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COMPARATIVE ECOPHYSIOLOGICAL SEED ADAPTATION OF THREE BARNYARDGRASS (*ECHINOCHLOA CRUS-GALLI* [L.] BEAUV) ECOTYPES.

By

KIPLANGAT J. RONO

A Thesis submitted to the Faculty of Graduate Studies of Dalhousie University in partial fulfilment of the requirements for the

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DEDICATION

To my parents, Mama Zedy Chepkemoi and the late Paul Kiprono Laboso, whose sacrifice, labour, love and discipline gave me the eyes for higher education and to see other parts of the world, something they wish but never succeeded in accomplishing. To my brother, Matthew Kipkirui Rono and the citizens of Mabasi for enabling me find my bearings in life, and Grace Chepkirui Rono and the kids for their patience, love and understanding in trying times. I hope one day they will understand my absence.

In fond and loving memory of Paul Kiprono Laboso, who did not live to see the success and vision he loved and cherished in his children.

BIOGRAPHY

Kiplangat J. Rono was born in Mabasi Village, Kericho District, Rift Valley Province, Kenya on May 25, 1955. He attended Mabasi Primary School before proceeding to Kabianga High School from 1971-75, then to Chania High School from 1976 to 1978.

In 1981 he went to India for further studies where he received his B.Sc in Agriculture from University of Rajasthan, graduating in 1984 and M.Sc in Botany from University of Udaipur, graduating in 1986. Currently, he is employed by the Kenya Agricultural Research Institute (KARI). He was granted a study leave from 1990-94 through sponsorship by KARI/CIDA scholarship, for the Ph.D degree at Dalhousie University, Canada.

The author is married to the former Grace Chepkirui Chepkwony and they have two children.

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ABSTRACT

Experiments were conducted under laboratory and greenhouse conditions to determine the longevity and germination pattern from seed burial, temperature effect, temperature and nitrate, temperature and water potential, and seeding depths and ecotype interactive effects, on seed germination and emergence; including photoperiodic effect, on barnyardgrass ecotypes originating from California (CA), Maryland (MD) and Prince Edward Island (PEI). Results indicated that the CA seed exhumed during the initial four months of burial had either germinated, died or rotted in the field. The MD and PEI ecotypes showed a seasonal cyclic germination pattern, corresponding to soil temperature changes. The temperature studies showed that the CA ecotype had over 80% germination at 10 to 40 °C, whereas the MD and PEI ecotypes displayed more than 80% germination at temperature between 15 and 20 °C, and decreased germination below 15 and above 20 °C. Temperature and nitrate interactive results, at 10-40 °C and 5-30 mM KNO_3, indicated that the CA ecotype had above 75% germination either imbibed in water or in KNO_3, hence suggesting that KNO_3 was not a factor in its germination. The MD and PEI ecotype germination, however were enhanced by the addition of KNO_3. The temperature and water potential interactive results indicated that the ecotypes displayed more than 86 and 80% germination at zero and -2 MPa, and decreased germination from -4 to -10 MPa, at 20 and 30 °C. The MD and PEI ecotype germination was affected more at 30 °C from -6 to -10 MPa, whereas the CA ecotype appeared better adapted at decreasing water potential and increasing temperature. The shoot and root lengths at 30 °C were generally longer than those at 20 °C. Seeding depth results indicated that highest percent emergence of more than 65% for all the ecotypes was obtained from 1 and 2.5 cm depths, and least percentages of less than 20% from 7.5 and 10 cm. Overall, the CA ecotype showed ability to emerge from greater depths, compared to the MD and PEI ecotypes. The photoperiodic effect showed that all the ecotypes under LD had vigorous vegetative growth, greater heights, large leaf area and greater fresh and dry weights, whereas the MD and PEI ecotype growth were severely inhibited, and the CA ecotype less inhibited under SD. Generally, these ecotype responses to different environmental factors reflect their adaptive strategies to their respective areas of collection.

GENERAL INTRODUCTION

Grass weeds are generally more troublesome than broad-leaved weeds in cereal crops (128). Based on Holm *et al.* (80), seven of the worst weeds on global scale are grasses. Four of these grasses are perennial. Barnyardgrass, an annual grass is ranked fourth globally. Two species of this annual of the genus Echinochloa (*Echinochloa colona* and *E. crus-galli*) each occur in about 60 countries (80). The reason attributed for grass weeds being more troublesome than broad-leaves is that grass weeds and cereal crops share similar ecological niches. Barnyardgrass, for example, has similar ecological preferences to that of rice, and young plants look similar (191). Also, several thousand years of hand weeding of rice in Asia may have selected for rice mimicry (14).

Barnyardgrass found infesting most agricultural crops in Atlantic regions appears to belong to more than one population. Floral observation and seed size showed that there are more than two groups. One group has green spikelets and the other pink. Among the groups with green spikelets, some plants have long awns whereas the others do not. In the group with pink spikelets, some plants showed spikelets having long awns while others do not. It was further noted that most of those groups with pink colouration have larger seed sizes (Personal observations).

Barnyardgrass has been known to spread rapidly. Its success is attributed to prolific seed set, seed dormancy, ability to grow and flower over a wide range of photoperiods, and relative resistance to herbicides (105).

The purpose of this research project was to determine the importance of some of

these adaptation factors to barnyardgrass growth and development using three barnyardgrass ecotypes originating from three contrasting geographical locations: California (CA), Maryland (MD) and Prince Edward Island (PEI). The project was done in the Atlantic region, to find out how some environmental factors could affect these ecotypes from different climates. The overall objective of this project was to characterize the seed biology and ecology of these ecotypes.

The sub-objectives of this research project were as follows:

1. To determine seed longevity and germination pattern of the three barnyardgrass ecotypes buried over a period of twenty-four months. The hypothesis was that these ecotypes would display similar longevity and germination patterns.

2. To determine effect of temperature under laboratory conditions on germination of the three ecotypes. It was hypothesized that ecotype would have similar germination response to temperature.

3. To determine the interactive effect of temperature and nitrate under laboratory conditions on the ecotype germination. The hypothesis was that ecotypes would respond similarly to more than one factor interacting together in influencing total germination.

4. To determine the interactive effect of temperature and water potential under laboratory conditions on the germination of the three ecotypes. Hypothesis was that ecotypes may display similar germination with declining water potential. Also, temperature and water potential interaction would influence the ecotypes germination performance.

5. To determine the effect of burial depths under growth chamber conditions on seedling emergence. The hypothesis was that burial depth would not affect ecotypes' seedling emergence.

6. To study the photoperiodic effect on growth and development of the three ecotypes under greenhouse conditions. The hypothesis was that the three ecotypes would display similar morphological response to photoperiod.

Chapter 1

GERMINATION PATTERN OF BURIED SEED OF THREE BARNYARDGRASS (*ECHINOCHLOA CRUS-GALLI* [L.] BEAUV) ECOTYPES.

INTRODUCTION

Barnyardgrass spikelets contain caryopses with associated palea, lemma and glumes. At maturity the surviving outer layers of caryopses form a hard covering (the caryopses coat) comprised of the suberized nucellar membrane, the aleurone, parts of the inner integument, exo- and endocarp layers of the pericarp. Within this protective covering are the embryo with attached scutellum, and the endosperm (117).

Caryopses are dormant when they are mature and require an afterripening period, that is a period of intense metabolic activity of dormancy-breaking processes, before they can germinate (43). High temperatures of 40 to 50 °C and low temperatures of 5 °C are known to overcome dormancy (174). Additionally, other factors like alcohols or nitrate treatment, prior to exposure of the seed to suitable thermic conditions (50), are found to enhance germination of dormant seed (85).

Buried seed of several summer and winter annuals are known to go through an annual cycle of decreased and increased dormancy (8, 86). In summer annuals, enforced dormancy, is alleviated during the winter, and induced again during the summer and

early autumn, thus the seedlings emerge during spring and early summer (15, 20,40, 85).

Seedling emergence studies in the field have shown that these cycles are largely controlled by temperature (16, 17, 40, 134). Germination of non-dormant seed may also show temporal patterns that relate to seasonal variation of different limiting environmental factors, for example temperature (169), soil moisture (158), or burial depth [in the sense that tillage may change] (79).

Cyclic changes in dormancy in response to temperature have been investigated primarily in annuals, most of them weeds of cultivated land, where burial and exhumation are also part of the annual cycle (110). Only a few perennial species have been investigated (18, 19, 21, 22).

Like many troublesome annual weeds that reproduce only by seed, the success of barnyardgrass as a weed is determined by seed persistence in the soil, rate of decay, and seed dormancy response to seasonal changes. Seed dormancy has been reported to range from 0 to 48 months. Viability of 100% has been recorded after 6 to 8 years (105). Dawson, (43) revealed that a few seed were able to germinate 13 years after burial in the soil; however viability had declined to 0 after 15 years in irrigated soil. Rahn *et al.* (134) found no evidence of deterioration in viability of barnyardgrass seed after storage for three years in dry or wet loam soil at a depth of 8 and 25 cm; respectively, in a glass jar in the laboratory.

Holm *et al.* (80) reported that generalizations about seed dormancy of barnyardgrass are meaningless, for this characteristic is specific to each ecotype (group of plants within a species adapted genetically to a particular habitat but able to cross

freely with other ecotypes of the same species) found around the world.

The objective of this experiment was to determine the longevity and germination pattern of buried seed of three barnyardgrass ecotypes from California (CA), Maryland (MD) and Prince Edward Island (PEI), buried for twenty-four months, under typical field conditions prevailing in Central Nova Scotia, which has a modified continental temperate climate.

It was hypothesized that these ecotypes would display similar seed longevity and germination patterns.

MATERIALS AND METHODS

Seed source[1]. The CA ecotype seed were obtained from seed harvested in 1989 at a latitude 37 ° 60' N, longitude 123° 18' W and altitude of 488 m above sea level; the MD ecotype seed, collected in May, 1988, were obtained at a latitude 39° 25' N, longitude 77° 25' W, and altitude of 91.5 m above sea level and PEI ecotype seed were collected in June, 1990, at a latitude 46° 20' N, longitude 62° 40' W, at sea level.

All seed lots were kept in the dark in paper bags, at 20±1 °C room temperature till the time of conducting the experiment.

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[1]Seed source: CA ecotype from San Jose Valley,CA; MD ecotype from Dept. Of Agric. Foreign Disease-Weed Sci. Res., Ft. Detrick, Bldg. 1301, Frederick, MD 21702., PEI ecotype from Agric. Canada, Res. Stn., Box 1210, Charlottetown, P.E.I., Canada, C1A 7M8.

Habitats. The barnyardgrass seed for the California ecotype were collected in 1988 as "certified" seed by Valley Seed Company, Fresno, CA. They were obtained from cropland which had been under different crop rotations over the years (Valley Seed Company communication).

Seed for Maryland ecotype (MD) were from greenhouse grown plants exposed to 14 hrs photoperiod and 660 to 700 μmol m^{-2} s^{-1} fluorescence lights. They were planted in March, 1988 and harvested in May, 1988 as seed lot D-5-88. At the time of harvest, seed were 80% dormant. This ecotype had been obtained earlier as a genetically pure bred plant of a 1981-82 clone from an Illinois Seed Company (G.R. Leather, personal communication).

The seed for Prince Edward Island ecotype (PEI) were collected from a crop production field at Charlottetown Research Centre, Charlottetown, PEI. The field has been in different rotations over the years, but had been mainly in potatoes/grain/forage grasses for the past 25 years. Prior to that the area was in free range chickens; barnyardgrass may have been a contaminate in chicken feed (J.A. Ivany, personal communication).

Seed weight. Four lots of fifty seeds of each ecotype were weighed before the start of the experiment. The CA, MD and PEI seed weighed 150, 80 and 90 mg per 50 seeds, respectively. In preliminary tests at room temperature, 75 to 80% germination was obtained for all ecotypes.

Chromosome evaluation. Fifty seeds of each ecotype were sent to Biosystematics Research Institute, Ottawa, for chromosome evaluation. The assay report showed that the three ecotypes each have 2n=54 (C.W. Crompton personal communication), hence confirming an earlier work (13)

The PEI ecotype was not available in sufficient quantity for the experiment; hence, seed was increased by growing the ecotype in the greenhouse. This was not necessary for the CA and MD ecotypes.

Batches of 100 seed/ecotype were placed in nylon net sachets[2]. Single sachets containing seed of each ecotype, were buried to a depth of 7 cm in soil in a 15-cm diameter clay pots having drainage holes. Direct contact of seed with nylon bags during incubation does not affect germination (112). Each pot contained a sachet, of each ecotype, and all were plastic tagged for ease of identification. The experiment was a randomized complete block design, with four replications. Seed were buried on 11 October, 1991 on a well prepared soil in a plot measuring 8 m by 3 m., containing 6 rows with 16 pots per row. Monthly soil temperature at 10 cm depth was recorded and precipitation data was obtained from the meteorological station, located approximately 300 meters from this site. Pots were covered with aluminum wire-mesh to give protection from rodents, then buried and three meter bamboo pegs were placed next to each pot to facilitate their spotting during retrieval, both in winter and summer over 24

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[2]Nylon Mesh HC3-151 40" wide of Tetko Inc. (B & SH Thompson and Coy. Ltd., Scarborough, Ontario, Canada, M1P 3B3).

months.

Dormancy changes of buried seed. Pots were exhumed on the 15th day of each month. Seed were protected from exposure to daylight during exhumation and transport. Seed were opened in a dark room under a green safelight (94).

Germination in the soil was determined by counting the non-germinated seed in each sachet and subtracting this figure from the total buried. To avoid infection of non germinated seed by micro-organisms like bacteria and soil fungus (especially *Fusarium spp.*), seed were treated with 10% sodium hypochlorite solution for 15 minutes and rinsed in distilled water before transferring onto filter paper. A germination test was performed on these seeds, in 9 cm Petri dishes containing two layers of Whatman #1 filter paper[3], moistened with tap water to saturation. Dishes, kept at a fixed temperature (20 ± 1 °C) were wrapped with aluminum foil to exclude light. Final percent germination was determined after 14 days of incubation. Protrusion of the radicle was the criterion for germination. Seed that did not germinate after 14 days were removed, washed with distilled water, cut in half along the long axis, and one half was dipped in 0.1% triphenyl tetrazolium chloride solution, while the other half was discarded. Seed that showed embryo colouration after 24 hours were considered viable and therefore dormant, the rest were considered non-viable.

Statistical analysis. Percent germination data were arcsin transformed to harmonize variability within data. Mean germination percentages and standard errors were

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[3]Whatman International Ltd., Maidstone, England.

calculated as per Baskin *et al.* (17, 20).

RESULTS AND DISCUSSION

Germination response to seasonal changes. During the first four months of retrieval, virtually all seed of CA ecotype had either germinated, died or rotted (Fig. 1.2). This indicates that the CA seed were not in a state of dormancy at the time of burial. This may be because dormancy had been broken during the three years of storage since harvest. During this initial seed exhumation, the mean daily temperature recorded for October, November and December, 1991, was 11.5, 7.1 and 1.7 °C, respectively. Most of the samples of the CA seed retrieved in the following twenty months were empty seed coats. Data for the CA ecotype used in figure 1.2 and 1.3, was for seed that had germinated in the field during the first four months.

Seed of the MD ecotype were non-dormant at the time of burial, and were able to attain a peak of 68% germination in the incubator at the first sampling date (Fig. 1.1). Thereafter, the germination declined continuously, until April at which time it was 27% germination. Seed germination followed a clear pattern in relation to the soil temperature, displaying 70% germination one month after burial, and as field soil temperature began to fall so did MD seed germination (Fig.1.1). This suggests that germination in the incubator is somehow related to the soil temperature. The number of seed germinating increased in May, June and July, attaining a peak of 45% in July, when the soil temperature was 15 °C. Soil temperature continued to increase during August, and seed became dormant again. Positive tetrazolium assays indicated that seed exhumed

during this time were viable but dormant. The prevailing soil temperature, recorded as more than 15 °C, might have exceeded the seed requirement. It is assumed that increase in soil temperature, decrease in soil moisture and other related factors interacting within the soil environment led to seed undergoing a dormancy state that resulted in lack of germination in July and August. Under controlled environmental conditions, however, barnyardgrass seed were capable of germinating at temperatures ranging from 10-40 °C (80, 91, Rono Chp. 2).

The MD seed dormancy imposed in summer was broken during September through December as the ecotype regained the ability to germinate, reaching a peak of 33% germination, in November. Field soil temperature for October and November was 9.5°C and 4.4°C, respectively. During winter, some seed again germinated when imbibed in the incubator.

The data suggest that buried seed samples of the MD ecotype were of a mixed population and some seed within this population were capable of germinating even after being subjected to extreme cold conditions. It is assumed that besides a rise in soil temperature, accumulated chilling requirements to end dormancy may have been satisfied during.

Germination in the incubator increased during April, May, June and July, with peak germination of 34% in July. Soil temperature recorded for June and July was 14 and 18 °C, respectively. Similar to the previous year, germination plummeted during August, September and October, 1993. This might indicate that again soil temperature during July and August caused the seed to become dormant because only 3% germination

was recorded in August when soil temperature was at its peak at 19 °C (Fig. 1.1). The factor(s) responsible for this dormancy may be interacting factors within the soil environment, such as temperature, oxygen, moisture and burial effects.

The two years cumulative percent data for field and incubator seed germination, dormant, and dead seed showed 21, 27, 49 and 4% for first year, compared to 0, 19, 33 and 43% for second year, respectively (Fig. 1.2, 1.3). Data indicate that the field and incubator seed germination as well as dormant seed were comparable in the two years. Additionally, 4% dead seed in the first season as compared to 43% recorded for the second season, shows that the MD ecotype buried seed survival decreased with the increasing burial duration (Fig. 1.2, 1.3).

The PEI seed appeared innately dormant at the time of burial, such that germination initially was low, and over time this dormancy was broken. At initial sampling in November, 1991, 14% of the seed germinated in the incubator (Fig. 1.1). Its germination increased to 81% in December and reached a peak at 84% in January, 1992. Thereafter germination declined in February to March reaching lowest level of 41% in May 1992 (Fig. 1.1).

During the first season of seed burial, 3% field germination was recorded, compared to 30% and 21% for CA and MD ecotypes, respectively. This support the above suggestion that the PEI seed, by the time of burial were newer seed (four months old), hence more dormant compared to either the MD or the CA seed which were two and three years old, respectively (Fig. 1.2, 1.3).

The PEI seed germination increased in June to 65%. Between March and June

of second year, soil temperature increased from -1 to 15 °C. The rise in soil temperature and other interacting environmental factors in the soil appeared to have stimulated the release from dormancy. In August, 1992, there was no germination recorded for the PEI seed. Lack of germination indicates that increased soil temperatures beyond 15 °C in summer, possibly coupled with decreasing soil moisture in the field, might have imposed secondary dormancy. Positive tetrazolium results on seed exhumed in August and September, 1992 showed that seed were dormant.

