THESIS

GERMINATION, EMERGENCE, AND SEED PERSISTENCE OF PANICUM MILIACEUM L.

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION

BY William Loyd Stump

ENTITLED GERMINATION, EMERGENCE, AND SEED PERSISTENCE OF PANICUM MILIACEUM L.

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ABSTRACT OF THESIS

GERMINATION, EMERGENCE, AND SEED PERSISTENCE OF PANICUM MILIACEUM L.

The effects of varying levels of temperature, moisture, and seed depth on wild proso millet (Panicum miliaceum L.) emergence were observed. The effects of depth and duration of seed burial and the effects of seed overwintering on the soil surface on modes of seed depletion and persistence were studied. Patterns of wild proso millet emergence in the field were studied under conditions of plus or minus intraspecific and corn competition, and with and without soil disturbance.

Emergence occurred over a range of 10 to 40 C with percent and speed of emergence increasing with temperature. Under simulated drought conditions induced by polyethylene glycol, germination was reduced at both temperatures tested (25, 30 C) as moisture stress increased. The greatest moisture stress that germination occurred at was -14 bars (1.5%) at 30 C and -10 bars (2%) at 25 C. Germination at 30 C was higher at all moisture levels than at 25 C. Emergence from soil moisture levels of 35 to 100% field capacity was greater than 87%. Emergence ceased below 25% field capacity. Fluctuations of soil moisture resulted in slightly higher emergence than at a constant soil moisture level. Emergence was equal from 1 to 8 cm of seed depth with 14 cm the maximum depth of emergence. After 21 months of seed burial loss was greatest at 5 cm, with only 23% viable seed remaining. Persistence

increased with soil depth with 77 and 93% viable seed at 10 and 30 cm, respectively. The main mode of depletion was *in situ* germination which decreased with depth. Seed death was not a major factor of depletion and was not affected by depth. The majority of depletion occurred within the first 12 months with seed populations stabilizing from 12 to 21 months of burial. Seeds overwintering on the soil surface were not greatly affected with more than 96% remaining viable seed. With high soil moisture, emergence patterns were influenced by fluctuations in temperatures in late May when emergence began, to June. In July and early August when emergence ceased, soil moisture became the limiting factor. Total emergence was greatest when all competition was removed. Both intraspecific and corn competition reduced emergence in July and early August. Cultivation acted to remove competition resulting in greater total emergence than treatments with competition.

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TABLE OF CONTENTS

TABLE OF CONTENTS (continued) page

LIST OF TABLES

LIST OF FIGURES

page

INTRODUCTION

Panicum miliaceum L., wild proso millet, has become established and spread rapidly throughout the North Central United States during the past ten years (3, 16, 27, 36). The weed is now present in the state of Colorado. The extent of the problem and its origin in Colorado are not known, however, it is becoming a major weed problem in several fields observed in Weld County. Wild proso millet is of great concern to farmers because it is highly competitive, a prolific seed producer, and is difficult to selectively control (3, 16, 27, 36, 62).

Because wild proso millet is a relatively new weed problem little work has been done on its biology. To best initiate any weed control program knowledge of a weed's biological characteristics is important. Weed seeds in the soil are dispersed with depth and degree of dormancy. These conditions create the periodic nature of emerging weeds. This periodicity of emergence can create problems for weed control when it does not correspond with control measures. Since each weed species is unique in its response to environmental conditions in terms of germination and emergence it is important to study factors which govern the establishment of a particular weed in question. Some of these factors include moisture requirements, absence or presence of light, temperature, dormancy, aeration, and depth of burial. When a weed is better understood there may be some aspects of its behavior

that can be exploited in a timely control measure. Examples could be control during periods of maximum emergence, seed responses to shallow or deep tillage, and manipulation of crop planting dates to maximize crop competition with later emerging weeds or to avoid early emerging weeds. This lack of biological information on Panicum miliaceum necessitates studies of its biology.

The investigation concentrated on three areas of wild proso millet biology. The first area, the range and optimum of temperature, moisture, and seed depth on germination, and emergence were established. Temperatures were constant and ranged from 10 to 40 C. Total emergence and speed of emergence were observed. Soil moisture levels of 20 to 100% field capacity and water potentials of 0 to -14 bars, established by polyethylene glycol, and their effects on total emergence and germination were observed. The effect of seed depth on total emergence was determined in pots and in the field, at depths from 0 to 18 cm.

In the second area, experiments were designed to study longevity of P. miliaceum seeds under field conditions. The effects of burial depth and duration on seed viability were studied. Seeds were buried in soil at 5, 10, and 30 cm and changes in persistence and depletion of the seed population monitored over 21 months. Persistence was partitioned into components of enforced and endogenous dormancy and depletion into nonviable and in situ germinated seed. In another study, seeds were exposed on the soil surface over winter and monitored the same way as in the previous study.

The third group of experiments were designed to observe patterns of P. miliaceum emergence in the field. Conditions with and without intraspecific competition, with and without interspecific competition

from corn (Zea mays L.), and with and without soil disturbance on emergence were studied.

The objectives of this investigation were to gain new insights on how Panicum miliaceum L. reacts to environmental stimuli and how these may relate to control measures.

CHAPTER 1

Literature Review

Botanical Description

Panicum miliaceum L. is an erect, branching annual grass which reproduces by seed. It is fast growing, highly competitive, and matures in 60 to 90 days (22). Plants often reach heights of 152 to 182 cm but may be decumbent at the base. Leaf blades are somewhat hairy, usually 30 cm long and 2 cm wide and rounded at the base. Seed production begins in mid-July and continues into late fall. The panicles range from 10 to 46 cm long and are erect or nodding at maturity. The numerous panicle branches are ascending and bear spikelets toward the end. Each spikelet is about 4 mm long and consists of two glumes, a sterile floret, and a fertile floret consisting of a caryopsis enclosed by a hard, smooth, shiny lemma and palea. Prominent light colored veins are evident on the fertile lemma and palea. The seed is olive-brown to brown-black and may darken with age. Seeds are 1.5 to 2 mm wide and 2.5 to 3 mm long and readily shatter from the panicle at maturity.

In the seedling stage wild proso millet resembles volunteer corn and later fall panicum (Panicum dichotomiflorum Michx.) or witchgrass (Panicum capillare L.). Upon close examination, wild proso millet can be distinguished from fall panicum and corn by the abundance of hairs on the stem found in all stages of its growth. Although

witchgrass also has hairs it does not grow as tall or vigorously. Another identifying characteristic is that with careful extraction of a wild proso millet plant from the soil the hull of the dark seed can often be found among the roots even in mature plants.

Location and Origin

At present, wild proso millet is a problem in Wisconsin and Minnesota, border areas of Illinois, Iowa, North and South Dakota, various parts of Ontario and Quebec, and scattered areas of Nebraska and Colorado (3, 27, 36). The weed, first discovered in Minnesota in 1970, has established itself in every county in the southern portion of the state (3). In Wisconsin, from a few isolated patches in the early 1970's, it has spread to an estimated million acres of corn (3). Wild proso millet is also found in Canada, Argentina, Southern and Eastern Africa, France, Central and Southeastern Europe, the British Isles, USSR, the Middle East, India, China, Japan, Australia, New Zealand, and several Pacific Islands (23).

There are many theories concerning the origin of wild proso millet in the United States. It is thought to be an escaped form of domestic proso millet (3, 36). This is grown in the Great Plains areas of Western Nebraska, Northeastern Colorado, and North and South Dakota for livestock feed and bird seed. Proso millet is also used for human consumption in many parts of the world like India and Africa (22). The crop has been cultivated so long by man that the wild ancestors are unknown (36). It is considered by Iltis and deWet to be Panicum miliaceum subsp. ruderale (Kitagawa) Tzvelv (syn. P. spontaneum Lyss. ex Zhukovsky) which is native to Manchuria, China (27).

If true, wild proso millet could have been introduced into the North Central region as a contaminant in imported proso millet seed. Or, it could have evolved from one of the domestic cultivars of proso millet. Morphologically, it is similar to a domestic cultivar "Crown" grown as a crop in Minnesota 30 to 40 years ago (24).

The source of wild proso millet infestations in Colorado is not known. In some areas it is believed that it was introduced by the spreading of manure from cattle fed contaminated weed seed screenings. The local farmers, that have this problem, believe that these seed screenings were obtained from areas of Nebraska with known wild proso millet infestations.

Several characteristics of wild proso millet enable it to compete vigorously with row crops. The weed's emergence and stage of growth closely parallel corn's emergence and development yet it also continues to emerge throughout the growing season (43). Its competitive ability and vigorous growth are probably due, at least in part, to its C_4 photosynthetic characteristic and low water requirements (17). The short maturity (60 to 90 days) enables it to flower and produce viable seed before corn or soybeans (Glycine max L.) are mature. Thus, seeds still remaining on the panicle can be spread from field to field by harvest machinery. Wild proso millet is a prolific seed producer. Strand and Behrens (62) reported it common to find 5,382 or more seeds/m^2 on the soil surface in infested fields.

Wild proso millet also shows tolerance to many commonly used herbicides. It is very tolerant to field rates of atrazine (2-chloro-4-ethylamino-6-isopropylamino-s-triazine) and somewhat less tolerant to cyanazine (2-[[4-chloro-6(ethylamino)-s-traizin-2-yl]amino]-

2-methylpropionitrile) (25, 62). However, several chemical programs have been developed over the past few years that offer satisfactory early suppression of wild proso millet in corn (39, 40, 41, 42). There is usually a positive yield response even though the weed is not controlled through harvest. Good wild proso millet control in corn has been obtained with EPTC (S-ethyl dipropylthiocarbamate) + R-25788 (N,N-diallyl-2,2-dichloroacetamide) at 6.7 kg/ha + cyanazine at 2.2 kg/ha both applied preplant incorporated (39). Other thiocarbamate herbicides such as butylate (S-ethyl diisobutylthiocarbamate) + R-25788, vernolate (S-propyl dipropylthiocarbamate) + R-25788, and cycloate (S-ethyl N-ethyl thiocyclohexanecarbamate) + R-25788 each at 6.7 kg/ha give satisfactory early season control (41). EPTC + R-25788 followed preplant or early post with pendimethalin (N-(1-ethylpropyl)-3,4 dimethyl-2,6-dinitrobenzeneamine) plus cyanazine also gives fairly good control provided the weeds are less than 1 inch tall (3). However, none of these treatments will give complete season control of wild proso millet in corn.

Cultural Control

The greatest wild proso millet control and corn yields were produced by planting in mid-May rather than late April and in 76 cm rather than 102 cm wide rows (39). Crop alternatives include early planted cover crops such as alfalfa (Medicago sativa L.), small grains, or peas (Pisum sativum L.). These crops establish quickly and have a growth advantage over later germinating wild proso millet. Of these, alfalfa seems to be the best long term method of controlling the weed (39). The combination of dense ground cover and frequent mowing (3 times/yr) suppresses the weed and prevents seed production (3, 36).

Weed Seeds in Soil

A potential weed problem exists as long as weed seeds remain in soil and the amount of viable weed seeds in soil is immense. In a recent review, Chancellor (11) reported on ten studies that found viable weed seed populations ranging from 3×10^6 to 860×10^6 seeds/ha and averaging 309×10^6 seeds/ha. In Denmark, Jensen (29) took soil samples from 57 cereal and root crop fields at depths of 0 to 20 cm and examined seed content. Total seed numbers ranged from 12,600 to 933,800/m^2 and the number of viable seeds from 600 to 496,200/m^2. Roberts and Ricketts (53) found 12.7 to 655.6 million viable weed seeds/ha in the upper 10 cm of soil on farms in the United Kingdom. In a study monitoring weed seed populations subjected to different weed management systems, Schweizer[1] found initial populations of 73.5 and 121.1 million seeds/ha present in the plow sole layer at Windsor and Akron, Colorado, respectively. At Windsor, barnyardgrass [Echinochloa crus-galli (L.) Beauv.] comprised 62% of the initial seed reservoir and redroot pigweed (Amaranthus retroflexus L.) 19%. At Akron, stinkgrass [Eragrostis cilianensis (All.) Lutati] was 37%, hoary vervain (Verbena stricta Vent.) 25%, and common lambsquarters (Chenopodium album L.) 16% of the initial seed bank. Leguizamon and Roberts (33) found that when stands of annual weeds were allowed to mature, a 14-fold increase in the seed bank resulted. After cultivation of the sandy loam in early April 9,500 seeds/m^2 were found at depths from

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[1]Schweizer, E.E. Systems Approach to Integrated Pest Management in Irrigated Crops. Not for publication.

0 to 10 cm. In November, 136,460 seeds/m^2 on the soil surface were returned.

In a model of soil seed banks, Thompson and Grimes (69) suggested that there are four types of soil seed reserves. Type I reserves are transient and do not last more than one year. This reserve is present during the summer and germinates in the fall. This is regarded as an adaptive characteristic for drier disturbed habitats and exploits gaps created by predictable seasonal changes. Type II seeds are also transient but are present during the winter and germinate in the spring. Type III seed reserves are intermediate with a portion germinating in autumn whereas another portion persists into subsequent years. Type IV reserves form the persistent seed bank. These seeds germinate in either the spring, fall, or at both times, with a portion persisting for several growing seasons. It is this type that is most adapted to regular and repeated disturbances common in American agriculture.

Buried Seed Persistence

Weed seeds in the soil can survive for many years. This was demonstrated by the classical experiment initiated by Beal (5) in 1879. In this experiment, seeds of 20 common Michigan weeds in 20 lots of 50 of each species were prepared for burial. Each lot was mixed with sand, placed in a pint glass bottle, and buried with the necks pointed down at a depth of 20 inches. After 40 years, seeds of ten species remained viable. After 80 years, three species still survived: curly dock (Rumex crispus L.) 2% survival, evening primrose (Oenothera biennis L.) 10% survival, and moth mullein (Verbascum blataria L.) 70%

survival (14). After 90 years, only moth mullein remained viable at 20% (32). In 1902, Duvel buried 107 crop and weed species in sterilized soil in flower pots covered with porous saucers. After 39 years, as reported by Toole and Brown (70), 36 species were still viable. In a more recent study, Lewis (35) buried seed lots of 7 cereals, 15 grasses, 8 legumes, and 9 weeds at depths of 13, 26, and 34 cm. After 20 years, Chenopodium album L. had 32%, Ranunculus repens L. 51%, and Rumex crispus L. 30% viability at the 13 cm depth.

Most weed seed longevity studies have been conducted in northern cooler climates of the U.S. or in areas outside the U.S. Since climatic conditions can influence seed longevity, information is lacking for soils of warm, humid areas. At Stoneville, Mississippi, Egley and Chandler (19) buried 20 weed species at 8, 23, and 38 cm and they were exhumed and tested for germination and viability 3.4, 4.5, and 5.5 years after burial. The 20 species were placed in five groups according to percent viable seeds remaining after 5.5 years. Group I, johnsongrass [Sorghum halepense (L.) Pers.], velvetleaf (Abutilon theophrasti Medic.), purple moonflower (Ipomoea turbinata Lag.), and spurred anoda [Anoda cristata (L.) Schecht.] had 30 to 48% seed viability after 5.5 years of burial. Hemp sesbania [Sesbania exaltata (Raf.) Cory] and pitted morningglory seeds (Ipomoea lacumosa L.) were 18 and 13% viable at 5.5 years and made up group II. Common eveningprimrose, sicklepod (Cassia obtusifolia L.), Florida beggarweed [Desmodium tortuosum (SW.) DC.], goosegrass [Eleusine indica (L.) Gaertn.], Texas panicum (Panicum texanum Buckl.), and prostrate spurge (Euphorbia supina Raf.) were 3 to 6% viable and were in group III. Large crabgrass [Digitaria sanguinalis (L.) Scop.], redroot pigweed, common purslane (Portulaca

oleracea L.), prickly sida (Sida spinosa L.), and common cocklebur (Xanthium pensylvanicum Wallr.) comprised group IV and were 0.1 to 1% viable. Group V was barnyardgrass [Echinochloa crus-galli (L.) Beauv.], redvine [Brunnichia cirrhosa (Gaertn.)], and common chickweed [Stellaria media (L.) Cyrillo] and all seeds were dead 5.5 years after burial. Loss rate for group I was 10%/year for the first 3.5 years and 26%/year thereafter. The average yearly loss for groups II, III, and IV were 26, 37, and 44%, respectively.

Since a vast, persistent reservoir of viable weed seeds exist in soil, knowledge of weed seed longevity in soil is important in developing long term weed control programs for target weeds. Some studies look at the length of time required to reduce soil seed reserves to a level at which effective weed establishment will not occur (12, 37, 49, 52). These studies frequently make the assumption that new seeds will not be reintroduced into the environment. Thus, studies of weed seed persistence in the soil may not accurately represent true life conditions but they do have some utility because of their predictive value. One such prediction is the Weed Predictive Index (WPI) developed by Naylor (46). With it one can correlate potential and actual weed flora by a measure of the expected weed density in the field derived from a soil sample taken before the crop is sown. Naylor found that WPI values derived for blackgrass (Alopecurus myosuroides L.) in each field sampled were positively correlated with the density of plants of this species at each site the following May.

Weed Seed Reduction Through Agricultural Practices

Through management, reduction of weed seeds in the soil is possible (10, 37, 58, 74, 75). Schweizer and Zimdahl (58) selected a field that contained over 1.2 million weed seeds/ha in the upper 25 cm of the soil profile. Corn was grown for six consecutive years under two weed management systems. In one system a mixture of 2.2 kg/ha of alachlor [2-chloro-2', 6'-diethyl-N-(methoxymethyl) acetanilide] plus 1.7 kg/ha of atrazine (2-chloro-4-ethylamino-6-isopropylamino-s-triazine) was applied preemergence each year followed by a postemergence application of 0.6 kg/ha of 2,4-D (2,4-dichlorophenoxyacetic acid). In the other system, only 2.2 kg/ha of atrazine, was applied preemergence each year. After the third year, herbicides were applied to only one half of each 42 by 70 m plot in each management system. After six cropping years, the total number of weed seeds declined by 98% in both systems. However, Amaranthus retroflexus L. rapidly increased in both management systems when herbicides were discontinued after three years. In a study by Wilson (74), the decline of a population of Avena fatua L., established in September 1971 and allowed to seed thereafter, was monitored in three successive barley (Hordeum vulgare L.) crops. Seedling numbers fell from 138/m^2 in 1972 to 9/m^2 in 1974 declining by 32% in the first, and by 89% in the second year. Numbers of viable seed in the soil in June, fell from 159/m^2 in 1972 to 1/m^2 in 1974 declining by 83% in the first, and by 96% the second year. Lueschen and Anderson (37) investigated longevity of velvetleaf seeds under agricultural conditions. They found that after four years of intensive tillage on fallow ground only 10% of the

original seed population remained. This 10%, however, was still 1,300 viable seeds/m^2 to a depth of 23 cm. Under undisturbed continuous alfalfa, 56% of the original population remained after four years. Under undisturbed continuous chemical fallow which consisted of 4.5 kg/ha of atrazine each spring with 1 kg/ha glyphosate [N-(phosphonomethyl)glycine] postemergence, only 37% of the seed population remained.

Factors Influencing Seed Persistence

Seed dormancy is the mechanism by which weed seeds persist in soil. Dormancy is defined as a state in which a viable seed will not germinate when exposed to the proper environmental conditions. Harper (24) recognized three types of dormancy: innate, induced, and enforced dormancy. With innate dormancy, dormancy is present at the time of seed maturation. This prevents untimely germination and assures germination dispersal in time. This type of dormancy may be physical or embryonic in nature. Induced dormancy is acquired after the seed is shed from the plant. Induced dormancy or secondary dormancy, is found when seeds are given all germination requirements but one (29, 38, 66). Restriction of water, light, too high or too low temperatures, low oxygen, and high carbon dioxide levels have all been cited in inducing dormancy in many seeds (38). Enforced dormancy is a function of the environment rather than the seed itself. Seeds are capable of germination as soon as environmental conditions are suitable. Thus, enforced dormancy is not really a dormancy in the strictest sense but a seed quiescence.

The possible causes of dormancy in seeds are numerous, can be quite complex, and in some cases, several dormancy mechanisms are present (66). A common physical cause of dormancy in seeds is the presence of a hard seed coat (38). A hard seed may be impermeable to water and/or gases or it may mechanically restrict embryo expansion. In nature, seed coats may be broken by mechanical abrasion, microbial attack, passage through animal digestive tracts, and by exposure to high and low temperatures where seed coats expand and contract causing seed coat rupture.

Whereas hard seed is mainly found in seeds with innate dormancy, results by Lueschen and Anderson (37) on longevity of velvetleaf seeds seem to suggest that water permeable (nonhard) seeds may later become water impermeable (hard). Stoller and Wax (61), in a study of seed viability of some annual weed seeds in soil, found that development or maintenance of hard seed coats was considered the principal mechanism for seed survival for three years in these species: jimsonweed (Datura stramonium L.), ivyleaf morningglory (Ipomea hederacea L. Jacq.), giant ragweed (Ambrosia trifida L.), yellow foxtail [Seteria lutescens (Weigel) Hubb.], velvetleaf, common ragweed (Ambrosia elatior L.), and Pennylvania smartweed (Polygonum pensylvanicum L.).

Other physical reasons for dormancy include the presence of various growth inhibitors such as abscisic acid in the seed coat or the seed coat may physically prevent radicle expansion. Removal of the embryo from the seed coat will allow germination to take place.

The other causes of dormancy are embryological and not as well understood. In many seeds, a period of after-ripening is needed to

overcome dormancy. Often this occurs when the seed is dry, and the length of time varies. Taylorson and Brown (65) found that after--ripening could be accelerated when dry seeds of many grass weeds were stored or incubated in sealed vials at 50 C for periods of 3 to 28 days.

Other seeds must be after-ripened in an imbibed state and often at lower temperatures, a procedure termed stratification. There are many reasons proposed for after-ripening requirements. In some seeds, the embryo is immature as in Orchidaceae and Orobanchaceae species and an after-ripening period is required for the embryo to reach maturity (38). In other seeds, chemical inhibitors may be present, or changes in storage materials composition required. Seed coat structures and permeability may undergo changes and chemical substances promoting germination may appear.

Soil disturbance. Many factors influence persistence and depletion of the soil seed reserve. In frequently disturbed soil, germination is believed to be the major cause of depletion of the soil reserve (49, 51, 74). Generally, germination loss is greatest during periods of maximal seasonal emergence and is species dependent. Roberts and Feast (51) found that seed reserves depleted exponentially whether the soil remained undisturbed or was subjected to constant cultivation. However, with increasing cultivation, there was a greater loss. For undisturbed soil, seed loss was 34%/year, with two disturbances, seed loss increased to 42%/year, and with seven disturbances, seed loss peaked at 56%/year. Similarly, Roberts and Dawkins (49) found that soil disturbance influenced the rate of depletion of the Poa annua seed bank.

Seed was buried nine inches deep and left undisturbed or was disturbed by being exhumed two to four times yearly. Undisturbed seed showed a 22% yearly loss in the soil seed reserve whereas the exhumed seed exhibited 30 to 36% annual loss.

Type of soil disturbance can also influence seed persistence. In England, the seed reserves of Avena fatua were less persistent under tine cultivation than moldboard plowing (75). Plowing generally resulted in fewer seedlings, but allowed more viable seeds to persist. Cultivation reduces seed longevity, apparently by increasing soil aeration, exposing seeds to light, and generally improving soil conditions for germination (52, 55, 73). On the other hand, deep soil tillage buries freshly shed seed enhancing persistence. With Avena fatua delayed fall cultivation led to increased seed mortality when compared to earlier fall cultivation (74). Seed persistence was attributed to deep (13 to 15 cm) moldboard plowing. In direct-drilled (minimum tillage) cereal production, 80 to 90% of new blackgrass seedlings originated from the previous years' seed production (45). In contrast, on moldboard plowed fields, the seeds shed the previous year did not contribute greatly to new seedlings. Tillage had brought up seed shed from previous years and buried new seed.

