With the exception of A. fatua and L. multiflorum lot 2, in situ germination was a more important mode of depletion than loss of viability among ungerminated seed after 30 days of burial. Closer examination of the original data indicates that this would be particularly true at intermediate soil moisture levels.

Table 13. Mode of viable seed depletion described as in situ germination/nonviability among ungerminated seed for five species after 30 days of burial. [1]

Species	Lot no.	In situ germination Nonviability among ungerminated seeds
A. fatua		0.59
A. tenuis		1.19
P. annua		2.73
L. multiflorum	-2	0.99
	-3	1.75
	-4	1.57
L. perenne	-2	1.80
	-3	1.71

[1] Ratios calculated from species means for in situ germination and nonviability among ungerminated seed.

DISCUSSION

I. The Population Model and Its Implications

An adequate population model, describing the status of seeds under natural environments, has not been reported in the literature. A model, such as that presented in the Results section of this thesis permits clarification of the components of seed populations at a point in time. This model also permits understanding of changes among components over a time course.

By studying the ratios of viable components over a time course, the mode of persistence can be ascertained. Likewise, the mode of seed depletion can be studied by using ratios of the nonviability components. This scheme is applicable to any seed population and could be utilized, for example in studying planting rates and field emergence of cultivated crops. It has been particularly useful in studying the components of buried seed populations.

The term quiescence, as used in this study is equivalent to environmental dormancy as used by Bibbey (6) to describe the dormant state imposed by adverse environmental conditions. When quiescent seeds are placed under favorable conditions, germination occurs readily.

Terminal dormancy was coined by the author to describe a

dormant state of seeds which may be a manifestation of primary dormancy, secondary dormancy or both. Seed in a state of terminal dormancy lack the capacity to germinate under favorable conditions. Since a low level of primary dormancy was present in most seed lots used in this study, only a statistically significant increase in the degree of terminal dormancy was interpreted to indicate the induction of secondary dormancy. When primary dormancy percentage exceeded that of terminal dormancy, it was impossible to determine the character of the latter, hence, the dormancy was called indeterminate. Secondary dormancy is a manifestation of the induction of internal changes within a seed, that opposes its germination when placed under favorable conditions. In the present study, primary and terminal dormancy must be regarded as relative since testing was not conducted under all combinations of environment (Vegis, 52, 53). The composite of environmental and terminal dormancy represents the viable contingent of a buried seed population.

The use of in situ germination as a nonviability parameter rests upon the assumption that germination below the maximum depth of emergence results in the elimination of the seed as a reproductive unit. The importance of in situ germination as a mode of viable seed depletion has generally not been recognized. In certain species, particularly L. perenne, this deep germination represents the principle channel of buried viable seed depletion. If, however, the

seeds are situated above the maximum depth of emergence, a proportion of in situ germinations result in functional plants.

Nonviability among ungerminated seed represents a loss of viability as a result of physiological ageing or through destruction by predatory organisms. This class also contains those seeds that were originally nonviable as a result of events that transpired during seed development.

The percentage of in situ germination plus nonviability among ungerminated seed represents the nonviable component of a given population of buried seeds.

II. Buried Seed Persistence and Depletion of Five Grass Species

A. L. perenne

The results of this study indicate that L. perenne is a nonpersistent species. In controlled environment studies, seed of L. perenne had virtually lost all viability after 30 days of burial at intermediate soil moisture levels. Placed under western Oregon field conditions during October, 1966, seed viability of this species was nearly exhausted after 60 days of burial. These findings are consistent with those reported by Kjaer (34, 35), and Rampton and Ching (43). These conclusions are further supported by Champness and Morris (9) and Milton (41) who reported less germinable seed of

L. perenne in recovered soil samples than would be expected from analysis of sward composition. However, the reports of Harris (24) and Lewis (38) suggest a more persistent nature for buried L. perenne seed. The conclusions reached by Harris are, however, open to question since he did not evaluate the status of ungerminated seeds. Harris also admitted that seed of L. perenne used in his study were infected with blind seed disease. In essence, germination alone cannot be used as a sole criterion of seed persistence.

Field studies revealed very low quiescence percentages among buried seed of L. perenne. Growth chamber studies showed that L. perenne maintained only limited numbers of quiescent seed at intermediate soil moisture levels and at higher temperatures. Also, terminal dormancy was very low in both field and growth chamber regimes.

The rapid loss of seed viability of L. perenne under field conditions is via in situ germination. This point is substantiated by high levels of in situ germination encountered at intermediate soil moisture percentage during growth chamber studies. The reason for this profuse in situ germination may be insensitivity of seed to darkness, limited oxygen level or high CO_2 levels. Bibbey (6), for example, found that species which are short lived in the soil did not show germination sensitivity to extremes of oxygen or CO_2 levels. Clarification of these points will require further study. Nonviability

among buried ungerminated seeds of L. perenne plays a lesser role in the depletion of viable seeds of this species. However, this mode of depletion was high in relation to the other species investigated.