Gradual decrease in soil temperatures from August towards November, 1992, led to stimulation of some seed which had been dormant to shift to a non-dormant state. Seed germination in the incubator during September, October, November and December was 11, 12, 16, and 31%, respectively. Temperature by then had fallen to 1.5 °C (Fig. 1.1). This observation followed a similar pattern as for MD, suggesting a cyclic seasonal change had been attained, with the seed germination having come full cycle. Dawson *et al.* (42) and Ogg *et al.* (121) had reported a similar pattern for barnyardgrass.

In January, February, and March, 1993 the PEI seed germination in the incubator was 23, 14 and 11%, respectively, indicating a decline. However, with warming of soil temperature, its germination increased. Germination recorded for April, May, June and July was 16, 25, 57 and 67% respectively (Fig. 1.1). Soil temperature by then had reached 19.2 °C in August, and as previously observed, this led to seed dormancy.

During the first season of seed burial; the total germination in the field and incubator germination, as well as dormant (induced) and dead seed were 3, 47, 51 and 2% as compared to 0, 23, 43 and 34% for second season, respectively. There was a

higher percentage for incubator germination and dormant seed during the first season as compared to high percentage for dormant and dead seed during the second year. Dead seed of 34% during the second year as compared to 2% during the first year, suggests that as the duration of PEI ecotype burial in the field increased, more seed die (Fig. 1.2, 1.3).

It should be pointed out that the percentage obtained for the MD and PEI ecotypes for the dormant and dead seed was from subtracting seed that germinated in the field and those in the incubator. The tetrazolium positive assay gave us the number of dormant seed. The remaining lot were considered dead.

The CA seed appeared to be completely non-dormant when buried with at least 40% germination in the field during the first four months, while still buried. This may be due to the effect of seed age (the CA seed at time of burial were 3 years old) which might have led to deterioration in dormancy. In contrast, seed of the MD and PEI ecotypes were probably innately dormant at the time of burial or became dormant soon after burial. The data indicates that PEI seed were dormant at burial. Seed were four months old when they were buried, in contrast to the MD seed, which were 3 years old, germinated at high percentage after one month in the soil suggesting its seed might have reduced in dormancy.

Seed have two major purposes: dispersal of new individuals of the same species with potential for colonisation of new habitats, and maintaining the survival of the species through conditions when the external environment is not conducive to active growth (122). Results obtained for barnyardgrass ecotypes agree with previous observations (17,

20, 40, 42, 85, 110, 134) that dormancy (induced dormancy) in buried seed can undergo a change in the field, which makes it possible for viable seed to remain through the burial period as a persistent seed bank. The CA, MD and PEI ecotypes results showed two types of seed banks: *Transient seed bank*, in which none of the seed output persists in the habitat in a viable condition for more then one year and *Persistent seed bank* in which some of the component seed are more than one year old (68, 69). The CA ecotype, apparently belongs to the former type (*Transient*), further sub-divided into *Type 1-2*, with its seed characterized by: (i) large size; (ii) lack of pronounced after-ripening or dormancy; (iii) capacity to germinate rapidly over a wide range of temperatures, (10°-40°C) (Rono Chp. 2). Grime, (68) referred to it as *Type 1a*, where seed in the seed bank lack dormancy thus facilitating rapid germination soon after seed fall and allowing exploitation of grasslands subjected to seasonally predictable damage by drought.

The germination of CA ecotype in the field might be attributed to effect of seed age, lack of dormancy or burial at a time when the soil temperature at 12 °C was still favourable for seed germination. Keeley *et al.* (90) reported that whenever the soil surface remains moist for periods of 1 to 2 weeks, emergence of barnyardgrass may be expected in California from the first of March when temperature is at 10 to 15 °C. There is also evidence that germination of buried seed *in situ* is often brought about by a response to the increased diurnal fluctuations in temperature which may result from the removal of the insulating effect of foliage, litter, or humus layers from the soil (69). It is assumed that the CA ecotype has adapted to an environment very different from that

of the MD and PEI ecotypes. Geographically, California is warmer in winter compared, for example, to the continental climate prevailing in Atlantic Canada regions. This might be a reason why the CA ecotype has no requirement for dormancy during winter. The other two ecotypes, however must undergo dormancy conditions if they are to survive the winter months in the region.

The MD and PEI ecotype results suggest that these ecotypes belong to the latter (*persistent*), referred to as *Type 3a*, (68) characterized by seed germinating in May through October with a small proportion becoming buried, and persistence in the soil. Germination occurs rapidly over a wide range of temperatures (for the MD and PEI: minimum 10, optimum 20 and maximum 40 °C, [Rono Chp. 2]).

Small seed size, and a light requirement for germination, are conducive to burial and persistence of buried seed. McRill *et al.* (109) pointed out that small seed are more likely than larger ones to be washed into small fissures in the soil surface and to be buried by the activities of the soil microfauna. The capacity to germinate in darkness in response to diurnal fluctuations in temperature appears to facilitate the colonisation of gaps in vegetation (168). The advantage of the persistent seed bank is obvious in ruderal species, barnyardgrass included, of the intermittently open habitats of farmland, since long-term survival of their populations more often depends upon the ability to remain in a dormant condition through periods in which the habitat is occupied by closed cover perennial species (69). The inhibition of germination for MD and PEI, might be attributed to the lack of promotive factors such as temperature and (or) light at increasing soil depths (27, 86).

Dawson *et al.* (43) reported a phenomena that was also observed in these three ecotypes. All ecotypes exhibited the presence of hulls which were intact (though empty for CA ecotype). Mummified caryopses became more common in the MD and PEI ecotypes as the duration of burial extended from one month to twelve months. At the end, samples of buried seed displayed almost a quarter mummified caryopses. They retained their original size and shape, but were black and crumbly like charcoal or chalky within. It is not known whether this was the result of some microbial parasitism or other related factors within the soil.

The results presented here for the MD and PEI ecotypes showed that seasonal changes in the environment influences the dormancy characteristics of the seed, which in turn causes a change in the sensitivity of the seed to their environment (86). There was a consistent pattern of germination of buried seed with the emergence from seed present in the soil with most seedlings appearing in April, May or June and sporadically until early autumn. This view was also shared by Robert *et al.* (141), when working on *Plantago major*, *P. lancelota*, *Silene alba*, *Utrica dioica* and *Stachys sylvatica.*

Overall, the outcome of the ecotypes' germination under buried conditions might have been affected by difference in age of the seed. The PEI ecotype seed were newer and probably innately dormant, whereas the MD and CA ecotype seed were old, hence their dormancy might have reduced over time.

Ecological and weed control implications. Transient seed banks, of which the data hypothetically suggests the CA ecotype may belong, are composed of seed that germinate when exposed to favourable conditions (69). If this was true, an infestation of the CA

ecotype might be eradicated in one season if all growing plants are prevented from setting mature viable seed. In practice, this may not be possible because of its likely chances to adapt genetically to any interference (herbicide use or other factors). Also, in most cropping systems, weed species are often allowed to set their seed. The ability of the CA ecotype for prolific seed production, ability to set mature viable seed in the field, as well as crop seed contaminant, are adaptations that will help it to survive. Additionally, it is more allied to the prolonged warm temperatures than the fluctuating winter temperatures. Its wide range of temperature (10-40 °C [Rono Chp. 2]) for seed germination is an asset, especially where competition and shading might be factors. Unless its survival mechanism is addressed, it will continue to pose a challenge to those trying to control it.

The persistent seed bank, of which MD and PEI ecotypes data suggest they belong, is very difficult to eradicate. Seed longevity, and the fact that a large proportion of the buried seed are dormant explains their success, and the difficulty to control them. Additionally, the task of forecasting weed infestation based on the seed bank is made even more difficult. Also the MD and PEI ecotypes, like many other troublesome weeds, germinate in flushes and therefore might be more of a challenge to control in their areas of origin than was previously thought.

Simpson, (152) stated that to argue that dormancy can be attributed to any single factor (e.g. a hormone, membrane, seed coat, or temperature) ignores the reality that a seed, like every other biological entity, is an exceedingly complex and dynamic living system situated, at all times, within a complex and ever-changing environment.

Therefore, to develop an effective integrated weed management system for controlling barnyardgrass (CA, MD and PEI) ecotypes, a better understanding of the factors that control the level of dormancy in the seed bank, and a knowledge of their emergence patterns as developed in this study is needed.

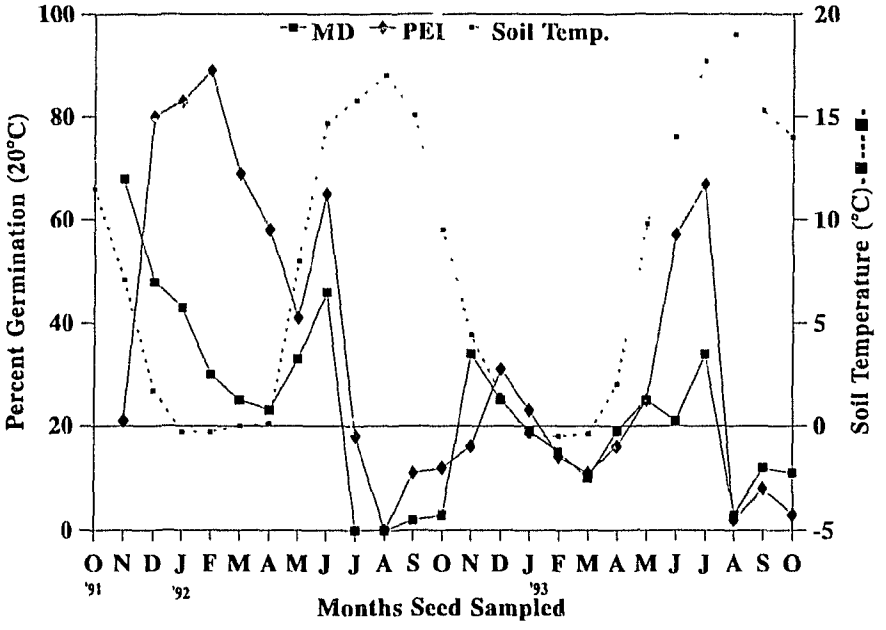

Fig. 1.1. Mean monthly maximum soil temperatures (--■--■--) and percent germination in the incubator for exhumed seed of the MD (-■-) and PEI (-▲-) ecotypes over 24 months. Data for the CA ecotype germination were not included in this figure.

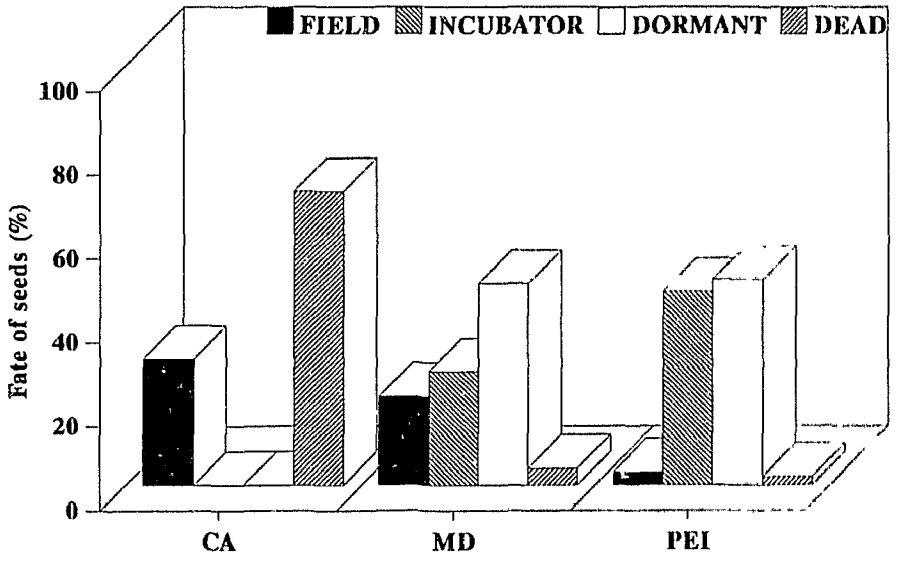

Fig. 1.2. Ecotype cumulative germination over first 12 months of burial.

Fig. 1.2. Mean percent seed fate for (i) Germination in the field, (ii) Exhumed seed and allowed to germinate in incubator at 20±1 °C, (iii) Dormant and (iv) Dead seed after exhumation, over the first 12 months of burial for the CA, MD and PEI ecotype.

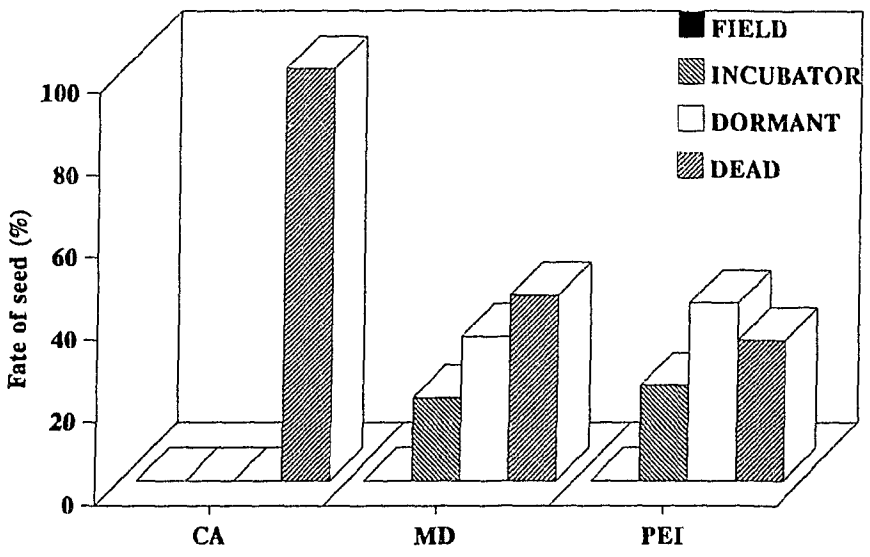

Fig. 1.3. Ecotype cumulative germination over second 12 months of burial.

Fig. 1.3. Mean percent seed fate for (i) Germination in the field, (ii) Exhumed seed and allowed to germinate in incubator at 20±1 °C, (iii) Dormant and (iv) Dead seed after exhumation, over the second 12 months of burial, for the CA, MD and PEI ecotype.

Chapter 2

EFFECT OF TEMPERATURE ON SEED GERMINATION OF THREE BARNYARDGRASS (*ECHINOCHLOA CRUS-GALLI* [L]. BEAUV) ECOTYPES.

INTRODUCTION

Many seeds do not germinate when placed under conditions which are normally regarded as favourable to germination, namely an adequate water supply, a suitable temperature and the normal composition of the atmosphere. Such seed are said to be viable, as they can be induced to germinate by various special treatments, and are said to be dormant or to be in a state of dormancy (107).

Basically, seed dormancy is the inability of seeds to germinate under favourable conditions. This condition may be due to one or several causes: (i) immature embryos, (ii) seed coats impermeable to water and/or gases, (iii) inhibitors, (iv) physiological immaturity, (v) light sensitivity or (vi) mechanical restriction by seed coats. Dormancy may also be secondarily induced by adverse environmental conditions (101). Wareing (175) defines dormancy as "Instances where the seed of a given species fails to germinate under conditions of moisture, temperature and oxygen supply which are normally favourable for the later stages of germination and growth of that species". Harper (74) indicated that "some seeds are born dormant, some acquire dormancy and some have dormancy thrust upon them". Harper (74) and called these three categories "innate",

"induced" and "enforced" dormancy. Innate dormancy is referred to at times as 'primary dormancy', induced and enforced dormancy as 'secondary dormancy'. Innate dormancy occurs when seeds are in a dormant state on release from the parent plant, whereas induced dormancy is used to describe the situation in which dormancy develops in response to some experience after release from the parent plant (31, 74).

Other terms like "relative dormancy" and "conditional dormancy", (which are synonymous are) conditions where a seed is able to germinate under a restricted range; for example, barley when freshly harvested has been shown to germinate at 10 °C but not at 15 °C, but after dry storage for some time, there is a widening of conditions under which germination will occur (31).

Germination is a complex process that is dependent upon several biological and environmental factors including temperature; which strongly affects primary dormancy and onset of secondary dormancy, in that seed which are primarily dormant undergo a period of after-ripening, and gradually this dormancy broken with the rise in temperature. Temperature fluctuation or shifts often promote germination (54).

Freshly collected seed of barnyardgrass exhibit innate dormancy, the duration of which varies considerably (13, 134). Rahn *et al.* (134) demonstrated that fresh seed had only 0.3 to 1.4% germination. Storage of seeds for 4 to 8 months increased germination to 19 and 44%, respectively. The dormancy has been attributed to the pericarp and epidermis (7). Various effective methods of breaking dormancy include removal of the outer seed covering or pericarp, freezing and thawing for 4 days, exposing moist seeds to 49 °C for 5 hours, soaking them in acetone for 20 minutes, in concentrated H_2SO_4 for

8 minutes, or in water for 4 days (134). Seed of barnyardgrass germinate over a wide range of temperatures, from 13 to 40 °C (80, 105, 134). The optimum temperature for seed germination from several regions had been estimated to range from 32 to 37°C, and germination decreases sharply at temperatures below 10 and above 40 °C (105). Arai *et al.* (7), found that the maximum temperature for germination was 45 °C, optimum was 30 to 35 °C, and minimum was 10-15 °C. Roche *et al.* (142), in Washington, obtained optimum germination with alternating temperatures of 20 to 30 °C, with light. The rate of germination of barnyardgrass seed is markedly affected by temperature. At 20 °C constant temperature the germination of barnyardgrass var. *praticola* seed, wintered in soil, was entirely dependent on exposure to sunlight or fluorescent light. The germination of barnyardgrass seed was not reduced by exposure to 60 and 80 °C temperatures for one hour but exposure to 100 to 130 °C for the same length of time significantly lowered percent germination (105).

The production of large numbers of easily dispersed seed, long seed viability, ability to flower under a wide range of photoperiods, and seed germination under a wide range of temperatures, contribute to the success of barnyardgrass as a weed (80, 105). Apparently the place of origin has an influence on barnyardgrass germination response.

The objective of this set of experiments was to determine the effect of temperature on germination of three barnyardgrass ecotypes collected from California (CA), Maryland (MD) and Prince Edward Island (PEI).

MATERIALS AND METHODS

Seed source. The CA, MD and PEI seed were obtained from greenhouse grown plants, seeded on 12 February, 1992 and harvested on 29 May, 1992. Ten seed for each ecotype were seeded on an amended steam sterilized soil (ratio of 2:1) having a pH of 6.4, filled into twenty-four 15 by 15 cm plastic pots (8 pots per ecotype). The plants were latter thinned in the third week after seeding, to three plants for each ecotype per pot. The greenhouse temperature was kept constant at 20/15$\pm$2 °C (day/night) and the growing plants were provided with 16 hrs long-day photoperiod and 600 to 670 μmol m^{-2} s^{-1}. The plants were watered daily when necessary, and flushed once every week with prepared nutrient solution of 15-15-18 (N-P-K) at the rate of 200 ppm of water. The mother plant seed source for the three ecotypes, is described in to Chapter 1. All the seed lots were kept in paper bags in the dark at room temperature prior to the time of conducting the experiment. The seed used were four months old at the start of this experiment. This experiment was initiated on 6 October, 1992 and terminated on 14 December, 1992.