Geographic location. Geographic location also has an influence on seed persistence. Loss of viability of shattercane [Sorghum bicolor (L.) Moench.] seeds was faster in Western Nebraska than in Eastern Nebraska (9). At both locations, seed was buried 22 cm deep and persisted for 11 and 13 years, respectively. Differences were attributed to biotype variation and total rainfall. Differences in

seed persistence at different locations have also been found in other studies. In Mississippi, Egley and Chandler (18) found only 1% of barnyardgrass persisted over 2.5 years in undisturbed soil. In the drier and cooler climate of Eastern Washington, Dawson and Bruns (15) found 3% of the barnyardgrass seed persisted 13 years. In the same study, Dawson and Bruns found considerable variation in samples buried under apparently uniform conditions. Preliminary results from a Colorado study of Triticum cylindricum (Host.) Ces. also show the importance of location on seed survival.[2] After two years of a six-year study, results suggest that there are substantial differences in persistence between five burial sites each in a different climatic area.

Soil conditions on seed survival. Ambient soil conditions influence the persistence of buried seed. Acid and waterlogged soils favor maintenance of dormancy and seed survival (34). Rampton and Ching (48) showed that seeds of annual ryegrass (Lolium multiflorum Lam.) were more persistence when buried in dense, poorly drained soils. Schafer and Chilcote (57) also found that annual reygrass dormancy could be induced by cold, wet conditions. Cold, wet soils also reduced in situ germination and viability loss of annual ryegrass. Evans (20) and Lewis (34) found, in separate studies, that buried seeds were more persistent below the water table than above it. They attributed the greater survival to enforced dormancy caused by cool temperatures and lack of aeration.

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[2]Donald, W.W. 198 . Jointed goatgrass (Aegilops cylindrica L.) seed persistence in Colorado. Unpublished data.

Soil atmosphere also plays a role in buried seed preservation. Bibbey (6) found that low oxygen or high carbon dioxide partial pressures depressed germination of Brassica arvensis L. and Thlaspi arvensis L. It appears that cool, wet (reduced O_2 levels) conditions enhance seed persistence whereas high soil temperatures favor germination (57) thus reducing seed survival.

Lewis (35) in looking at longevity of crop and weed seeds after 20 years in the soil found that soil type influenced seed persistence. After 20 years at a soil depth of 26 cm, Polygonum persicaria L. and Matricaria inodora L. had 17% and 12% survival in a peat soil, respectively, and zero survival in a mineral soil. These differences were not explained by the author.

Wild proso millet was buried 25 cm deep in a sandy loam and in a silt loam for 54 months (39). Millet seed loss six months after burial in the sandy loam and silt loam was 26% and 19%, respectively. Twelve months after burial, more than half (58%) of the seed had lost its viability in silt loam and 47% in sandy loam. However, after 54 months of burial viability loss was identical for sandy loam and silt loam with 90% and 89% loss, respectively.

Depth of seed placement. In general, increasing soil depth favors greater seed longevity (19, 28, 48, 54, 61, 70, 76). The effect of depth and duration of burial on persistence of Avena fatua L. and Kochia scoparia (L.) Schrad. seed populations was investigated by Zorner (76). Nondormant and dormant seed populations of each seed were placed in separate nylon mesh packets and buried at soil depths

of 1, 3, 5, 10, 15, and 30 cm and recovered after 1, 2, 4, 5, 9, 12, 18, 24, 30, and 36 months. Seeds were tested for germination, viability, and innate, enforced, or induced dormancy. Avena fatua seed persistence increased with depth and the mode of population depletion varied with depth. Seed death decreased, and in situ germination increased as burial depth increased. Seed persistence was a function of innate dormancy and was enhanced by deep burial. Seed populations were completely depleted at all depths after 24 months burial. Initial rates of viable seed loss were much greater in the nondormant, than in the dormant, seed populations. However, after one month, the remaining viable seeds from the nondormant population acquired induced dormancy and had a depletion rate similar to the dormant population. Like wild oats, kochia seed persistence increased with depth. In situ germination was the primary mode of seed population depletion and seed persistence was a function of innate, enforced, and induced dormancy. In the initially nondormant seed population, loss of seed viability was more apparent than in the dormant population especially at the shallow depths. Depending on depth, from 1 to 3% of initially buried seed was still viable after 36 months of burial.

In the final results of Duvel's buried seed experiment reported by Toole and Brown (70) there was a general tendency for seeds buried at 42 inches to have a greater percent viability than seeds buried at 8 inches. Jacques et al. (28) studied the effects of depth and duration of burial on shattercane. They found that the number of viable seeds increased with depth regardless of time duration. Taylorson (64) buried nondormant and dormant populations of redroot

pigweed, yellow rocket (Barbarea vulgaris R. Br.), and barnyardgrass at depths of 2.5, 7.6, and 17.2 cm with recovery at 3, 6, 9, and 12 months. Shallowly placed seeds lost viability more than seeds placed at 15.2 cm. Seeds that were initially nondormant were less persistent than the dormant seeds.

Cooler soil temperatures at greater soil depths seem to affect seed persistence at greater soil depths. This is supported in Egley and Chandler's (19) 50-year buried seed study at Stoneville, Mississippi, only four of the twenty weed seed species buried at 8, 23, and 38 cm showed a depth effect on seed longevity after 5.5 years. They attributed this to warmer soil temperatures. Reduced oxygen levels and generally less fluctuation in soil conditions are other reasons for increased seed persistence at deeper soil depths (5).

Methods for the Study of Seed Persistence

Several methods have been devised to study weed seed behavior and persistence in the soil. More recently, nylon mesh seed packets have been utilized to bury a known number of seeds at varying depths and exhume them at predetermined intervals (15, 18, 19, 61, 76). By using nylon mesh packets the seed is exposed to natural, or near natural, soil conditions of temperature, moisture fluctuations, and microbial activity and yet seed recovery is still possible. Other methods using inverted jars, earthen pots, or columns filled with seeds at known depths can be criticized because of the failure to expose the seeds to the full range of soil conditions. Yet the data from such studies do demonstrate the potential longevity of many weed seeds in the soil.

In short term studies, weed seeds have been marked or 'tagged' in various ways and their fate monitored over a period of time. Naylor (46) painted blackgrass seed with fluorescent paint so the seed could be recovered the following season. Radioactive tracers have also been employed to trace seeds in the soil environment (62).

In order to analyze and interpret buried seed persistence and depletion data Schafer and Chilcote (57) devised a model that described the parameters of persistence and depletion within a buried seed population. The basis of these parameters is given by the following equation which defines the status of buried seed: $S = P + D$. S represents the total number of buried seed of a species at any time. P is the persistent segment of the total seed population, and D is the depleted or nonpersistent segment. The P component of the equation can be expanded to $P = P_{ex} + P_{end}$ where P_{ex} represents the percentage of seeds that possess exogenous or enforced dormancy. These seeds are able to germinate under favorable conditions. P_{end} is the percentage of seeds that possess endogenous dormancy which is composed of innate and induced dormancy. Seeds possessing endogenous dormancy fail to germinate under favorable conditions. The D component is also expanded to $D = D_g + D_n$. D_g represents seeds that have germinated <u>in situ</u>. D_n represents dead seed. Thus, the complete equation describing the components of a buried seed population is $S = P_{ex} + P_{end} + P_g + P_n$. The use of this equation requires a controlled study with a known number of seed buried and recovered. P_{ex} is estimated using standard laboratory germination tests established by the researcher. P_{end} is estimated by the seeds that

fail to germinate in laboratory germination tests and are then separated by several methods from nonviable seeds. The nongerminated seed can be treated to overcome dormancy by scarification, growth regulators, or stratification. A fast and frequently used method of estimating seed viability is the tetrazolium acid stain (13). The 2,3,5-triphenyl tetrazolium chloride stains respiring; hence, viable, embryo tissue a pink or red color. The test is not an absolute indication that the seed has sufficient vigor for germination. Thus, using tetrazolium chloride to determine seed viability will not underestimate the percentage of viable seeds but can slightly overestimate them (21). The D component is the seeds that are dead or have germinated in situ. Separation of the two may be difficult in a long term study because of deterioration of the plumule and radicle of germinated seed.

Seedling Emergence

Many weed species exhibit seasonal or periodic flushes of emergence. In a five year study by Roberts and Feast (50) average patterns of monthly emergence of seedlings of twenty annual weeds were derived from observations made under field conditions. Many species produced seedlings throughout the year, although there was a general tendency toward peaks during spring and autumn. Species that showed a gradual increase during early months peaking in April or May were groundsel (Senecio vulgaris L.), lambsquarter, corn spurry (Spergula arvensis L.), and annual nettle (Urtica urens L.). These species continued to produce seedlings in lesser amounts throughout summer and autumn. Hairy vetch (Vicia hirsuta L.) had an emergence peak in April with a few seedlings appearing from June onwards.

In a study by Chepil (12) the period of maximum emergence varied with species. The majority of the species studied had a peak emergence occurring within a relatively short period of about three weeks commencing about April 23. This was followed by a tapering off in emergence until midsummer or fall. For a few species emergence was more or less haphazard and showed no pattern. Stoller and Wax (60) found that giant ragweed and common ragweed (Ambrosia elatior L.) emerged in April followed closely by common cocklebur, velvetleaf, Pennsylvania smartweed, and yellow foxtail. Ivyleaf morningglory and Jimsonweed (Datura stramonium L.) were later in their emergence and emerged throughout the summer. A significant portion of common cocklebur, velvetleaf, and to some extent yellow foxtail also emerged after May 15. In contrast, giant ragweed, common ragweed, and Pennsylvania smartweed completed their emergence before May 15.

The periodicity of emergence can, in part, help determine which species are the most serious weeds. Weeds that germinate earlier in the spring are more easily controlled before or at planting. Weeds that emerge all season or later in the season after planting, are more difficult to control.

The underlying mechanisms involved in regulating seasonal emergence of many weeds have, in many cases, not been understood (38). Such mechanisms are undoubtedly complex and involve the seed and its interaction with the environment. Roberts and Potter (54) in a four year study of seedling emergence found the overall patterns were different in each year. The results indicated, however, that once the spring flush occurred, because of general soil warming,

rainfall was the most important influence on the distribution of seedling emergence. Stoller and Wax (60) also found that rainfall resulting in adequate soil moisture was the primary factor responsible for weed emergence after mid-May.

Germination Factors

Some of the factors found to influence weed seed germination and emergence in these studies were temperature, moisture, and depth of seed placement. The proper germination temperature varies with species. There is a minimum temperature below which germination will not occur and a maximum temperature above which germination will cease. The optimum temperature is that where germination is greatest in the shortest amount of time. Fluctuation of temperature rather than a fixed optimum is required by many weed species before germination can take place (30, 31, 38, 59, 71). Steinbaur and Grigsby (59) in a germination study involving 85 weed species found that alternating, rather than constant, temperature increased germination in more than 75% of the species. Striegel and Boldt (63) reported that wild proso millet had maximum germination at 30 C and that germination occurred from 10 to 40 C.

Soil moisture is a critical and often limiting factor for seed germination. Moisture requirements, like temperature requirements, vary with species. Weeds that are able to germinate and become established under less than optimal conditions get a competitive jump on crop seeds that might require more water. Therefore, it is useful to identify weed seeds that can become established under low

moisture conditions. Osmotic solutions are commonly used by researchers to simulate soil water stress. Osmotic pressures can be controlled by simple salts, such as NaCl or sugars like mannitol. However, because of toxic effects and experimental difficulties in using the aforementioned, polyethylene glycol (PEG) has been found superior because of its biological inertness and stability (44, 47, 68). In a study by Hoveland and Buchanan (26) weed species were germinated in 0, -3, -6, and -10 bar water solutions of PEG to simulate drought. Prickly sida, sicklepod (Cassia obtusifolia L.) and morningglory (Ipomoea lacunesa L.) were the most drought tolerant weeds tested. The first two exhibited some germination at -10 bars and 90% of the morningglory germinated after 72 hours at -6 bars. Hemp sesbania (Sesbania exaltata L.) was the least tolerant of drought. Germination was sharply reduced at -3 bars and only 2% germinated at -6 bars. Barrett and Peters (4) studied germination of corn, lambsquarters, and fall panicum (Panicum dichotomiflorum Michx.) under osmotic solutions of 0, -5, -10, and -15 bars. Corn and lambsquarter germination was only reduced 19 and 14%, respectively, in the -15 bar treatment. In comparison, fall panicum germination was significantly lowered over all osmotic levels from 20% reduction at -5 bars to 80% reduction at -15 bars. Thill, Schirman, and Appleby (67) investigating downy brome (Bromus tectorum L.) germination found it had 61% germination at 0 bars down to 10% germination at -15.6 bars. They found that at higher matrix potentials, germination was increased by warmer temperatures. In the three seedlots tested little variation in drought tolerance occurred implying that downy brome response to soil moisture should not vary much from year to year.

Blackshaw et al. (7) studied the influence of soil temperature and soil moisture on green foxtail [Setaria viridis (L.) Beauv.] establishment in wheat (Triticum aestivum) and found that soil moisture had a greater effect than soil temperature. At water potential of -6.5 bars, green foxtail germination was reduced to zero at 15, 25°C and to 8% at 20°C. At -7.8 and -15.3 bars there was no germination at all temperatures. Wheat had 100% germination from 0 to -15.3 bars water tension at 15, 20, and 25°C. In the field, when the soil was moist (0 to -4 bars) and warm (20 to 25°C) green foxtail emerged within a few days of wheat. However, when in dry (-4 to -6.5 bars) and cool (15 to 20°C) soil, green foxtail emerged 7 to 14 days after wheat. The time of emergence of green foxtail relative to the wheat was found to be critical to potential competition with the greatest yield decrease of wheat with earlier green foxtail emergence.

Depth of emergence varies with species, soil, and environmental conditions. Brecke and Duke (8) in a study of fall panicum germination found the maximum number of seedlings (39%) emerged in the field when the seed was placed 1.3 cm below the soil surface, 7% emerged from 5.1 cm. They concluded that fall panicum must be relatively close to the soil surface for maximum emergence. Alex (1), also studied fall panicum emergence and found that soil texture strongly influenced emergence. At 1 and 2 cm, emergence from a silt loam was twice as great as from a gravelly loam. At 5 cm the trend was reversed. Depth had a greater negative effect on emergence in the silty loam than in the gravelly loam. The explanation given was that soil moisture may have been more limiting near the surface and aeration greater in the gravelly loam than in silt loam.

Striegel and Boldt (63) found wild proso millet emerged from 0.1 to 13.6 cm. Anderson and McLaren (2) found the average depth for wild proso millet germination was 3.5 cm and maximum emergence depth was also 13.6 cm. This deepest emergence occurred on a sandy soil. Like corn, the first internode and the coleoptile of wild proso millet elongate during emergence, thus permitting the plant to germinate and emerge from deep in the soil.

CHAPTER 2

Materials and Methods

Seed Source

Panicum miliaceum seed was collected in October, 1981, in a corn field three miles southeast of Ault, Colorado. After shaking loose seed from mature panicles, the seed was cleaned in an air flow separator and stored at room temperature in unsealed plastic bags. Viability at collection was 100% and germination was 46%. In 1982 more seed was collected due to the exhaustion of the 1981 seed. The seed was collected from the same area and at the same stage of maturity except seeds were collected from the ground since it was more efficient. Seeds were 100% viable with 37% germination at collection. After approximately six weeks of dry storage, seeds from both years were 95-100% germinable.

Soil Preparation for Greenhouse Studies

Soil used was steam sterilized, air dried, and sieved through a 0.63 cm mesh screen.

Soil Water Holding Capacity Determination

Following the methods described by Klute[3] five sections of PVC pipe each 5 cm long and 3 cm in diameter were taped together to form a column which was filled with air dried soil. Three such columns were constructed. Water was added to each column until water came out from the base of the column indicating saturation. Water saturated columns were not disturbed for 24 hr. The three middle sections were separated from each column and the wet soil was removed and weighed. The soil sections were dried at 180 C for 24 hr and weighed again. The percent water needed for 100% field capacity for a given soil type and weight was determined from the formula:

$$\frac{\text{dry weight of soil}}{\text{wet weight-dry weight}} \times 100$$

Soil Temperature Effects on Emergence

The range and optimum temperature for P. miliaceum emergence was established using water temperature baths[4]. Eighty 10 by 10 cm square pots were filled with 625 g of air dried Nunn clay loam (43% sand, 25% silt, 32% clay, 1.7% O.M., pH 8.0) and 50 nondormant P. miliaceum seeds were planted at 0.6, 1.2, 2.5, or 5.0 cm in each pot. Each pot was placed inside another pot which had its drain holes

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[3]Black, C.A. 1965. Methods of Soil Analysis. Part 1. American Society of Agronomy, Inc. Publ. Madison, Wis. p. 273-278.

[4]ESCO, West Chester, PA

sealed with silicone sealant to prevent water from the temperature tanks from entering the pots. Sixteen (4 depths X 4 observations) pots were immersed to the soil level in a completely random design in constant temperature baths held at 15, 20, 25, 30, or 35 C. One hundred and twenty four mls of water were added to each pot to bring the soil to field capacity. Seedling emergence was recorded every day and moisture levels were maintained at field capacity as determined by pot weights. For the 20, 25, 30, and 35 C tanks the experiment lasted 10 days whereas the 15 C experiment lasted 17 days. Speed of germination was determined for each temperature using the coefficient of germination mathematical expression.[5]

$$C.G. = \frac{100\ (A_1 + A_2 + \ldots A_x)}{A_1T_1 + A_2T_2 + \ldots A_xT_x}$$

Where A = number of seeds germinating per day

T = time in days for count

Subscript = number of days

Since the temperature tanks could not be held at 40 or 10 C, two closed incubators were used. Four pots with 50 P. miliaceum seeds at 2 cm in the same soil and moisture level as the preceding experiments were placed in each incubator. The experiment lasted 2 and 4 weeks for 40 and 10 C, respectively.

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[5]Kotowski, K. 1926. Temperature relations to germination of vegetable seeds. Proc. of the Amer. Soc. of Hort. Sci. 23:176-184.

Germination Under Simulated Drought Conditions

Osmotic solutions of 0, -2, -4, -6, -8, -10, -12, and -14 bars were prepared using aqueous solutions of polyethylene glycol 6000 (Peg 6000). The amount of Peg 6000 needed for each osmotic potential was derived from the formula $\psi_s = -(1.18 \times 10^{-2})\ C - (1.18 \times 10^{-4})\ C^2 + (2.67 \times 10^{-4})\ CT + (8.39 \times 10^{-7})\ C^2\ T$ where C is the concentration of Peg 6000 in g/kg H_2O and T is the temperature in degrees celsius (44). The amounts of Peg 6000 used for the two experiments are shown in Table 1.

Table 1. Amounts of polyethylene glycol 6000 used to establish osmotic potentials.

Osmotic potential	T = 25 C Peg 6000 g/ml	T = 30 C Peg 6000 g/ml
0	0	0
- 2	120	128
- 4	178	188
- 6	202	234
- 8	262	273
-10	296	308
-12	326	339
-14	355	368

Fifty nondormant P. miliaceum seeds were placed on a blotter in a petri dish and 12 ml of osmotic solution were added. The covered petri dishes were incubated in the dark at 25 or 30 C in two separate experiments for 14 days. Every one or two days petri dishes were removed and germinated seeds counted and removed. Seeds were considered germinated with radicle extension of 1mm or more. Deionized water was added to resaturate the blotter when needed.

Emergence as Influenced by Different Levels of Soil Moisture

Six hundred and seventy five g of air dried Nunn clay loam soil were placed in 10 by 10 cm square pots lined with 10 by 30 cm plastic bags. Appropriate amounts of water were added for each moisture level: 100% field capacity (135 ml H_2O), 75% (101 ml), 50% (68 ml), and 25% (34 ml). For the 50 and 25% levels soil and water were mixed in a twin shell blender[6] for five minutes to achieve uniform wetting. For the higher two levels water was added directly to the pots. Fifty nondormant P. miliaceum seeds were planted at 2 cm in each pot, and the plastic bags were sealed approximately 15 cm above the soil surface to maintain moisture levels and allow room for plant growth. A total of sixteen pots (4 water levels and 4 observations) were arranged in a completely random design at a temperature of 25 C for three weeks. Pots were weighed, emergence recorded every two days, and water added when necessary to bring the soil to its respective moisture level as determined by pot weights. Pots required about 1 ml of water every four days. Using the same techniques outlined above, an additional

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[6]The Patterson-Kelly Co., Inc., East Stroudsburg, Pennsylvania.

experiment was set up with field capacity levels of 45, 40, 35, 30, 25, and 20% field capacity.

The Effects of Continuous Moisture (100% field capacity) vs Fluctuating Moisture (100-25% field capacity) on Emergence

Twenty four 10 by 10 cm square pots were filled with 675 g of air dried Nunn clay loam soil and 50 nondormant P. miliaceum seeds were sown at 1, 2, and 4 cm. Soil in all pots was brought to field capacity initially with 135 ml of water. Pots were arranged in a completely random design on a greenhouse bench. Soil in one-half of the pots was maintained at 100% field capacity by placing them in shallow dishes filled with 2 cm of water. Soil in the remaining pots was allowed to dry down to 25% field capacity confirmed by weighing and then water added to bring the soil back to 100% field capacity. This wet/dry cycle occurred four times during the two weeks of the experiment. Emergence and pot weights were checked daily. Soil temperature ranged from 25 to 35 C.

The Effect of Depth of Planting on Emergence

Greenhouse. Thirty eight hundred g of air dried Thedalund loam (33% sand, 29% silt, 38% clay, 1.3% O.M., pH 7.8) was placed in 20.3 cm tall styrofoam pots and 100 nondormant P. miliaceum seeds were placed into each pot at soil depths of either 0, 1, 2, 4, 6, 8, 10, 14, or 18 cm with four replicate pots per depth. Thirteen hundred ml of water were added to each pot to bring the soil to field capacity. This moisture level was maintained throughout the four weeks of the experiment by monitoring pot weights. Pots were arranged in a completely random

design on a greenhouse bench. Soil temperature range was 22 to 25 C. Four weeks after the initial watering the number of emerged plants was counted in each pot.

Field. Experiments were conducted at two sites: at Ault, CO on a Thedalund loam and at the Colorado State University Bay Farm on a Nunn clay loam. At Ault, May 25, 1983, 21 holes 10.5 cm in diameter were made using a golf hole corer[7], and 50 nondormant P. miliaceum seeds were placed at depths of 2, 4, 6, 8, 10, 12, and 14 cm. Holes were filled with soil, from the same field, that had been steam sterilized to kill existing P. miliaceum seeds. Plot design was a randomized block with three replicates. Soil temperature and moisture were monitored and recorded (Figure 11). On June 22, 1983, emerged seedlings were totaled for each depth. At the Bay Farm, July 25, 1983, 28 holes were dug and 50 nondormant P. mileaceum seeds were placed at 2, 4, 6, 8, 10, 14, or 18 cm of depth. Plot design was a randomized block with four replicates. On August 24, 1983, emerged seedlings were totaled for each depth.

The Effects of Depth and Duration of Seed Burial on Dormancy and Seed Viability

Two hundred seeds that had been collected in 1981 were placed into 8 cm square, 113 mesh polypropylene screen cloth packets[8]. Treatments involving burial duration and seed depth were established in a split plot with 4 blocks at Colorado State University Bay Farm on a Nunn

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[7]PAR-Aide Corp.

[8]Tetko, Inc., Elmsford, N.Y.

clay loam. Total plot size was 2 by 4 meters with four 60 by 120 cm blocks. In each main block (time) 8 holes 2.5 cm in diameter were dug October 21, 1981. Within each hole (subplot of depth factor) one seed packet was placed at 5, 10, and 30 cm and recovered with soil. Plots were undisturbed and kept weed free by surface hoeing or applications of glyphosate. Plots received only incident rainfall as shown in Table 2.

One, 4, 6, 8, 12, 16, 19, and 21 months after burial one subplot containing seed packets at the three depths was exhumed in each of the four blocks. Recovered seed was analyzed immediately or frozen at -20 C to maintain dormancy levels and viability, for future analysis.