Thus, very high in situ germination associated with loss of viability among ungerminated seed explains the limited persistence of buried seed of this species.

B. L. multiflorum

The persistence of buried seed of L. multiflorum was evident in all phases of experimentation. This persistence is in agreement with the findings of Rampton and Ching (43). Persistence of buried seed of this species was manifest in large numbers of quiescent and terminal dormant seed maintained during burial.

Quiescent seed was evident among samples of L. multiflorum recovered after one year of burial. The three lots of L. multiflorum produced large numbers of germinable seed upon recovery from burial during the period of October, 1966 through April, 1967. High levels of quiescence were also found among seed samples of L. multiflorum tested under controlled environment. High percentages of quiescent seed were evident in the data of Rampton and Ching (43).

While appreciable levels of terminal dormancy were recorded after one year of burial of lot 1, the presence of secondary dormancy could not be ascertained. However, high percentages of terminal

dormancy present in lots 2, 3 and 4 after two, four and six months of burial (Experiment II) were adequate to establish the presence of secondary dormancy. The deep dormancy of L. multiflorum seeds, recovered from burial in Experiment II, may play an important role in the long range persistence of this species. Terminal dormancy was highest for lot 2, intermediate for lot 4, and lowest for lot 3 in Experiment II. This same relationship was also evident in the growth chamber study where terminal dormancy was particularly noticeable at 5 C X 22. 5 percent soil moisture and 5 C X 40. 5 percent soil moisture regimes. Again, the magnitude of terminal dormancy was adequate to establish the induction of secondary dormancy. High levels of terminal dormancy among seed of L. multiflorum have been reported by Rampton and Ching (43).

Variable degrees of in situ germination were encountered among lots of L. multiflorum after 60 days of burial (October, 14 through December, 14, 1966). Lots 2 and 4 were relatively low in this aspect, 39. 5 percent and 44. 5 percent respectively, while lot 3 underwent much higher (63. 7 percent) in situ germination. This same relationship held true in the growth chamber study, where the in situ germination for 10 C X 22. 5 percent soil moisture closely resembled the in situ germination of Experiment II. At 5 C X 22. 5 percent soil moisture, in situ germination was less than that observed in Experiment II while in situ germination at 15 C x 22. 5

percent soil moisture exceeded the magnitude of in situ germination of Experiment II.

Loss of viability among ungerminated seed was relatively low for all 3 lots in Experiments II and III. The total nonviability was lower among lots 2 and 4 than among lot 3 in both the short term burial study and the growth chamber investigation.

The nature of buried seed persistence in L. multiflorum must be related to high levels of quiescence and terminal dormancy found under field conditions. Persistence of L. multiflorum must also be related to limited in situ germination and limited loss of viability among ungerminated seed.

As evident in the previous discussion, considerable variation was encountered among the three lots of L. multiflorum studied in Experiments II and III. Generally speaking, lot 2 possessed the most persistent characteristics while seed of lot 3 was least persistent. Several hypotheses can be presented to explain such variation.

(a) Variation among lots could be the result of exposure to different environmental conditions during floral and seed development.

(b) Considerable genetic variability may exist among populations of L. multiflorum, thus accounting for variation among lots.

(c) Original seed vigor may differ among lots.

The clarification of these alternatives warrents additional study. Should extensive genetic diversity among L. multiflorum populations be established, plant breeding procedures could be utilized to change the dormancy and persistence characteristics of this species.

C. P. annua

Examination of dormancy and seed depletion data for this species, suggests that it may persist for several years. A small percentage of viable seed was found after one year of burial. Controlled experimentation on the longevity of this species has not been previously reported. However, a number of British workers (9, 12, 40, 41) have reported extensive numbers of P. annua seedlings arising from soil samples recovered from several cropping systems and land forms. This, of course, gives indirect evidence for the persistence of this species.

The percentage of quiescence seed recorded after one year of burial (October, 1965 through October, 1966) was greater than quiescence recorded during the period of October, 1966 through April, 1967 (Experiment II). Since the same seed lot was used for both experiments, the decreased germinability subsequent to recovery, noticeable in Experiment II, may reflect ageing of the seed during storage. It is also possible that the dormancy, induced during the cold, wet period of the year, is overcome during the warm,

dry period. Consequently samples of buried seed recovered in October, 1966 would show increased quiescence/terminal dormancy ratios. Testing of samples recovered from burial in Experiments I and II indicate that terminal dormancy plays an important role in the persistence of seed of this species. In particular, the deep dormancy recorded in Experiment II may be the principle mode of long term persistence in P. annua.

In situ germination appears to be the principle route of viable seed depletion in P. annua. Nonviability among ungerminated seed was not consistent between Experiment II and III. Under field conditions, P. annua developed high percentages of nonviability among ungerminated seed. In the controlled environment study, the nonviability among ungerminated seed was relatively low. Such differences might be the result of soil, temperature or soil moisture variation between the two studies.