Influence of temperature. Fifty seeds of each ecotype, were placed in 9-cm Petri dishes, on two layers of Whatman #1 filter paper[1], moistened with tap-water. The experiment was prepared in a dark room under a green safe light. Petri dishes were wrapped with aluminium foil to exclude light, and seed lots were allocated to two

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[1]Whatman International Ltd., Maidstone, England.

incubators set at 0 to 45 °C constant temperatures, at increments of 5 °C. The design was a split-plot with temperature levels as main-plot, and ecotypes as sub-plots. The treatments were replicated four times (one dish per replication for each ecotype). Germination was scored simultaneously each day for seven days, under a green safe light, with protrusion of the radicle to about 2 mm as the criterion for germination. Seed that had germinated were counted and discarded, whereas the seeds that had not germinated after seven days were removed, and cut into halves, along the long axis. One half was soaked in 0.1% triphenyl tetrazolium chloride solution. Those embryo halves that took the red stain after 12 hrs were considered viable but dormant, the rest were considered non viable. Total germinated seed were converted into percentages.

Statistical analysis. Final percent germination data were arcsin transformed to harmonize the variability within the data. Transformed data were subjected to a general linear model procedure of SAS (Statistical Analysis System) and means were separated using LSD (0.05). Main effects and interaction were tested with the appropriate error terms.

RESULTS AND DISCUSSION

Significant ($P > 0.0001$) main effects of temperature, ecotype and ecotype by temperature interaction were detected for germination data. Incubator and any factor involving its interaction had no effect on germination (Table 2.1). The results indicates that the effect of temperature on germination varied among ecotypes. The CA ecotype had more than 90% germination at temperatures between 10 to 40 °C, whereas the MD

and PEI ecotypes showed above 90% and 80% germination, respectively at 15 to 20 °C. Overall, the MD and PEI ecotypes showed more than 75% germination at temperatures between 15 and 35 °C, but germination decreased below 15 and above 30 °C (Fig. 2.1). These results confirm previous studies by other workers (80, 90, 105) who reported that seed of barnyardgrass germinated over a temperature range of 13 to 40 °C. They further reported that the optimum temperatures from several regions range from 32 to 37 °C and germination decreased sharply at temperatures below 10 and above 40 °C.

The rate of seed germination at 10 °C was very slow; the CA ecotype took five days to attain 97% germination, compared with the MD and PEI, attaining 45 and 35% germination, respectively, after seven days. All ecotypes germinated faster at temperatures above 15 °C, compared to lower temperatures.

Germination over a wide range of temperatures (Fig. 2.1), obtained in this study, agree with results of Maun *et al.* (105) and Rahn *et al.* (134). Holm *et al.* (80), however pointed out that ecotypes showed different levels of temperature responses. It was apparent in this study that, though all ecotypes exhibited germination over a wide range of temperature, the percentage germination was markedly affected. The CA ecotype displayed greater temperature tolerance by germinating with greater percentages from 10° to 40 °C, and exhibited very little dormancy. Keeley *et al.* (90) reported that the germination of a high percentage of barnyardgrass seeds under controlled temperature regime of 15/10 °C accounts for the early emergence of this weed in California in March when air and soil temperatures do not exceed 14 and 17 °C, respectively. The MD and PEI ecotypes on the other hand showed germination minimum at 10 °C,

optimum at 20 °C and maximum at 40 °C. Additionally, they exhibited greater dormancy at temperatures below 10° and above 30 °C.

There was no germination detected at 5° or 45 °C (Fig. 2.1), for all ecotypes, and the explanation for this apparent lack of germination is still obscure. Di Nola *et al.* (49) found that a brief exposure of dormant barnyardgrass seed to 46 °C, affects the composition of soluble and membrane-bound proteins in the cell, and thus stimulates subsequent germination at favourable temperatures. These changes occur during the transition of the seed from a dormant to a non-dormant state and are reversed when the seed are exposed to the same temperature for prolonged periods of time, which inhibits subsequent germination. Di Nola *et al.* (45, 46, 47, 48) further found that a brief exposure to 5 °C during imbibition strongly affects membranes and ultra-structural changes in the embryonic axis cells of *Pisum sativum* L. (Pea) seeds, ultimately delaying subsequent germination at favourable temperatures.

Mayer *et al.* (107), states that changes in membranes or denaturation of protein might be the cause of seed failure to germinate at low or high temperatures. Di Nola *et al.* (49) and Mayer *et al.* (107) divergent views may assist in resolving some causes of seed failure to germinate at low or high temperatures.

Ecological implications. The CA ecotype temperature tolerance and ability to germinate at temperatures as low as 10 °C and as high as 40 °C, demonstrates how successfully this weed has adapted over time to the local environment. Furthermore, the results suggest that it will germinate throughout the year in the field in California, provided

other environmental requirements are met. Though this may be a positive asset for the weed in its early establishment, this factor may expose the weed to other environmental hazards. The CA ecotype capacity to germinate with higher percentages in the dark may indicate that light is not a limiting factor to its germination, and could reduce its ability to accumulate seeds in the soil seed bank.

The MD and PEI ecotypes on the other hand, appeared adapted to temperate conditions and germinated well when incubated under temperatures typical of warm spring temperatures (15 to 20 °C) attaining their optimum at 20 °C. They also exhibited very high seed dormancy at unfavourable temperature (below 10° and above 30 °C), so therefore are capable of accumulating considerable amounts of seed in the seed bank.

Agricultural implications. The fact that CA ecotype does germinate over a wide range of temperatures suggests an ability to maximize its reproductive potential, to get established, and utilize limited natural resources for growth, as long as the environmental conditions are favourable. This may confer some distinct competitive advantage in relation to crops. This ecotype, however, may not be a serious problem in cooler climates because of its inability to accumulate dormant buried seeds during cold seasons and as a result seed reserve may be depleted.

The MD and PEI ecotypes ability to accumulate considerable amounts of dormant seeds below 10 and above 30 °C, suggests a capability for a large reserve in their seed banks, increasing the difficulty to eliminate them. This characteristic is an invaluable asset to these ecotypes since they are capable of surviving cropping and cultivation as

buried seed. Once the spring season starts, a few seeds will germinate in flushes, and weed flushes will occur throughout the cropping season.

Table 2.1. Ecotype, temperature and their interactive effect on germination of three barnyardgrass ecotypes. Data arcsin transformed.

Source	Df	MS	F-value[a]
Model	41	1735.7	30.7*
Error	126	56.6	
Incubator(BK)	1	19.0	0.34[ns]
Ecotype (E)	2	18538.1	20823.1*
Error (BK x E)	2	0.9	0.02[ns]
Temperature (T)	6	3670.1	673.5*
Error (BK x T)	6	5.4	0.10[ns]
E x T	12	994.0	142.1*
Error (BK x E x T)	12	7.0	0.12[ns]
		R-square 0.91	

[a] *, significant at $P < 0.0001$.

ns= not significant at $P<0.0001$

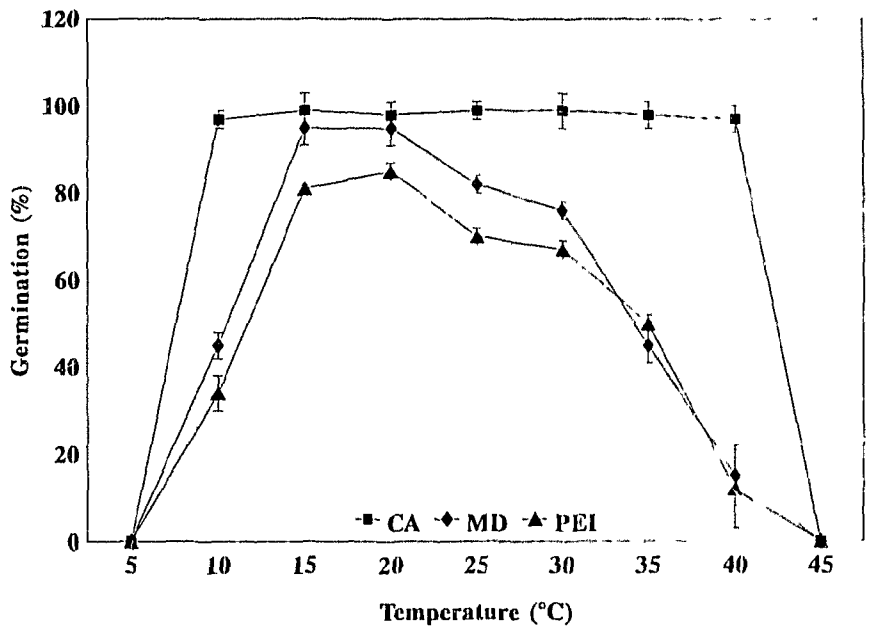

Fig. 2.1. Effect of temperature on seed germination (actual percentage) of three (CA, MD and PEI) barnyardgrass ecotypes. Vertical bars are standard errors (±SE).

Chapter 3

TEMPERATURE AND NITRATE INTERACTIVE INFLUENCE ON GERMINATION OF THREE BARNYARDGRASS (*ECHINOCHLOA CRUS-GALLI* [L.] BEAUV) ECOTYPES.

INTRODUCTION

Many important, successful weeds, barnyardgrass included, have viable but dormant seed which remain in the soil for variable periods and may accumulate to population densities as high as 10 to 100 million per hectare (135, 179). Most of these seeds exhibit sporadic release from dormancy, which leads to sporadic emergence of weed seedlings from the soil-borne reservoir of dormant seed. This creates a formidable obstacle to efficient and lasting weed control, and therefore repeated measures are required to keep the weed population under control (12, 145). Efficiency of weed control could be improved if reliable methods were available to induce synchronous germination of dormant seed in the field (144). Many chemicals have been known to overcome weed seed dormancy under controlled environmental conditions (27, 139). Ethylene and nitrate, for example, are the most promising among very limited numbers of dormancy-breaking chemicals that are suitable for field application (53, 55). Agricultural use of most germination stimulants is impractical because of their high costs, toxic effects in the environment, and difficulty of field application (144). Field applications of nitrate have been generally unsuccessful in inducing adequate increases

in weed seed germination (62, 150) although some stimulative effects have been reported (151).

The physiological role of KNO_3 in promoting seed germination is not clearly understood. Some workers are of the opinion that KNO_3 treatment renders the seed more susceptible to the promotive effects of light and alternating temperatures to which the seed may be exposed during germination (100). Hendricks *et al.* (75), proposed that nitrate action in seed germination depends on nitrite or hydroxylamine or nitric oxide produced from nitrate reduction to nitrite, rather than a reduction to ammonium ions or a process of reduction *per se*. Adkins *et al.* (2), argued that nitrogenous compounds of higher nitrogen oxidation level (sodium nitrate, potassium nitrate and nitrite) are probably active by virtue of their ability to act as electron acceptors, and by so doing induce oxygen uptake by seed. Roberts (136, 138) proposed that nitrate acts as an oxidizing substrate in a metabolic regulatory process involving NADPH - $NADP^+$ in the pentose pathway of glucose metabolism. The pentose shunt and nitrate as electron acceptor were proposed by Roberts *et al.* (139). Also, alternative respiration (58, 59, 60, 171, 188) has been proposed as avenues by which various nitrogen compounds act as agents of dormancy-breaking . However, this pentose shunt hypothesis is not supported by the latest evidence (1, 65, 170); therefore the requirement for alternative respiration as a prerequisite for dormancy breaking by nitrate and nitrite has been questioned (3). These explanations on the effects of different temperature levels and KNO_3 concentrations, might shed some light in the present study on seed germination in the dark. It might indicate whether the three ecotypes have the same habitat, that is, arable or transient,

and what effect nitrate fertilization has on barnyardgrass ecotypes seed germination

Dormancy in any one weed species may be terminated not just by one factor, such as light, but by a combination of factors such as chilling, fluctuating temperatures, or after-ripening. It is commonly found that two or three factors interact to release seed from dormancy (27). *Phytolacca americana* seed, for example, respond only marginally to light, nitrate, or alternating temperatures, but a combination of all three factors succeeds in breaking dormancy (157).

Because large numbers of weed seed in the soil are below the soil surface and not exposed to light, it was decided to investigate the two factors of temperature and nitrate that might influence barnyardgrass seed germination in the dark. The objective of this set of experiments was to determine in the dark the temperature by nitrate interaction on seed dormancy of three barnyardgrass ecotypes originating from California (CA), Maryland (MD) and Prince Edward Island (PEI).

MATERIALS AND METHODS

Seed source. The seed source and their storage condition prior to conducting the experiment are described in Chapter 2.

Chemical preparation. A stock solution of 200 mM Potassium nitrate (KNO_3), was diluted with deionised water to obtain the required solutions of 5 to 30 mM KNO_3 concentration, at increments of 5 mM. Pure deionised water was used as a control for

all treatments. These concentrations were confirmed with a Nitrate Electrode[1].

Seed incubation in Petri dishes. Fifty seeds of each ecotype, were placed on two layers of 9-cm Whatman #1 filter paper[2], in 9-cm diameter Petri dishes. The seeds in each dish, moistened with 10 ml of water or nitrate solution, was prepared under green safe light. These dishes were wrapped with aluminum foil to exclude light from the treatment. All the treatments were conducted at constant temperatures of 10 to 40$\pm$1 °C at increments of 10 °C. The dishes were arranged as split-plot design with incubators as block, temperature level as main-plot, ecotypes and nitrate as sub-plots. The treatments were replicated four times (one dish per replicate for each ecotype and nitrate level). Germination counts were conducted under green safe light after 48 hrs and every day thereafter for 7 days. Protrusion of the radicle was the criterion for germination. Seed germinated were counted daily and discarded, whereas those that had not germinated after 7 days were removed, washed with distilled water, dried on a blotting paper, and each seed cut into half, along the long axis. One half was soaked in 0.1 % triphenyl tetrazolium chloride solution, the other half discarded. Those embryos which took the red stain after 12 hrs were considered viable but dormant. The rest were considered non viable. Cumulative seed germination was converted into percentages.

Statistical analysis. Germination data was arcsin transformed to harmonize the

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[1]Agricultural Combination Nitrate Electrode Model 46132, Hach Company, Box 389, Loveland, Colorado, 80539, U.S.A.
[2]Whatman International Ltd., Maidstone, England.

variability within ecotypes and nitrate. Final percent germination data were analyzed as a factorial (2 blocks x 4 temperatures x 3 ecotypes x 7 KNO_3 concentrations), using general linear model. Where F-values were significant at the 5% level, means were compared using tests for least significant difference (LSD).

This experiment was performed twice, on 6 January, 1992 and terminated on 28 February, 1992 and repeated on 15 April, 1992 and terminated on 4 May, 1992. The data presented are the means of the two runs.

RESULTS AND DISCUSSION

Significant ($P > 0.0079$) ecotype (E), ($P > 0.0001$) temperature (T) and nitrate (N), ($P > 0.0011$) temperature by nitrate (T x N), ($P > 0.0001$) ecotype by temperature (ExT), ecotype by nitrate (E x N) and ($P > 0.0850$) ecotype by temperature by nitrate (E x T x N) interactive effects were detected for seed germination. Block (BK) as a factor was not significant ($P > 0.7616$), however, error terms associated with blocks as a factor was significant ($P > 0.0001$) (Table 3.1). This suggests that total germination was influenced by more than one factor acting alone or interacting with other factors. Incubators (blocks) had no effect on seed germination. These results supports views held by other investigators (27, 105), that the fate of seed germination is not the result of one factor but several factors interacting together. By statistical means separation, except for the CA ecotype at 0 NO_3^-, the germination of the CA and MD ecotypes did not differ between them at 20 °C, whereas the PEI ecotype showed a decline in percent germination at 30 °C from 10 mM to 30 mM (Table 3.2). The PEI ecotype, showed

a decline in germination from 15 to 30 mM KNO_3 at 30 and 40 °C. The MD and PEI ecotypes water-treated seed displayed low percent germination at 10, 30 and 40 °C, compared to CA ecotype seed (Table 3.2).

Average percent germination differences between untreated and KNO_3-treated MD and PEI seed were 21 and 17% at 10 °C, 19 and 17% at 20 °C, 54 and 48% at 30 °C, and 25 and 21% at 40 °C, respectively. This indicates that the increase in germination due to KNO_3 is comparable at 10, 20, and at 40 °C, but differed at 30 °C.

The CA ecotype at 10 to 40 °C showed more than 95% germination, regardless of KNO_3 treatment used (Table 3.2). Germination at 20 °C, for all ecotypes showed no apparent difference at all KNO_3 levels of 5 to 30 mM. The germination of the CA, MD and PEI ecotypes at 30 °C in the absence of KNO_3 was 98, 45 and 50%, respectively (Table 3.2). The decline in percent germination might indicate that the PEI ecotype has an optimum germination limit at 25, 10 and 15 mM KNO_3 concentration at 10, 30 and 40 °C, respectively and addition KNO_3 beyond these treatment levels caused decrease in germination. The CA ecotype maintained above 95% germination at 0 to 30 mM, at 40 °C, whereas the MD and PEI ecotypes, at 40 °C showed gradual germination increase, peaking at 15 mM, before declining (Table 3.2).

This lack of response by the CA ecotype to KNO_3 might be attributed to an assumption of pre-existing Pfr and endogenous nitrate, already charged on mature seed (76, 91), or lack of dormancy. The CA ecotype appeared to have a germination threshold level that allowed seed to germinate in the dark, without showing any response to KNO_3 treatment.

The result showed that the MD and PEI ecotypes exposed to increasing KNO_3 concentration, at lower temperature were stimulated to germinate better, compared to the same concentrations at higher temperatures. Also, KNO_3 stimulation appeared ecotype dependent and the extent of this stimulation was affected by KNO_3 concentration and temperature levels.

Maguire *et al.* (105), pointed out that KNO_3 does not overcome dormancy *per se* but may act in conjunction with dormancy-breaking treatments such as light and alternating temperatures to increase germination. The KNO_3 treatment might have sensitized the seed response to temperature and thus enhanced germination at 20 °C and to a greater extent at 30 and 40 °C for the MD and PEI ecotypes.