Partitioning recovered seed populations into model components. To analyze and interpret buried seed persistence, the model described by Schafer and Chilcote (56) was used. In this model the parameters of persistence and depletion are described by the equation $S = P_{ex} + P_{end} + D_g + D_n$ (Chapter 1, p. 21). D_g was assessed by counting and removing germinated seeds. To determine P_{ex} the remaining seeds were subjected to a germination test. This involved placing 50-100/seeds between two water saturated 8.5 cm diameter blotting paper discs in 9.5 cm diameter glass petri dishes. Petri dishes were wrapped in aluminum foil to retard moisture loss. The dishes were put in a dark growth chamber set at 30 C for two weeks. Every two days the dishes were removed, germinated seeds counted and removed, and water was added to resaturate the blotting paper discs. Seeds were considered germinated when the radicle extended 1 mm or more. The number of seeds that germinated in this time period made up the P_{ex} (enforced dormancy) component. Seeds remaining

Table 2. Monthly precipitation, Colorado State University Weather Station.

Year	Month	Precipitation (inches)
1981	October	0.75
	November	0.10
	December	0.65
		1.50 total
1982	January	0.25
	February	0.05
	March	0.73
	April	0.37
	May	5.14
	June	4.34
	July	4.86
	August	0.45
	September	3.51
	October	0.74
	November	0.48
	December	0.41
		21.33 total
1983	January	0.01
	February	0.04
	March	2.89
	April	4.10
	May	3.21
	June	3.52
	July	1.57
		15.34 total

were made up of P_{end} and D_n seed fractions. To separate the two, the remaining nongerminated seeds were removed and stored dry at room temperature for two weeks. Seeds were then resubjected to the standard germination test for an additional week. The seeds that germinated were placed in the P_{end} component. To separate D_n from the rest of the still nongerminated seed a tetrazolium acid stain test was performed. Caryopsis were split longitudinally and one half placed in a 0.1% tetrazolium chloride solution for three hours. Pink staining of the embryo indicated viability.

The Effects of Overwintering of Seed on the Soil Surface

Experiments were conducted on the CSU Bay Farm. The 1981-1982 experiment used seed collected in 1981 and the 1982-1983 experiment used seed collected in 1982. One hundred seeds were placed inside 8 cm square 113 mesh polypropylene screen cloth packets. These seed packets were wrapped in 0.63 cm mesh hardware cloth to protect the seed from birds or rodents. On November 8 in 1981 and 1982, a total of 20 wrapped seed packets were placed on the bare surface of a Nunn clay loam in a completely random design within a 2 by 4 meter area. Five seed packets were removed at each of four exposure periods which were different in the two years (Table 3). Recovered seed were then tested and partitioned into the components previously described.

Panicum miliaceum Induction of Dormancy

In order to determine if cold moist storage could induce dormancy one hundred nondormant P. miliaceum seeds were placed in 8 cm square nylon mesh packets. Sixteen packets were arranged in a 50 by 34 by 10

Figure 1. Schematic diagram of procedures used to partition weed seed recovered from the soil into components of persistence and depletion.

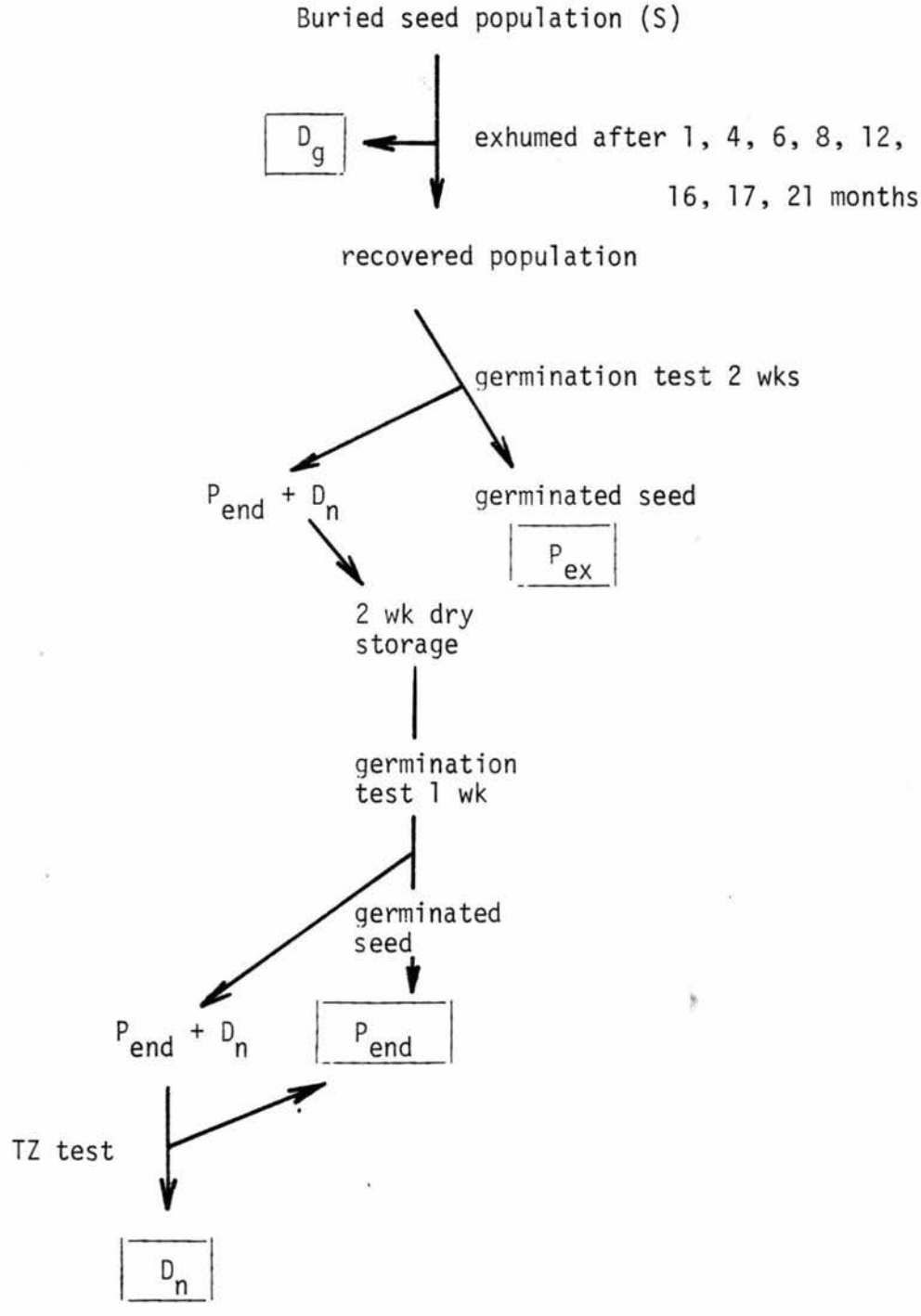

Table 3. Effects of overwintering of seed on the soil surface seed recovery times for the two experiments.

Experiment initiated	Treatments of length of seed exposure (months)			
November, 1981	1	2	3	5
November, 1982	1	3	5	7

cm deep metal flat and a 7-cm deep moist peat/vermiculite mix was added to cover the seeds. The flat was stored in a constant temperature cold room set at 8 C and the peat/vermiculite mix was kept moist. After 2, 4, 6, or 8 weeks or storage, four packets were removed and the standard germination tests performed.

Panicum miliaceum Emergence Patterns in the Field

The 1982 experiment was located at Ault, CO on a Thedalund loam with P. miliaceum seed populations in excess of 28 million seeds per acre at 15.2 cm as determined by soil sampling. Four soil cores 2.5 cm diameter, 15.2 cm deep were taken in each treatment plot. Soil samples from each plot were combined, air dried, and a 100 g subsample removed. The sample was placed in a No. 18 brass sieve[9] and washed with tap water to remove all silt, clay, and fine sand. Remaining seeds were counted and seeds per acre determined from the formula:

$$\frac{\text{\# of seeds}}{100\text{ g soil}} \times \frac{454\text{ g}}{1\text{b}} \times \frac{2 \times 10^6\text{ 1b}}{\text{Acre}}$$

[9]U.S.A. standard testing sieve, W.S. Tyler, Inc., Mentor, Ohio.

Plot size was 1 by 1.5 meters with a 0.3 by 0.6 meter subsample observed. Plot design was a randomized block with ten replicates. The objective was to study seedling emergence with and without intraspecific competition. In the latter case, emerged seedlings were counted and removed every 3 to 7 days until emergence ceased in late August. For intraspecific competition emerged seedlings were counted, recorded, and labeled with a small spot of white paint to avoid duplicate counting. A center pivot sprinkler applied 2.5 cm of water per week.

The plots for the 1983 experiment were located in Ault and Severance, CO. Plot dimensions and design were the same as those used in the 1982 study. In Ault, four treatments were used with and without intraspecific competition and two levels of soil disturbance. The soil was disturbed two and four times on 6/11, 7/15, and 6/8, 6/18, 7/2, and 7/12, respectively. Disturbance was accomplished by hoeing to a depth to 8 cm.

In Severance plots were established on a Nelson fine sandy loam (57% sand, 22% silt, 21% clay, 1.2% O.M., pH 7.6) in a corn silage field. P. miliaceum seed populations were 15.4 million seeds per acre at 15.2 cm. Treatments were with and without intraspecific competition and with and without intraspecific competition but with corn present in the plots. Plots were furrow irrigated.

For both locations continuous soil temperatures were recorded with a soil temperature disc recorder[10] at a depth of 8 cm. Soil moisture

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[10]Model 1000, Dial Thermometer Division, Marshalltown Manufacturing, Inc., Marshalltown, Iowa, U.S.A.

samples were taken every 3 to 6 days and by sampling 0 to 8 cm and soil moisture content was determined by weighing before and after oven drying.

CHAPTER 3

Results and Discussion

Temperature and Seed Depth on Emergence

As a reminder the 40 and 10 C temperature treatments were conducted in a growth chamber at one depth (2 cm), and rate of germination was not recorded. All other treatments were conducted in the water baths. Greatest emergence (98.5%) occurred at 40 C (Table 4).

Table 4. Total emergence and speed of germination averaged over the four depths.

	Temperature C						
	40	35	30	25	20	15	10
% germination	98.5	87.9	66.9	64.9	54.5	49.3	45.5
Coefficient of germination	-	2.0	1.6	1.4	0.8	0.7	-

As temperature dropped emergence decreased to 45.5% at 10 C. The coefficient of germination, a measure of rate, was highest at 35 C (could not be calculated at 40 C) and decreased with temperature. Although the coefficient of germination was not recorded for the 40 and 10 C treatments, emergence took 3 and 40 days, respectively, for 50% or greater of the total emergence to occur. Although experimental design did not permit statistical comparison between temperatures there was a direct correlation between temperature and its effect on percent and rate of emergence. For all temperatures, depth did not have an effect on total emergence (Table 5). Germination rate was faster at 0.6 and 1.2 cm than at 2.5 and 5.0 cm of seed depth at all temperatures except 20 C. The reason for this is not known.

Germination Under Simulated Drought

The greatest reduction of germination (30%) for both temperatures occurred between the control (no water stress) and -2 bars (Table 6). For both temperatures germination was reduced as moisture stress increased. The exception is the increase of % germination from -4 to -6 bars at 25 C. However, the difference was not significant. Germination essentially ceased from -10 to -14 bars at 25 C but continued to -14 bars at 30 C. Germination was greater, at 30 C, at tension levels from 0 to -10 bars. Differences in germination at 0 tension between the two temperatures (22%) is surprising since in the previous experiment germination differences between 30 and 25 C was only 2% (Table 4). Differences between 35 and 25 C (23%) in this experiment were more like the differences found here. A possible reason for the differences

Table 5. Effect of temperature and seed depth on percent germination and rate of germination[a].

Temperature C	Seed depth (mm)	% Germination	Coefficient of Germination
35	6.35	91.5 a	2.3 a
	12.7	86.0 a	2.4 a
	25.4	84.0 a	1.9 b
	50.8	90.0 a	1.3 c
30	6.35	68.0 ab	1.8 a
	12.7	66.0 ab	1.7 a
	25.4	62.0 b	1.5 b
	50.8	71.4 a	1.4 b
25	6.35	64.5 ab	1.5 a
	12.7	63.5 ab	1.5 a
	25.4	61.5 b	1.2 b
	50.8	70.0 a	1.2 b
20	6.35	54.0 ab	1.0 a
	12.7	51.5 b	0.9 a
	25.4	51.0 b	0.8 a
	50.8	61.5 a	0.7 a
15	6.35	50.0 ab	0.8 a
	12.7	44.5 b	0.8 ab
	25.4	47.5 ab	0.7 b
	50.8	55.0 a	0.6 c

[a]Means within a column for % germination or coefficient of germination and within each temperature followed by the same letter are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

Table 6. Percent germination of wild proso millet under moisture stress induced by solutions of polyethylene glycol 6000.[a]

Water potential	Percent germination at	
Bars	25 C	30 C
0	76.5 a	98.5 a
- 2	44.0 b	69.5 b
- 4	18.0 c	54.5 bc
- 6	27.5 c	46.0 bc
- 8	2.0 d	40.5 c
-10	0 d	36.5 c
-12	0 d	4.0 d
-14	0.3 d	1.5 d

[a]Means within a column for temperature followed by the same letter are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

could be in seed stock since a period of one year occurred between the two experiments. Also in looking at the replicated data (Appendix II) one rep was only 62% whereas the other three were 80, 82, and 82% germination resulting in a lower average.

Although the purpose of this experiment was not to observe the effects of temperature on germination under moisture stress the results indicate that increasing temperatures increase wild proso millet's ability to germinate under greater moisture stress. However, to properly answer this question an experiment with a full range of temperatures from 10 to 40 C and various levels of moisture stress should be performed. In the field this phenomenon would be important in predicting wild proso millet emergence because both temperature and moisture must be taken into consideration. Caution must be observed when applying simulated moisture stress data to field situations. Although radicle emergence was noted at high moisture stress levels, further growth was reduced especially at levels above -8 bars hence emergence in the field under such conditions cannot be predicted with confidence.

Germination as Influenced by Different Levels of Soil Moisture

The greatest emergence was at 50% field capacity (Table 7). Higher moisture levels did not differ greatly but were significantly different from 50%. The differences observed could be due to slightly reduced oxygen levels on the higher moisture levels. At 25% emergence was reduced to 3%. To find the break between 50 and 25% field capacity and to find the minimum moisture level for emergence an additional experiment was conducted.

Table 7. Effects of soil moisture level on emergence.[a]

% field capacity	% germination
100	87 b
75	90 b
50	98.5 a
25	3 c

[a]Means within the column for % germination followed by the same letter are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

In this experiment greatest emergence occurred at 45, 40, and 35% field capacity (Table 8). Thus, wild proso millet is capable of 87% or higher germination in the soil moisture range of 100 - 35% field capacity. At 30% emergence dropped to 59.5 % and from 30 to 25% field capacity, the critical moisture level, emergence decreased to 8.5%. No emergence occurred at 20%. How these soil moisture levels and osmotic potentials from polyethylene glycol compare in terms of moisture availability is not known so no comparisons between these two experiments will be attempted.

Table 8. Effects of soil moisture level on emergence.[a]

% field capacity	% germination
45	94.5 a
40	97 a
35	93.5 a
30	59.5 b
25	8.5 c
20	0 c

[a]Means within the column for % germination followed by the same letter are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

The Effect of Continuous vs Fluctuating Soil Moisture on Emergence

The effect of depth on emergence was not significant at both moisture levels (Table 9). Moisture did affect total average emergence when the two levels were compared. Wetting and drying of the soil must encourage seed germination of wild proso millet probably by weakening of the lemma and palea. Wild proso millet seeds are not hard but do seem to restrict radicle emergence. In a separate observation when seed coats were removed, germination was greater and quicker than when seed coats were intact. However, this was not confirmed by an experiment. Another possible explanation is the soil with fluctuating moisture levels will have oxygen levels higher than the constantly wet soil.

Table 9. Percent emergence as influenced by moisture level and seed depth.[a]

Seed depth (cm)	100% field capacity	100/25% field capacity
1	85.5 b	98.0 a
2	94.5 ab	99.5 a
4	82.5 b	98.5 a
Total average	87.5 b	98.7 a

[a]All means followed by the same letter are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

Depth of Emergence

In the pot studies, emergence showed no general trends with respect to depth. Between 1 and 10 cm emergence was from 68.5 to 95% (Table 10).

At 14 cm of depth, emergence was drastically reduced with only 4.8% emerging. At 18 cm there was no emergence. Examination of the seeds showed that they had germinated and attempted, but failed to emerge. Thirty-one percent of the seeds on the surface germinated and this number is artificially high because some seeds were washed into soil cracks during watering and covered by soil. Seeds placed between 1 and 10 cm emerged the second week all within a few days of each other with the shallowly placed seeds emerging first. Seedling emergence from 14 cm occurred after 3 weeks.

Table 10. Percent emergence as influenced by seed depth.[a]

depth (cm)	% emergence
0	31 d
1	74.3 bc
2	68.5 c
4	78.5 bc
6	86.3 ab
8	95 a
10	83.8 abc
14	4.8 e
18	0 f

[a]Means followed by the same letter are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

Emergence results for both field sites were variable. At Ault, greatest emergence occurred between 2 and 8 cm (Table 11), however, the only significant differences were between emergence at 2 cm and 10, 12, and 14 cm. All other comparisons were identical. At the Bay Farm, the greatest emergence was from 2, 4, and 6 cm with 29.5, 37.5, and 20%, respectively (Table 11). Emergence decreased to 4.5 and 2% at 8 and 10 cm and no emergence was recorded at 14 and 18 cm. Total emergence and maximum depth of emergence for this site was less than that at Ault. The most probable cause was moisture availability. Soil moisture at Ault was high (Figure 11, page 84) whereas at the Bay Farm in August plots received less than 2 inches of precipitation (Figure 2).

Table 11. Percent emergence as influenced by seed depth at two field sites.[a]

Depth (cm)	% emergence	
	Ault	Bay Farm
2	66.0 a	29.5 a
4	35.9 ab	37.5 a
6	47.9 ab	20.0 a
8	39.0 ab	4.5 b
10	11.4 b	2.0 b
12	9.9 b	---
14	10.4 b	0 b
18	---	0 b

[a]Means within a column for site followed by the same letter are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

The general conclusion is that total emergence is equal from 1 to 8 cm of seed depth. The amount of emergence depends on conditions present. Since experiments were designed to observe wild proso millet emergence from various depths environmental and soil conditions were not closely monitored. Because of this it is difficult to determine why differences in emergence between the studies were found. However, emergence was higher when moisture was not limiting, as in the pot experiments, than emergence under field conditions. Emergence up to 95% occurred in the pot experiments where the soil

Figure 2. Average daily air temperature and precipitation, Bay Farm, Colorado State University from July 25 to August 24, 1983.

Temperature
Precipitation
Temperature C
25
20
15
10
1.2
1.0
0.5
Precipitation (inches)
7/25
8/1
August
8/24

was maintained at 100% field capacity, whereas 66% emergence was the highest in the field studies. The greatest depth of emergence was from 14 cm. At the Bay Farm this was not the case with 10 cm being the greatest depth of emergence. Again this can be due to moisture or different soil type since the pot experiments and Ault plots had the same soil. Reduced germination of seeds on the soil surface was probably due to reduced availability of water. Additional studies should be designed to observe the interactions of moisture, temperature, soil types, and soil compaction on depth of emergence.

Depth and Duration of Seed Burial

Total seed depletion is composed of seeds germinated in situ (D_g) and nonviable seeds (D_n). The greatest seed depletion occurred at 5 cm where more than 76% of the population was lost after 21 months of burial (Figure 3).[11] Depletion rates for the 10 and 30 cm depths were 23.1 and 7.3%, respectively, after 21 months. The majority of seed loss for all depths occurred between 6 (April) and 12 (October) months after burial. From 12 to 21 months after burial, depletion rates remained constant (Appendix VI).

In situ germination (D_g) decreased with depth and was the major avenue of seed depletion at 5 and 10 cm (Figure 4). D_g was greatest 6 to 12 months after burial. In situ germination at 5 cm became greater than at the other depths after 8 months (Appendix VI). After 12 months it became difficult to differentiate between seeds germinated in situ and nonviable seeds because of decay of the radical

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[11] Experimental means and mean comparisons for all data in this section are presented in tabular form in Appendix VI and VII.

Figure 3. Percent total depletion ($D_g + D_n$) of Panicum miliaceum seed populations buried in the soil at 5, 10, and 30 cm over a period of 21 months. Experimental means and mean comparisons of data are presented in tabular form in appendices VI, VII.