Persistence in P. annua seems to be characterized by high levels of terminal dormancy, which may be a more important mode of persistence than quiescence. In spite of rather large losses of viable seed through in situ germination, intermediate duration of persistence in P. annua is highly probable.

D. A. tenuis

Evidence gathered in this thesis indicates that A. tenuis seed

can survive for prolonged periods under burial. Such a conclusion is agreeable with the reports of Lewis (38), and Rampton and Ching (43). Additional evidence for the persistence of A. tenuis buried seed is supplied by the British investigators (7, 9, 12, 40, 41). These workers found appreciable numbers of Agrostis spp., including A. tenuis, in soil samples recovered from various localities.

The lot of A. tenuis used in these investigations maintained appreciable numbers of quiescent seed during burial. Terminal dormancy was not as extensive as quiescence in Experiment I, but exceeded quiescence in Experiment II, conducted during the following year. The high percentage of deep dormant seed, recorded in Experiment II indicates that this state may be of considerable importance for the persistence of buried A. tenuis seed. The low staining potential of the tetrazolium chloride used in Experiment I may partly account for the differential importance of terminal dormancy between the two experiments. In both experiments, evidence of secondary dormancy, as a constituent of terminal dormancy was presented. The growth chamber study showed that terminal dormancy was prevalent at low temperature associated with intermediate soil moisture levels.

Both field and growth chamber studies showed that A. tenuis undergoes only limited in situ germination. This may indicate the presence of a sensitivity mechanism operative in seed of this species, that prevents germination under adverse conditions, i. e. deep burial.

This is very conceivably an evolutionary characteristic since the limited nutrient reserves found in the small seed of A. tenuis would not permit emergence from deep burial depths. The principle mode of viability loss in A. tenuis was found to be nonviability among ungerminated seed.

E. A. fatua

The persistence of A. fatua was quite variable among the experiments conducted in this thesis. The results of Experiment I conducted from October, 1965 to October, 1966 indicated extensive persistence among buried seed of A. fatua. Subsequent experimentation with the same seed lot showed rapid depletion of buried viable seeds. On the basis of results of the first experiment, one must recognize the fact that extensive persistence of buried seed of A. fatua is possible. Such persistence has been reported by Thurston (47, 48). Lesser degrees of persistence have been reported by Lewis (38) and Toole and Brown (49). These differences may be the result of (a) climatic differences from experiment to experiment, or (b) presence of ecological races of A. fatua.

In regard to quiescence, A. fatua had 16.8 percent germination after one year of burial, which was the highest percentage of the species investigated. However, quiescence among buried seeds during the subsequent year (Experiment II) was limited. While terminal

dormancy was high in all experiments, the high level of primary dormancy precluded any statement concerning induction of secondary dormancy. The differential response of A. fatua between Experiments I and II could be the result of different climatic conditions prevalent during each study. A more plausible explanation of this disparity is ageing of seed during storage. For example, Lewis (38) found that seed of several species had greater longevity when buried in the soil than while stored in the air.

Examination of the nonviability parameters shows that extensive in situ germination and loss of viability occurred under field conditions (Experiment II) and under the controlled environments of Experiment III.

III. Influence of Environment Upon Buried Seed Persistence and Depletion

A. Depth of Burial

The results of Experiment I show that germinability among buried seeds was maintained at higher levels at the deeper depth of burial. Total nonviability, on the other hand, was highest at the shallow burial depth. These results are in agreement with the findings of several workers (6, 11, 43, 47, 48, 51). Only the report of Lewis (38) opposes the concept of greater preservation of seeds at deeper burial depths. This evidence suggests that seed having been

deeply buried by the action of livestock during winter grazing, by entrance through cracks in the soil, or by cultivation practices are longer lived than seeds remaining on the surface or under shallow burial. This preservation of seed at deeper burial depth may be related to: (a) lower and more stable temperature, (b) higher, more stable soil moisture levels, (c) lower oxygen and higher CO_2 composition of the soil atmosphere.

Rampton and Ching (43) have reported that dormancy of seeds were more pronounced at deeper burial depths. This occurrence was not observed in Experiment I. Detailed comparison of the results of these two studies is difficult since Rampton and Ching did not apply statistical analysis to their data. It may be possible that imposition of dormancy in buried seeds is brought about by conditions that differ from, or are unrelated to those factors responsible for the maintainance of quiescence in buried seeds. These factors will be discussed in part C of this section.

B. Vegetative Cover Type

Relatively high levels of terminal dormancy were noted among seed samples recovered from perennial ryegrass plots. This occurrence may be the result of unique characteristics of the rooting media of perennial ryegrass, i. e. gaseous composition, soil moisture, or the presence of inhibitory materials exuded from perennial

ryegrass roots. However, the exact cause of this heightened dormancy is unclear. The reason for high dormancy percentages among buried seed as contrasted to rather low germinability under perennial ryegrass cover also remains obscure.

C. Soil Temperature and Moisture

Of the numerous environmental factors influencing buried seed persistence, temperature and moisture are undoubtedly the most important.