Ecological and agricultural weed implications. The results of this study suggest that nitrates do not influence germination of the CA ecotype. Its ability to respond favourably to water-treated or KNO_3 concentration suggests that field application of nitrate or lack of it would not increase its germination above the 90% laboratory value. This response is attained at temperatures from 10-40 °C. The CA ecotype seed hence might germinate in the field with high percentage, throughout the growing season regardless of the presence or absence of nitrate in the soil. Unless otherwise capable of sporadic seedling emergence, like many soil-borne dormant seed, the disadvantage of the CA ecotype seed's indiscriminate germination could be the possibility of total eradication in one season, if timely application of herbicide or tillage was performed and growing plants prevented from setting mature seed. However, this assumption is not practical or

likely to occur, in that any disturbance within its environment will lead to some selection pressures resulting in seeds or weeds which will be resistance to the intended changes or herbicide applications.

The MD and PEI ecotype germination, unlike the CA ecotype displayed a strong temperature by nitrate interaction. Nitrate enhanced seed germination at all concentration levels tested (5-30 mM), from 10 to 40 °C, except the PEI ecotype at 30 mM at 10 °C, and 15 to 30 mM, at 30 and 40 °C. As mentioned earlier, it might indicates that the PEI has an optimum germination limit at the above KNO_3 concentration at 10, 30 and 40 °C. This result might indicate that nitrate fertilization could influence the fate of the MD and PEI ecotypes, by breaking their dormancy and thus more seed germination might be expected. Also, in an agricultural field situation there might be less dormant seed, and more seed would die before germination, because most of the seed will be stimulated by the nitrate to either germinate or break their dormancy. The consequences might be unfavourable for the perpetuation of the weed species. To the farmers, however, this situation will be favourable for optimal weed control through more rapid depletion of barnyardgrass ecotype seed from the soil. Fawcett *et al.* (61), reported a similar situation with field fertilizer application of $NH_4(NO_3)$ resulting in the production of common lamb's-quarters seed with less dormancy. Following such treatment, more germination might be expected the next spring with less dormant seed to carry over to other growing season. The consequence of having large seedling emergence during the second spring means that the farmers face a worst scenario of having to deal with weedy fields. This could lead to more expense to achieve weed control. Timely application of

herbicides and prevention of mature plants from setting seed might be the best option, to avoid having to deal with the same situation during the next spring.

It is concluded from this study that the CA ecotype total germination was not influenced by addition of KNO_3, whereas the MD and PEI ecotypes responded with high percent germination to the addition of KNO_3, even though the PEI ecotype appeared to show germination optimum limit at some temperature by nitrate interaction. Also, germination was influenced by interacting ecotype, nitrate and temperature. Overall, the data showed that the CA ecotype behaved differently from the MD and PEI ecotypes.

Table 3.1. Analysis of percent germination of three barnyardgrass ecotypes[§] incubated in darkness at constant temperatures (10, 20, 30 and 40 °C) and nitrate concentrations ranging from 0-30 mM.

Source	DF	MS	F-Value	P>F
Model	171	1745.3	38.9	0.0001
Error	500	44.8		
Block (BK)	1	0.7	4.1	0.7616
Ecotype (E)	2	29467.2	125.0	0.0079
Error (BK x E)	2	235.8	5.3	0.0055
Nitrate (N)	6	7127.1	28.4	0.0001
Error (BKxTxN)	29	251.4	5.6	0.0001
Temperature (T)	4	21466.6	85.3	0.0001
Error (BKxTxN)	29	251.4	5.6	0.0001
E x T	6	4760.5	18.0	0.0001
E x N	12	1735.6	6.5	0.0001
E x N x T	36	399.4	1.5	0.0850
Er[‡].(BKxExTxN)	54	265.2	5.9	0.0001
		R-square 0.92		

Abbreviation: [§] E, Ecotype=California (CA), Maryland (MD) and Prince Edward Island (PEI).
[‡] Er.= error term.

Table 3.2. Effect of temperature by nitrate on percent germination of three barnyardgrass ecotypes, at 4 constant temperatures and 7 KNO_3 levels.

		Temperature (°C)			
		10	20	30	40
Ecotypes[§]	KNO_3(mM)	Germination (±SE)[d] (%)			
CA	0	98±2(1)	98±2(1)	100±0(0)	96±3(1)
	5	98±0(1)	99±0(1)	100±0(0)	98±1(1)
	10	99±1(0)	100±0(0)	100±0(0)	98±2(1)
	15	99±1(0)	100±0(0)	100±0(0)	99±0(1)
	20	100±0(0)	100±0(0)	100±0(0)	98±2(1)
	25	100±0(0)	100±0(0)	100±0(0)	96±3(2)
	30	100±0(0)	100±0(0)	100±0(0)	96±4(2)
MD	0	45±3(52)	95±4(5)	45±5(55)	15±7(85)
	5	66±1(43)	99±1(0)	99±1(1)	40±4(58)
	10	72±2(27)	99±1(0)	99±1(1)	42±4(58)
	15	86±2(12)	100±0(0)	100±0(0)	96±4(4)
	20	86±2(12)	100±0(0)	100±0(0)	84±3(11)
	25	88±1(12)	100±0(0)	98±1(1)	84±3(11)
	30	76±6(24)	100±0(0)	98±1(1)	74±4(25)
PEI	0	34±4(65)	85±2(13)	50±2(48)	12±9(86)
	5	51±3(48)	96±4(4)	98±2(2)	33±2(66)
	10	66±2(34)	99±1(0)	98±2(2)	33±4(66)
	15	78±2(21)	100±0(0)	95±2(4)	90±3(9)
	20	86±3(14)	100±0(0)	92±3(7)	66±4(34)
	25	92±2(8)	100±0(0)	89±2(10)	63±5(36)
	30	68±3(31)	100±0(0)	89±3(11)	54±4(45)

Abbreviation: Ecotype[§]=California (CA), Maryland (MD) and Prince Edward Island (PEI). [d] Numbers in bracket are mean percent dormant seed obtained by tetrazolium assay analysis.

Chapter 4

EFFECTS OF TEMPERATURE AND WATER POTENTIAL ON GERMINATION OF THREE BARNYARDGRASS (*ECHINOCHLOA CRUS-GALLI* [L.] BEAUV) ECOTYPES.

INTRODUCTION

In many environments availability of water at the time of seed germination may be critical (87). Water availability for seed germination is determined by the osmotic and matric potential of the water in the seedbed and the substrate hydraulic conductivity (186). Drought studies have been restricted to field conditions and often lack precise experimental control, measurement, or method of controlling water potential, resulting in problems of interpretation (87, 123). Early studies (52, 67) showed that soluble salts in excess of immediate plant requirements caused decreased water absorption, disturbed nutrient uptake, caused abnormal metabolism, and reduced growth.

Simulating seed environments in dry soils is often accomplished by adding solutes to water to lower the water potential. Solutions of mannitol, sodium chloride, and polyethylene glycol (PEG) have been widely used to provide a range of water potential regimes (87, 123, 150, 181). Polyethylene glycol (PEG) particularly, has been used to maintain experimental media at predetermined water potential values (87, 123, 161, 167). PEG of high molecular weight (4,000 or more) cannot pass through materials made of plant cell fibres (35, 162) so it has been suggested to be superior to other solutes for

work with plants than PEGs of lower molecular weight (89, 111). Its suitability has been demonstrated for peas (*Pisum sativum* L.) by Manchar (102) and corn (*Zea mays* L.) by Parmar et al. (124).

It has been reported that some osmotic substrates used in research may enter germinating seeds and induce effects, including toxicity, which are more complex than drought (9, 88, 103). Several researchers have reported that PEG has toxic effects on plants (81, 97). The toxicity of PEG 6,000, for example, was attributed to associated heavy metals. Dialysis or passage through ion exchange columns to remove these impurities is recommended (95). The different osmotica have a specific effect on germination, independent of water potential (23, 123, 150).

Though this type of experiment is conducive to laboratory work, seeds imbibed with PEG solutions versus seeds imbibed in soil with the same water potential can be quite different. The reason for this difference can be explained partially in that seeds imbibed in an osmotic solution have approximately 100% seed and water (solution) contact. In soil media, the seed has less soil water contact and new water has to move further to replace imbibed water (123).

Although there have been relatively few studies of interaction between varying water potentials and temperature, temperature and moisture stress interaction is known to influence seed germination (167, 186). Kaufmann *et al.* (88) reported that the effect of both temperature and water potential on germination was significant for lettuce (*Lactuca sativa*) but not for wheat (*Triticum aestivum* L.).

McGinnes, (108) and Tadmor *et al.* (161), working on mannitol solutions, suggested

that the effect of water potential on germination of perennial grasses was dependent on temperature, but this was not true for wheat and barley (*Hordeum vulgare* L.). Woods *et al.* (184) further reported that the interaction between temperature and osmotic stress on the germination of *Lotus corniculatus* (L.) changed with time. Most rapid germination occurred at 25 °C with no moisture stress. Lower temperatures and lower water potentials each delayed germination and intensified the effects of the other.

Soils with relatively high water potential and high fertility have been found to provide an ideal substrate for barnyardgrass. It germinated best under wet conditions and its seedlings headed earlier. Dry conditions depressed germination and morphological development. Barnyardgrass can thrive very well under extremely high moisture conditions, and seedlings do emerge under conditions of low oxygen (134). However, Jones (83), suggested that partial control of barnyardgrass could be achieved by flooding the seed bed with 10 to 20 cm of water. Moisture conditions that are favourable for most crops are apparently optimum for barnyardgrass (134). Increasing moisture stress not only delayed initial germination but also slowed shoot and root elongation (7, 33). Similar results (72, 146, 187) of insufficient moisture, simulated by using osmotica with decreasing water potentials, have been reported to affect root and shoot length of wheat seedlings, and to delay the initiation of germination, rate and percent germination in faba bean and chickpea (*Acer arietinum*).

The objective of the following set of experiments was to determine the germination response of three barnyardgrass ecotypes originating from California (CA), Maryland (MD) and Prince Edward Island (PEI), to simulated environmental conditions

of temperature by moisture stress interaction.

MATERIALS AND METHODS

Seed source. For the seed source and storage conditions prior to conducting this experiment, refer to Chapter 2.

This experiment used a cellulose membrane to separate PEG solution from direct contact with the seeds (88). The effects of temperature from 10 to 40 °C and water potential on germination was studied using the osmoticum, polyethylene glycol (PEG 8000)[1]. Water potential of zero (deionised water) to -10.0 MPa at a decrement of 2.0 MPa were prepared by dissolving PEG (8000) at the rate of 0, 90, 150, 195, 223, 240 g, respectively, in 1 L of deionised water (123). The water potential for each solute was measured on a Wescor Model 5130 vapour pressure osmometer, calibrated with NaCl standard solutions available from Wescor, Inc. (Logan. UT). Approximate values were determined from published curves (96).

The experiment was a three-factor factorial (3 ecotypes x 6 water potential x 4 temperatures). The factors were ecotypes (CA, MD, PEI), water potential ranging from 0.0 to -10 MPa at decrements of 2.0 MPa and temperature (10, 20, 30 and 40°C). Experimental design was split-plot with (a) incubators as blocks, (b) temperature and water potential as main-plots and (c) ecotypes as sub-plot. During data analysis, temperature levels were reduced to two levels (20 and 30 °C).

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[1]Carbowax PEG 8000. Fisher Scientific, 711 Forbes Ave., Pittsburgh, PA 15219.

Germination tests were conducted in a Shel-Lab low temperature incubator (Model 2005), with deviation from targeted temperature at $\pm$ 0.2 °C. The ecotype seeds and solution were held separately for 12 to 16 h at the tested temperature before initiating the experiment. At the start of the experiment, plexi glass support stands for each germination vessel were covered with two layers of paper towels. A third of the paper on both edges was allowed to fold over towards the inside of the germination vessel. On top of the paper towels, a cellulose membrane treated earlier with distilled water, was placed to cover the paper's entire surface. At one side, between the vessel and the support stand's edge, a plastic funnel was wedged at an angle. With this funnel, 800 ml of deionised water or osmotic solution were poured into the germinating vessel until it came in contact with seed-support material (paper towel). This procedure was repeated for the other vessels (two vessels per osmotic solution or deionised water and temperature). Fifty seeds for each ecotype, replicated four times, were placed on a cellulose membrane surface. The paper towels were fully saturated with deionised water or osmotic solution. Since the germinating vessels were maintained with a large reservoir of osmoticum or deionised water, it was not necessary to constantly add the solutes. The vessels were covered, with the lid placed to allow space for gas exchange, while minimizing any moisture escape from the vessels. Also, the vessels were encased in black polythene bags, to prevent light interference. The seed were incubated for 10 days, after which germination counts were taken. Germination was defined as plumule and radicle response. A definition used in the previous studies where germination was defined as the emergence of the radicle, became unsuitable and questionable in osmotic

stress studies (186). For this study, low water potential (-6 to -10 MPa) showed instances which occurred where there was radicle emergence but no plumule, hence were considered abnormal germination (119) or incomplete germination (73). Percent germination data was arcsin transformed to normalize the variance within the data (156).

Growth of seedling shoots and roots was also determined by taking at random eight seedlings of each ecotype (2 per replicate) and measuring their length in centimetres after 10 days. Abnormal (or incomplete) seedlings were not considered.

Data from treatments at 10 and 40 °C were not used in data analysis because the seeds at 10 °C incubated for more than 30 days did not yield any germination. The data at 40 °C was abandoned, because of fungal infection on the seeds and resultant damage to the cellulose membrane. Fungal growth in germination environment is thought to reduce germination directly through disease and indirectly by changing the osmotic potentials of the solution (186).

Statistical analysis. This experiment was repeated and the following data represent the average of the two experiments. All factors of blocks $(BK)^{B}$, ecotypes $(E)^{\S}$, temperature $(T)^{\dagger}$, and water potential $(WP)^{\P}$ were subjected to analysis of variance, using the general linear model of SAS (Statistical Analysis System); the means were separated at 5% level of significance using Fisher's Protected LSD Test.

Abbreviation: bk^{B}=incubators, $E^{\S}$=ecotypes, $T^{\dagger}$=temperatures, $WP^{\P}$=water potential.

RESULTS AND DISCUSSION

Significant ($P > 0.0188$) ecotype [E], ($P > 0.0001$) temperature [T], water potential [WP]), temperature by water potential [T x WP] and temperature by ecotype by water potential [E x T x WP] interactions were detected for percent germination. No significant difference was detected for block [BK] ($P > 0.1526$), block by temperature by water potential [BK x T x WP] ($P > 0.9654$), block by ecotype [BK x E] ($P > 0.4663$), ecotype by temperature [E x T] ($P > 0.3417$) or block by temperature by ecotype by water potential [BK x T x E x WP] interactions ($P > 0.7980$) (Table 4.1).

The results showed that total percent germination responses were influenced by main factors and interactive factors. Lack of interaction between ecotype and temperature appears to suggest that the three-way interaction of ecotype x temperature x water potential, might have masked the two-way interaction (Table 4.1). The results demonstrate that in nature, several factors interacting together determine the germination of weed seeds. Also, it was noted that among all the main factors, ecotype though significant, is having the least less influence. This may suggest that the three ecotypes responded almost equally to declining water potential and changes in temperature (Table 4.1).

At 20 °C, the CA, MD and PEI ecotypes had more than 80% germination, from zero to -8 MPa water potential (Fig. 4.1). Germination at -10 MPa, however, showed the CA, MD and PEI ecotypes with 85, 57 and 30%, respectively. The CA, MD and PEI ecotypes, at 30 °C, displayed a gradual decline in germination, showing above 85% for the CA and MD ecotypes and above 70% germination for the PEI ecotype, from 0

to -4 MPa. However, from -6 to -10 MPa, the CA had 64 to 12%, the MD 47 to 7% and the PEI 32 to 5% germination, respectively (Fig.4.2). Tadmor *et al.* (161), working with wheat and barley reported similar results and commented that osmotic stress exerted the greatest effect on percent germination at higher temperatures. Greater than 65% germination by these ecotypes at both 20 and 30 °C, from 0 to -4 MPa water potential showed how these ecotypes have adapted to areas that maintained relatively high moisture levels which place relatively little stress on seed germination (134).

Generally, at zero and -2 MPa water potential, all ecotypes had above 95% germination, over the range of tested temperatures (Fig. 4.1; 4.2). Temperature increases from 20 to 30 °C and decreasing water potential from -6 to -10 MPa led to decrease in germination. Though all ecotypes showed the same germination behaviour the MD and PEI ecotypes at 30 °C, from -6 to -10 MPa appeared more affected, whereas the CA ecotype might be better adapted at this temperature and water potentials (Fig. 4.1; 4.2).

Shoot and root growth effects. Significant differences ($P > 0.0001$) among ecotype, temperature, water potential, ecotype by temperature, temperature by water potential and their error term interactions were detected for shoot and root growth. The block (BK) effect was significant ($P > 0.0001$) for root but not shoot growth ($P > 0.0551$). Also, block by ecotype (BK x E) error term for ecotype was not significant (Table 4.2; 4.3).

Generally, shoot and root lengths were gradually reduced with decreasing water

potential. However, the relationship between ecotype, temperature and water potential showed that the shoot and root length were greater at 30 °C than at 20 °C, especially at low water potential of 0 to -2 MPa, but became less with decreased water potential. The CA ecotype, however, at these temperatures showed greater root length at 0 to -2 MPa, but was comparable at lower water potentials with other ecotypes. Shoot lengths unlike root lengths, were progressively reduced, as water potential decreased (Table 4.4). The growth of the root even at declining water potential may be due to plants' attempt to extract water by root extension at greater soil depths. In this case root length extension was prompted by limiting water potential. Additionally, as in seed germination, among the main factors, ecotype appeared to have less influence on short and root growth.

Shoot growth for all ecotypes was more temperature and water potential sensitive than root growth. This observation agrees with work done on wheat by Hampson *et al.* (73) and that of Cooper (38) in which root/shoot ratio was reportedly lower at higher temperatures and decreasing water potential.

Germination and seedling growth was affected differently by temperature and water potential. Hadas *et al.* (71) noted that growth probably requires higher turgor pressure and less negative water potential than does germination. While shoot lengths were progressively reduced as water potential was lowered, roots tended to grow persistently as water potential declined. Some seedlings (about 10%), described here as abnormal (119) or incomplete germination (73), had root growth but inhibited shoot growth. This suggests that shoots and roots have different water potential requirements for growth. Incomplete germination has been demonstrated in γ-irradiation experiments

(26) and may have occurred in high salt treatments (73). In this study this phenomenon occurred at low water potential at both temperatures.

Ecological and agricultural implications. The effects of different levels of water potential at two constant temperatures on the germination, coupled with shoot and root growths on the three barnyardgrass ecotypes, could not reliably show adaptation to their provenance. This was because of restriction by two levels temperature, however, it could be extrapolated to indicate that possibility. Ecotypes germination at water potentials as low as -10 MPa demonstrated their ability to survive in areas of low water potential. Germination rates of more than 80% at high water potential (0 to -4 MPa) showed that barnyardgrasses have adapted well to areas of relatively high moisture levels (irrigated conditions included) without their seeds experiencing moisture saturation stress. Though this study may not reflect the field situations, it is an indicator of what to expect. Field water potential, for example, is known to range from -1 to -3 MPa. The three barnyardgrass ecotypes from this study, can germinate at less than -1 to -3 MPa. In agricultural terms, barnyardgrass success in such conditions complicates weed control methods. This is one of the reasons why barnyardgrass has been a serious weed in flooded rice fields or fields maintained at high soil moisture.