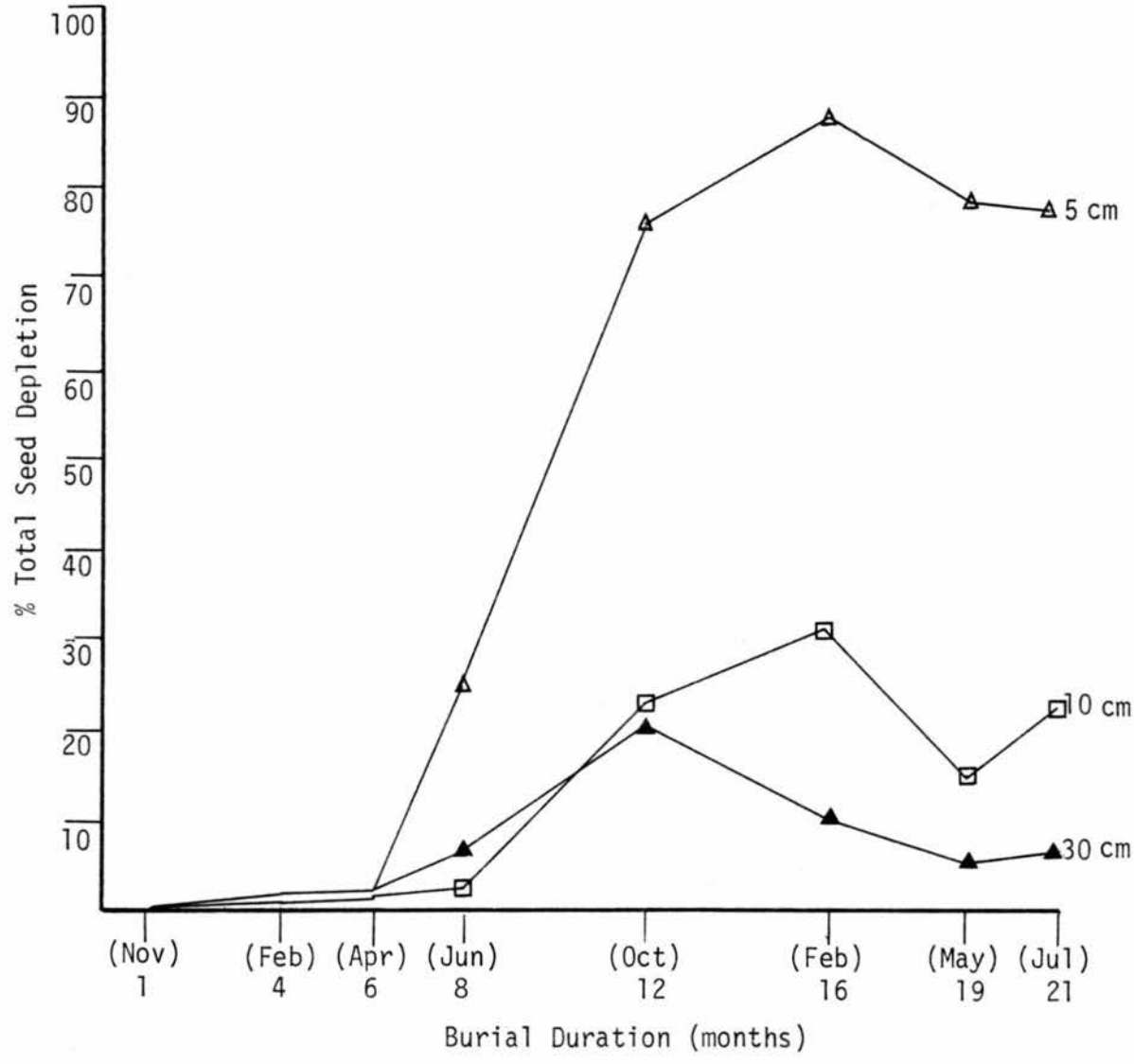
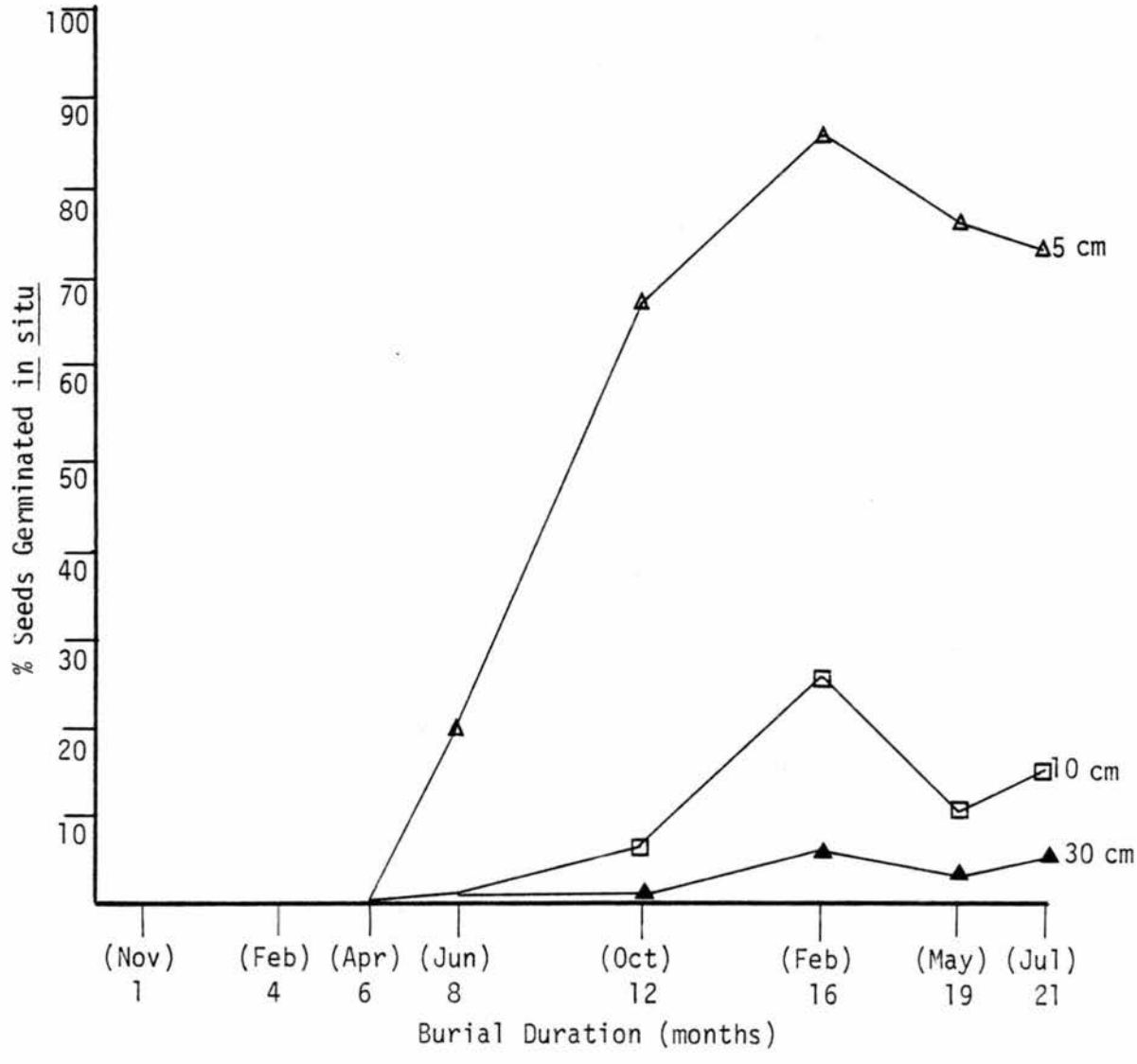

100
90
80
70
60
50
40
30
20
10
% Total Seed Depletion
5 cm
10 cm
30 cm
(Nov) 1
(Feb) 4
(Apr) 6
(Jun) 8
(Oct) 12
(Feb) 16
(May) 19
(Jul) 21
Burial Duration (months)

Figure 4. Percent *in situ* germination (D_g) of *Panicum miliaceum* seed populations buried in the soil at 5, 10, and 30 cm over a period of 21 months. Experimental means and mean comparisons of data are presented in tabular form in appendices VI, VII.


% Seeds Germinated in situ
100
90
80
70
60
50
40
30
20
10
5 cm
10 cm
30 cm
(Nov) 1
(Feb) 4
(Apr) 6
(Jun) 8
(Oct) 12
(Feb) 16
(May) 19
(Jul) 21
Burial Duration (months)

and plumule. Hence, the germination peak at 16 months is probably overestimated because in situ germination should not have increased from October to February. However, the last three time periods were not different within each depth (Appendix VI).

Seed death (D_n) was not affected by depth or duration of burial (Figure 5). Seed death began after one month of burial with an average of 1.6% dead seed for all depths and did not increase significantly over the 21 months except at 12 months (Appendix IV). The peak in seed death at this point is questionable since the amount of dead seed was less than the next three time periods. This could have been caused by confusing the dead seed with in situ germinated seed. Overall, seed depletion by loss of viability was not as important as in situ germination, with dead seed amounting to less than 8% after 21 months of burial.

Seeds buried at 30 and 10 cm were the most persistent with 92 and 77% of these seeds still viable after 21 months of burial, respectively (Figure 6). Seeds at 5 cm were the least persistent. Persistence was constant for all depths the first six months. Between 8 and 12 months (June to October) in situ germination took place and persistence was lost especially at 5 cm. After the first year populations stabilized and persistence did not change from 12 to 21 months at any depth. Low points in total persistence for each depth at 12 and 16 months are confusing because it is not logical for persistence to increase at 19 and 21 months, but statistically these numbers are the same and minor variation accounts for the effect (Appendix VI).

Figure 5. Percent viability loss (D_n) of Panicum miliaceum seed populations buried in the soil at 5, 10, and 30 cm over a period of 21 months. Experimental means and mean comparisons of data are presented in tabular form in appendices VI, VII.

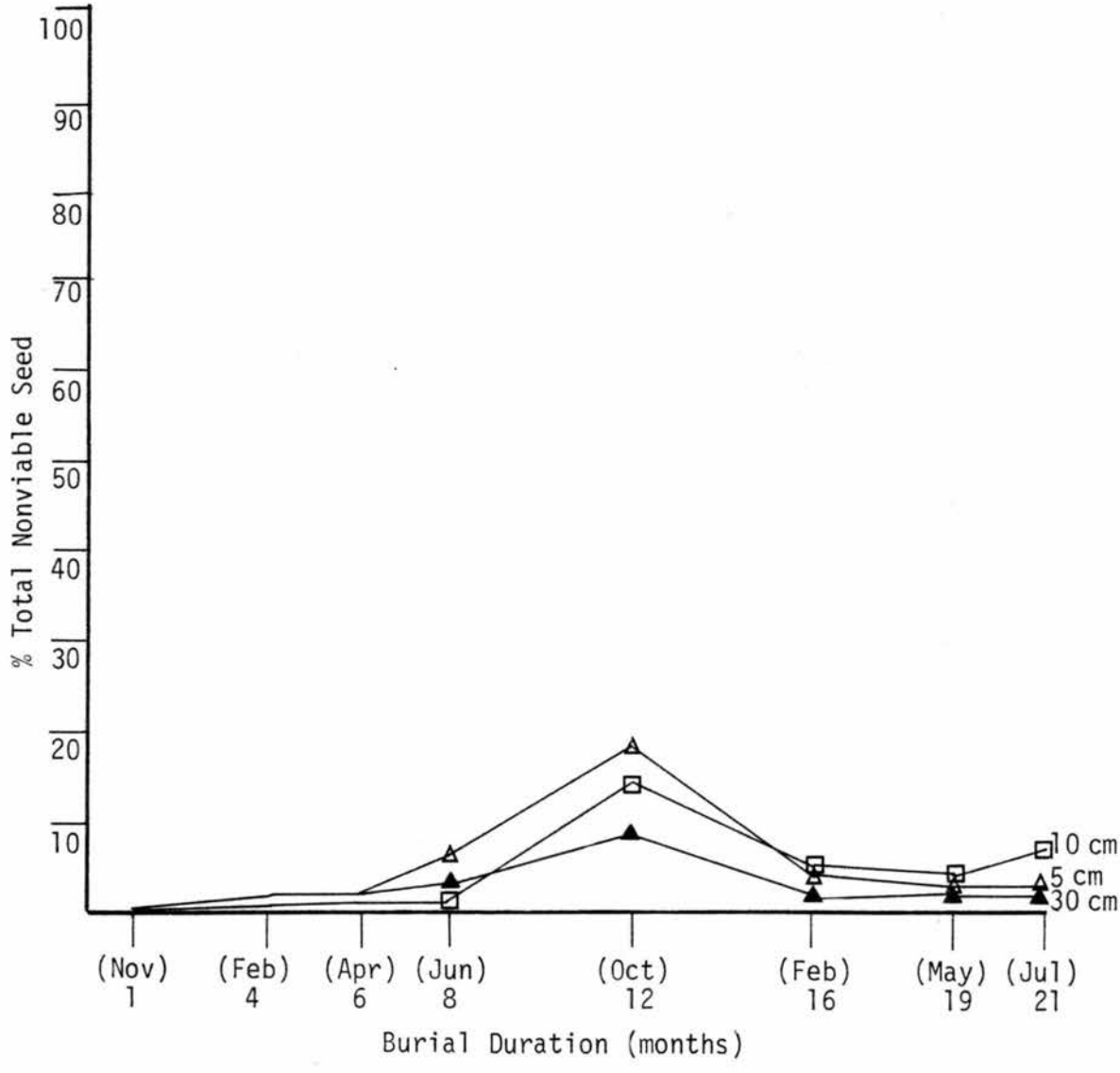
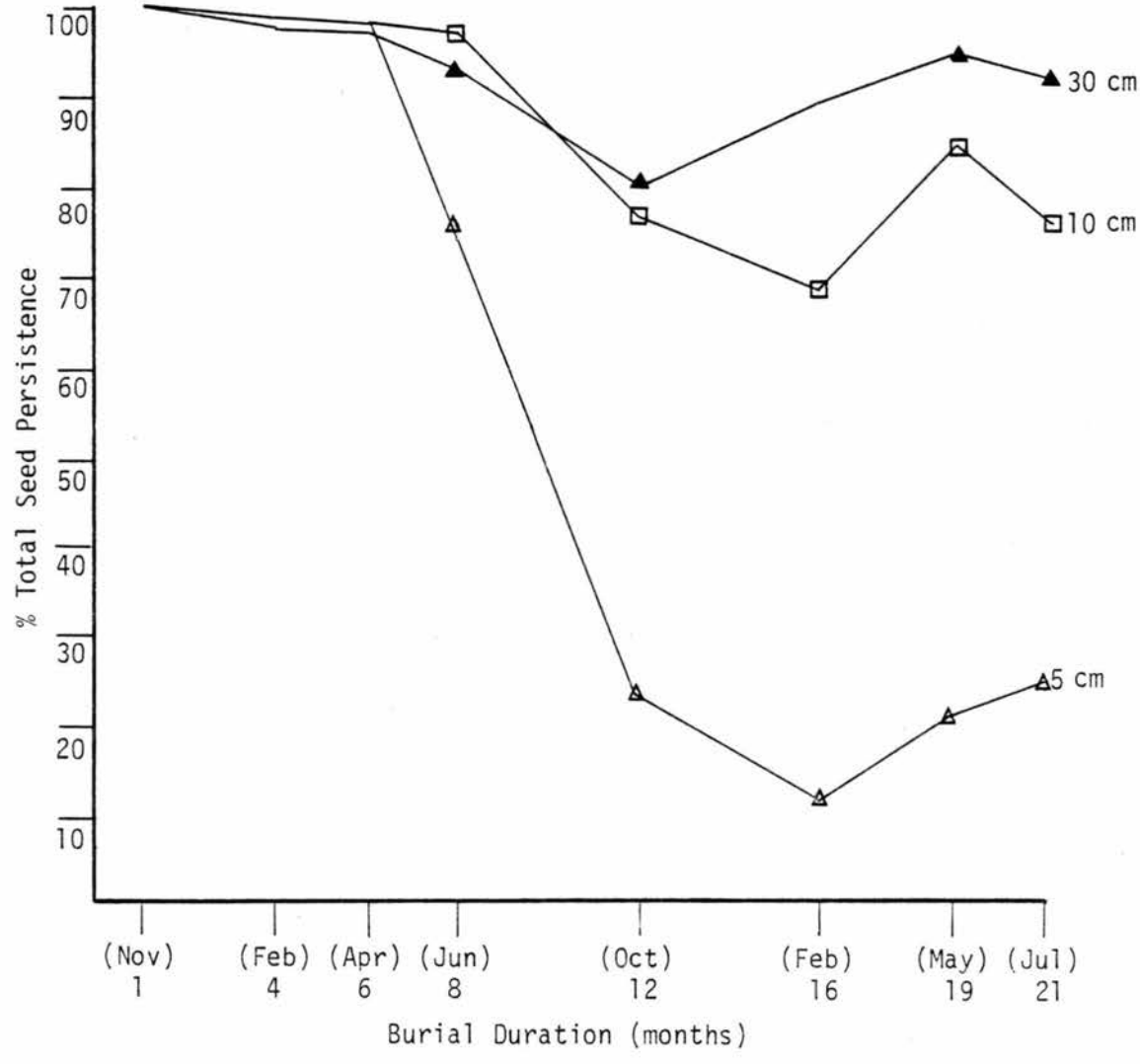

100
90
80
70
60
50
40
30
20
10
% Total Nonviable Seed
10 cm
5 cm
30 cm
(Nov) 1
(Feb) 4
(Apr) 6
(Jun) 8
(Oct) 12
(Feb) 16
(May) 19
(Jul) 21
Burial Duration (months)

Figure 6. Percent total persistence ($P_{ex} + P_{end}$) of Panicum miliaceum seed populations buried in the soil at 5, 10, and 30 cm over a period of 21 months. Experimental means and mean comparisons of data are presented in tabular form in appendices VI, VII.


100
90
80
70
60
50
40
30
20
10
% Total Seed Persistence
30 cm
10 cm
5 cm
(Nov) 1
(Feb) 4
(Apr) 6
(Jun) 8
(Oct) 12
(Feb) 16
(May) 19
(Jul) 21
Burial Duration (months)

The components of total seed persistence (P_{ex}, P_{end}), representing enforced and endogenous dormancy, are shown in Figures 7 and 8. At 5 cm the level of enforced dormancy is fairly constant through the 8 months (Figure 7). After 8 months the percentage of seeds exhibiting enforced dormancy dropped rapidly from 62% to 12%. This was due to loss through in situ germination, since enforced dormant seeds will germinate under the proper conditions. After 12 months the P_{ex} level did not change significantly (Appendix VI). In the 10 and 30 cm seed populations, P_{ex} increased from time 0 to 8 months, after 8 months it decreased at a rate similar to the 5 cm seeds. However, this drop was not due to in situ germination but to an increase in the endogenous dormant (P_{end}) seed fraction (Figure 8). From 12 to 21 months seeds with enforced dormancy (P_{ex}) increased and seeds with endogenous dormancy (P_{end}) decreased (Figures 7, 8). The level of endogenous dormant seeds at 5 cm increased slightly from 0 to 6 months then decreased sharply after 6 months. This represents endogenous dormant seeds losing dormancy and germinating in situ. P_{end} levels then remained stable up to 21 months. For all depths endogenous dormancy made up less than 10% of the total seed population after 21 months of burial.

In summary, seed depletion occurred over time up to 12 months after burial. From 12 to 21 months the seed depletion rate did not change at any one depth. Seed persistence increased with seed depth. Seeds at 5 cm exhibited the greatest seed loss over time (77%), due primarily to in situ germination (D_g). This is understandable since seeds at this depth are subjected to more favorable germination

Figure 7. Changes in percent exogenous dormancy (P_{ex}) of Panicum miliaceum seed populations buried at 5, 10, and 30 cm over a period of 21 months. Experimental means and mean comparisons of data are presented in tabular form in appendices VI, VII.

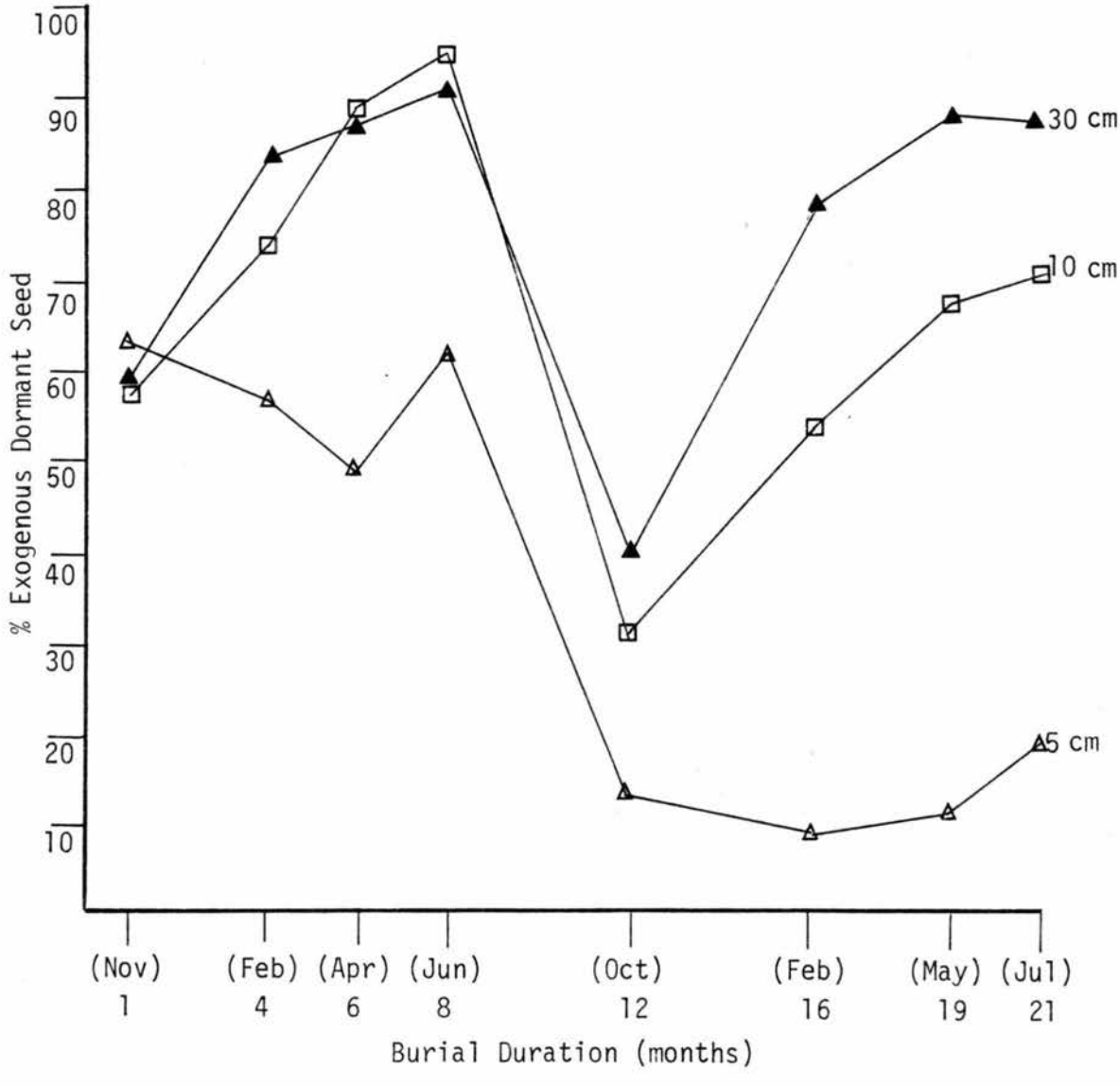
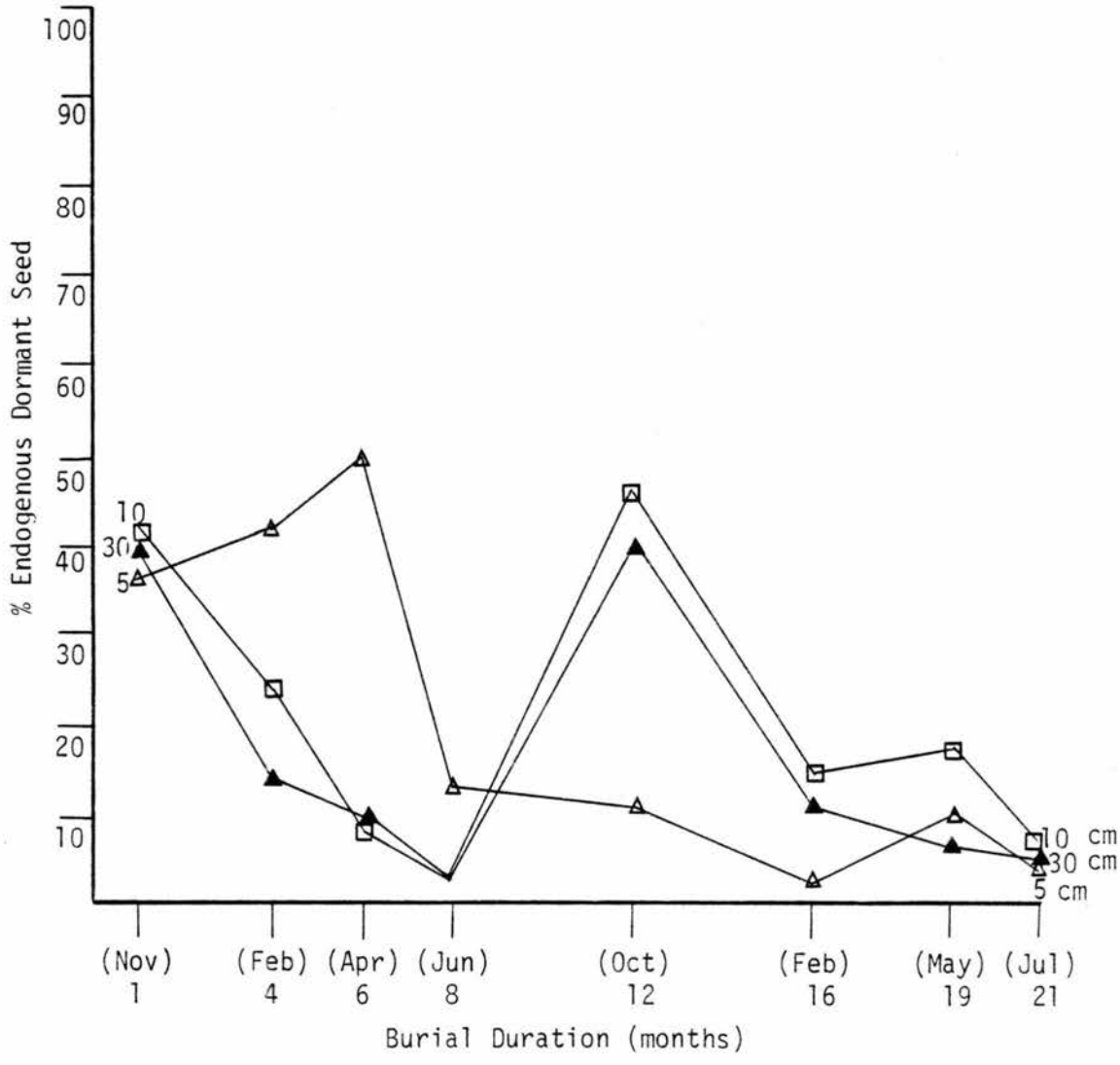

100
90
80
70
60
50
40
30
20
10
% Exogenous Dormant Seed
30 cm
10 cm
5 cm
(Nov) 1
(Feb) 4
(Apr) 6
(Jun) 8
(Oct) 12
(Feb) 16
(May) 19
(Jul) 21
Burial Duration (months)

Figure 8. Changes in endogenous dormancy (P_{end}) of Panicum miliaceum seed populations buried at 5, 10, and 30 cm over a period of 21 months. Experimental means and mean comparisons are presented in tabular form in appendices VI, VII.