While seed quiescence decreased continuously over the course of Experiment II, the rate of decrease was noticeably attenuated during the period of December, 1966 through April, 1967. Climatological data indicated that the most noticeable trend during this period was low soil temperature (less than 10 C during December through February) associated with high soil moisture (greater than 27 percent). The results of Experiment III show that seed quiescence increased with decreasing temperature. Also, due to extensive *in situ* germination at 22.5 percent soil moisture, quiescence was maintained at high levels only in very dry or very wet soil. Under western Oregon field environments, conditions are alternately favorable and unfavorable for maintainance of seed quiescence. Quiescence is drastically reduced under field environments prevailing during autumn when existing conditions are favorable for *in situ* germination. Presumably, a

similar period of germination activity occurs in the spring. The prevalence of low temperature coupled with high soil moisture during winter in western Oregon imposes principle limitations upon in situ germination of viable seed. This cessation of germination activity is probably a result of low temperature interaction with limited oxygen availability in the soil. The effect of low oxygen availability on the suppression of germination has already been discussed (6, 29). The suppressive action of CO_2 during the dormant period must also be considered (6). The principle limitation imposed upon in situ germination, during summer in western Oregon is undoubtedly that of insufficient soil moisture.

Comparison of terminal dormancy recorded in Experiment II with climatological data shows that maximum terminal dormancy was induced during the period when prevailing conditions in the field were low soil temperature and high soil moisture. The same observation was made for "deep dormancy". Such occurrences were reproduced in the growth chamber experiment. Again, terminal dormancy increased with decreasing temperature when associated with intermediate and high soil moisture percentages. Five degrees C coupled with 22. 5 percent soil moisture was found to be particularly effective for dormancy induction in L. multiflorum and A. tenuis. Terminal dormancy was most effectively induced in P. annua at 5 C X 40. 5 percent soil moisture.

This evidence strongly suggests that terminal dormancy in buried seed of L. multiflorum, A. tenuis and P. annua can be induced by high soil moisture associated with low temperatures indigenous to western Oregon during winter periods. Under field conditions, the induction of dormancy would occur subsequent to the flush of autumn germination. Germination could result if this dormancy were overcome at later periods--perhaps in the spring. Certainly, the cessation of germination and the induction of dormancy provides an effective protective mechanism that prevents germination during periods of adverse weather conditions. Seed in a deep state of dormancy could provide a reservoir of propagules with the capability of long term survival. The role of low temperature associated with high soil moisture (limited gaseous exchange) appears unique since high temperature and limited gaseous exchange has been presumed to be the principle environmental cause of secondary dormancy induction (16, 17, 54).

Extensive in situ germination was recorded after recovery of seed from two months of burial during the fall of 1966. Climatological data indicate that soil temperature generally was greater than 5 C and that intermediate soil moisture levels were prevalent. High percentages of in situ germination were also brought about in the growth chamber by maintaining seed at various temperatures associated with a soil moisture of 22.5 percent. Since in situ

germination is irreversible and since the parameter of total nonviability in Experiment II was not different at each of the three sampling dates, it can be concluded that low temperature and high soil moisture held in check further in situ germination from December, 1966 through April, 1967. The effectiveness of high soil water tables on the suppression of in situ germination has been reported by Evans (19, 20). The present study supports his findings.

Appreciable loss of viability among ungerminated seeds were found after the first two months of burial under the conditions described in Experiment II. Similarly, the loss of viability among ungerminated seeds in Experiment III increased with temperature and soil moisture. Although a complete time course study of nonviability among ungerminated seed was not made, it seems possible that a mechanism similar to that theorized by Barton (4) or Toole and Toole (50) may be responsible for preservation of seed in the imbibed state during periods of low temperature. Such a mechanism, through the moderation of metabolic processes, could prevent seed deterioration or untimely germination.

IV. The Mode of Persistence and Depletion of Viable Seeds

While quiescence plays an important role in early stages of burial, terminal dormancy seems to play an increasingly important role with the progression of time. This relationship was evident in

data presented on Table 5 of Results. This alteration in the mode of persistence is due to depletion of quiescence seeds via in situ germination and to conversion of quiescent seeds to dormant types by inductive conditions. The data of Rampton and Ching (43) indicates that both quiescence and terminal dormancy are operative as modes of persistence near the termination of viability of a buried seed population.

No time course evaluation of mode of depletion is available. However, the results of Experiments II and III show that in situ germination of most species studied in these investigations is the principle route of viable seed depletion when favorable conditions are present. The obvious exception to this statement was the response observed for A. tenuis. This species was characterized by extensive loss of viability among ungerminated seed. Since in situ germination is an irreversible process, it is logical to assume that it is the principle route of eliminating viable buried seeds.

SUMMARY AND CONCLUSIONS

Field and growth chamber studies were conducted to ascertain the effects of environment on the persistence and depletion of buried seed of five grass species.

A population model describing the components of viability and nonviability was constructed. This model is applicable to all seed populations and is useful in studying the relationships between population components at a point in time and over a time course.