The emergence of the radicle and inhibition of the plumule at low water potential of -8 to-10 MPa and high temperatures of 30 °C has led some investigators to conclude that such phenomena may be of considerable ecological significance. The failure to produce coleoptiles may be a form of induced epicotyl dormancy (186), a dormancy that

might be broken by some environmental occurrence, for example cool moisture conditions. This concept was not investigated in this experiment.

The significant findings of this study were that the CA ecotype was better adapted to high temperature of 30 °C and water potential of -6 and -8 MPa, in comparison to the MD or PEI ecotypes. This suggests that the CA, in comparison to either MD or PEI ecotypes, could thrive better in areas experiencing high temperatures and low water potential. This adaptive difference reflects the area of origin of the ecotypes and their adaptation to the prevailing environment in their provenance.

It was also found that declining water potential led to plumule inhibition and elongation of the radicle. It is not known why this phenomenon happened, but speculatively this may be of ecological significance to plants experiencing moisture stress, in that the radicle will continue to nurture the plumule and once favourable environmental conditions occur, the plumule might be stimulated to grow.

Table 4.1. Effects of six water potentials and two constant temperatures on percent germination of three barnyardgrass ecotypes, analyzed by general linear model (GLM).

Source	Df	Mean square	F-value	P > F
Model	71	2524.4	31.3	0.0001
Error	216	80.7		
Block (BK)	1	166.2	2.1	0.1526
Temperature (T)	1	36619.9	1217.4	0.0001
Error (BK x T x WP)	11	30.1	0.4	0.9654
Ecotype (E)	2	3216.1	52.7	0.0188
Error (BK x E)	2	61.8	0.8	0.4663
Water potential (WP)	5	20767.7	690.4	0.0001
Error (BK x T x WP)	11	30.1	0.4	0.9654
E x T	2	67.1	1.1	0.3417
E x WP	10	179.7	3.0	0.0146
T x WP	5	5039.0	62.5	0.0001
E x T x WP	10	256.3	3.2	0.0008
Error (BKxTxExWP)	22	59.5	0.7	0.7980

R-square = 0.91

Table 4.2. Influence of six water potential and two constant temperatures on shoot length of three barnyardgrass ecotypes analysed by general linear model (GLM).

Source	Df	Mean square	F-value	P > F
		Shoot length		
Model	71	28.1	115.2	0.0001
Error	504	0.24		
Block (Bk)	1	0.9	3.7	0.0551
Ecotype (E)	2	28.5	116.6	0.0001
Error (BK x E)	2	2.4	9.9	0.0001
Temperature(T)	1	89.3	365.8	0.0001
Error (BK x T x WP)	11	7.4	30.4	0.0001
Water potential (WP)	5	269.8	1105.3	0.0001
E x T	2	4.4	18.0	0.0001
E x WP	10	2.9	12.0	0.0001
T x WP	5	46.2	189.2	0.0001
E x T x WP	10	5.5	22.7	0.0001
Error (BKxTxExWP)	22	4.1	16.6	0.0001
		R-square =0.94		

Table 4.3. Influence of six levels of water potential and two constant temperatures on root length of three barnyardgrass ecotypes analysed by general linear model (GLM).

Source	Df	Mean square	F-value	P>F
		Root length		
Model	71	22.9	31.8	0.0001
Error	504	0.7		
Block (BK)	1	219.2	304.6	0.0001
Ecotype(E)	2	30.4	42.2	0.0001
Error (BK x E)	2	1.1	1.6	0.2034
Temperature (T)	1	543.5	755.4	0.0001
Error (BKxTxWP)	11	21.1	29.4	0.0001
Water potential (WP)	5	68.1	94.6	0.0001
Error (BKxTxWP)	11	21.1	29.4	0.0001
E x T	2	2.3	3.2	0.0401
E x WP	10	10.3	14.3	0.0001
T x WP	2	5.9	8.2	0.0001
E x T X WP	10	5.1	7.0	0.0001
Error (BKxExTxWP	22	1.8	2.6	0.0001
		R-square = 0.81		

Table 4.4. Mean shoot and root length (cm ±SE) response of three barnyardgrass ecotypes to varying osmotica and temperatures.

Ecotype[§]	CA		MD		PEI		
T[†] (°C)	20	30	20	30	20	30	
WP[¶]	Shoot length (cm)						Mean
0	4.1±0.2	5.6±0.3	2.9±0.2	5.5±0.2	3.4±0.2	5.4±0.2	4.5[a]
-2	1.4±0.1	5.2±0.2	1.2±0.1	3.0±0.4	1.1±0.2	3.5±0.5	2.6[b]
-4	1.2±0.1	3.1±0.6	0.6±0.1	0.6±0.1	0.9±0.1	0.6±0.1	1.2[c]
-6	1.2±0.3	0.3±0.1	0.5±0.0	0.2±0.0	0.5±0.0	0.2±0.0	0.5[d]
-8	0.7±0.0	0.4±0.1	0.4±0.1	0.2±0.0	0.3±0.0	0.1±0.0	0.4[d]
-10	0.4±0.1	0.4±0.1	0.3±0.0	0.1±0.0	0.3±0.0	0.1±0.0	0.3[d]
Mean[*]	1.5[xy]	2.5[x]	1.0[yz]	1.6[xy]	1.1[yz]	1.7[xy]	
	Root length (cm)						Overall mean
0	3.5±0.2	6.2±0.4	2.5±0.2	3.4±0.1	2.4±0.1	3.2±0.1	3.5[ab]
-2	4.0±0.2	7.4±0.4	3.6±0.2	5.2±0.3	2.7±0.1	5.0±0.4	4.7[a]
-4	4.0±0.3	5.8±0.5	4.0±0.2	6.5±0.4	3.7±0.2	5.2±0.4	4.9[a]
-6	4.2±0.3	4.8±0.4	3.9±0.3	4.8±0.2	2.7±0.3	4.9±0.4	4.2[a]
-8	2.0±0.1	3.9±0.5	2.3±0.3	4.6±0.4	1.7±0.3	4.5±0.4	3.2[b]
-10	1.6±0.2	3.7±0.4	1.9±0.1	3.9±0.5	1.4±0.2	4.2±0.3	2.8[b]
Mean[*]	3.2[y]	5.3[x]	3.0[y]	4.7[x]	2.0[y]	4.5[x]	

Ecotypes[§]: California (CA), Maryland (MD) and Prince Edward Island (PEI); T[†]., temperatures (20 and 30 °C); WP[¶]., Water Potentials.

[*]Overall means followed by the same letter within and across ecotypes and temperatures are not significantly different ($\alpha = 0.05$).

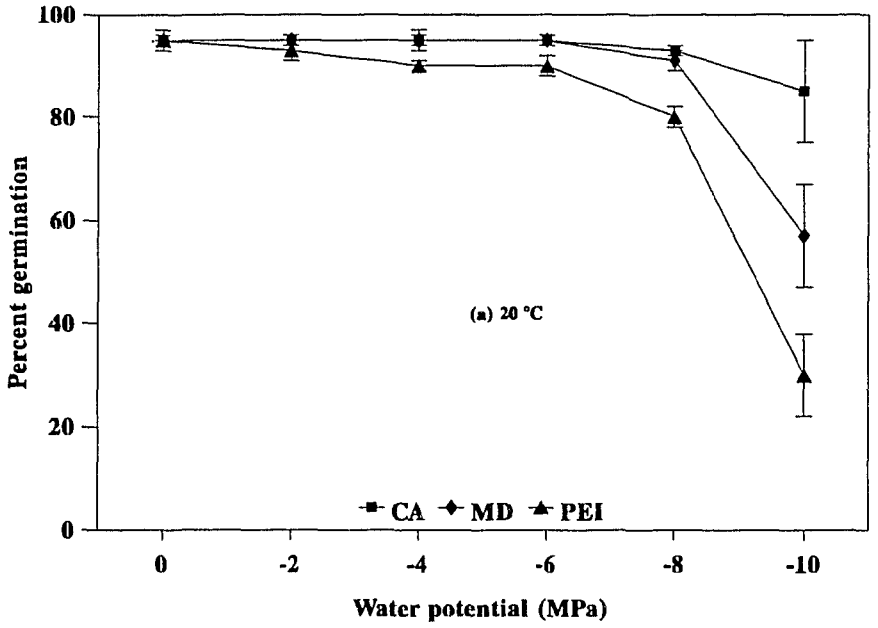

Fig. 4.1. Effect of six water potential on germination of three barnyardgrass ecotypes at 20 °C. Vertical bars are standard errors (±SE).

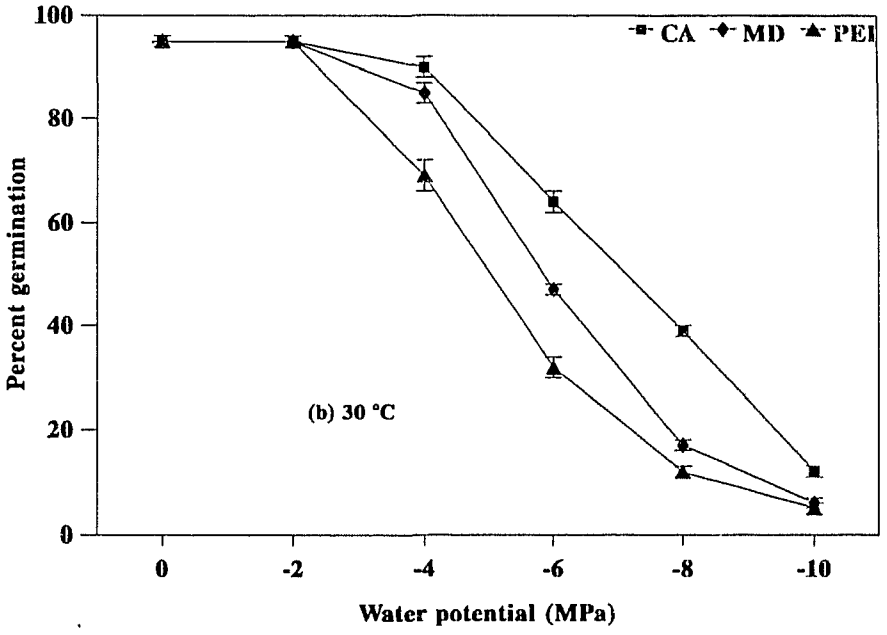

Fig. 4.2. Effect of six water potential on germination of three barnyardgrass ecotypes at 30 °C. Vertical bars are standard errors (±SE).

Chapter 5

EFFECT OF SEEDING DEPTH ON THE EMERGENCE OF THREE BARNYARDGRASS (*ECHINOCHLOA CRUS-GALLI* [L.] BEAUV) ECOTYPES.

INTRODUCTION

Troublesome annual weeds propagated by seeds, barnyardgrass included, can infest agronomic crops to a marked extent. These seeds, distributed in the soil surface layers, principally by tillage implements, can eventually germinate and establish plants that compete with crop plants for water, nutrients, and light. The crop yield can be reduced when weeds are not controlled (161). Knowledge of the timing and extent of different weed species emergence before and immediately after seedbed preparation is important, especially when planning control measures through mechanical and/or chemical methods. Seedbed preparation at or near the natural peak of seedling emergence is essential to reduce the density of weeds after crop emergence; this reduces the use of herbicides (5, 57).

Time of crop emergence in relation to associated weeds can markedly affect subsequent crop-weed competition (190). Radosevich *et al*, (133) considers germination and emergence timing as key factors in crop-weed competition. Knowledge of these factors may be used to forecast weed competition and subsequent crop yield reductions (5, 28). Different germination and emergence requirements between crops and weeds

vary considerably under different environmental conditions, and potentially may be exploited to reduce weed impact (29). For example, wheat (*Triticum aestivum*) is capable of emerging from drier soils than some weed species, thus conferring an advantage to wheat's ability to compete with them (28, 98, 120). Field and pot studies of plant competition have shown early emergence of one competitor to give a distinct advantage over another in gaining resources (74). Crop yield losses are less when weed emergence is delayed after sowing of crops (118, 176).

Crop emergence is generally more uniform than weed emergence because populations of weed seeds are more variable with respect to germination requirements and burial depth in the soil (133). Germination of non-dormant seeds is largely a function of soil temperature, soil moisture and for many weed species exposure to light (74, 76). Decrease in temperature from 22 to 14 °C was found to cause a 6-d delay in emergence of green foxtail (*Setaria viridis* L.) relative to that of wheat (*T. aestivum* L.) and to result in lower crop yield losses and lower weed seed production (28). Soil temperature, soil moisture and light requirements, may vary within a soil profile interactively.

Seedling emergence at various depths in soil has been investigated under field and laboratory conditions (41, 180). Chepil (37) reported that seeds of various weeds emerged best near the soil surface and emergence decreased as seed depth increased. Other workers (62, 74, 106), have reported that depth of burial strongly influences percent emergence of many weed seedlings. Barnyardgrass has been reported to emerge

best at shallow soil depths (1.5 or 2.5 cm) and to decrease as depth of seeding increases. However, it is capable of emergence at depths of 10 to 15 cm (41, 134, 142).

Depth of burial was found to affect emergence of lamb's-quarters and eastern black nightshade, where percent emergence was higher when seeded near the soil surface than when buried (178). Redstem filaree (*Erodium cicutarium*) shows greatest emergence at soil depths of 1 cm or less, but no emergence occurs at depths of 8 cm or more (29); wheat grass (*Agropyron psammophilum*) shows higher percent emergence at 2 and 4-cm burial depth and no seedlings emerged from depths greater than 8 cm (189); *Ammophila breviligulata*, *Elymus canadensis*, *Cakile edentula* and *Corispermum hyssopifolium*, all show higher seedling emergences at 2 to 4 cm, but decreased emergence at depths greater than 4 cm (106).

A close association between seed size (weight) and maximum depth in soil has been observed (106, 158), with the largest seeds emerging from the greatest depths. Baker (11) showed that plant species with large seeds are associated with drier habitats, under California conditions. Schimpf (147) showed that ecotypes of redroot pigweed (*Amaranthus retroflexus*) from drier regions, may have larger seeds than ecotypes from more mesic regions. Large seed size in plants exposed to drought, is thought to be due to selection pressure in favour of seedlings which establish an extensive root system quickly, by drawing on their food reserves in the seed (62). *Erigeron canadensis* and *Solidago semipervirens*, species that have very small seeds, are known to emerge only from shallow depths in sand (172).

Seed size (weight) is an important element of adaptive strategy for reproduction

of a plant. Size adopted by each species probably represents a compromise between the requirements for dispersal (in favour of small seeds) and the requirements for seedling establishment (in favour of large seeds). For plants of transient, widely scattered open sites, wide dispersal is essential for their colonization of new areas, while the lack of competition from surrounding plants renders large seed reserves less important. Such species have large numbers of small seeds. For species that grow in more stable environments with closed vegetation, wide dispersal may be of less importance than the ability to establish seedlings in a highly competitive environment. These species give priority to seed size rather than numbers (62).

The effect of seed depth in soil of different barnyardgrass ecotypes is little known. The objective of this experiment was to determine the influence of seed depth on germination and emergence of barnyardgrass ecotypes, originating from three contrasting geographical environments - California (CA), Maryland (MD) and Prince Edward Island (PEI). The information obtained from this study will aid in developing cultural methods for their control, particularly when trying to reduce the use of herbicides.

MATERIALS AND METHODS

Seed source. Seed source and storage conditions prior to conducting the experiment are described in Chapter 2.

Soil amendment and seeding. Experiments were conducted in a steam sterilized loam soil, having a pH of 6.0, amended in the ratio of 2:1 (loam soil: sand). Soil was

amended to increase soil aeration and to avoid soil compaction, which might result from differences in field versus potted soil water content. Soil was placed into plastic pots, 15 cm diameter by 15 cm depth. The soil was watered and allowed to settle overnight. Each ecotype was planted at depths of 0.0, 1.0, 2.5, 5.0, 7.5 and 10 cm; one hundred seeds were used per pot for each ecotype and planting depth. After seeding, pots were filled to within 1 cm of the rim; seeds were not sown within 2 cm of the edge of the pot. Pots were arranged in a completely randomized design, replicated four times and placed in a growth chamber maintained at 20 ± 1 °C. The growth chamber had a 16-h photoperiod and 300 μE $m^{-2}s^{-1}$ photon flux with relative humidity maintained at 70%. Pots were watered regularly for the duration of the experiment, with water applied gently to minimise seed disturbance.

Seedling emergence was counted and emerged plants removed daily until a low emergence percentage level was reached or emergence ceased.

This experiment was repeated with similar procedures and requirements. The first run was initiated on 15 April, 1992 and terminated on 2 May, 1992 and the second run on 21 January, 1993 and terminated on 8 February, 1993.

Statistical analysis. This experiment was duplicated and the following data represented the average of the two experiments. Emergence data was arcsin transformed and subjected to analysis of variance (ANOVA) using the general linear model of SAS (Statistical Analysis System) procedure, as 'repeated measure analysis'. Experimental run (R) was analysed as block, seed depths (D) as main-plot treatment, Ecotype (E) as sub-plot treatment. Mean separation was done, using Fisher's Protected LSD test.

RESULTS AND DISCUSSION

Significant ($P > 0.0001$) ecotype (E), seed depth (D) effects and ecotype by run (E x R), ecotype by seed depth (E x D) and ecotype by seed depth by run (E x D x R) interaction was detected for ecotypes' seedling response to seed depths. There was no significant effect by experimental run (R) (Table 5.1). The results suggest that the type of ecotype, seed depths and their interaction influences seedling emergence of the three ecotypes.

Also, significant ($P > 0.0001$) time (t), time by run (t x R), time by ecotype (t x E), time by seed depth (t x D) and time by ecotype by seed depth by run (t x E x D x R), was detected for seedling response. This indicate that seedling emergence was influence by interacting tested variables over time (Table 5.1).

Daily seedling emergence, as affected by ecotype and seed depth effects, showed that the ecotypes are different from each another. Seedling emergence commenced 3 DAS[1] and continued until 17 DAS (after a low emergence levels was reached or emergence ceased) (Fig. 5.1, 5.2, 5.3). The first 9 DAS of seedling emergence showed significant ($P > 0.0001$) interaction for ecotype and seed depths and their interaction (Table 5.1).

Across the ecotypes and seed depths, germination generally plateaued beyond 9 DAS, except at 0 cm depth where emergence did not plateaued but instead showed an elevated trend. The seedling emergence at shallow (1, 2.5 and 5 cm) depths plateaued

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DAS[1] = Days after seeding.

at 5 DAS for the CA ecotype and 8 DAS for the MD and PEI ecotypes (Fig. 5.1 to 5.3). Thereafter, main effects were significant but not for interactive effects.