% Endogenous Dormant Seed
100
90
80
70
60
50
40
30
20
10
10
30
5
10 cm
30 cm
5 cm
(Nov) 1
(Feb) 4
(Apr) 6
(Jun) 8
(Oct) 12
(Feb) 16
(May) 19
(Jul) 21
Burial Duration (months)

conditions than seeds at the deeper depths. Seed depletion at 10 and 30 cm after 21 months was 23 and 7%, respectively. Depletion was due primarily to in situ germination. Thus, seed death was not a major depletion route within 21 months of burial and depth of seed placement did not affect that rate. The trend that increasing soil depth favors seed persistence has been established in many studies (17, 21, 46, 53, 54, 60, 66). Seeds buried deep in the soil are subjected to cooler temperatures, reduced O_2, and generally less fluctuation of environmental conditions enhancing seed persistence (4, 5, 17, 18, 30).

Dormancy fluctuations occur and may also play a role in enhancing seed persistence at the 10 and 30 cm seed depths. Endogenous to enforced dormancy ($P_{end} \rightarrow P_{ex}$) occurred from 0 to 8 months encompassing late fall and winter. Loss of dormancy may have been caused by a cold, moist stratification. From 8 to 12 months this trend reversed as enforced goes back to endogenous dormancy ($P_{ex} \rightarrow P_{end}$). This is probably due to one or more germination factors such as water or oxygen being limited during spring and summer and inducing dormancy. Again, from 12 to 16 months $P_{end} \rightarrow P_{ex}$ occurs over fall and winter. During the summer (19-21 months) seeds remained predominantly in the enforced dormancy state.

These results show that wild proso millet is much more persistent in Colorado soils than in Wisconsin where a burial study indicated that more than 50% of seeds at 25 cm were depleted after 12 months (39). Differences found are probably due to variations in soil and climatic conditions between Colorado and Wisconsin, but to prove this additional studies are required.

Limitations to this study were in separating the components of depletion. Separation of seeds that had germinated *in situ* and nonviable seeds was a problem because of decay of seed germination structures, hence this model is best suited for short term seed studies. In order to use *in situ* germination as a parameter of depletion in relation to a natural buried seed population an important assumption must be made. Germination below the maximum depth of emergence results in the elimination of that seed as a reproductive unit. Seeds that germinated at 30 cm fall into this category since 30 cm is below the maximum depth of emergence. In nature seeds that germinate at 5 and 10 cm of depth will probably produce a seedling. Thus in order for *in situ* germination at these depths to be considered a parameter of depletion it must be assumed that any emerged seedlings are controlled in order to prevent additional seed production.

The Effects of Overwintering of Seed on the Surface.

In the 1981-82 experiment seeds went from 46% initially, to 98.2% enforced dormancy (P_{ex}) after one month on the soil surface (Table 12). The next four months P_{ex} remained essentially static decreasing to 90.5% after 5 months. Endogenous dormancy (P_{end}) decreased from 54% to 1.5% after one month and increased to 9.1% after 5 months. Nonviable seed (D_n) was less than 0.5% over 5 months. No seeds were lost by *in situ* germination (D_g).

Table 12. Components of seed persistence and depletion as influenced by exposure of populations on the soil surface in two subsequent winters.[a]

Year/month	Months of seed exposure	Components of Population, Depletion, and Persistence			
		P_{ex}	P_{end}	D_n	D_g
1981-1982					
Nov[b]	0	46	54	0	0
Dec	1	98.2 a	1.6 a	0.2 a	0
Jan	2	97.5 a	2.4 a	0.1 a	0
Feb	3	96.2 a	3.3 a	0.5 a	0
Apr	5	90.5 b	9.1 b	0.4 a	0
1982-1983					
Nov[b]	0	37	63	0	0
Dec	1	32.2 b	66 b	1.8 b	0
Feb	3	61.6 a	33.9 a	4.5 b	0
Apr	5	18 b	62.6 b	19.4 a	0
Jun	7	24.2 b	70.8 b	3.8 b	1.2

[a]Means within a component row and year followed by the same letter are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

[b]Initial seed status before seed exposure.

Results for the 1982-83 experiment which utilized a different years seed source, were markedly different. Initially P_{ex} was 37% and after 1 month little change occurred. After 3 months P_{ex} increased to 61.6% then decreased again to 18 and 24% after 5 and 7 months, respectively (Table 12). P_{end} changed little after 1 month then decreased to 34% after 3 months. At 5 and 7 months P_{end} increased again to 63 and 71%, respectively. Seed death was slightly higher in this experiment with 3.8% dead after 7 months. The high D_n value reported at 5 months is probably due to failure of the tetrazolium acid test. In situ germination was only 1.2% after 7 months.

Results indicate that wild proso millet can survive quite well on the soil surface overwinter, losing less than 5% of the original seed population. Dormancy status of the viable seed in the spring, however, was different between the two studies with 9% endogenous dormant seed in 1982 and 63% in 1983. Results can be due to differences in seed used and/or differences in environmental conditions thus it is difficult to elicit reasons for observed differences.

One striking difference between the two years was total precipitation. In 1982-83 there was over twice as much precipitation than in 1981-82, in the months of November through April (Table 13). Dormancy fluctuations and subsequent greater dormancy (P_{end}) in April may be the result of increased metabolic activity in the imbibed seed. Temperatures for both studies fluctuated and were different at many points of time (Appendix VIII), but no influential

Table 13. Monthly precipitation.

Month	Precipitation (inches)	
	1981-82	1982-83
November	0.10	0.48
December	0.65	0.41
January	0.25	0.01
February	0.05	0.04
March	1.61	3.77
April	0.16	2.0
May		3.07
June	____	0.08
Total	2.82	9.86

pattern could be identified. The differences in seed source may be the most important factor involved. After only one month on the soil surface the differences between the two studies, representing different seed population, was large.

Dormancy Induction

Starting with nondormant seed after two weeks of cold (8 C) moist storage, 14.3% of the seeds became dormant (Table 14). After four weeks, seed dormancy increased to 30.5% and to 56% after six weeks. At eight weeks dormancy decreased slightly. Seed death was 1% after four weeks and 6% after eight weeks.

Table 14. The effects of cool[a] moist storage on seed status over a period of 2, 4, 6, and 8 weeks.[b]

Storage duration (weeks)	% of total		
	nondormant	dormant	nonviable
2	85.8 a	14.3 c	0.0 b
4	68.5 b	30.5 b	1.0 b
6	38.5 c	56.0 a	5.5 a
8	43.8 c	50.3 a	6.0 a

[a] 8 C.

[b] Means within each column of seed status followed by the same letter are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

These results show that dormancy can be induced by a cool moist storage. Whether this happens in the field is difficult to conclude because of conflicting results from the field experiments. In the depth and duration of seed burial experiments seeds at 10 and 30 cm lost dormancy during the cold months of November to February. In the previous section, seeds overwintering on the surface in the first years experiment also lost dormancy from February to April. Differences from the field and lab study are probably due to fluctuations of temperature and moisture in the field as compared to the constant moisture and 8 C temperature in this experiment.

These effects of environmental conditions on dormancy are biochemical in nature and beyond the scope of this investigation. Since seeds were constantly in the inbibed state and germination did not occur at this temperature, seeds went into a state of dormancy.

Seed death was high in this study as compared to the field studies. Six percent of the seeds were nonviable after only 8 weeks whereas in the field studies this rate was much smaller. Reasons for this again are probably due to the imbibed state of the seed. It is generally known that seeds remain viable for longer periods if they are dry (38).

Patterns of Emergence

Total emergence for the nine plots with intraspecific competition in Ault was 825 plants from May 25 to August 8, 1982 (Table 15). For the plots that had intraspecific competition removed almost five times as many plants emerged (4,111) in the same time period.

In 1983, plots again with intraspecific competition had the fewest emerged plants at 458 (total emergence for 5 plots) as compared to 1655 emerged plants in plots with intraspecific competition removed. The treatments of two and four cultivations resulted in 710 and 1524 plants, respectively (Table 15). Since these cultivations removed competing wild proso millet additional seedlings could emerge. However, the month between cultivations (Figure 14, page 90) for the two cultivation treatment was long enough for existing plants to become well established

Table 15. Total emergence of wild proso millet in Ault, CO in the period of May 27 to August 3, 1982 and May 25 to August 8, 1983 as influenced by intraspecific competition and cultivation.

Emergence conditions	Total emergence	
	1982[a]	1983[b]
1. + intraspecific competition	825	458
2. - intraspecific competition	4,111	1,655
3. 2 cultivations	-	710
4. 4 cultivations	-	1,524

[a]Total emergence represents sum of nine 0.3 by 0.6 meter plots.

[b]Total emergence represents sum of five 0.3 by 0.6 meter plots.

and reduce additional emergence as compared to those plots with no competition. Treatment 4 with four cultivations 10 to 12 days apart (Figure 15, page 92) did not give plants sufficient time to become well established. Thus, additional emergence was not reduced as much resulting in a total emergence of 1,524 close to total emergence of plots with no competition.

Total emergence in Severance was much less than in Ault (Table 16).

Table 16. Total emergence of wild proso millet in Severance, CO in the period of May 24 to August 3 as influenced by competition from corn and/or wild proso millet.

	Emergence conditions		Total emergence[a]
	Corn	Intraspecific competition	
1.	+	+	106
2.	+	-	118
3.	-	+	118
4.	-	-	274

[a]Total emergence represents sum of five 0.3 by 0.6 meter plots.

Treatment 4, which had no competition, had the greatest emergence. The other treatments which had one or more form of competition resulted in similar emergence. Possible reasons for less emergence for all treatments include the smaller initial seed population in Severance as compared to Ault (15.4 and 28 million seeds/acre/6 inch, respectively). Also, the presence of corn as a competitor reduced emergence. Although some plots contained no corn, neighboring corn plants bordered the plots and formed canopies over the plots by early July.

Emergence patterns varied with year, site, and treatment. In Ault, in 1982, emergence began May 27 with an initial emergence peak for both treatments (Figures 9 and 10). Then both experienced

Figure 9. The effects of intraspecific competition on emergence patterns of Panicum miliaceum from May 27 to August 3, 1982 in an Ault, Colorado field.

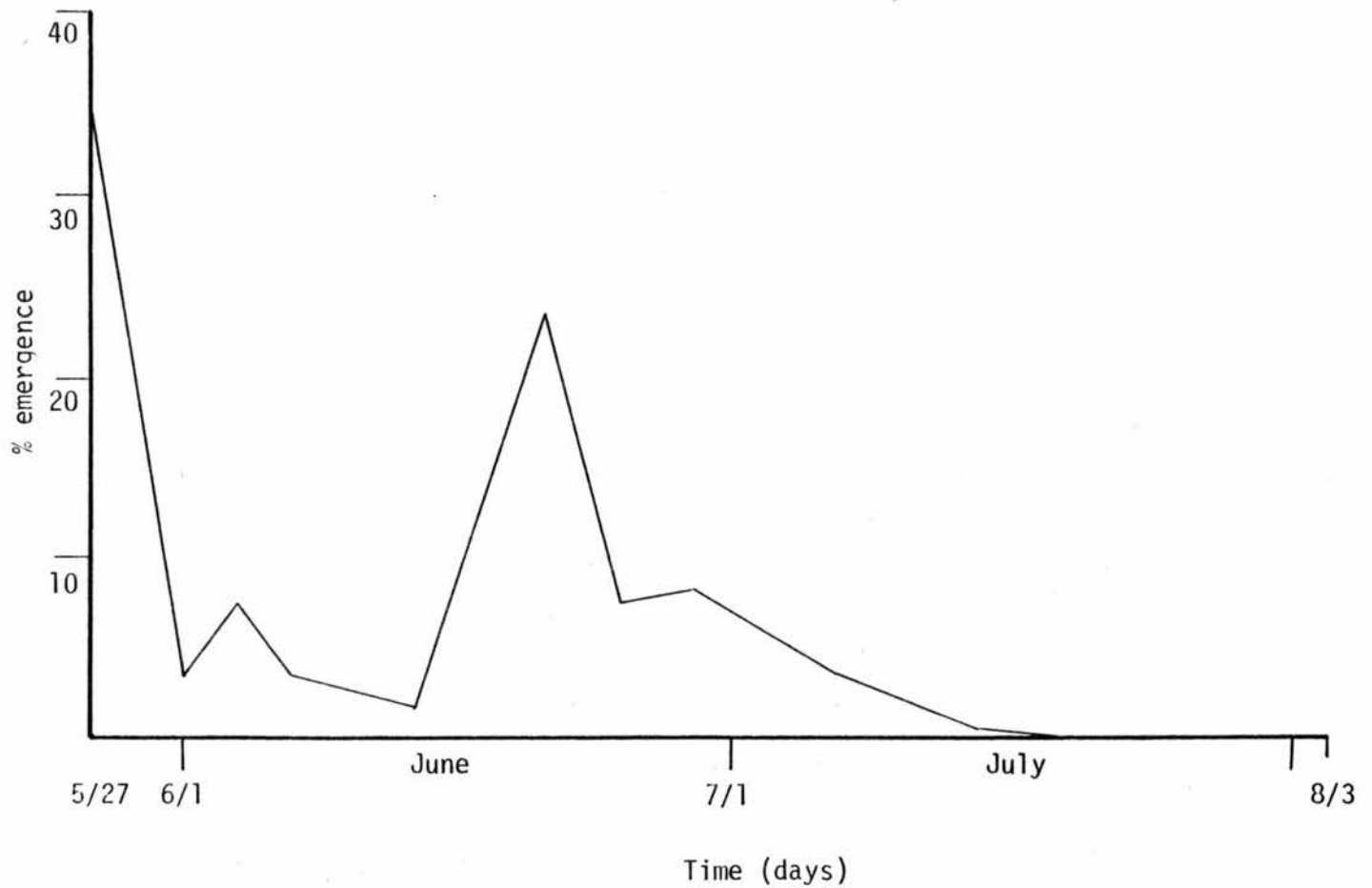
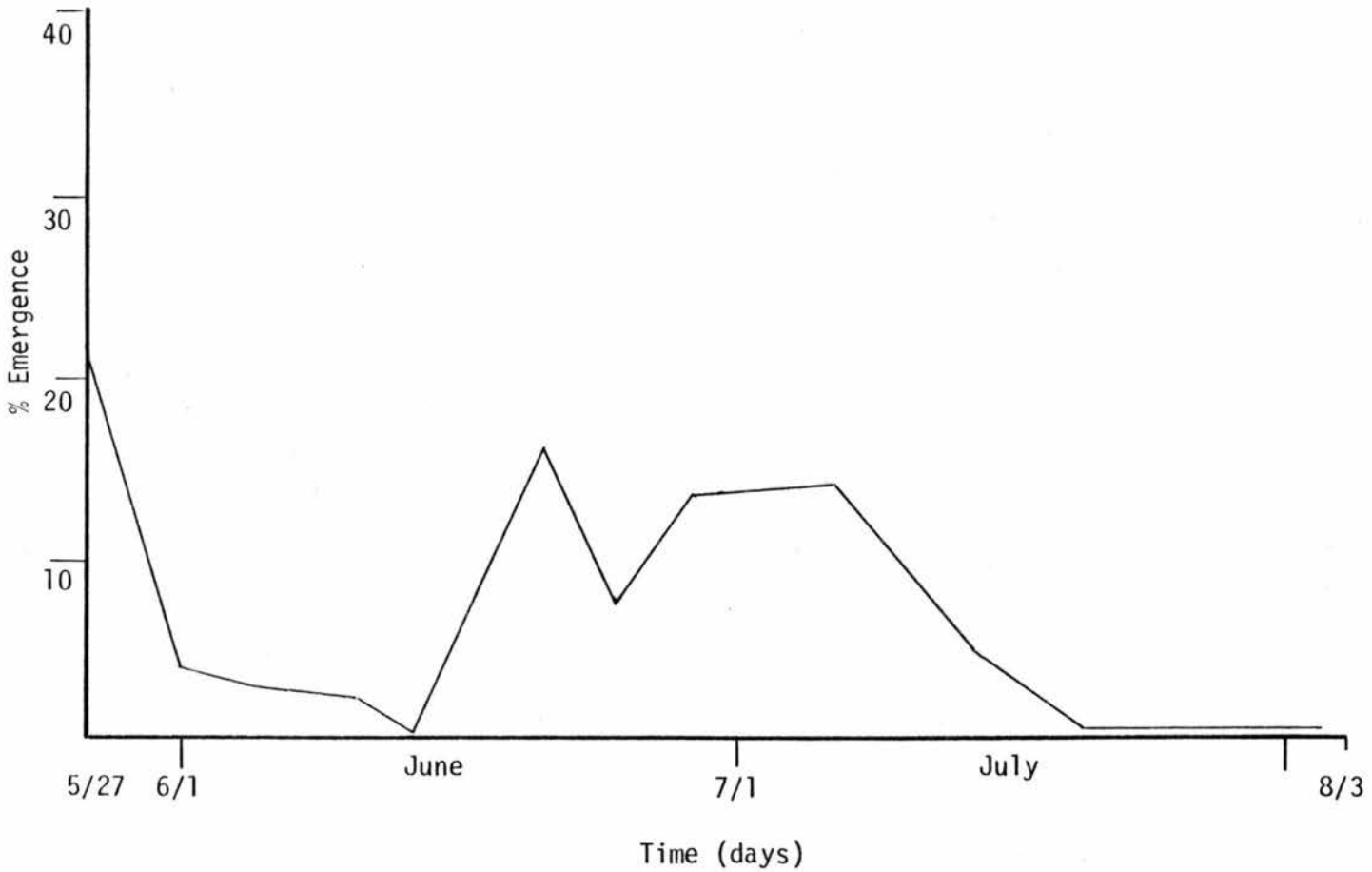

40
30
20
10
% emergence
5/27
6/1
June
7/1
July
8/3
Time (days)

Figure 10. The effects of intraspecific competition removal on emergence patterns of Panicum miliaceum from May 27 to August 3, 1982 in an Ault, Colorado field.


40
30
20
10
% Emergence
5/27
6/1
June
7/1
July
8/3
Time (days)

a sharp drop in emergence in June. Since detailed environmental conditions were not monitored for this experiment, exact reasons for this are not understood. Low temperatures are the most probable reason as soil moisture is usually still high early in the season. Both treatments showed another emergence peak in late June. The emergence in plots with intraspecific competition tapered off in late June and ceased in late July (Figure 9). Plots without competition had an extended emergence peak through mid-July and tapered off early August (Figure 10).

Patterns of emergence for Ault in 1983 are shown separately in Figures 12,13,14,15). Emergence began May 27 when the temperature ranged from 15 to 20 C and the soil moisture was 46% of field capacity. In plots with intraspecific competition the highest emergence (83.6%) occurred from May 25 to June 25 (Figure 12). There were two small emergence peaks in July and emergence ceased July 29. The environmental data (Figure 11) show that soil moisture was adequate during the period of maximum emergence with soil field capacities in the range of 40 to 50%. Temperature during this period fluctuated from 10 to 20 C reducing emergence when temperatures fell to 10 C. A warming trend corresponded with the largest emergence peak. At the end of June, soil moisture was low and emergence decreased. The two small emergence peaks in July corresponded with two distinct moisture peaks at the time of emergence. Temperature was not limiting with mean temperatures above 20 C. These emergence peaks were small because of emergence reduction from intraspecific competition.

Figure 11. Weather data for emergence plots in Ault, Colorado from May 25 to August 8, 1983. Upper line is the soil temperature at a depth of 8 cm and the lower line is soil moisture reported in terms of percent of the field capacity.

30
25
20
15
10
5
Mean Daily Temperatures (C)
60
40
20
% Field Capacity
5/25
6/1
June
7/1
July
8/1
8/8
Time (days)

Figure 12. The effects of intraspecific competition on emergence patterns of Panicum miliaceum from May 25 to August 8, 1983 in an Ault, Colorado field.

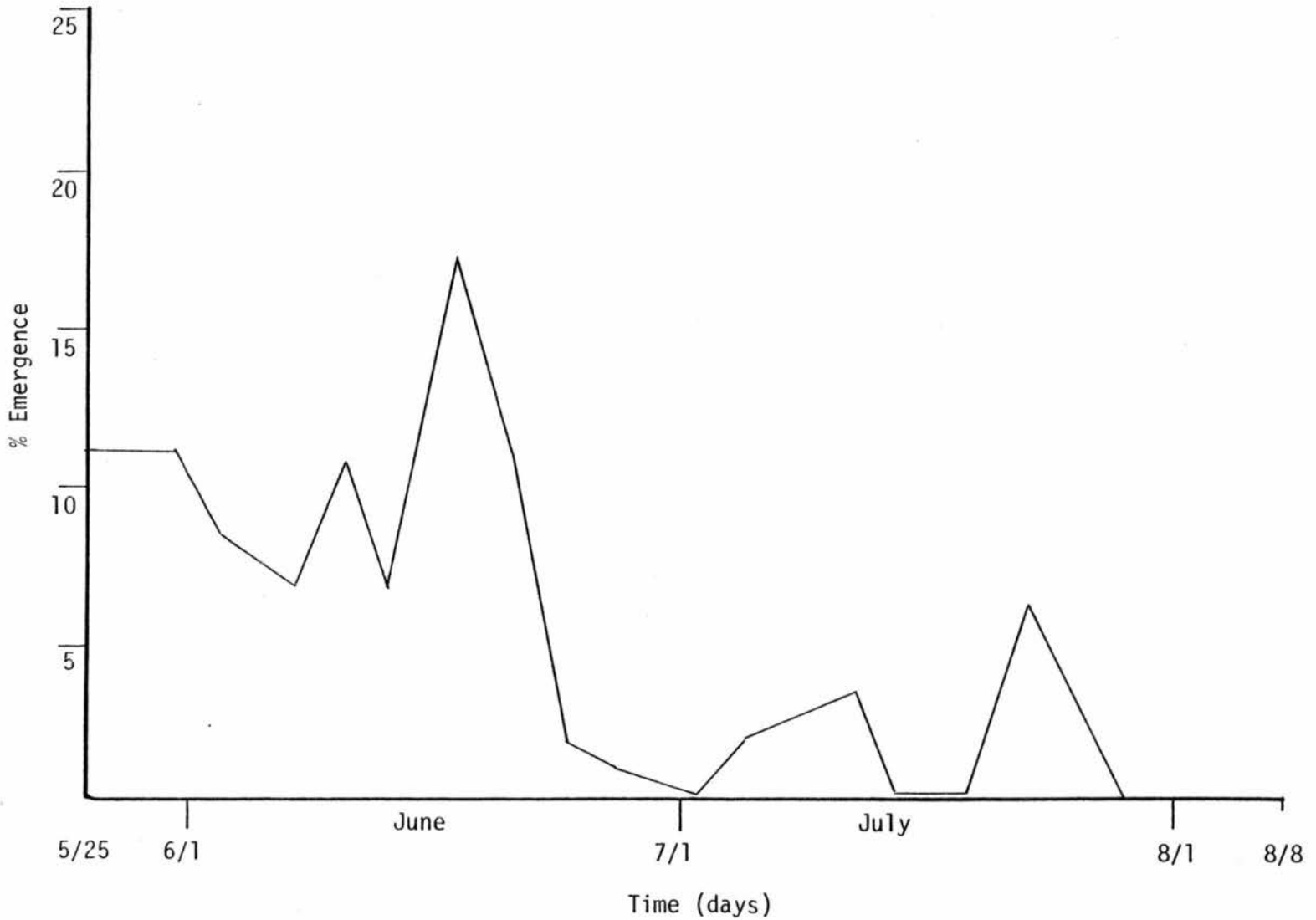

25
20
15
10
5
% Emergence
June
July
5/25
6/1
7/1
8/1
8/8
Time (days)

Figure 13. The effects of intraspecific competition removal on emergence patterns of Panicum miliaceum from May 25 to August 8, 1983 in an Ault, Colorado field.