Of the five species investigated in this thesis, L. perenne was found to be the least persistent. Field studies indicated that L. perenne lost virtually all viability after 60 days of burial. This rapid loss of viability was found to occur through in situ germination. In addition, loss of viability among ungerminated seed of L. perenne was relatively high.

A high degree of persistence among buried seed of L. multiflorum was encountered in these studies. This persistence was a manifestation of both quiescence and terminal dormancy. Variation in persistence was encountered among different seed lots of L. multiflorum.

Persistence among buried seed of P. annua was due to both quiescent and terminal dormant seed. Also, relatively high percentages of seed in a deep state of dormancy were found among seed

lots buried under field conditions. Large numbers of buried seed of this species were found to be lost through in situ germination.

A. tenuis, like L. multiflorum and P. annua maintained viability through the components of quiescence and terminal dormancy. Buried seed in a deep state of dormancy may play an important role in the persistence of A. tenuis. Very low percentages of in situ germination occurred among buried seed of this species. The principle route of seed depletion appears to be via loss of of viability among ungerminated seed.

On the basis of the long term burial study, A. fatua was concluded to possess considerable seed persistence. Quiescence was found to be the principle mode of persistence among buried seed of this species.

Seed buried at 10 cm depth were found to have a higher percentage of quiescence and a lower level of nonviability than seed buried at 5 cm depths. The degree of terminal dormancy was not influenced by depth of burial.

Seed lots recovered from perennial ryegrass cover were found to be significantly higher in terminal dormancy than seed recovered from weed, wheat and alfalfa plots.

Soil temperature and moisture was found to exert a profound influence upon seed persistence and depletion. Loss of seed quiescence was minimized over time when conditions of low temperature

and high soil moisture were prevalent. Terminal dormancy was found to be present after buried seed were subjected to regimes of low temperature and high soil moisture. Higher temperatures associated with intermediate soil moisture levels were effective in depleting viable seed through in situ germination. High temperatures associated with high soil moisture was found to increase nonviability among ungerminated seed.

Seed quiescence was found to play an important role in the early stages of seed persistence in L. multiflorum, P. annua, A. tenuis and A. fatua. With the progression of time, terminal dormancy was found to play an increasingly important role as a mode of persistence. The importance of terminal dormancy as a mode of persistence was confirmed by the findings that seed in a state of terminal dormancy were capable of producing normal seedlings subsequent to stratification.

With the exception of A. tenuis, in situ germination was found to be the principle mode of viable seed depletion. Loss of viability among ungerminated seed was the primary mode of viable seed loss in A. tenuis.

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APPENDIX

Appendix Table 1. Analysis of variance of quiescent, terminal dormant and total nonviable seed recovered after one year of burial at two depths under four vegetative cover types.

Source of Variation	df	Quiescence Mean Square	Terminal Dormant Seed Mean Square	Total Nonviability Mean Square
Replications	1	83.37	62.00	138.18
Cover Type	3	101.85	87.01*	105.54
Depth of Burial	1	543.53*	29.24	522.35*
Species	4	2,335.64*	407.96*	2,834.65*
C X D	3	74.69	12.54	57.58
C X S	12	105.20	21.09	72.97
D X S	4	65.67	12.66	77.82
C X D X S	12	41.08	19.18	146.98
Experimental error	39	57.77	17.65	54.37
Sampling error	80	13.77	12.69	16.54
Total	159			

*Significant at the five percent probability level.

Appendix Table 2. Quiescence of seed recovered after one year of burial at two depths under four vegetative cover types. [1]

Species of buried seed	Depth of burial (cm)	Vegetative Cover Type: Weed	Wheat	Perennial Ryegrass	Alfalfa	Species Means
A. fatua	5	21.75 abc	8.00 c-f	8.50 c-f	9.75 cde	16.84 a
	10	33.25 a	10.50 cde	15.75 bcd	27.25 ab	
A. tenuis	5	2.00 e-h	3.50 d-h	2.75 e-h	7.50 c-g	4.84 b
	10	2.75 e-h	10.50 cde	4.75 d-h	5.00 d-h	
P. annua	5	2.25 e-h	1.00 e-h	0.75 fgh	2.00 e-h	1.94 c
	10	1.25 e-h	0.50 fgh	5.50 d-g	2.25 e-h	
L. multiflorum	5	1.75 e-h	0.00 h	0.25 gh	1.00 e-h	2.37 c
	10	2.00 e-h	0.75 fgh	10.50 cde	2.75 e-h	
L. perenne	5	0.00 h	0.00 h	0.00 h	0.00 h	0.06 d
	10	0.00 h	0.00 h	0.50 fgh	0.00 h	
Cover type means [2]		6.70	3.47	4.93	5.75	
Burial depth means [3]		5 cm - 3.64 10 cm - 6.79				

[1] Values in a section not having a letter in common are different at the five percent level of significance according to Duncan's Multiple Range Test. Continuity among long sequences of letters is indicated by a dash.