Data indicate that seedling emergence is primarily influence by the characteristic of each ecotype and seed depths in soil. The CA, MD and PEI ecotypes showed greatest percent emergence at 1 and 2.5 cm, lower emergence at 5 and 0 cm and least emergence at 7.5 and 10 cm depths (Fig. 5.1 to 5.3). The significant interactive effect between 3 to 9 DAS suggests that the first few days are critically important in seedling emergence. Thereafter, interactive effects appeared less important, since most of the seedling that will emerge have emerged by 9 DAS, and any difference observed thereafter might be related to ecotype and seed depths. It was also observed that interactive effects influence the rate of emergence, with shallow seed emerging first. This rate varies significantly with ecotype and seed depths. The CA ecotype emerge much faster at 3 DAS from 1 to 2.5 cm, 4 DAS from 0, 5 and 7.5 cm and 7 DAS from 10 cm seed depths, whereas the MD ecotype took 4 DAS to emerge from 1, 2.5 and 5 cm seed depths; 5 DAS from 0 cm, 6 and 7 DAS to emerge from 7.5 cm and 10 cm seed depths, respectively. The PEI ecotype took 3 DAS to emerge from 1 cm seed depth, 4 DAS from 0, 2.5 and 5 cm seed depths, 6 DAS from 5 cm, and 7 DAS from 10 cm seed depths respectively (Fig. 5.1, 5.2, 5.3). Even though the ecotypes emerged faster at 1 and 2.5 cm seed depths, the CA ecotype showed greater percent emergence compared to the MD or PEI ecotypes.

Seedling emergence at 0 cm depth for all ecotypes commenced between 4 and 5

DAS and increased progressively, and by 17 DAS, the CA, MD and PEI ecotypes had 89, 78 and 89% cumulative seedling emergence (Fig. 5.1, 5.2 and 5.3). Emergence at 0 cm though showing consistency across ecotypes and seeding depths, it is noted that there was variation amongst ecotypes and other seed depths which may have been due to exposure to greater environmental fluctuations, including constant fluctuating soil moisture levels, temperature, light quality and intensity. These factors, though they were not measured in this study, appeared detrimental to the three ecotypes seed planted on the surface.

The highest cumulative percent emergences recorded were at 1 and 2.5 cm seed depths. Average germination of the CA ecotype was 95 and 98%; 94 and 93% for MD, and 83 and 79% for PEI ecotypes, respectively (Fig. 5.1, 5.2, and 5.3). Overall cumulative germination among ecotypes showed no significant difference at the above depths, however, rate of emergence and the time it took each ecotype to peak and plateaued appeared to favour the larger seed of CA ecotype than the smaller seed of the MD and PEI ecotypes.

These results confirm (29, 41, 104, 106, 134, 142, 155, 158, 164, 182 and 185) work done on other weed species by other investigators; that seedling emerged better at 1 and 2 cm depths with greater percentages than at other burial depths and emergence decreased as seed depth increased (Fig. 5.1, 5.2 and 5.3). The difference however, between this experiment and results by other worker is the fact that comparison was made among the three ecotype instead of studying an individual or group of weed species. The proximity of the seeds to the soil surface, without being exposed to variable

conditions appears to sensitize them to prevailing interacting environmental factors. This enable them to germinate and emerged with greater percentages.

Ecotype emergence at 5 cm depth commenced at 4 DAS, attaining maximum emergence at 6 DAS for the CA, 7 and 8 DAS for the MD and PEI, respectively. Maximum cumulative percent emergence recorded at 17 DAS for the CA, MD and PEI ecotypes were 82, 81 and 65%, respectively. The CA and MD ecotypes showed similar maximum emergence at this seeding depth in relation to the PEI ecotype (Fig. 5.1, 5.2 and 5.3).

Emergence at 7.5 cm depth for the CA, MD and PEI, commenced at 4, 6 and 5 DAS, respectively. Comparatively, seedling emergence for all ecotypes were significantly different, with the CA showing greater percent emergence, and PEI showing lowest emergence. Cumulative percent emergence recorded for the CA, MD and PEI ecotypes at 17 DAS was 56, 46 and 26% (Fig. 5.1, 5.2 and 5.3). The data suggests that at this depth more than half of the CA and MD and a two-third of the PEI seedlings did not emerge (Fig. 5.1 to 5.3). At the conclusion of the experiment, it was noted that some these seed did germinate but did not emerge.

The 10-cm depth had the lowest percent seedling emergence for all ecotypes. Seedlings from this depth took a long time to emerge; with all ecotypes emergence beginning at 7 DAS. Total cumulative emergence recorded for the CA, MD and PEI ecotypes was 12, 7 and 4%, respectively (Fig. 5.1, 5.2 and 5.3). Also, most of the emerged seedlings at this depth displayed chlorotic leaves which may be due to the

absence of light and reduced food reserves used to emerge. Also as noted for seeds at 7.5 cm depth, some seeds did germinate but did not emerge.

Low percent emergence recorded at 7.5 and 10 cm, for all ecotypes was attributed to either, greater depths enforcing seed dormancy mediated by higher soil moisture, lower oxygen content at greater depths (36, 74).

Additionally, it was observed that total emergence for the CA and MD ecotypes at 7.5 and 10 cm, like at 5 cm depth, was similar, relative to the PEI ecotype. It appeared that emergence of the PEI ecotype was consistently lower than emergence of the CA and MD ecotypes, regardless of seed depths. It was assumed that this was because the PEI seed were less vigorous such that fewer seedlings reached the surface.

Differences observed in the cumulative percent emergence between ecotypes supported the hypothesis that these were actual ecotypes. This difference is likely a reflection of their areas of origin and how they have adapted to these areas.

Higher percent seedling emergences displayed by the CA in relation to either the MD or PEI, at tested depths, also reflects their characteristic differences. The CA ecotype has large seed size as compared to the MD or PEI ecotypes, and therefore had a larger food reserve that might sustain germination and emergence from greater depths. Additionally, seed germination from greater depths of 7.5 and 10 cm suggests that light is not the only factor influencing the fate of seed germination. Other related factors like temperature, soil moisture and oxygen content, which are equally important as light are acting singly or in combination in affecting seed germination. It may be argued that light

at 0 depth may be inhibitory, but other factors like fluctuating soil moisture and temperature, do play a role at this depth.

Since this study was conducted under controlled conditions, it should be borne in mind that the results obtained may differ from those occurring in a field situation. These results, however, indicate that barnyardgrass ecotypes respond to specific stimuli and emergence, may not necessarily be the same in a field soil environment (164). In soil, several variables often interact simultaneously to varying degrees on weed seed (barnyardgrass included). These variables include changes in exposure to light, moisture, temperature, and gaseous environment. Depending upon the location of the seed in the soil profile and the season, exposure of seeds to these variables differs considerably.

These ecotypes demonstrated varying rates of emergence and total emergence. The CA ecotype emerged with greater numbers at all seed depth, followed by the MD and PEI ecotypes, respectively. It is assumed that the MD and PEI ecotype low percent emergence across depths, unlike the CA ecotype may be attributed to their seed dormancy status, seed sizes, less seed vigour and their adaptive strategy to "budget" seed release.

Seed of the CA ecotype emerged sooner after seeding, compared to the seed of the MD and PEI ecotypes, regardless of seeding depths. Maximum emergence was obtained from seed planted at 1 or 2.5 cm depth. Fewer seedlings established from seed planted on the surface, and the rate of establishment was slower.

The unpredictable nature of seedling emergence at 0 cm reflects seed behaviour

to uncertain environmental exposure. In this study, drying in between watering, light exposure, and unpredictable gaseous exchange might have contributed to the results obtained 0 cm depth. In a field situation, however, the soil surface tends to dry rapidly after a rainfall, resulting in inadequate moisture and probably accounts for unpredictable seedling emergence or a low number of seedlings (41). It is also likely that the opposite of the above field situation could occur. Additionally, light quality, particularly the red: far red ratio that changes as it passes through a crop canopy or a direct contact with the soil may differentially affect dormancy in seed (151, 153, 163).

The ecotype seedling emergence at 1 and 2.5 cm depths displays greatest percent emergence, suggesting that these ecotypes' optimum depth of emergence was at 1 and 2.5 cm. It was further observed that the CA ecotype showed greater emergence at 2.5 cm than at 1 cm, whereas the MD and PEI ecotypes had greater emergence at 1 cm than at 2.5 cm. This may suggest that those ecotypes with large seed size, such as the CA ecotype, has better chance of emergence at 2.5 cm than at 1 cm, whereas the MD and PEI ecotypes with small seed size do well at shallow (1 cm) depth. It might also be possible that interacting environmental factors within these depths might sensitize ecotypes' seed to germinate. Timely control measures taken once seedlings have emerged at these depths, application of pre-emergent herbicides, or cultivation at the peak of seedling emergence, will reduce weed density and control the infestation.

The results further showed the ability of the three ecotypes to germinate and emerge from great soil depths (7.5 to 10 cm). Although light has been shown to stimulate germination of other weed seed (79, 137, 164, 179), it appears that this

stimulus at greater depths might not have been a factor in this study; since light could not penetrate soil to stimulate the seeds buried at 7.5 to 10 cm (165).

Ability to emerge from soil depths of 5 to 10 cm, makes barnyardgrass a serious weed, as indicated by Roche *et al.* (142). The emergence from these depths, though less in percentages than at 1 to 2.5 cm, must be considered a potential source of weed infestation. Later emerging plants might escape pre-emergence or early post-emergence herbicides, and further complicate future weed control measures (41). Stoller *et al.* (158) reported that weeds emerging after planting, in agronomic crops, require different and usually more difficult methods of control than those emerging together with or before the crops.

It could be concluded in this study that the three ecotypes are distinctly different in their seedling emergence from 0 to 10 cm depths. Increasing seed depths, especially from 1 to 10 cm, led to a decrease in total percent emergence, and a delay in time of emergence. Overall, the CA ecotype showed higher percent emergence between 3 to 9 DAS, followed sequentially by the MD and PEI, respectively. At greater depths of 7.5 and 10 cm, the CA ecotype was a better performer. Additionally, the ecotype seeding depth, their characteristics, and seed sizes determine seedling emergence.

Table 5.1. Barnyardgrass ecotype seedling emergence response over time to main and interacting factors, analysed by orthogonal polynomial (Data arcsin transformed).

Source	Df	MS	F-Value
Run (R)	1	4.58	1.15ns[a]
Ecotype(E)	2	17207.2	30.1*
Depth (D)	5	84864.0	149.3*
E x R	2	121.4	0.25ns
E x D	10	1347.1	2.4*
(E x D x R)	54	553.6	0.14ns
Time (t)	14	15101.4	1062*
t x R	14	1526.8	2242.1*
t x E	28	47251.1	1560.4*
t x D	70	629.7	273.4*
t x E x D x R	140	0.28	30*

[a] Not significant at $P < 0.0001$;

*, Significant at $P < 0.0001$

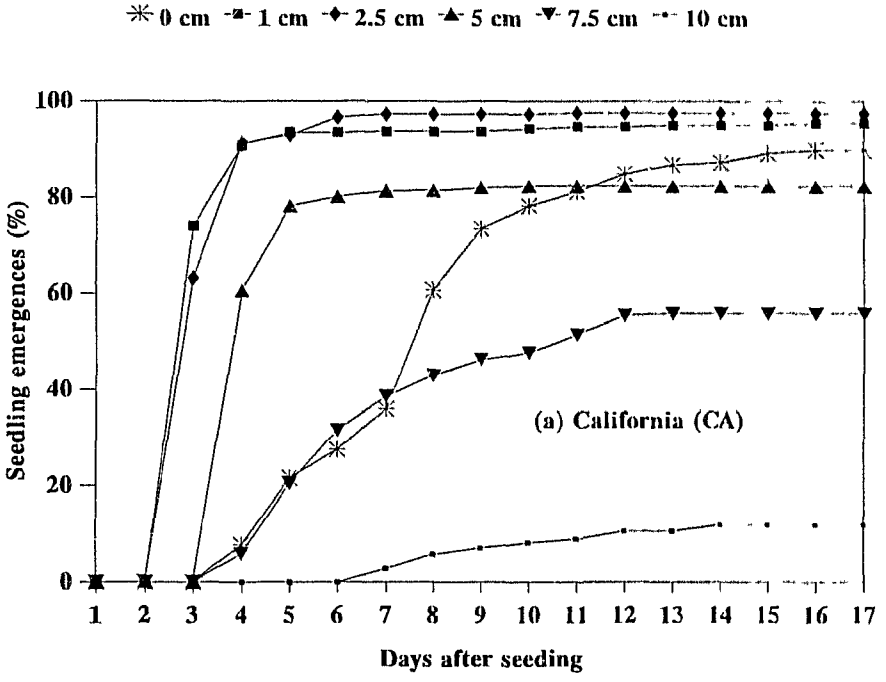

Fig. 5.1. Effect of seed depth on California ecotype cumulative seedling emergence.

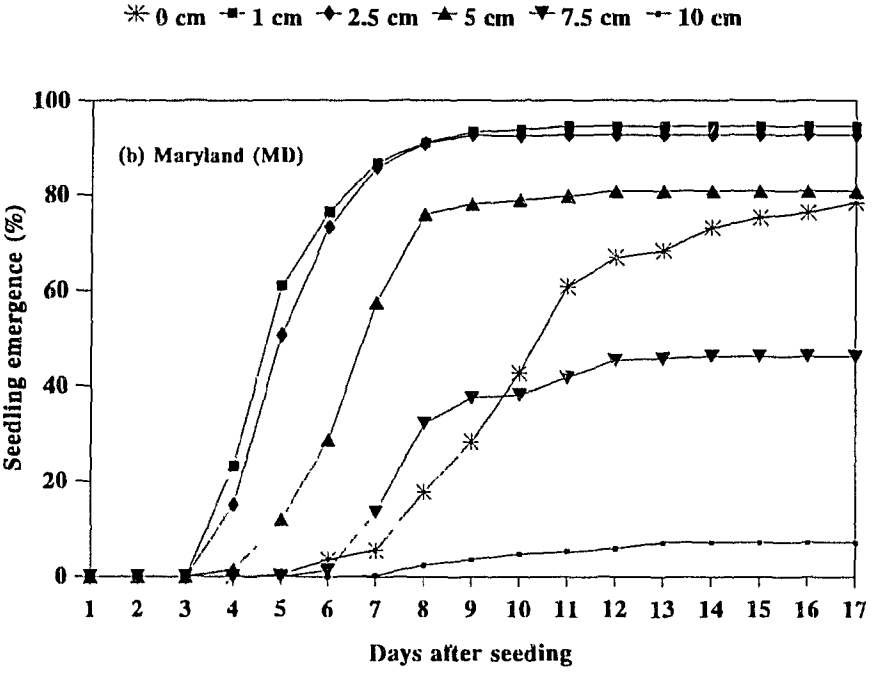

Fig. 5.2. Effect of seed depth on Maryland (MD) ecotype cumulative seedling emergence.

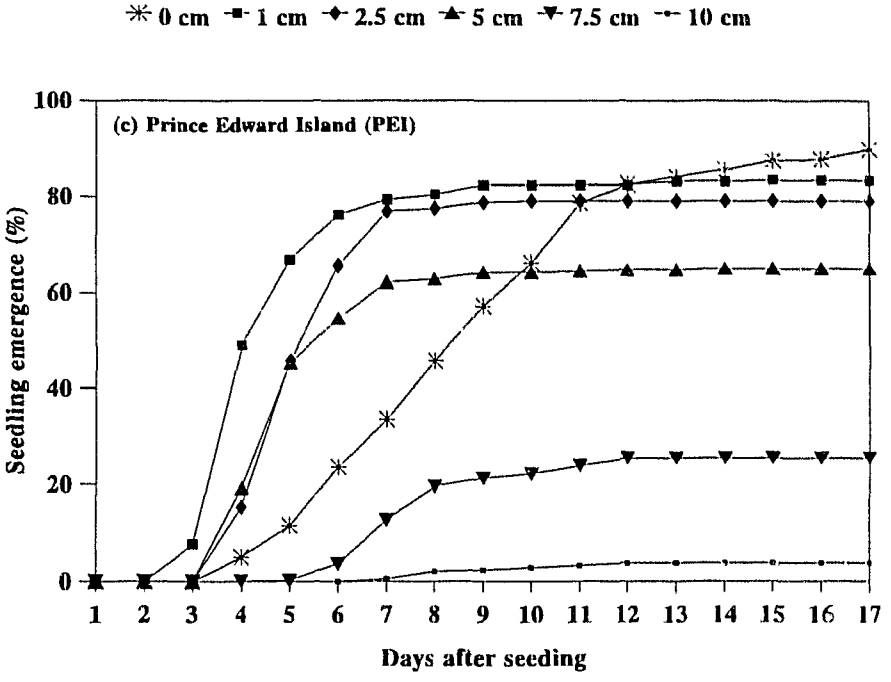

Fig. 5.3. Effect of seed depth on Prince Edward Island ecotype cumulative seedling emergence.

CHAPTER 6

THE EFFECT OF PHOTOPERIOD AND TEMPERATURE ON GROWTH AND DEVELOPMENT OF THREE BARNYARDGRASS (ECHINOCHLOA CRUS-GALLI [L.] BEAUV) ECOTYPES.

INTRODUCTION

Barnyardgrass is reported to be a short day (SD)[1] plant (134); but is adapted to flower under a wide range of photoperiodic conditions. This adaptation may be a significant factor to its wide distribution globally (80). Barnyardgrass under SD, of 8 to 13-hr day length, headed and produced mature seeds much earlier when they are 70 cm tall compared to plants under long-day (LD)[1] of 16-hr conditions, flowering much later at 150 cm plant height. The LD plants also produce large inflorescences with greater seed output compared to small inflorescences and low seed output under SD conditions (13, 80, 90, 143).

Barnyardgrass plants are highly susceptible to shading. The number of tillers and panicles per plant are always greater in full sunlight than in heavy shade (24). The growth, leaf area and net assimilation rate also increases with increasing light intensity and temperature (8).

The objective of this set of experiments was to determine the effects of long (16 hr) and short (9 hr) day photoperiods on germination, growth and development of

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[1]Abbreviations: SD and LD for short-day and long-days.

three barnyardgrass ecotypes, originating from contrasting environments - California (CA), Maryland (MD) and Prince Edward Island (PEI).

MATERIALS AND METHODS

Seed source. For the seed source and storage conditions for seed used, prior to conducting the experiment, are described in Chapter 2.

Soil treatment. A loam-soil was used, amended with sand, in the ratio of 2:1, a ratio established on volume basis. The soil had a pH of 6.4 (measured using a pH glass electrode metre, after preparing a 2:1 water and soil ratio solution, and allowing to stand for 30 minutes). The soil amendment, increased soil aeration and deterred soil compaction, that might occur due to differences between field and potted soil, in the course of plant germination and development. Amended soil was steam sterilized and filled into 108 plastic pots, each 15 cm diameter by 15 cm depth, then transferred to the greenhouse.