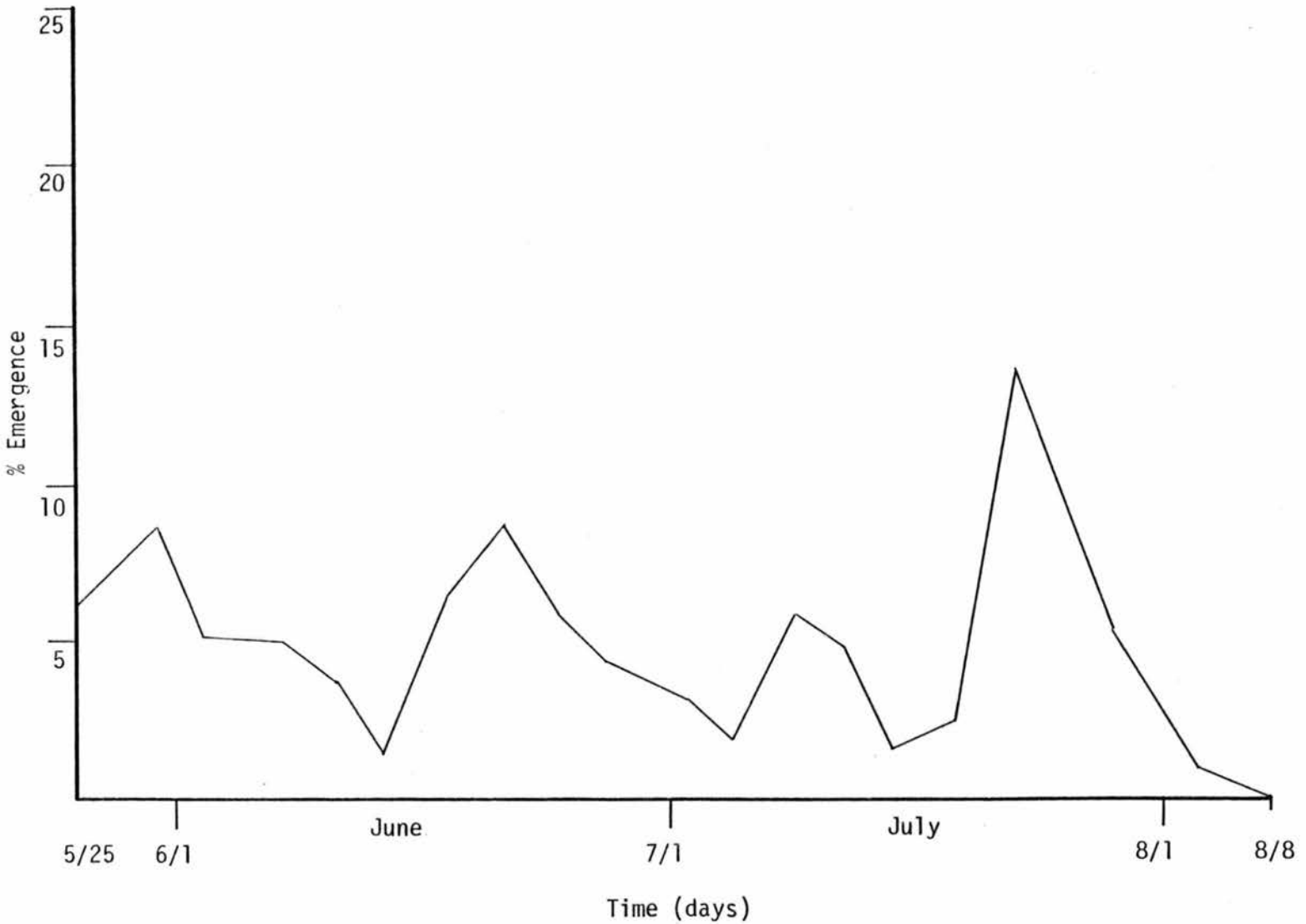

25
20
15
10
5
% Emergence
June
July
5/25
6/1
7/1
8/1
8/8
Time (days)

Figure 14. The effects of two cultivations (6/11, 7/15, denoted by *) 8 cm deep on emergence patterns of Panicum miliaceum from May 25 to August 8, 1983 in an Ault, Colorado field.

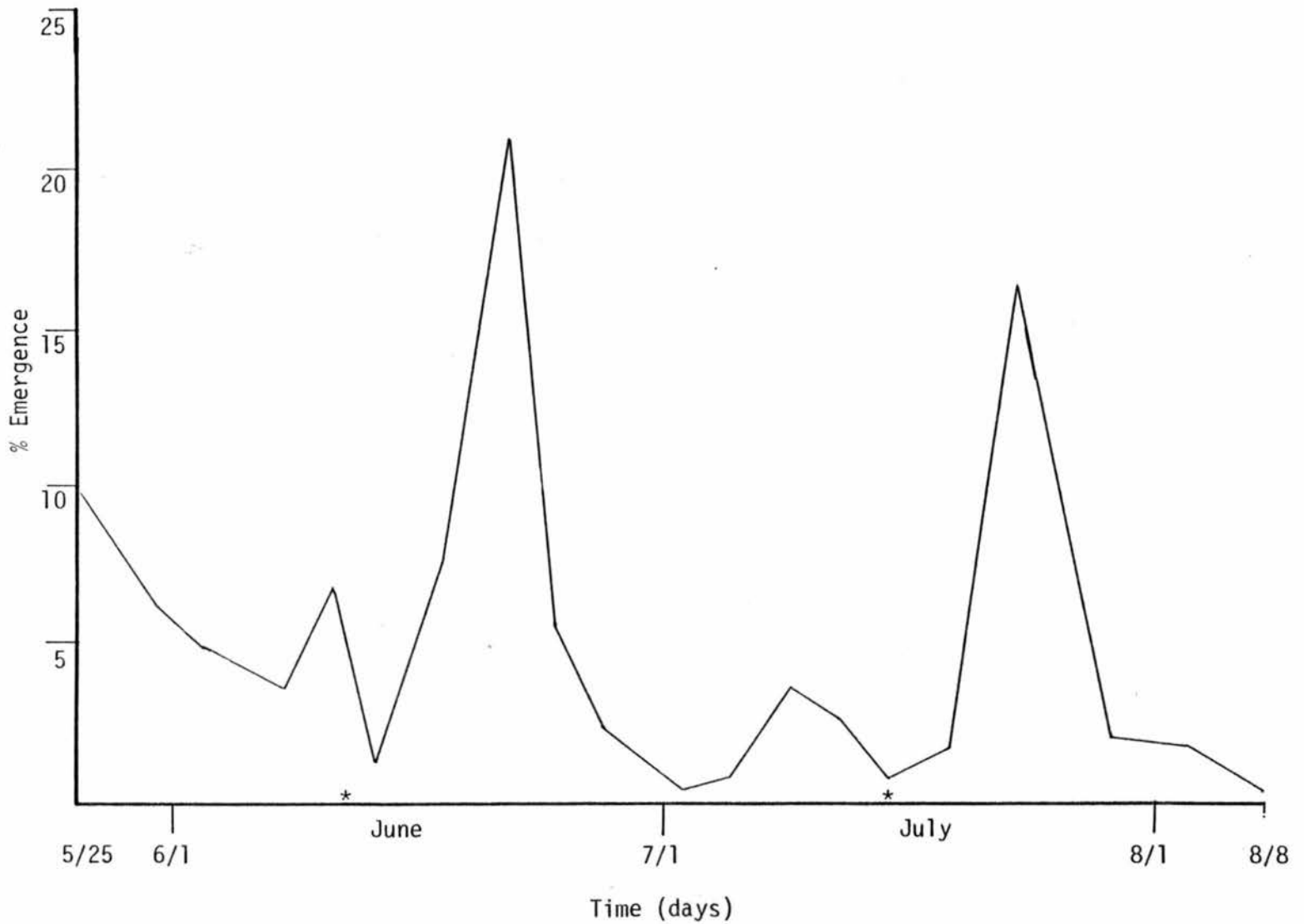
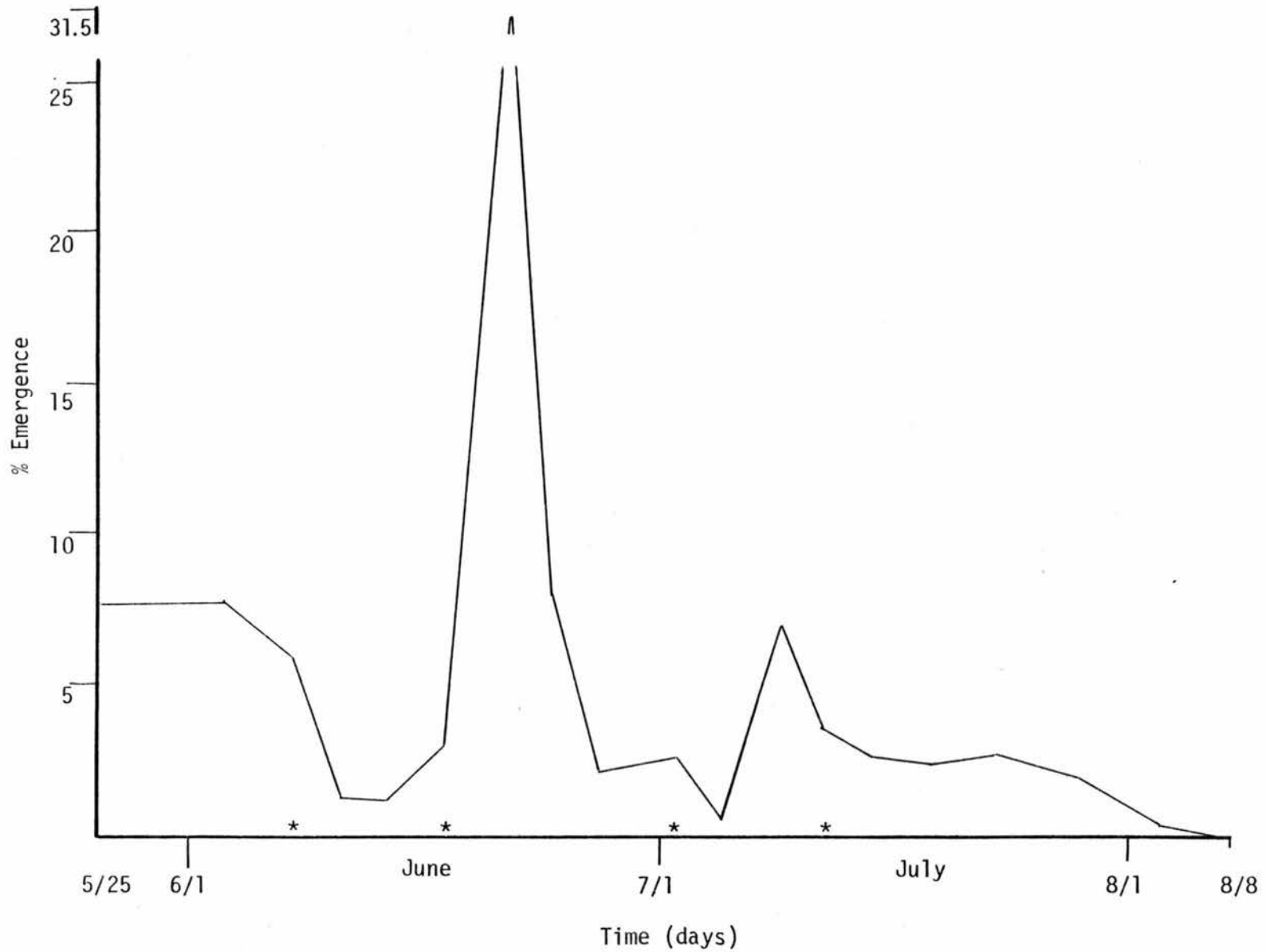

25
20
15
10
5
% Emergence
*
*
June
July
5/25
6/1
7/1
8/1
8/8
Time (days)

Figure 15. The effects of four cultivations (6/8, 6/18, 7/2, 7/12, denoted by *) 8 cm deep on emergence patterns from May 25 to August 8, 1983 in an Ault, Colorado field.


31.5
25
20
15
10
5
% Emergence
5/25
6/1
June
7/1
July
8/1
8/8
Time (days)

With intraspecific competition removed emergence continued throughout the season from May 25 to August 8 with four emergence peaks apparent (Figure 13). With competition removed, emergence was regulated by temperature and moisture. In June, when moisture was not limiting, emergence peaks were influenced by temperature with low temperatures reducing emergence. Later in the season when temperatures were constant, moisture became the limiting factor with the two peaks occurring with high moisture. The reason for emergence cessation on August 8 is not clear since moisture and temperature were not limiting at that time (Figure 11).

Emergence patterns for two and four cultivations were similar except for a peak of emergence on July 29 for the two cultivation treatments (Figure 14 and 15). Emergence peaks and valleys corresponded to environmental conditions of temperature and soil moisture. Cultivation, or frequency of cultivation, did not have an effect on the patterns of emergence but did affect the number of emerged plants.

In Severance, all treatments had similar emergence patterns (Figures 17, 18, 19, 20). Wild proso millet and corn emergence began May 24. The bulk of the emergence occurred in June with two large peaks for all treatments except four (no corn or intraspecific competition) which had a small second peak (Figure 20). Moisture for June was adequate for emergence never going below 35% field capacity and temperatures fluctuated yet stayed above 14.5 C (Figure 16).

Figure 16. Weather data for emergence plots in Severance, Colorado from May 24 to August 3, 1983. Upper line is the soil temperature at a depth of 8 cm and the lower line is soil moisture reported in terms of percent of the field capacity.

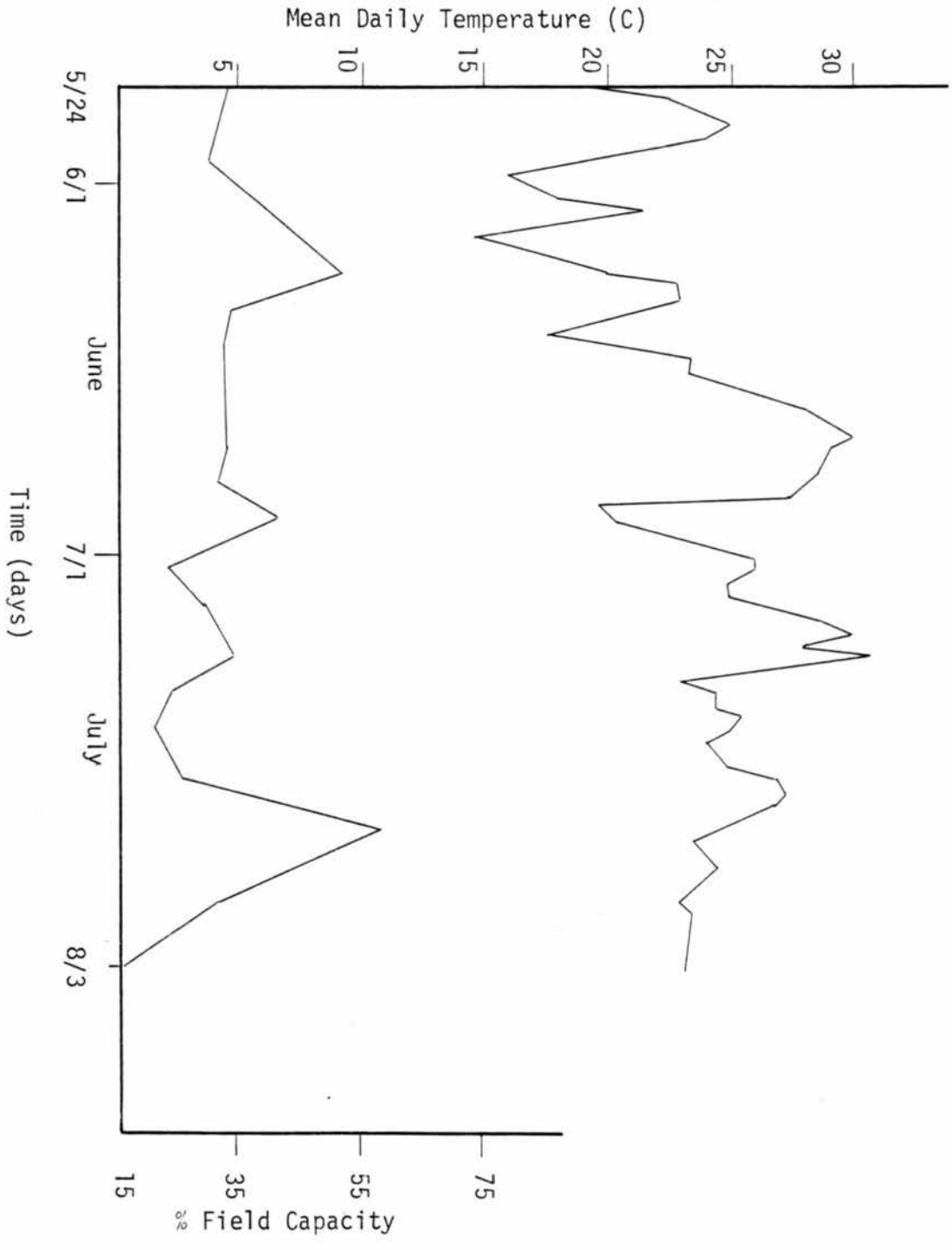

Mean Daily Temperature (C)
5
10
15
20
25
30
5/24
6/1
June
7/1
July
8/3
Time (days)
15
35
55
75
% Field Capacity

Figure 17. The effects of intraspecific and corn competition on emergence patterns of Panicum miliaceum from May 24 to August 3, 1983 in a Severance, Colorado corn field.

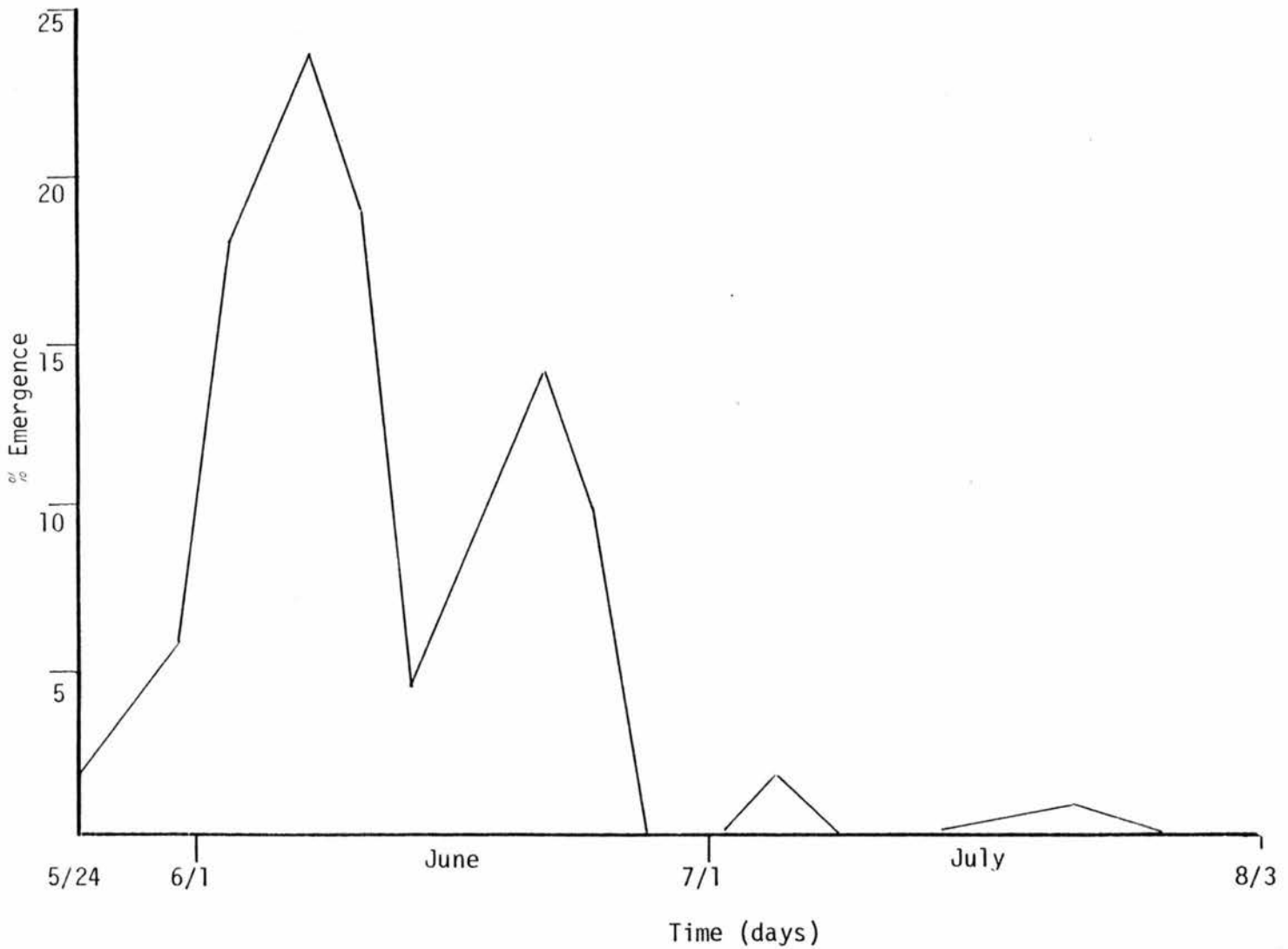

25
20
15
10
5
% Emergence
5/24
6/1
June
7/1
July
8/3
Time (days)

Figure 18. The effects of corn competition with intraspecific competition removed on emergence patterns of Panicum miliaceum from May 24 to August 3, 1983 in a Severance, Colorado corn field.

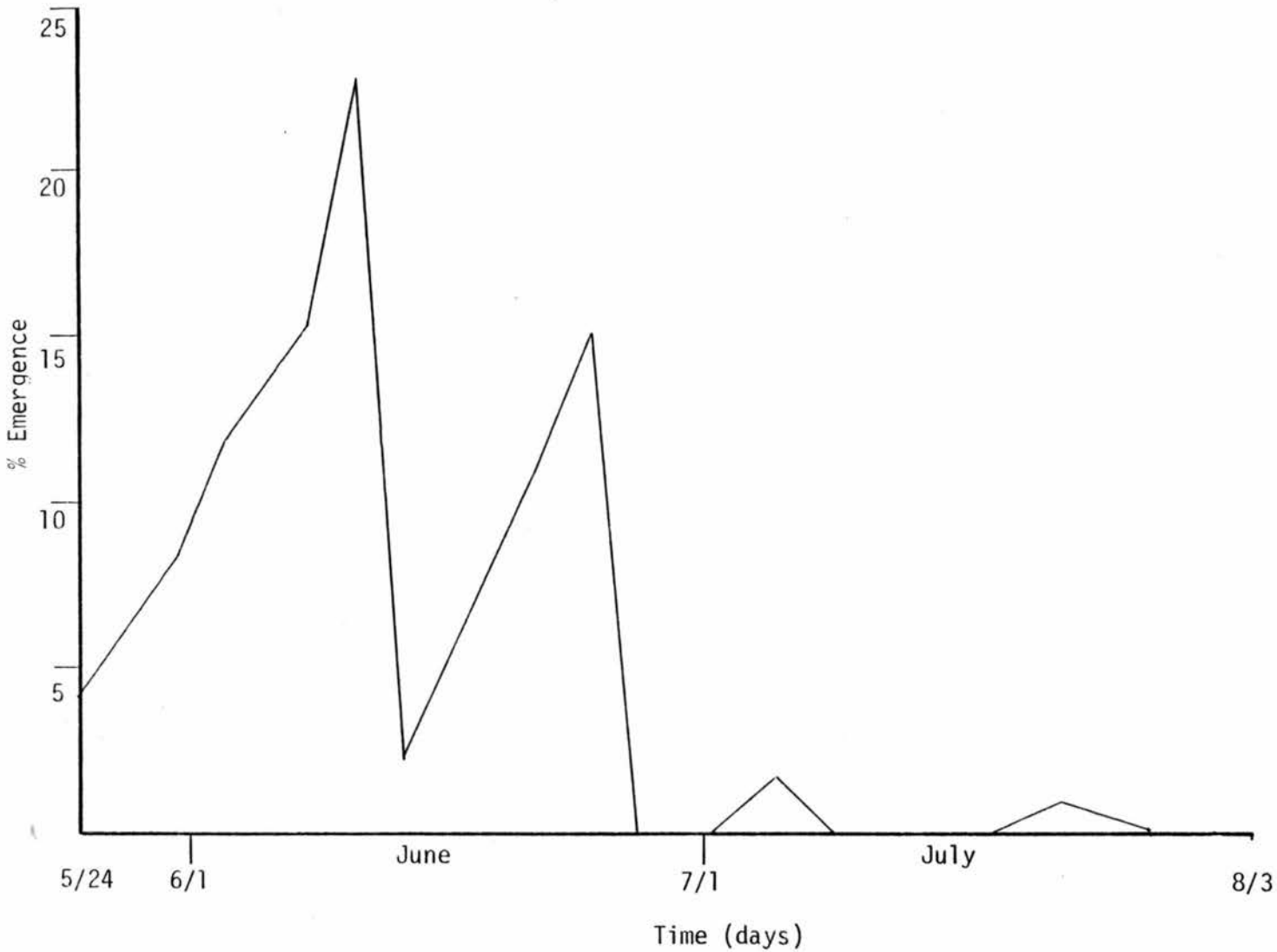

25
20
15
10
5
% Emergence
5/24
6/1
June
7/1
July
8/3
Time (days)

Figure 19. The effects of intraspecific competition on emergence patterns of Panicum miliaceum from May 24 to August 3, 1983 in a Severance, Colorado corn field.