[2] Cover type means were not significantly different.

[3] Burial depth means differed at the five percent level of significance.

Appendix Table 3. Terminal dormancy percentage of seed recovered after one year of burial at two depths under four vegetative cover types. [1]

Species of buried seed	Depth of burial (cm)	Vegetative Cover Type: Weed	Wheat	Perennial Ryegrass	Alfalfa	Species Means
A. fatua	5	2.50 a-d	1.75 bcd	6.00 ab	2.50 a-d	3.50 a
	10	2.50 a-d	2.50 a-d	6.75 a	3.50 abc	
A. tenuis	5	4.25 abc	1.50 b-e	1.00 cde	1.00 cde	2.22 b
	10	2.50 a-d	2.00 a-d	3.50 abc	2.00 a-d	
P. annua	5	0.75 cde	0.75 cde	2.25 a-d	1.25 cde	1.16 c
	10	0.75 cde	1.00 cde	2.25 a-d	0.25 de	
L. multiflorum	5	0.25 de	0.75 cde	0.75 cde	0.25 de	0.84 c
	10	1.00 cde	0.25 de	2.25 a-d	1.25 cde	
L. perenne	5	0.00 e	0.00 e	0.00 e	0.00 e	0.03 d
	10	0.00 e	0.00 e	0.25 de	0.00 e	
Cover type means		1.45 b	1.05 b	2.50 a	1.20 b	
Burial depth means [2]				5 cm - 1.38 10 cm - 1.73		

[1] Values in a section not having a letter in common are different at the five percent level of significance. Continuity among long sequences of letters is indicated by a dash.

[2] Burial depth means were not significantly different.

Appendix Table 4. Percent total nonviable seed recovered after one year of burial at two depths under four vegetative cover types.[1]

Species of buried seed	Depth of burial (cm)	Vegetative Cover Type: Weed	Wheat	Perennial Ryegrass	Alfalfa	Species Means
A. fatua	5	75.75 ghi	90.25 c-g	85.50 e-h	87.75 d-g	79.66 d
	10	64.25 i	87.00 efg	77.50 f-i	69.25 hi	
A. tenuis	5	93.75 b-e	95.00 b-e	96.25 a-e	91.50 b-f	92.94 c
	10	94.75 b-e	87.50 d-g	91.75 b-f	93.00 b-e	
P. annua	5	97.00 a-e	98.25 abc	97.00 a-e	96.75 a-e	96.91 b
	10	98.00 a-d	98.50 abc	92.25 b-f	97.50 a-d	
L. multiforum	5	98.00 a-d	99.25 ab	99.00 abc	98.75 abc	96.84 b
	10	97.00 a-e	99.00 abc	87.25 efg	96.00 a-e	
L. perenne	5	100.00 a	100.00 a	100.00 a	100.00 a	99.91 a
	10	100.00 a	100.00 a	99.25 ab	100.00 a	
Cover type means[2]		91.90	95.48	92.58	93.05	
Burial depth means[3]				5 cm - 95.01 10 cm - 91.49		

[1]Values in a section not having a letter in common are different at the five percent level of significance according to Duncan's Multiple Range Test. Continuity among long sequences of letters is indicated by a dash.

[2]Cover type means were not significantly different. [3]Burial depth means differed at the five percent level of significance.

Appendix Table 5. Analysis of variance for quiescent, terminal dormant and total nonviable seed recovered after two, four and six months of burial.

Source of variation	df [1]	Quiescence mean square	Terminal dormancy (tetrazolium positive) mean square	Terminal dormancy (delayed germination) mean square	Deep terminal dormancy (tetrazolium positive) mean square	Total nonviability mean square
Replications	3	7.58	23.81	3.30	19.10	13.92
Species	7	2,252.92*	1,106.58*	1,504.40*	437.88*	4,602.92*
Duration of burial	2	328.00*	138.22*	145.64*	21.57	75.03
S X D	14	50.79*	209.08*	99.50*	34.27	69.88
Error	65	9.72	15.90	20.27	19.93	27.65
Total	92					

[1] Error and total degrees of freedom were corrected for missing data.

* Significant at the five percent probability level.

Appendix Table 6. Analysis of variance for *in situ* germination and nonviability among ungerminated seed after two months of burial.

Source of variation	df	*in situ* germination mean square	nonviability among ungerminated seed mean square
Replications	3	8.46	8.93
Species	7	2,639.34*	778.41*
Error	21	51.91	44.64
Total	31		

*Significant at the five percent probability level.