Experiment I. ***Short days***.

This experiment was initiated on 16 October, 1991 and terminated on 1 January, 1992. It was repeated on 14 October, 1992 and terminated on 30 January, 1993. Short-day photoperiod of 9 hr, and a natural light of 600-670 μmol m^{-2} s^{-1}, without supplemental light was provided throughout the study. Greenhouse temperature was maintained at 18/15 °C (day/night). Ten seeds of each ecotype were planted at a depth of 2 cm. The experiment was replicated three times (3 pots x 3 ecotypes), in a randomized complete block. Seedling emergence for each ecotype, 5

to 8 days after seeding, was noted. One week after seeding, one of the emerged seedlings was selected at random, removed and plant height, numbers of leaves, leaf area, and dry weight were determined. Two weeks later, each ecotype was thinned to two plants per pot. Each pot of two plants, was treated as an experimental unit. One plant per pot per replicate for each ecotype, was subjected to a weekly suite of measurements. The other plants were photographed and seed yield was recorded at the conclusion of the experiment. The plants were watered daily with tap water when necessary, and once a week flushed with prepared nutrient solution of 15-15-18 (N-P-K) at the rate of 1 gm of this product per litre of water. Pots were rearranged weekly within replications for the entire duration of the experiment.

Experiment II. ***Long days.***

This experiment was provided with long-day photoperiod of 16 hrs, 670 μmol m^{-2} s^{-1} supplemental light and 21/16 °C (day/night) constant temperature. It was initiated on 12 February, 1992 and terminated on 29 April, 1992; repeated on 1 February, 1993 and terminated on 15 April, 1993. The procedures and other requirements for the repeat were the same as for the above experiment.

Plant height. Plant height was measured weekly, from the soil surface to the tip of the inner and most recent unfolding leaf. Once the plant headed, flag leaf tip was used; later, the measurement was shifted to the tip of the spikelets.

Tillering. The onset of tillering, under SD and LD conditions, was noted, and once this had occurred, the number of tillers produced by each ecotype was recorded weekly until the conclusion of the experiment.

Plant leaf area. Plants used for height measurement were also utilized for leaf area measurement. Leaf area was measured with a Li-Cor leaf area metre (Li-Cor model LI-3100)[2], which was calibrated with a standard calibration disk (50 cm^2 for 1.0 mm^2 resolution). Measurement was made for each individual plant, on fully developed expanded leaves. The leaves were cut at the collar where the leaf blade met the leaf sheath. At later stages of plant maturation, the lower senescing leaves were omitted. Measured leaves, representing each ecotype per replicate were placed in labelled paper bags, then transferred to the oven.

Plant dry weight. The above ground plant materials, were placed in paper bags and transferred into a Fisher Isotemp Oven set at 80 °C. The dry weight was obtained after 24 hours.

Statistical Analysis. The data for each day length for both experimental runs were combined and each variable was analyzed separately. Data were analyzed using SAS Statistical Package (SAS Institute, 1985) as 'repeated measures analysis'. Each experimental run $(R)^b$ for each day-length was analysed as (a) block, (b) temperature and photoperiod $(TP)^\dagger$ as whole plot treatment, and (c) ecotype $(E)^\S$ as sub-plot treatment. Data for height and leaf area were log transformed in order to stabilize the variance within the data. Leaf and tiller number, fresh and dry weights were not

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[2]LI-Cor, Inc., P.O.Box 4425, Lincoln, Nebraska 68504, USA.
Abbreviations: $(R)^b$=Experimental run, $(TP)^\dagger$=temperature and photoperiod, and $(E)^\S$=ecotype.

transformed.

RESULTS AND DISCUSSION

Seedling emergence. The seedling emergence for the CA ecotype, from 2 cm soil depth under both SD and LD conditions, exceeded 90% within five days after seeding, whereas the MD and PEI ecotypes displayed above 85% emergence after eight and five days, under SD and LD conditions, respectively (Appendix II).

The early emergence of the CA seedling may give it an initial competitive edge over late emerging species or ecotypes. The first plants up, however, are not necessarily the most competitive. If a late-emerging crop or other weed species, for example, has a faster growth rate than the weed, then it may surpass the other species and become the dominant one in its area of influence (70). Weed emergence time relative to crops is critically important in weed-crop competitive outcome (133). It was apparent in this study that under LD conditions, all ecotypes displayed similar time of seedling emergence.

Plant height. Ecotypes' growth stages attained at each date provided an assessment of barnyardgrass vegetative development. There was clear evidence that ecotype height response to runs (R), photoperiod/temperature (TP), ecotype (E) effects, and runs by temperature/photoperiod (R x TP), ecotype by temperature/photoperiod (E x TP), runs by ecotype by temperature/photoperiod ($P > 0.0001$), and ecotype by temperature/photoperiod at ($P > 0.0931$) interaction, was significantly different,

respectively, over time to SD and LD conditions (Table 6.1). This indicate that the ecotypes height over time was influenced by tested variables.

Significant ($P > 0.0001$) time (t), time by runs (t x R), time by temperature and photoperiod (t x TP), time by temperature/photoperiod by runs (t x TP x R), time by ecotype (t x E), time by ecotype by runs (t x E x R), time by temperature/photoperiod by ecotype (t x TP x E) and time by ecotype by temperature/photoperiod by runs (t x E x TP x R), were detected. The data suggests that the ecotypes' height response to runs, ecotype, temperature/photoperiod varied significantly over time (Table 6.1).

Individual observations indicated that under SD conditions, the CA ecotype, from seedling emergence to maturation, showed greater height in comparison to the MD and PEI ecotypes (Fig. 6.1a-b). This trend, however, differed remarkably under LD conditions, where difference in height between ecotypes was noticeable only during the first three weeks; thereafter, the ecotypes displayed similar height up to the eighth week, when the MD and PEI ecotype floral initiation commenced. Floral initiation appeared to trigger culm elongation, which increased rapidly in comparison to overall vegetative growth. This elongation appeared to be independent of temperature and photoperiod. Elongation in most grasses is a requirement which separates leaves from the spikelets, hence elevating and exposing the inflorescence to a solar energy-rich environment at some height above the ground (6). The stem elongation for the CA ecotype was not as rapid as for the other two ecotypes (Fig. 6.1a-b).

High temperatures and long days increased ecotype height. Although the CA

ecotype responded favourably to both conditions, the MD and PEI ecotypes responded favourably to the LD but were inhibited by the SD conditions. Individual ecotype observations indicated that ecotypes under LD conditions were taller unlike ecotypes under SD conditions (the CA ecotype aside). The differences in height among the ecotypes, under SD was conspicuous when the MD and PEI ecotypes were compared with the CA ecotype. Similar results have been reported by other workers (80, 99, 127), and indicated that rate of plant vegetative growth, measured by plant height, appears to be directly related to temperature and photoperiod effects, with slow extension of shoots in spring and very rapid growth in the heat of summer.

Also, the MD ecotype displayed a prostrate habit during LD, which might suggests that it belongs to an open habitat (105). The MD and PEI ecotypes under LD condition also displayed distinct anthocyanin pigmentation, which became obvious in the fourth week and lasted to maturity of the ecotypes. The CA ecotype, under the same condition, showed leaf chlorosis, and senescence of lower leaves. This may be attributed to plants' preparation to channel most energy and food requirement to the developing seed instead of other organs.

A positive relationship between height and competitive ability has been found in rice varieties (82), corn varieties (127), *Amaranthus* spp. (177) and in wheat and weeds (126). In this study, the CA ecotype showed greater height during both photoperiods, and depending upon the extent to which its leaves can rapidly penetrate to superior positions in the canopy (69), the data might suggest that it is capable of successful competition for light, either under SD or LD conditions, and would be a

threat to crops either during warm or cool growing conditions. Additionally, the MD and PEI ecotypes might be considered serious weeds, especially during warm growing conditions (LD), but not during cool conditions (SD), because of their small stature under this latter condition. It has been noted that in a year with cool summer on PEI, the PEI ecotype is less competitive with crops than in warm seasons (Ivany, personal communication). This confirms an earlier report (134), that the LD plants grow tall, produce a large amount of foliage, and are very competitive. The SD ecotypes, (the CA ecotype aside), might have less competitive influence on crop plants (Fig. 6.1 a-b).

Tillers. The CA ecotype, under SD conditions, tillered late, in its tenth week of growth. Its mean tiller number recorded varied from 0.3 to 2.3. The MD and PEI ecotypes, on the other hand, started tillering on the sixth and seventh week. Their mean tiller number recorded varied from 2 to 6.8 tillers (Fig. 6.2a). Mean maximum tillers for the CA, MD and PEI ecotypes were 2.3, 6.2 and 6.8, respectively. Comparatively, the MD and PEI ecotypes, besides tillering late, tillered profusely under SD, hence corroborating an earlier report (132) that a photoperiod of 13 hr produced plants markedly different from those in 14.5 and 16 hr treatments, in that they have more tillers and panicles.

Ecotypes tillering under LD commenced early, three weeks after seeding, and unlike the SD conditions, mean tiller number recorded varied from two to four tillers. Maximum tillers recorded for the CA, MD and PEI ecotype under LD were 2.8, 4.2 and 3.8, respectively. There was no difference in maximum tiller numbers recorded

under SD or LD for the CA ecotype. However, tiller numbers for the MD and PEI ecotypes, under LD were less than those under SD (Fig. 6.2b). In this study, the SD conditions, besides influencing tillering time, also produce ecotypes with weak tillers, unlike the robust ones under LD conditions. In both conditions, it appeared that the CA ecotype was a poor tiller producer.

Leaf number. Significant ($P > 0.0001$) runs (R), temperature and photoperiod (TP), ecotype (E) effects; runs by temperature/photoperiod (R x TP), runs by ecotype (E x R), and temperature/photoperiod by ecotype by runs (TP x E x R) interactive effects detected, respectively, for main shoot leaf number response over time (Table 6.2). The results indicate that the ecotypes' leaf numbers were influenced both by the experimental runs, temperature/photoperiod, ecotype and their interactions.

Also, significant ($P > 0.0001$) time (t), time by runs (t x R), time by temperature/photoperiod (t x TP), time by temperature/photoperiod by runs (t x TP x R), time by ecotype (t x E), time by ecotype by runs (t x E x R), time by temperature/photoperiod by runs (t x TP x R), time by temperature/photoperiod by ecotype (t x TP x E) and time by temperature/photoperiod by ecotype by runs (t x TP x E x R), respectively. This suggests that leaf numbers response over time to the tested variables varied with increase influenced across time (Table 6.2).

Ecotype leaf number under either SD or LD over time showed that ecotype specific number of leaves must be attained before flowering. Additionally, this number was influenced by the ecotype and day-length (Fig. 6.3 a-b). The graph presented (Fig. 6.3), showed that leaf numbers increase initially up to the seventh

week after seeding, then levelled off. The levelling off appeared to have been caused by floral initiation and leaf senescence.

It has been reported that the number of leaves produced on a shoot or tiller is determined at inflorescence initiation; since floral initiation terminates any further leaf development. Characteristic leaf numbers are 7 to 9 for wheat, oats, and barley; 7 to 14 for sorghum; 14 to 21 for most corn hybrids; and 10 to 16 for soybean cultivars (66). In this study, number of leaves recorded varied by ecotype, with the greatest number of leaves for MD and PEI ecotypes for primary culm and tillers being 5 to 6, and 6 to 10, respectively, under SD condition. The CA ecotype, on the other hand, recorded 8 to 9 for the culm and 4 to 7 for the tillers. Under LD, these ecotypes had 8 to 9 leaves, confirming earlier studies (134) that a definite number of leaves must be attained before floral initiation.

Plant leaf area. Significant ($P > 0.0001$) runs (R), temperature/photoperiod (TP), ecotype (E) effects, and temperature/photoperiod by runs (TP x R), ecotype by runs (E x R), temperature/photoperiod by ecotype (TP x E) and temperature/photoperiod by ecotype by runs (TP x E x R) was detected for leaf area response over time to SD and LD conditions (Table 6.3).

Significant ($P > 0.0001$) time (t), time by runs (t x R), time by ecotype (t x E), time by temperature/photoperiod (t x TP), time by temperature/photoperiod by runs (t x TP x R), time by ecotype by runs (t x E x R), time by temperature/photoperiod by ecotype (t x TP x E) and time by temperature/photoperiod by ecotype by runs (t x TP x E x R) interactive effects was detected for leaf area response over time. The

results suggests that there is a significant change in leaf area in response to the studied variables over time (Fig. 6.4a-b).

The data further suggest that the CA, MD and PEI ecotypes were closely related under LD condition, whereas under SD, the MD and PEI ecotypes showed closely related small leaf area compared with the CA ecotype which displayed greater leaf area under SD condition (Fig. 6.4a-b). The MD and PEI ecotype leaf areas were significantly affected by SD. The maximum mean leaf area attained for the MD and PEI ecotypes was 68 and 71 cm^2, compared to 229 cm^2 for the CA ecotype (data backtransformed). This clearly showed that the CA ecotype was less inhibited by the SD condition (Fig. 6.4a-b). The MD and PEI ecotypes confirm an earlier report (125, 134), that reduction of leaf area at short day length and lower temperatures is one of the more noticeable morphological effects. Anslow (6) reported that smaller leaf areas may be due to reduction of the rate of appearance of leaves at the growing tip.

Ecotypes under LD displayed larger leaf area, with no significant difference among them, unlike plants under SD conditions. Though the MD and PEI ecotypes headed 7 weeks after seeding, two weeks earlier than the CA ecotype, their leaf areas appeared to level off at week nine.

Flower initiation occurred 7 and 8 weeks after seeding under LD. As a result, upper leaf expansion ceased, confirming earlier studies (113) that the length of leaf lamina decreases with flower initiation in grasses like barley. The cause of the diminution of upper leaves is not known but might be due to competition with the

inflorescence for nutrients (113). The flag leaves for these ecotypes were shorter, narrower and had less area than the primary leaves (Fig. 6.4a-b).

Potter *et al.* (129), showed that leaf area partitioning, or the rate of expansion of new leaf area, was highly correlated with rapid growth, confirming the results reported in this study for ecotypes grown under LD conditions. They all exhibited large leaf areas and rapid, robust, vegetative growth. Roush *et al.* (143), reported that growth parameters related to plant size and leaf area was the best predictor of competitiveness in mixtures of weeds. Holt (80), suggested that rapid leaf area production, which results in rapid canopy development is critical for the success of either weeds or crops in the agricultural environment. Success of plants in isolation and in mixture is associated with early and rapid establishment, rapid canopy development, and rapid root growth (74). Generally, a disproportionate share of the available resources, to the detriment of its neighbours, is used by species that grow faster than their neighbours. Hence, growth rate may reflect potential relative competitive ability of the plants (143). It is apparent in this study that the CA ecotype may be a better competitor under SD conditions, compared to either the MD or PEI ecotypes, because of its large leaf area that might capture incoming light more effectively, and its wider canopy area might cut off available light for the other species. However, under LD condition, all ecotypes appeared equally competitive.

Plant dry weight. Significant ($P > 0.0001$) runs (R), temperature/photoperiod (TP), and ecotype (E) effects; temperature/photoperiod by runs (TP x R), ecotype by runs by temperature/photoperiod (E x R x TP), ($P > 0.0019$) ecotype by runs (E x R), and

($P > 0.0009$) temperature/photoperiod by ecotype by runs (TP x E x R) interactive effects was detected for the ecotypes above ground dry-weight response (Table 6.5).

The results indicate that ecotypes dry-weights were influenced by individual as well as interacting variables tested. Also, temperature/photoperiod (TP) has greater influence on the above ground dry-weight, whereas ecotype by run (E x R) and ecotype by temperature/photoperiod (E x TP) both showed less influence on the ecotypes dry-weight (Table 6.4)

Significant ($P > 0.0001$) time (t), time by runs (t x R), time by ecotype (t x E), time by temperature/photoperiod (t x TP), time by temperature/photoperiod by runs (t x TP x R), and ($P > 0.0459$) for time by temperature/photoperiod by ecotype by runs (t x TP x E x R) was detected for the ecotypes' dry-weight response. No significant difference was detected for time by ecotype by runs ($P > 0.3063$) and time by ecotype by temperature/photoperiod ($P > 0.3893$) (Table 6.4). This suggest that ecotypes' dry weight was influenced over time by the main factors (ecotype, runs and temperature/photoperiod), whereas time and its interaction with ecotype by run and ecotype by temperature showed no influence (Table 6.4).

The SD conditions produced ecotypes that had no significant difference in their above ground dry weight, from the time of seedling emergence up to the sixth week. Thereafter, the CA ecotype dry weight increased, relative to either the MD or PEI ecotype. There was no significant difference in the MD and PEI ecotypes dry weight, implying a close relationship in energy efficiency and food accumulation. Maximum average dry-weight recorded for the CA, MD and PEI ecotypes was 3.0, 0.6 and

0.9 gm, respectively (Fig. 6.5a-b).

The ecotypes under LD conditions had no significant difference in their above ground dry-weights. The greatest mean dry-weight recorded was 14.0, 12.2 and 12.0 gm for the CA, MD and PEI ecotypes, respectively. The data showed that all ecotypes under LD produced greater dry-weight, compared to ecotypes under SD (Fig. 6.6a-b). Additionally, the three ecotypes appeared to have accumulated more dry matter under LD than SD conditions (Fig. 6.5 a-b).

Plant dry weight is the most meaningful parameter for measuring growth analysis, and plant efficiency in utilizing limited natural resources. Total dry matter yield for field crops or weeds results from accumulation of net CO_2 assimilation throughout the growing season. The CO_2 assimilation results from solar energy (irradiance) absorption and because of its wide range, on seasonal basis, the primary factors affecting total dry matter yield are solar radiation absorbed and the efficiency of utilizing that energy for CO_2 fixation (66). The CA ecotype displayed greater ability to produce dry weight and large leaf areas, regardless of the conditions. It is assumed that the CA ecotype may be capable of fixing CO_2 and utilizing light energy more efficiently regardless of the photoperiods used in this study. The MD and PEI ecotypes, on the other hand, were severely inhibited in their dry matter accumulation under SD conditions (Fig. 6.6a-b). It may be assumed that the MD and PEI ecotypes, at low temperatures and photoperiods, were less efficient in fixing CO_2 and utilizing light energy, while at high temperatures and photoperiods (LD), they might be very efficient.