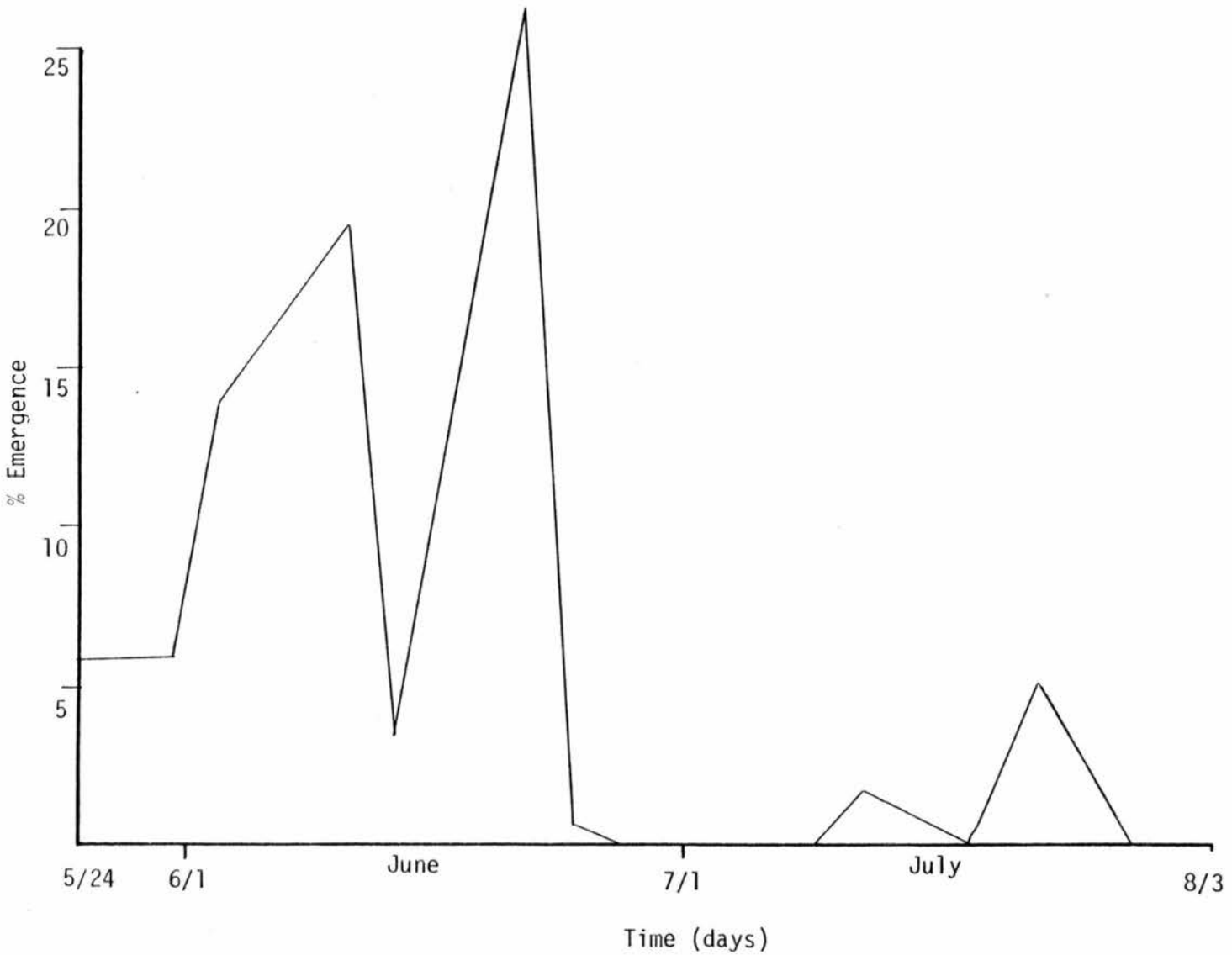
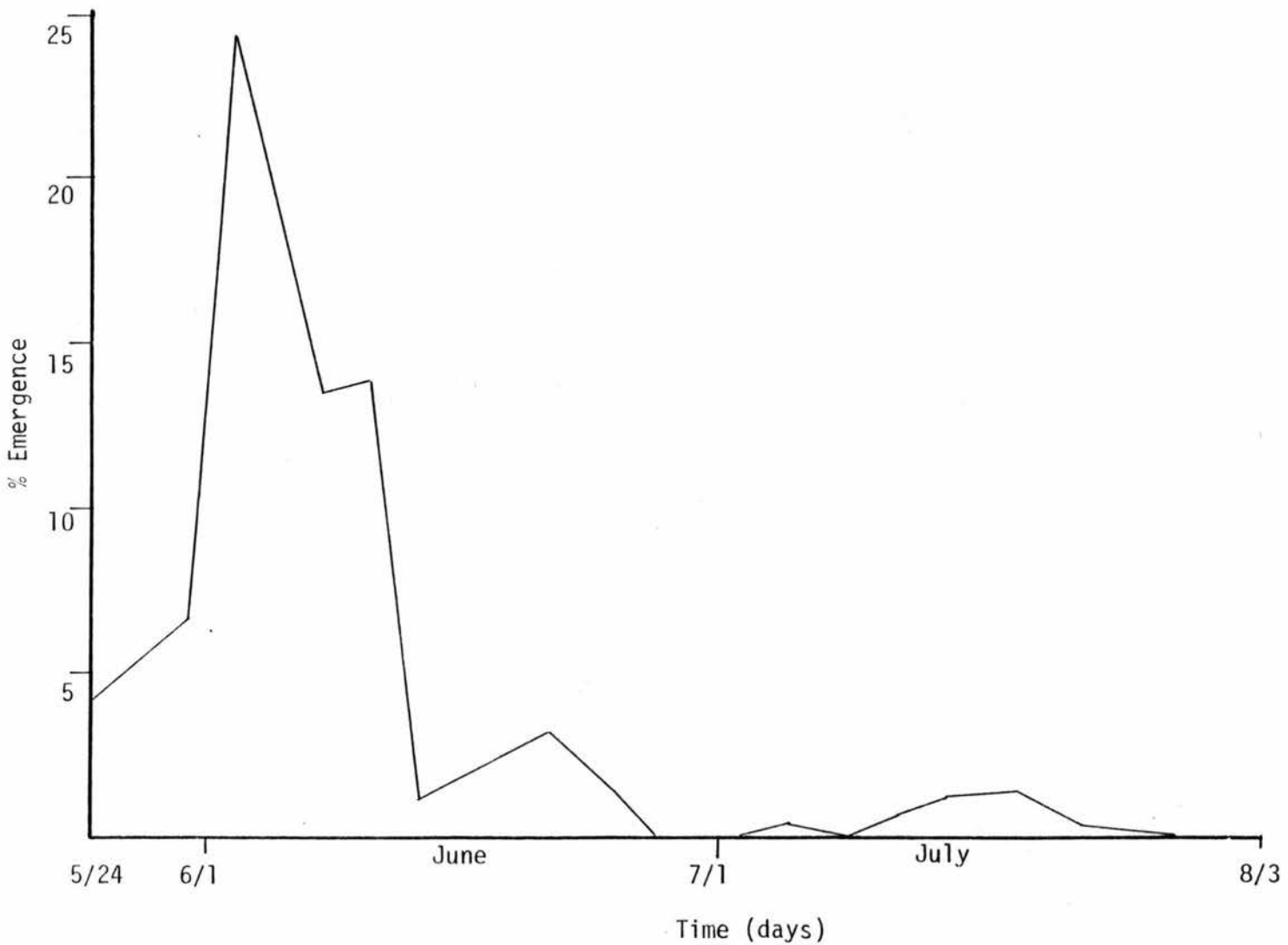

25
20
15
10
5
% Emergence
5/24
6/1
June
7/1
July
8/3
Time (days)

Figure 20. The effects of intraspecific competition removal on emergence of Panicum miliaceum from May 24 to August 3, 1983 in a Severance, Colorado corn field.


25
20
15
10
5
% Emergence
5/24
6/1
June
7/1
July
8/3
Time (days)

Near the end of June, no emergence was recorded because corn rows were cultivated and irrigation furrows made. Corn at this time was in the 11 to 12 leaf stage and 58 cm tall. In July all treatments had two small emergence peaks which again corresponded to moisture peaks. Emergence ceased July 29. Since corn was over 183 cm tall at this time it is likely that the corn canopy reduced additional emergence during late July and August.

From these studies it is apparent that temperature, moisture, and competition were the primary factors influencing wild proso millet emergence. How exactly competition affects its emergence is beyond the scope of this investigation. Other factors such as seed distribution in the soil profile and soil type probably also influence emergence patterns but were not within the scope of this investigation. In general, emergence patterns in 1983 for both sites and all treatments consisted of four peaks of emergence. The magnitude of peaks, of course, differed. The first two peaks occurred in late May to late June and were influenced by temperature fluctuations. In treatments that involved competition, these peaks represented the majority of the season's total emergence. This was especially apparent in Severance where corn was present. Later in the season, two more peaks occurred in early and late July corresponding to moisture fluctuations. Other researchers studying emergence have also found that temperature was the limiting factor early in the season and moisture was limiting later in the season to emergence (47, 52). Emergence patterns the previous year, 1982, in Ault, however, were different with two major emergence peaks; at the end of May and from mid-June to mid-July. Differences were probably due to different environmental conditions that year.

CHAPTER 4

Conclusions

The results indicate that wild proso millet is capable of germination and emergence over a fairly broad range of temperatures, moistures and seed depths. They, partially, explain wild proso millet's competitiveness and rapid spread. Emergence occurred at temperatures from 10 to 40 C and the amount and rate increased with temperature. In field studies, temperatures from 10 to 20 C regulated emergence in May and June.

The effects of daily fluctuating temperature were not investigated on emergence. But since temperatures in the field are rarely constant, especially early in the season, temperature fluctuation may influence emergence in the field.

Emergence occurred over a broad range of soil moisture levels but soil moisture limited emergence in the field in July. Plants frequently showed drought stress during July and August. Also germination under simulated drought conditions indicated that wild proso millet is not as drought tolerant as some weed and crop species (4, 7, 26). Thus, one must ask if wild proso millet could become established on dryland. In Colorado, there have been no such reports yet the possibility warrants investigation. The maximum depth of emergence was 14 cm but will vary with soil texture and moisture. Total emergence was equal from 1 to 8 cm.

The persistence of many weed species increases with depth of burial, and wild proso millet was no exception. Seeds at 5 cm showed the greatest depletion after two years because of in situ germination which was the main mode of seed depletion at all depths. Because germination at 10 cm in the depth of emergence studies, where moisture was not limiting, was 84% depletion at greater depths by in situ germination may have been higher, in the field, where water was limiting. In the non-irrigated field burial study, in situ germination was only 7% after one year, which was similar to emergence from depth of emergence studies in Ault and Severance of 11 and 2%, respectively. Seed death was not an important depletion factor, with less than 10% dead seed at all depths after two years. However, in the induced dormancy experiment continuously imbibed seed at 8 C had 6% seed death after only 8 weeks. Because of differences found between studies additional studies are needed to test seed persistence under varying moisture conditions and longer burial duration.

Emergence patterns in the field were affected by temperature and moisture, and were influenced by competition. With intraspecific competition from wild proso millet or interspecific competition from corn, late emergence was drastically reduced. The exact competitive mechanism was beyond the scope of this investigation.

One of the objectives of this study was to develop control strategies based on the knowledge developed. By no means were all aspects of wild proso millet biology and response to environmental conditions covered, but what has been found provides some bases for understanding and better control.

Because wild proso millet is found in irrigated row crops in Colorado, control strategies for corn and dry beans will be proposed. Alfalfa will also be discussed. The intent of these control strategies is to reduce current year weed pressure, seed production, and soil seed reserve. The proposed control measures are primarily cultural and should be integrated with chemical control when possible. It should be noted that these control strategies are based on predictions of wild proso millet behavior established by this study.

Wild proso millet emerges concurrently with corn, thus no emergence gaps can be exploited by later crop planting dates. Wild proso millet is also capable of emergence up to early August and it will still mature and set seed before corn harvest. When these factors are coupled with the present unavailability of a full season chemical control program, wild proso millet becomes difficult to control. As with many weeds early season control is essential. Current chemical control strategies call for Eradicane or Sutan + at 6.1 lb/A plus Bladex at 1.0 lb/A preplant incorporated. Later in the season, when corn is tall enough to hill, wild proso millet must be cultivated and Prowl applied at 1.0 lb/A. Prowl must be soil incorporated and the treated soil should be moved into the corn row. After July, emergence is greatly reduced. In Severance, emergence during July and August represented only 3% of the season's total emergence because of competition from corn.

For long term reduction of the soil seed reserves prevention of the reintroduction of seed is very important so that net loss of the seed reserve will occur. In a minimum or no-till system seeds

around 5 cm lose up to 75% of their viability after two years. Seeds at deeper depths will be more persistent but will not emerge if they are below 14 cm. After two years seed depletion at these depths will be only 20%. Perhaps after two years seed death will increase to reduce their numbers. In Colorado, many farmers do not practice minimum or no-till cropping thus buried seed will be subjected to annual burial and exhumation in a conventional tillage system. If reintroduction of seed is prevented total seed reduction should be quicker as persistent seed from deeper depths is brought up each year to shallower depths where more rapid depletion can take place.

With dry beans, a planting date from late June to July 1 can be employed and wild proso millet emerging in late May and June can be controlled. To achieve maximum emergence during this period a shallow cultivation should be done about mid-June to remove intra-specific competition so additional emergence can occur that is controlled prior to planting. Fifty percent of the total years emergence may occur prior to planting. Intensive use of herbicides and cultivation is needed to control weeds emerging in July. To date, the work done on chemical control has not developed completely effective strategies for wild proso millet in dry beans. However, there may be more chemical control strategies in beans because of the postemergence grass herbicides like the diphenyl ethers currently available. In terms of total seed reserve reduction, this cropping system should result in a quicker reduction than in corn because of the opportunity to control the early emerging weeds. The production of new weed seeds must be avoided to most effectively reduce the soil seed bank.

If the acreage infested is small and the grower can afford to grow a lower value crop for at least a few years, an alfalfa rotation would be a good alternative in a long term program. Alfalfa may be planted in early to mid-May before wild proso millet seeds germinate. Use of a preplant herbicide such as EPTC can help suppress wild proso millet until alfalfa is established. Competition from the crop will reduce seedling establishment and a frequent mowing schedule will prevent seed production on plants that become established. Seedlings that might emerge after the last cutting in late summer may produce seeds but the number will be small and viability questionable because of immaturity. This sytem will have the quickest soil seed depletion because it minimizes reintroduction of new seeds and keeps others buried. After several years of alfalfa the remaining viable seeds at the deeper depths will be placed nearer the surface by spring plowing and may then be depleted more rapidly.

In summary, some aspects of wild proso millet biology have been explored and new insights have been gained on some factors that govern its germination, emergence and seed persistence in the field. However, as with any preliminary investigation, more questions have been raised than answered. Other researchers should continue to investigate wild proso millet so we can increase our understanding of its biology.

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Appendix I. Effect of temperature and seed depth on percent and rate of germination.

Temperature/ seed depth (mm)	Replication	Elapsed time at emergence readings (hrs)																Total emergence	Coefficient of germination
		27	39	44	51	64	68	75	88	112	117	121	137	153	170	177	192		
35 C																			
6.35	I	5[a]	35	7	0	0	0	0	0	0	0	0	0	0	0	0	0	47	2.6
	II	2	29	4	0	5	0	2	0	0	0	0	0	0	0	0	0	42	2.3
	III	1	33	2	0	8	0	0	0	0	0	0	0	0	0	0	0	44	2.3
	IV	0	31	8	2	8	0	0	0	0	0	0	1	0	0	0	0	50	2.2
12.7	I	1	26	14	1	2	0	0	0	1	0	0	0	0	0	0	0	45	2.3
	II	0	35	0	7	4	0	1	0	0	0	0	0	0	0	0	0	47	2.3
	III	0	30	5	4	2	0	0	0	0	0	0	0	0	0	0	0	41	2.4
	IV	1	31	1	0	3	0	0	0	0	0	0	0	0	0	0	0	39	2.5
25.4	I	0	27	6	0	14	2	1	0	0	0	0	0	0	0	0	0	50	2.1
	II	0	17	6	0	3	3	1	0	1	0	0	0	0	0	0	0	31	2.0
	III	0	31	1	0	7	0	1	0	3	0	0	0	0	0	0	0	43	2.0
	IV	0	22	2	4	7	0	0	2	0	9	0	0	0	0	0	0	44	1.6
50.8	I	0	0	20	0	6	2	0	0	0	6	5	4	2	0	0	3	48	1.2
	II	0	0	23	5	0	1	1	0	0	10	4	3	0	0	0	0	47	1.3
	III	0	0	13	5	1	5	0	0	0	4	6	3	3	0	0	0	40	1.2
	IV	0	8	15	2	5	6	0	0	0	8	6	0	0	0	0	0	45	1.7

Appendix I (continued).

Temperature/ seed depth (mm)	Replication	Elapsed time at emergence readings (hrs) 27	39	44	51	64	68	75	88	112	117	121	137	153	170	177	192	Total emergence	Coefficient of germination
30 C																			
6.35	I	0	5	4	8	9	3	2	2	0	0	0	0	0	0	0	0	33	1.7
	II	0	6	7	10	7	2	2	0	0	0	0	0	0	0	0	0	34	1.9
	III	0	4	4	0	16	2	4	1	0	0	0	0	0	0	0	0	31	1.6
	IV	0	12	7	5	14	0	0	0	0	0	0	0	0	0	0	0	38	2.0
12.7	I	0	5	3	14	9	2	2	2	0	0	0	0	0	0	0	0	37	1.8
	II	0	3	6	3	12	1	4	0	0	0	0	0	0	0	0	0	29	1.7
	III	0	1	3	2	19	3	1	2	0	0	0	0	0	0	0	0	31	1.6
	IV	0	9	5	6	10	1	0	3	0	1	0	0	0	0	0	0	35	1.8
25.4	I	0	1	4	6	5	4	1	2	3	1	0	0	0	0	0	0	26	1.3
	II	0	0	5	4	14	4	0	2	0	0	0	0	0	0	0	0	29	1.6
	III	0	0	1	5	14	4	2	2	0	0	2	0	0	0	0	0	30	1.5
	IV	0	0	2	5	16	6	4	4	1	1	0	0	0	0	0	0	39	1.5
50.8	I	0	0	0	8	19	6	5	0	0	0	0	0	0	0	0	0	38	1.6
	II	0	0	0	10	8	7	3	4	0	0	3	0	0	0	0	0	35	1.2
	III	- - - - - - - - - - - - - - pot leaked -																	
	IV	0	0	0	1	12	6	4	8	3	0	0	0	0	0	0	0	34	1.3

Appendix I (continued).

Temperature/ seed depth (mm)	Replication	Elapsed time at emergence readings (hrs)																Total emergence	Coefficient of germination
		27	39	44	51	64	68	75	88	112	117	121	137	153	170	177	192		
25 C																			
6.35	I	0	1	5	5	9	3	6	6	0	0	0	0	0	0	0	0	35	1.5
	II	0	1	2	10	11	1	5	3	1	0	0	0	0	0	0	0	34	1.6
	III	0	0	5	5	10	1	9	4	0	0	0	0	0	0	0	0	34	1.5
	IV	0	0	1	9	11	1	8	3	1	0	0	0	0	0	0	0	34	1.5
12.7	I	0	0	1	8	14	0	7	3	0	0	0	0	0	0	0	0	33	1.5
	II	0	0	4	8	8	1	7	3	0	0	0	0	0	0	0	0	31	1.5
	III	0	0	0	4	11	1	11	5	2	0	0	0	0	0	0	0	33	1.3
	IV	0	0	1	1	16	4	4	3	1	0	0	0	0	0	0	0	30	1.4
25.4	I	0	0	0	0	6	4	13	12	5	0	0	0	0	0	0	0	40	1.2
	II	0	0	0	2	9	4	7	8	3	0	0	0	0	0	0	0	33	1.3
	III	0	0	0	1	5	3	2	12	2	1	0	0	0	0	0	0	27	1.1
	IV	0	0	0	0	6	3	6	7	1	0	0	0	1	0	0	0	23	1.3
50.8	I	0	0	0	0	15	0	11	8	3	0	0	0	0	0	0	0	37	1.3
	II	0	0	0	0	6	3	7	16	3	0	0	0	0	0	1	0	36	1.2
	III	0	0	0	0	1	4	10	10	6	0	2	0	0	0	0	0	33	1.1
	IV	0	0	0	1	4	3	4	18	4	0	0	0	0	0	0	0	34	1.2

Appendix I (continued).

Temperature/ seed depth (mm)	Replication	Elapsed time at emergence readings (hrs) 95	103	107	121	144	152	167	179	202	208	217	241	Total emergence	Coefficient of germination
20 C															
6.35	I	14	3	3	3	1	0	0	0	0	0	0	0	24	1.0
	II	11	10	0	8	4	0	0	0	0	0	0	0	33	0.9
	III	7	7	1	5	0	0	0	0	0	0	0	0	20	0.9
	IV	20	6	0	4	0	1	0	0	0	0	0	0	21	0.9
12.7	I	0	5	0	20	1	0	1	0	0	0	0	0	27	0.8
	II	7	11	0	6	0	0	0	0	0	0	0	0	24	0.9
	III	4	12	3	7	2	0	0	0	0	0	0	0	28	0.9
	IV	0	7	5	12	0	0	0	0	0	0	0	0	24	0.9
25.4	I	0	6	4	14	2	1	0	0	0	0	0	0	27	0.7
	II	0	2	7	10	5	0	1	0	0	2	0	0	27	0.8
	III	0	5	5	9	2	0	1	0	0	1	0	0	23	0.8
	IV	0	0	0	17	5	3	0	0	0	0	0	0	25	0.8
50.8	I	0	0	0	2	18	5	2	0	0	0	0	0	27	0.7
	II	0	0	0	2	26	6	4	1	0	0	0	0	39	0.7
	III	0	0	0	2	13	9	5	0	0	0	0	0	29	0.7
	IV	0	0	0	7	12	6	3	0	0	0	0	0	28	0.7

Appendix I (continued).