Appendix Table 7. Quiescence among seed of five species after three durations of burial. [1]

Species	Lot no.	Days of Burial 60	120	180	Species Means
A. fatua		0.00 e	0.00 e	0.00 e	0.00 e
A. tenuis		8.75 c	0.75 d	0.25 de	3.25 c
P. annua		0.75 d	0.00 e	0.00 e	0.25 d
L. multiflorum	-2	33.75 a	21.25 b	22.50 b	25.83 a
	-3	21.50 b	11.00 c	9.50 c	14.00 b
	-4	38.75 a	24.00 b	17.33 b	27.54 a
L. perenne	-2	0.00 e	0.25 de	0.33 de	0.18 de
	-3	0.00 e	0.25 de	0.00 e	0.09 de
Burial duration means		12.94 a	7.42 b	6.28 b	

[1] Duncan's Multiple Range Test was independently applied to treatment, species and burial duration means. Means having a common letter do not differ at the five percent level of probability.

Appendix Table 8. Terminal dormant seed of five species, estimated by tetrazolium chloride reaction, after three durations of burial. [1]

Species	Lot no.	Days of Burial 60	120	180	Species Means
A. fatua		3.00 ghi	3.00 ghi	2.00 hi	2.66 d
A. tenuis		27.50 a	4.50 fgh	15.00 bcd	15.66 b
P. annua		13.00 cde	0.00 j	15.00 bcd	9.33 c
L. multiflorum	-2	12.00 de	26.25 a	25.50 a	21.25 a
	-3	2.75 ghi	9.75 def	9.50 def	7.33 c
	-4	6.75 efg	20.00 abc	22.60 ab	16.50 b
L. perenne	-2	1.00 ij	0.00 j	0.00 j	0.33 e
	-3	0.50 ij	0.50 ij	0.50 ij	0.50 e
Burial duration means		8.3 b	8.0 b	11.3 a	

[1] Duncan's Multiple Range Test was independently applied to treatment, species and burial duration means. Means having a common letter do not differ at the five percent level of probability.

Appendix Table 9. Terminal dormant seed of five species, estimated by delayed germination response, after three durations of burial. [1]

Species	Lot no.	Days of Burial 60	120	180	Species Means
A. fatua		1.00 ijk	0.00 k	1.00 ijk	0.73 d
A. tenuis		24.00 abc	13.50 de	13.50 de	17.00 b
P. annua		5.50 fgh	4.00 ghi	10.50 ef	6.66 c
L. multiflorum	-2	14.75 cde	25.75 ab	32.00 a	24.17 a
	-3	1.50 h-k	11.50 ef	9.50 efg	7.50 c
	-4	3.50 hij	16.75 b-e	20.66 bcd	13.00 b
L. perenne	-2	0.00 k	0.50 jk	0.00 k	0.18 de
	-3	0.00 k	0.00 k	0.00 k	0.00 e
Burial duration means		6.28 b	9.29 a	11.31 a	

[1] Duncan's Multiple Range Test was independently applied to treatment, species and burial duration means. Means having a common letter do not differ at the five percent probability level. Continuity among long series of letters is indicated by a dash.

Appendix Table 10. Percentage of seed in deep dormancy, estimated by tetrazolium chloride reaction subsequent to delayed germination tests. [1]

Species	Lot no.	Days of Burial 60	120	180	Species Means
A. fatua		3.00 cde	1.33 def	1.50 def	2.00 b
A. tenuis		3.50 cde	3.50 cde	15.00 a	7.33 a
P. annua		6.50 bc	6.50 bc	9.50 ab	7.50 a
L. multiflorum	-2	1.50 def	1.50 def	1.50 def	1.50 b
	-3	0.00 f	0.50 ef	0.00 f	0.17 c
	-4	1.50 def	4.00 bcd	1.33 def	2.55 b
L. perenne	-2	0.00 f	0.00 f	0.00 f	0.00 c
	-3	0.00 f	0.00 f	0.00 f	0.00 c
Burial duration means		2.00 b	2.17 b	3.60 a	

[1] Duncan's Multiple Range Test was independently applied to treatment, species and burial duration means. Means having a common detter do not differ at the five percent level of probability.

Appendix Table 11. In situ germination and nonviability among ungerminated seeds recovered after 60 days of burial. [1]

Species	Lot no.	in situ germination (percent)	nonviability among ungerminated seed (percent)
A. fatua		72.00 b	21.50 b
A. tenuis		10.75 d	53.00 a
P. annua		69.00 b	18.25 bc
L. multiflorum	- 2	39.50 c	10.50 c
	- 3	63.70 b	13.25 bc
	- 4	44.50 c	11.75 bc
L. perenne	- 2	87.00 a	13.00 bc
	- 3	84.00 a	16.00 bc

[1] Within each column, means having a common letter do not differ significantly at the five percent level.

Appendix Table 12. Percentage total nonviable seed of five species after three durations of burial. [1]

Species	Lot no.	Days of Burial 60	120	180	Species Means
A. fatua		96.00 ab	98.66 a	97.50 a	97.27 a
A. tenuis		63.75 g	82.25 cde	71.25 f	72.42 d
P. annua		87.25 cd	89.50 bc	80.00 de	85.58 b
L. multiflorum	-2	50.00 ij	51.50 ij	44.00 j	48.50 f
	-3	77.00 ef	77.00 ef	81.00 de	78.33 c
	-4	56.25 ghi	55.25 hi	60.66 gh	57.09 e
L. perenne	-2	100.00 a	98.66 a	99.66 a	99.63 a
	-3	100.00 a	99.75 a	100.00 a	99.90 a
Burial duration means [2]		78.78	81.10	78.48	

[1] Duncan's Multiple Range Test was independently applied to treatment, species and burial duration means. Means having a common letter do not differ at the five percent level of probability.

[2] Burial duration means were not significantly different at the five percent level of probability.

Appendix Table 13. Analysis of variance of viability and nonviability parameters of seed buried for 30 days under combinations of three temperatures and three soil moistures.

Source of variation	df	Quiescence mean square	Terminal dormancy mean square	*in situ* germination mean square	Nonviability among ungerminated seed mean square	Total nonviability mean square
Temperature	2	5, 349. 42*	304. 62*	346. 25*	4, 173. 38*	6, 145. 51*
Soil moisture	2	50, 830. 56*	290. 12*	70, 520. 20*	19, 987. 74*	49, 142. 84*
Species	7	2, 992. 56*	302. 69*	600. 16*	1, 357. 44*	2, 558. 51*
T X S_m	4	3, 107. 58*	91. 52*	297. 35*	3, 475. 61*	3, 294. 55*
T X S_p	14	177. 26*	19. 21	52. 04*	324. 88*	149. 59*
S_m X S_p	14	693. 41*	64. 01*	598. 50*	1, 020. 05*	752. 35*
T X S_mX S_p	28	234. 53*	19. 32	54. 65*	234. 63*	220. 76*
Error	144	18. 46*	12. 02	5. 87	18. 15	18. 69
Total	215					

*Significant at the five percent probability level.

Appendix Table 14. Percentage *in situ* germination of five species after 30 days of burial at nine combinations of temperature and soil moisture.[1]

Species	Lot no.	Temperature: 5 C, Soil moisture percent 4.5	5 C, 22.5	5 C, 40.5	10 C, 4.5	10 C, 22.5	10 C, 40.5	15 C, 4.5	15 C, 22.5	15 C, 40.5	Species $\bar{x}$
A. fatua		0.0 n	46.7 ij	0.0 n	0.0 n	67.7 ef	0.0 n	0.0 n	70.0 e	1.0 m	20.6 c
A. tenuis		0.0 n	6.3 l	0.0 n	0.0 n	51.0 hi	0.0 n	0.0 n	61.3 fg	0.0 n	13.2 e
P. annua		0.0 n	40.0 j	0.0 n	0.0 n	78.3 d	0.0 n	0.0 n	71.3 e	0.0 n	21.6 c
L. multiflorum	-2	0.0 n	29.3 k	0.0 n	0.0 n	40.7 j	0.0 n	0.0 n	49.0 i	0.7 m	13.3 e
	-3	0.0 n	68.0 ef	0.0 n	0.0 n	74.3 de	0.0 n	0.0 n	78.3 d	0.0 n	24.5 b
	-4	0.0 n	44.3 ij	0.0 n	0.0 n	56.7 gh	0.0 n	0.0 n	58.0 gh	0.0 n	17.6 d
L. perenne	-2	0.0 n	94.0 ab	0.0 n	0.0 n	95.0 a	0.0 n	0.0 n	88.3 c	0.7 m	30.9 a
	-3	0.0 n	93.0 ab	0.0 n	0.0 n	92.0 abc	0.0 n	0.0 n	90.0 bc	0.0 n	30.5 a
Temperature means			17.7 c			23.1 b			23.7 a		
Soil moisture means					4.5 percent		0.0 c				
					22.5 percent		64.3 a				
					40.5 percent		0.1 b				

[1]Duncan's Multiple Range Test was applied independently to species, temperature, soil moisture and treatment means. Means having a common letter do not differ at the five percent level of probability.

GLOSSARY

The following terms are used throughout the text of this thesis. These definitions are given to eliminate any confusion arising from their use.

Deep dormancy — A term used in this thesis to describe a terminal dormancy which cannot be broken by stratification or chemical treatment. This dormancy type could include primary dormancy, secondary dormancy or both.

Germination — Emergence and development of the radicle and shoot from the seed.

Indeterminate dormancy. Dormancy among seeds in which further characterization of dormancy type i. e. primary or secondary is impossible.

In situ germination. Germination of a seed at depths that preclude successful emergence of the seedling. This term, although not used as such in this thesis, could also be used to describe germination at shallow burial depths.

Primary dormancy. A dormancy originally present in the seed which prevents germination under favorable conditions.

Quiescence — Seeds remain ungerminated as a result of environmental limitations only. Germination occurs as soon as favorable conditions prevail.

Secondary dormancy. A dormancy condition in seed induced by unfavorable germination conditions. Germination is prevented under favorable conditions.

Terminal dormancy. A term used in this thesis to describe dormancy among seed estimated at the end of an experimental duration. This dormancy may be composed of primary dormancy, secondary dormancy or both.