Temperature/ seed depth (mm)	Replication	Elapsed time at emergence readings (hrs) 88	112	116	121	136	144	161	169	183	193	209	232	256	279	313	333	361	Total emergence	Coefficient of germination
15 C																				
6.35	I	0	7	3	2	6	0	0	2	1	0	1	0	0	0	0	0	0	22	0.8
	II	0	20	0	0	4	0	1	0	0	0	0	0	0	0	0	0	0	25	0.8
	III	0	22	3	0	4	0	0	0	0	0	1	0	0	0	0	0	0	30	0.9
	IV	2	13	0	0	4	0	1	2	0	0	0	0	0	0	0	0	0	23	0.9
12.7	I	0	10	1	10	3	1	1	0	0	0	0	0	0	0	0	0	0	25	0.8
	II	0	6	1	6	4	0	0	0	0	0	0	0	0	0	0	0	0	17	0.8
	III	0	1	0	12	13	1	0	0	0	0	0	0	0	0	0	0	0	27	0.8
	IV	0	7	2	2	8	1	0	0	0	0	0	0	0	0	0	0	0	20	0.8
25.4	I	0	0	1	3	11	12	2	0	0	0	1	0	0	0	0	0	0	29	0.7
	II	0	2	1	0	10	2	3	0	0	0	0	0	0	0	0	0	0	18	0.7
	III	0	5	0	2	11	2	4	0	0	0	0	0	0	0	0	0	0	24	0.7
	IV	0	1	0	0	10	3	10	0	0	0	0	0	0	0	0	0	0	24	0.7
50.8	I	0	0	0	0	0	4	10	10	4	2	1	0	0	0	0	0	0	31	0.7
	II	0	0	0	0	1	4	14	4	1	0	0	0	0	0	0	0	0	24	0.6
	III	0	0	0	0	0	0	0	0	1	3	13	6	9	3	0	0	0	35	0.4
	IV	0	0	0	0	0	2	8	5	1	4	0	0	0	0	0	0	0	20	0.6

Appendix I (continued).

Temperature	Replication	Percent emergence at 40 and 10 C
40 C	I	100
	II	100
	III	100
	IV	84
10 C	I	20
	II	30
	III	86
	IV	46

[a]Values presented are amounts of emerged seedlings at time of reading. Fifty seeds were planted in each replicate.

Appendix II. Percent germination under simulated drought.

Water potential Bars	25 C				30 C			
	Rep				Rep			
	I	II	III	IV	I	II	III	IV
0	62	80	82	82	98	98	98	100
- 2	48	40	40	48	64	62	86	66
- 4	22	22	12	16	50	40	56	72
- 6	26	22	26	36	46	68	44	26
- 8	2	2	4	0	42	46	30	44
-10	0	0	0	0	36	34	46	30
-12	0	0	0	0	4	8	2	2
-14	0	1	0	0	4	0	2	0

Appendix III. Germination as influenced by different levels of soil moisture.

% Germination:	% Field Capacity									
	100	75	50	25	45	40	35	30	25	20
Replication										
I	88	88	98	2	100	100	92	78	8	0
II	88	94	96	2	78	100	96	20	12	0
III	90	94	100	12	100	100	92	70	2	0
IV	82	84	100	8	100	88	100	70	12	0

Appendix IV. The effect of continuous vs fluctuating soil moisture on emergence.

Seed depth (cm)	Rep.	Moisture level: 100% field capacity	Moisture level: 100/25% field capacity
		% emergence	
1	I	88	98
	II	86	100
	III	86	100
	IV	82	94
2	I	92	100
	II	86	98
	III	100	100
	IV	100	100
4	I	74	100
	II	88	96
	III	96	100
	IV	72	98

Appendix V. Percent emergence as influenced by seed depth.

Seed depth (cm)	Replication I	II	III	IV
Pot experiments				
0	23	32	26	43
1	68	71	77	81
2	71	70	69	64
4	95	75	75	69
6	97	84	87	77
8	90	96	97	97
10	77	83	87	88
14	6	3	5	5
18	0	0	0	0
Field, Ault, CO				
2	84	70	44	
4	12	50	45.5	
6	40.5	61.5	41.5	
8	29.5	27.5	60	
10	2.5	12	19.5	
12	5	21.5	3	
14	1	22	8	
Field, Bay Farm				
2	18	2	54	44
4	50	32	46	22
6	22	26	12	20
8	12	6	0	0
10	6	0	2	0
14	0	0	0	0
18	0	0	0	0

Appendix VI. Effects of depth and duration of seed burial on components of persistence and depletion.[a]

Months of burial	Depth (cm) 5	10	30
% total persistence (P)			
1	100 a	100 a	99.8 a
4	98.8 abc	98.8 ab	97.2 a
6	98.3 ab	98.1 abc	97.5 abcd
8	75.8 defg	97.5 abc	93.1 abcdef
12	24.0 h	77.3 efg	80.0 cdefg
16	11.8 h	68.7 g	89.5 abcdef
19	21.4 h	85.2 bcdefg	95.1 abcde
21	23.2 h	76.9 fg	92.7 abcdefg
% Exogenous dormancy (P_{ex})			
1	63.6 abcdef	56.2 bcdefg	58.8 abcdefg
4	56.9 defgh	74.2 abcdef	83.3 abcd
6	48.4 cdefgh	89.4 abc	87.5 abc
8	62.5 abcdef	94.9 a	81.1 ab
12	12.9 h	31.0 fgh	39.0 efg
16	9.1 h	54.2 bcdefg	78.0 abcde
19	10.9 h	67.3 abcdef	88.3 ab
21	19.1 gh	69.7 abcdef	87.7 abc
% Endogenous dormancy (P_{end})			
1	36.4 abc	42.5 a	41.1 ab
4	41.9 ab	24.5 abcd	14.5 cdef
6	49.9 a	8.8 def	10.3 def
8	13.3 cdef	2.1 ef	2.0 f
12	11.1 def	46.3 a	41.0 ab
16	2.6 ef	14.5 cdef	11.6 def
19	10.5 def	18.0 bcde	6.8 def
21	4.1 ef	7.2 def	5.5 ef

Appendix VI (continued).

Months of burial	Depth (cm) 5		10		30	
% Total depletion (D)						
1	0.0	f	0.0	f	0.2	f
4	1.3	cdef	1.3	def	2.2	cdef
6	1.7	ef	1.9	cdef	2.0	cdef
8	24.4	bcde	3.0	cdef	6.9	bcdef
12	76.0	a	22.8	bcd	20.0	bcde
16	88.3	a	31.3	b	10.5	bcdef
19	78.7	a	14.8	bcdef	6.1	bcdef
21	76.8	a	23.1	bc	7.3	bcdef
% In situ germination (D_g)						
1	0.0	e	0.0	e	0.0	e
4	0.0	e	0.0	e	0.0	e
6	0.0	e	0.0	e	0.0	e
8	20.6	bc	1.3	de	0.3	e
12	66.4	a	7.0	bcde	1.0	de
16	86.0	a	26.3	b	6.3	bcde
19	76.3	a	10.3	bcde	3.1	cde
21	73.4	a	15.5	bcd	4.8	bcde
% Seed death (D_n)						
1	0.0	c	0.0	c	0.2	c
4	1.3	c	1.3	c	2.2	c
6	1.7	c	1.9	bc	2.0	bc
8	3.6	abc	1.8	c	6.6	abc
12	9.6	abc	15.7	ab	19.0	a
16	2.3	abc	5.1	abc	4.2	abc
19	2.4	bc	4.5	abc	1.8	c
21	3.4	abc	7.6	abc	2.5	abc

[a]Means followed by the same letter for each component are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

Appendix VII. Effects of depth of seed burial on components of persistence and depletion.[a]

Depth (cm)	Percent
Total persistence (P)[b]	
5	56.6 a
10	87.8 b
30	93.2 c
Exogenous dormancy (P_{ex})[b]	
5	35.4 c
10	67.2 b
30	76.2 a
Endogenous dormancy (P_{end})[b]	
5	21.2 a
10	20.5 a
30	16.6 a
Total depletion (D)[b]	
5	43.4 a
10	12.3 b
30	6.9 b
In situ germination (D_g)[b]	
5	40.3 a
10	7.5 b
30	1.9 c
Seed death (D_n)[b]	
5	3.0 a
10	4.7 a
30	4.8 a

[a]Means followed by the same letter for each component are not significantly different at P = 0.05 according to Tukey's test for mean comparison.

[b]Represents average of all time periods.

Appendix VIII. Depth and duration of seed burial replicated data.

Duration (months)	Depth	Replication	% components of population depletion and persistence					
			P	P_{ex}	P_{end}	D	D_g	D_n
1	5	I	100	50.2	49.8	0.0	0.0	0.0
		II	100	75.8	24.2	0.0	0.0	0.0
		III	100	54.1	45.9	0.0	0.0	0.0
		IV	100	74.4	25.6	0.0	0.0	0.0
	10	I	100	54.2	45.8	0.0	0.0	0.0
		II	100	75.4	24.6	0.0	0.0	0.0
		III	100	48.7	51.3	0.0	0.0	0.0
		IV	100	51.8	48.2	0.0	0.0	0.0
	30	I	100	65.5	34.5	0.0	0.0	0.0
		II	99.3	58.7	40.6	0.7	0.0	0.7
		III	100	53.5	46.5	0.0	0.0	0.0
		IV	100	57.4	42.6	0.0	0.0	0.0
4	5	I	99.5	65.3	34.2	0.5	0.0	0.0
		II	98.0	59.3	38.7	2.0	0.0	2.0
		III	98.6	51.2	47.4	1.4	0.0	1.4
		IV	98.9	51.6	47.3	1.1	0.0	1.1
	10	I	97.5	80.9	16.6	2.5	0.0	0.0
		II	98.5	74.7	23.8	1.5	0.0	1.5
		III	100	66.0	34.0	0.0	0.0	0.0
		IV	99.0	75.3	23.7	1.0	0.0	1.0
	30	I	93.2	80.0	13.2	6.8	0.0	0.0
		II	99.5	89.9	9.6	0.5	0.0	0.5
		III	100	85.1	14.9	0.0	0.0	0.0
		IV	98.6	78.3	20.3	1.4	0.0	1.4

Appendix VIII (continued).

Duration (months)	Depth	Replication	% components of population depletion and persistence					
			P	P_{ex}	P_{end}	D	D_g	D_n
6	5	I	98.6	53.6	45.0	1.4	0.0	1.4
		II	95.0	40.6	24.2	5.0	0.0	5.0
		III	100	63.0	37.0	0.0	0.0	0.0
		IV	99.5	36.2	63.3	0.5	0.0	0.5
	10	I	98.5	87.4	11.1	1.5	0.0	1.5
		II	96.5	91.4	24.6	3.5	0.0	3.5
		III	99.5	70.0	9.5	0.5	0.0	0.5
		IV	98.0	88.7	93.0	2.0	0.0	2.0
	30	I	97.0	83.6	13.1	3.0	0.0	3.0
		II	94.5	85.4	40.6	3.5	0.0	3.5
		III	99.0	84.3	14.7	1.0	0.0	1.0
		IV	99.5	96.6	2.9	0.5	0.0	0.5
8	5	I	71.6	52.2	19.4	28.4	23.4	5.0
		II	73.1	60.4	38.7	26.9	21.3	5.6
		III	58.9	44.1	14.5	41.1	37.2	3.9
		IV	99.5	93.0	6.5	0.5	0.5	0.0
	10	I	92.0	90.5	1.5	8.0	4.0	4.0
		II	100	99.0	23.8	0.0	0.0	0.0
		III	99.0	96.1	2.9	1.0	0.0	1.0
		IV	97.0	94.0	3.0	3.0	1.0	2.0
	30	I	99.0	98.5	0.5	1.0	0.5	0.5
		II	76.6	72.1	9.6	23.4	0.0	23.4
		III	97.9	96.9	1.0	2.1	0.5	1.6
		IV	99.0	97.0	2.0	1.0	0.0	1.0

Appendix VIII (continued).

Duration (months)	Depth	Replication	% components of population depletion and persistence					
			P	P_{ex}	P_{end}	D	D_g	D_n
12	5	I	35.0	12.0	23.0	65.0	37.5	27.5
		II	8.0	5.0	3.0	92.0	86.5	5.5
		III	3.0	2.0	1.0	97.0	97.0	0.0
		IV	50.0	32.5	17.5	50.0	44.5	5.5
	10	I	79.0	31.0	48.0	21.0	2.5	18.5
		II	83.0	24.0	59.0	17.0	0.5	16.5
		III	60.0	26.0	34.0	40.0	17.1	22.9
		IV	87.9	13.0	44.0	13.0	8.0	5.0
	30	I	78.0	24.0	54.0	22.0	3.5	18.5
		II	93.0	39.0	54.0	7.0	0.0	7.0
		III	94.0	77.0	17.0	6.0	0.5	5.5
		IV	55.0	16.0	39.0	45.0	0.0	45.0
16	5	I	20.0	20.0	0.0	80.0	75.0	5.0
		II	6.0	2.5	3.5	94.0	92.0	2.0
		III	5.0	4.0	1.0	95.0	94.0	1.0
		IV	16.0	10.0	6.0	81.0	83.0	1.0
	10	I	93.4	86.7	6.7	6.6	2.0	4.6
		II	51.2	33.8	17.4	48.8	42.6	6.2
		III	79.8	75.3	4.5	20.2	17.7	2.5
		IV	80.3	21.1	29.2	49.7	42.7	7.0
	30	I	96.1	88.3	7.8	3.9	0.6	3.3
		II	75.3	49.7	25.6	24.7	18.0	6.7
		III	90.7	79.3	11.4	9.3	5.7	3.6
		IV	96.0	94.5	1.5	4.0	1.0	3.0

Appendix VIII (continued).

Duration (months)	Depth	Replication	% components of population depletion and persistence					
			P	P_{ex}	P_{end}	D	D_g	D_n
19	5	I	46.6	19.5	25.1	55.4	54.9	0.5
		II	5.0	3.5	1.5	95.0	92.0	3.0
		III	20.8	8.6	12.2	79.2	73.6	5.6
		IV	15.0	12.0	3.0	85.0	84.5	0.5
	10	I	88.6	61.2	27.4	11.4	5.0	6.4
		II	76.7	51.3	25.4	23.3	20.3	3.0
		III	78.6	63.8	14.8	21.4	14.8	6.6
		IV	97.0	92.8	4.2	3.0	1.0	2.0
	30	I	95.4	86.2	9.2	4.6	0.0	4.6
		II	86.6	71.1	15.5	18.4	11.8	1.6
		III	99.0	98.5	0.5	1.0	0.0	1.0
		IV	99.5	97.5	2.0	0.5	0.5	0.0
21	5	I	12.0	4.0	8.0	88.0	86.0	2.0
		II	40.9	39.4	1.5	59.1	50.2	8.9
		III	10.5	9.0	1.5	89.5	88.5	1.0
		IV	29.5	24.0	5.5	70.5	69.0	1.5
	10	I	71.0	61.9	7.1	29.0	17.8	11.2
		II	87.0	83.0	4.0	13.0	9.0	4.0
		III	77.1	62.8	14.3	22.9	12.2	10.7
		IV	72.5	71.0	1.5	27.5	23.0	4.5
	30	I	95.5	91.5	4.0	4.5	2.5	2.0
		II	93.9	92.4	1.5	6.1	4.6	1.5
		III	86.5	76.4	10.1	13.5	11.2	2.3
		IV	95.0	88.6	6.4	5.0	0.9	4.1

Appendix IX. Monthly mean temperatures in Fort Collins, Colorado for the periods of November 1981 to April 1982 and November 1982 to June 1983.

Year	Month	Temperature (C)		
		max	min	mean
1981	November	13.9	- 2.1	5.9
	December	7.6	- 6.7	0.5
1982	January	5.6	-10.1	-2.3
	February	8.5	- 9.0	-0.3
	March	11.9	- 2.2	4.9
	April	19.7	- 0.7	9.5
1982	November	7.9	- 5.8	1.1
	December	6.2	- 8.6	-1.2
1983	January	8.7	- 7.0	0.9
	February	10.1	- 4.1	3.0
	March	10.6	- 2.8	3.9
	April	11.4	- 1.4	5.0
	May	18.6	4.2	11.4
	June	24.5	9.4	17.0

Appendix X. The effects of overwintering of seed on the soil surface.

Month	Replication	%			
		P_{ex}	P_{end}	D_n	D_g
1981-1982					
Dec	I	98.5	1.5	0	0
	II	97.5	2.0	0.5	0
	III	96.0	3.5	0.5	0
	IV	99.5	0.5	0	0
	V	99.5	0.5	0	0
Jan	I	99.0	1.0	0	0
	II	98.5	1.5	0	0
	III	96.1	3.9	0	0
	IV	97.6	2.4	0	0
	V	96.4	3.1	0.5	0
Feb	I	94.1	6.0	0	0
	II	98.0	1.0	1.0	0
	III	97.0	3.0	0	0
	IV	96.0	3.5	0.5	0
	V	95.9	3.1	0.5	0
Apr	I	94.0	6.0	0	0
	II	91.8	8.2	0	0
	III	91.1	7.9	1.0	0
	IV	80.7	18.8	0.5	0
	V	95.0	4.5	0.5	0
1982-1983					
Dec	I	35.0	65.0	0	0
	II	42.0	58.0	0	0
	III	14.0	84.0	2.0	0
	IV	26.0	71.0	3.0	0
	V	44.0	52.0	4.0	0
Feb	I	77.0	19.0	4.0	0
	II	41.1	53.3	5.6	0
	III	54.0	41.0	5.0	0
	IV	67.0	30.0	3.0	0
	V	69.0	26.0	5.0	0

Appendix X (continued).

Month	Replication	%			
		P_{ex}	P_{end}	D_n	D_g
Apr	I	15.0	56.0	29.0	0
	II	23.0	60.0	17.0	0
	III	8.0	62.0	30.0	0
	IV	5.0	80.0	15.0	0
	V	39.0	55.0	6.0	0
Jun	I	28.0	67.0	5.0	0
	II	23.0	73.0	4.0	0
	III	25.0	69.0	4.0	2
	IV	25.0	70.0	3.0	2
	V	20.0	75.0	3.0	7

Appendex XI. The effects of cool moist storage on seed dormancy induction.

Storage duration (weeks)	Replication	% Seed status		
		Nondormant	Dormant	Nonviable
2	I	85	15	0
	II	84	16	0
	III	86	14	0
	IV	88	12	0
4	I	78	21	1
	II	67	33	0
	III	64	33	3
	IV	65	35	0
6	I	44	50	6
	II	37	56	7
	III	31	64	5
	IV	42	54	4
8	I	52	44	4
	II	39	54	7
	III	41	55	4
	IV	43	48	9

Appendix XII. Patterns of emergence, Ault, CO, 1982.

Treatment	Replication	Date													
		5/27	6/1	6/4	6/7	6/11	6/14	6/21	6/25	6/29	7/7	7/15	7/21	7/26	8/3
1	I	55	11	8	5	1	1	34	7	6	6	1	0	0	1
	II	45	3	2	5	3	0	15	5	4	9	6	0	0	1
	III	221	31	38	67	60	9	403	175	381	361	121	53	4	5
	IV	49	7	11	6	5	0	34	26	55	34	9	0	2	0
	V	65	14	2	12	8	0	28	11	16	11	2	1	0	0
	VI	41	6	5	10	9	1	22	22	51	58	34	2	0	2
	VII	54	7	7	7	3	4	27	5	16	20	5	1	0	1
	VIII	25	7	8	7	5	3	34	25	41	74	22	4	0	1
	IX	200	47	26	13	10	4	138	130	132	103	42	16	0	3
2	I	22	3	5	4	4	1	19	9	4	1	0	2	0	0
	II	14	4	4	1	0	3	22	5	3	12	0	1	0	0
	III	35	2	10	4	1	1	28	16	7	10	2	0	0	0
	IV	29	0	4	1	3	0	12	2	1	0	0	0	0	0
	V	30	0	4	2	2	6	13	2	4	1	1	0	0	0
	VI	113	36	15	10	3	2	37	10	4	0	0	0	0	0
	VII	9	0	4	5	1	0	22	8	6	1	1	0	0	0
	VIII	52	0	8	3	3	1	9	3	2	0	3	1	0	0
	IX	14	3	7	1	1	0	14	6	36	0	0	0	0	0

Appendix XII (continued). Patterns of emergence, Ault, CO, 1983.

Treatment	Replication	Date																			
		5/25	5/30	6/3	6/8	6/11	6/14	6/18	6/22	6/25	6/28	7/2	7/5	7/9	7/12	7/15	7/19	7/23	7/92	8/3	8/8
1	I	2	10	6	7	12	5	3	5	0	1	1	0	0	1	1	0	0	0	0	0
	II	5	5	2	3	5	4	7	2	1	0	0	1	1	0	0	4	0	0	0	0
	III	22	17	7	8	11	9	21	9	3	2	0	2	0	0	0	5	0	0	0	0
	IV	16	5	11	8	5	8	28	9	4	0	0	3	11	0	0	2	0	0	0	0
	V	6	15	5	5	17	4	20	17	0	2	1	3	4	1	0	18	0	0	0	0
2	I	5	4	2	4	8	1	11	17	20	7	16	5	20	38	3	0	31	6	0	0
	II	16	17	10	3	7	0	13	20	8	10	2	9	1	0	0	0	6	3	0	0
	III	7	11	9	10	9	3	3	17	2	3	4	3	7	4	1	2	27	10	0	0
	IV	45	62	41	38	17	7	38	58	32	26	17	7	23	13	9	12	31	22	0	0
	V	32	50	22	25	19	8	52	115	33	29	13	8	45	24	11	26	127	46	12	0
3	I	1	1	0	0	2	1	1	7	9	2	1	0	0	0	2	0	7	2	2	0
	II	14	15	5	6	8	4	17	9	8	7	0	1	2	6	2	1	17	2	1	0
	III	14	18	19	7	17	4	14	35	11	0	1	2	2	1	1	0	11	5	6	0
	IV	6	1	9	4	4	0	10	24	7	6	1	1	9	0	0	0	9	1	3	1
	V	35	9	2	8	17	0	12	74	6	3	0	2	13	13	0	12	73	4	0	0
4	I	5	5	5	11	2	0	3	20	4	2	4	0	6	3	1	5	2	3	1	0
	II	11	1	9	5	2	3	5	96	16	7	7	1	22	5	3	7	11	8	1	0
	III	11	27	31	15	5	6	7	10	21	7	9	2	23	12	11	3	8	6	1	0
	IV	6	6	7	7	0	0	2	47	24	9	8	1	11	9	10	6	6	4	3	0
	V	84	80	67	59	7	10	26	307	60	7	12	2	45	24	15	16	13	7	0	0

Appendix XII. Patterns of emergence, Severance, CO, 1983.

Treatment	Replication	Date															
		5/24	5/30	6/3	6/8	6/11	6/14	6/22	6/25	7/5	7/9	7/12	7/15	7/19	7/23	7/29	8/3
1	I	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0
	II	1	1	1	7	4	0	0	10	0	0	0	0	0	1	0	0
	III	1	2	7	7	4	2	4	0	0	0	0	0	0	0	0	0
	IV	0	1	4	6	5	1	2	0	0	0	0	0	0	0	0	0
	V	1	1	7	4	7	2	8	0	2	0	0	0	0	0	0	0
2	I	2	2	2	0	2	0	1	2	0	0	0	0	0	0	0	0
	II	0	1	4	0	3	0	0	4	0	0	0	2	0	0	0	0
	III	2	1	3	7	11	2	4	2	0	0	3	0	0	0	0	0
	IV	0	5	2	5	9	1	4	5	2	0	0	2	0	1	0	0
	V	1	1	3	6	2	0	4	5	0	0	0	0	0	0	0	0
3	I	2	1	3	4	2	0	6	0	0	0	1	0	0	1	0	0
	II	2	3	2	4	6	0	0	0	0	0	0	0	0	2	0	0
	III	1	0	4	7	6	0	7	0	0	0	0	0	0	0	0	0
	IV	0	2	6	3	5	3	7	0	0	0	0	0	0	1	0	0
	V	2	1	1	2	4	1	11	1	0	0	1	1	0	2	0	0
4	I	6	2	16	13	12	0	29	1	0	0	0	2	0	0	0	0
	II	2	9	11	2	3	0	7	0	0	0	1	0	0	1	0	0
	III	2	3	27	12	14	2	34	2	0	0	1	1	0	0	0	0
	IV	1	2	13	7	7	0	13	1	0	0	0	0	0	0	0	0
	V	0	2	0	3	2	1	2	0	1	0	0	0	4	0	0	0