Floral initiation. The CA ecotype, regardless of photoperiods, booted 8 weeks after seeding and did not flower until after 9 to 10 weeks. The MD and PEI ecotype, under SD conditions, booted 6 weeks after seeding and flowered after 7 to 8 weeks, whereas under LD conditions they booted at 8 weeks and flowered 9 to 10 weeks after seeding, respectively. These ecotypes therefore displayed similar flowering time under LD but differed widely under SD. Under SD, the ecotypes matured faster, and flowered earlier, compared to the ecotypes under LD. Holm *et al.* (80) reasoned that plants grown under 8- to 13-h day lengths passed into flowering stage quickly and remained small in stature because vegetative development had been reduced or ceased altogether. Besides flowering and maturing earlier, the SD ecotypes produced very few seeds, whereas the LD ecotypes had rapid, vegetative growth and massive seed production. It was recorded, for example, the CA, MD and PEI ecotypes had an average of 1,511, 3,682 and 3,448 seeds per plant, respectively, under LD conditions, whereas under SD conditions, the CA, MD and PEI ecotypes had 97, 130 and 114 seeds per plants, out of 36 plants per each ecotype (Appendix III). The floral initiation and seed production reported in this study confirmed findings by other workers (80, 90, 105, 134),

The fact that the MD and PEI ecotypes matured fast and did produce some viable seeds under SD, provides evidence that they are successfully adapted to a cool environment. They tolerate low temperatures and a short life cycle (130, 131). Reduction in their life cycle enables such ecotypes to set seed before the frost, an example of the 'avoidance strategy' for their survival (99). Additionally, under LD

by the twelfth week any slight disturbance of the MD and PEI ecotypes' spikelets caused seed shattering and fall. The CA ecotype appeared to lack avoidance strategy. Under controlled conditions, it booted and initiated flowering late and produced mature viable seeds, but in the field onset of frost might occur before seed set and affect its chance of successful production of viable seed. The CA ecotype is adapted to a warm environment and might not do well in a cooler environment.

It has been reported that barnyardgrass might be an (SD) plant. It is apparent, however, that it is adapted to a wide range of photoperiodic conditions. It flowers early under SD and thus appears to be an SD plant. Under LD, it displays vigorous vegetative growth, extremely large plants with large inflorescences, often producing more seed than comparable panicles under SD. The grass then might be a delayed LD plant (134). It appeared that the CA ecotype fit into an LD, whereas the other two ecotypes corroborate the view held by Rahn *et al.* (134), that of appearing to fit into the two day lengths. The ability of these ecotypes to flower under a wide range of temperatures and photoperiods explains the wide range of distribution of barnyardgrass (80).

Ecological and agricultural implications. It is concluded from this study that the CA ecotype is different form the MD and PEI ecotypes in its photoperiodic and climatic adaptation. The three ecotypes' morphological and physiological characteristics reflect adaptation to their zones of collection. The ecotypes grown under LD conditions exhibited greater heights, larger leaf area, greater number of leaves, greater fresh and dry weights and more prolific seed production than those

grown under SD. The vigorous vegetative growth under LD suggests that all three ecotypes may be more competitive to crops, especially if they establish earlier, and utilized available food resources before the crops, whereas ecotypes (the CA ecotype aside) under SD may not be competitive to crops, especially if their height and leaf area are taken into consideration.

The response to a wide range of photoperiods demonstrated the suitability of the ecotypes for distribution globally and their adaptive success to different thermal ecological zones. This wide adaptation, means that as a successful weed, most of the crops world wide, temperate and tropical alike, will not be spared of its interference.

Early maturity under SD, and rapid seed fall under LD conditions, especially by the MD and PEI ecotypes, showed an adaptive avoidance strategy to allow survival over winter. This strategy allows them to flower and set mature seed into the soil seed bank, before the frost onset. Regardless of the conditions thereafter, future survival is ensured until favourable conditions occur again.

The prolific production of seed by all ecotypes under LD achieves two purposes: a) predation budgeting, and b) seed bank reserves. Large seed production is seen as a safety net, to ensure that in case of seed predation, there will be some seed spared for future propagation. The CA ecotype, for example, because of its large seed size, may be prone to destructive predators, unlike the small seeded MD and PEI ecotypes, which may benefit from some "facilitator" like the earthworms, which pass them with their cast to deeper soil depth, where they remain buried until exposed to favourable environmental conditions. Large amounts of dormant seed

ploughed back into soil seed bank ensures a seed reserve in the soil for future propagation. This strategy may explain the success of the MD and PEI ecotypes in temperate climates.

Table 6.1. Analysis of variance for three barnyard grass ecotypes' height responses to main and interactive effects by 'repeated measures analysis' (Data log transformed).

Source	Df	MS	F-Value
Runs (R)	1	0.91	806.5*[a]
Temperature/ photoperiod (TP)	1	9.32	242.1*
Ecotype (E)	2	2.11	713.6*
TP x R	1	0.04	34.2*
E x R	30	0.03	2.6*
TP x E	2	0.58	37.4*
TP x E x R	2	0.02	13.8*
Time (t)	11	7.3	2108.9*
t x R	11	0.06	17.3*
t x TP	11	0.03	8.04*
t x TP x R	11	0.08	23.2*
t x E	22	0.02	7.18*
t x E x R	22	0.01	2.5*
t x E x TP	22	0.02	5.75*
t x E x TP x R	22	0.01	3.29*

[a]=Significant at $P < 0.0001$ level of confidence

Table 6.2. Analysis of three barnyardgrass ecotype leaf number response to main and interacting factors by 'repeated measure analysis'.

Source	Df	MS	F-Value
Runs (R)	1	4.48	101.9*[a]
Temperature/ photoperiod (TP)	1	363	200.0*
Ecotype (E)	2	70.53	33.3*
TP x R	1	1.81	41.2*
E x R	2	2.1	48.2
TP x E	2	11.58	263.4*
TP x E x R	2	5.01	113.9*
Time (t)	11	210.6	2013.6*
t x R	11	0.82	7.9*
t x TP	11	3.33	31.8*
t x TP x R	11	0.66	6.3*
t x E	22	4.46	42.7*
t x E x R	22	0.84	8.0*
t x TP x E	22	1.54	14.8*
t x TP x E x R	22	0.27	2.6*

[a]=Significant at $P < 0.0001$ level of confidence

Table 6.3. Analysis of three barnyardgrass ecotype leaf area response to main and interacting factor by 'repeated measures analysis' (Data log transformed).

Source	Df	MS	F-Value
Runs (R)	1	2.41	428.6*[a]
Temperature/ photoperiod (TP)	1	65.96	20.9*
Ecotype (E)	2	6.73	1048*
TP x R	1	3.16	561.9*
E x R	2	0.01	1.14ns[b]
TP x E	2	1.69	30.7*
TP x E x R	2	0.06	9.8*
Time (t)	11	23.66	2954.1*
t x R	11	0.21	26.7*
t x TP	11	1.31	163*
t x TP x R	11	0.34	42.7*
t x E	22	0.08	10.3*
t x E x R	22	0.01	1.11ns
t x TP x E	22	0.10	13.1*
t x TP x E x R	22	0.02	2.9*

[a]=Significant at $P < 0.0001$ level of confidence

[b]=Not significant at $P < 0.0001$

Table 6.4. Analysis of three barnyardgrass ecotype dry weight response to main and interacting factors by 'repeated measure analysis'.

Source	Df	MS	F-Value
Runs (R)	1	24	44.3**[a]
Temperature/ photoperiod (TP)	1	1018.52	17.2*
Ecotype (E)	2	23.44	5.3*
TP x R	2	59.1	109*
E x R	2	4.45	8.2*
TP x E	2	5.19	9.58*
TP x E x R	2	10.5	19.4*
Time (t)	11	154.1	226.5*
t x R	11	5.78	8.49*
t x TP	11	100.6	147.5*
t x TP x R	11	9.96	14.6*
t x E	22	1.87	2.7*
t x E x R	22	0.77	1.14 ns[b]
t x TP x E	22	0.72	1.06 ns
t x TP x E x R	22	1.09	1.60*

[a]=Significant at $P<0.0001$ level of confidence

[b]=Not significant at $P<0.0001$.

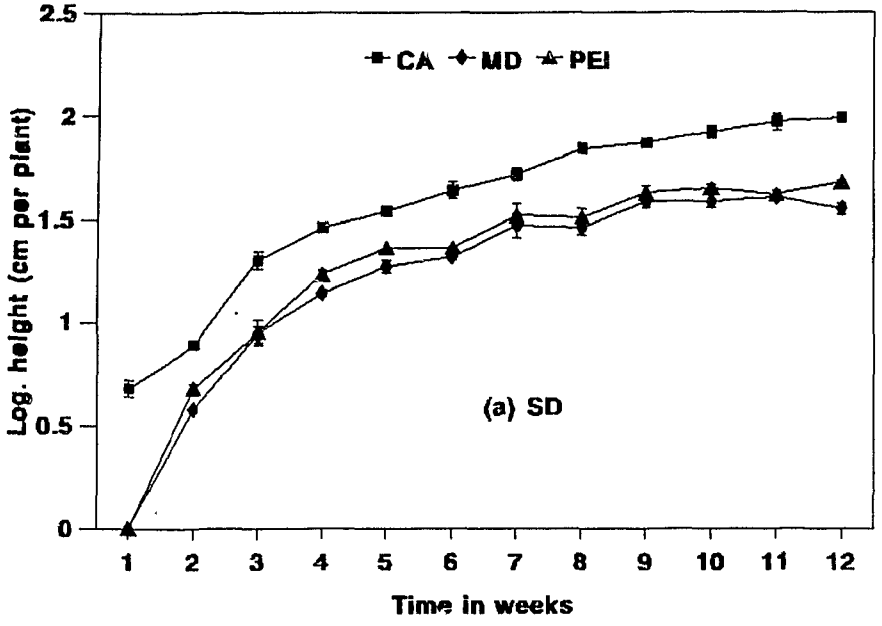
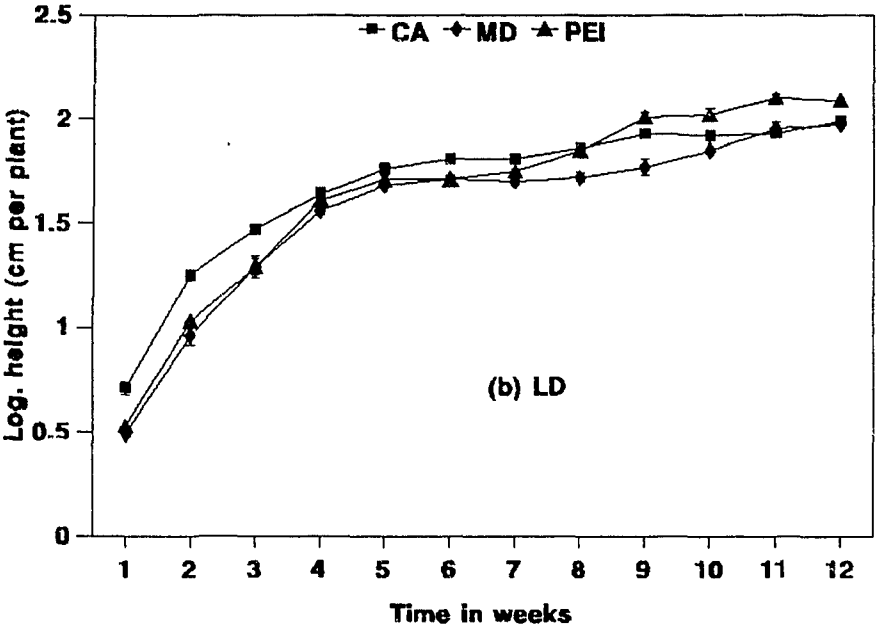


Fig. 6.1a, b. Effect of SD and LD on three barnyardgrass ecotype plant height (data log transformed).



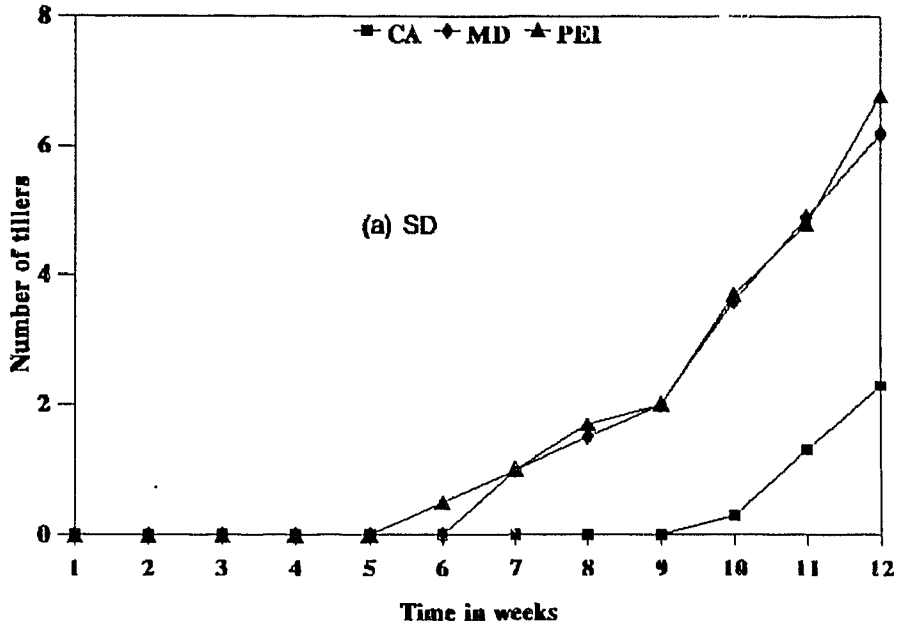
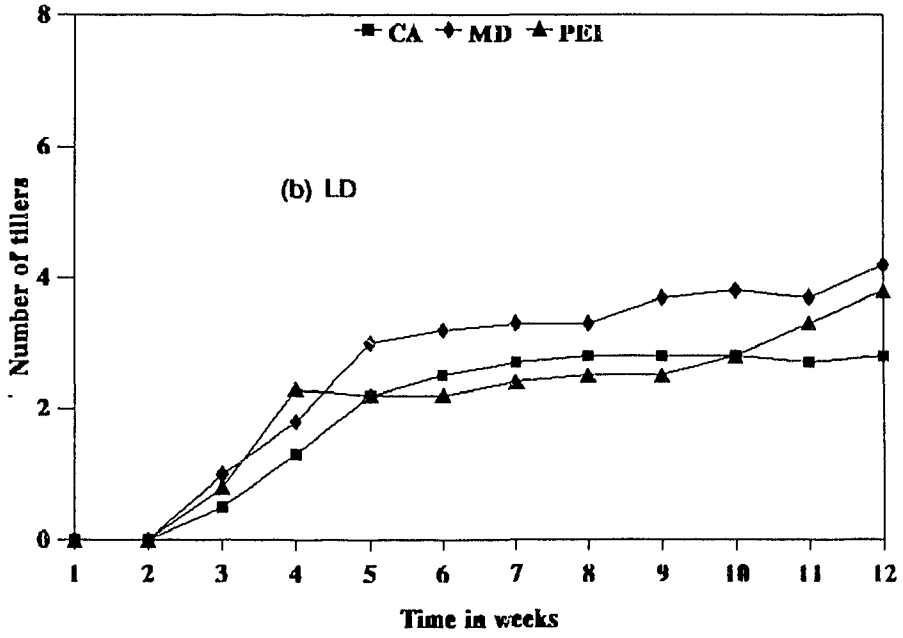


Fig. 6.2a, b. Effect of SD and LD on three barnyardgrass ecotype number of tillers.



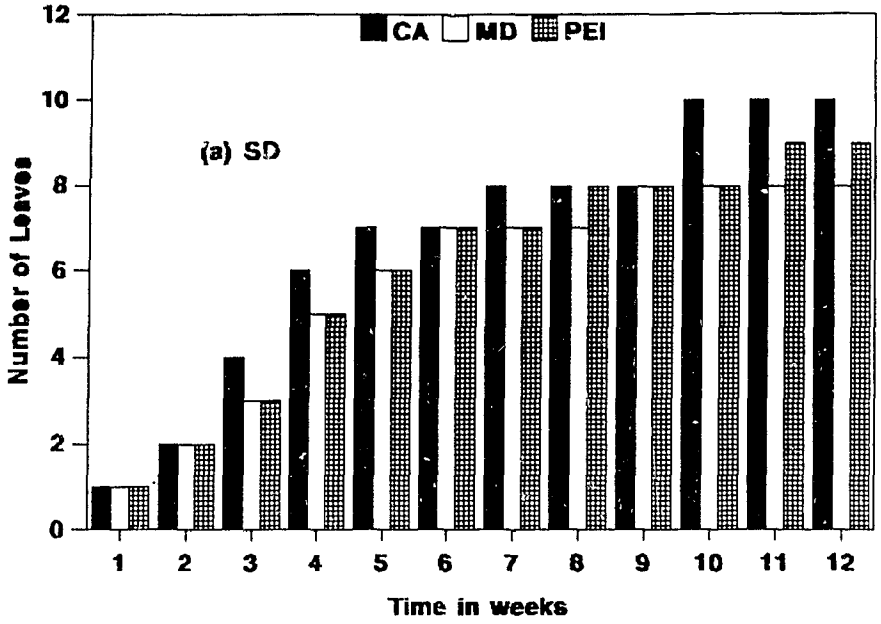
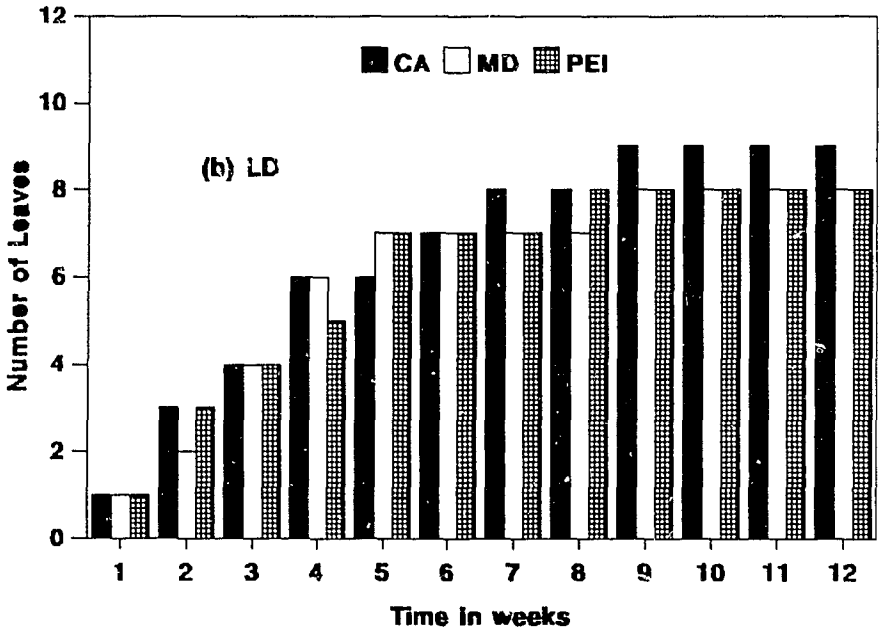


Fig. 6.3a, b. Effect of SD and LD on three barnyardgrass ecotype number of leaves.



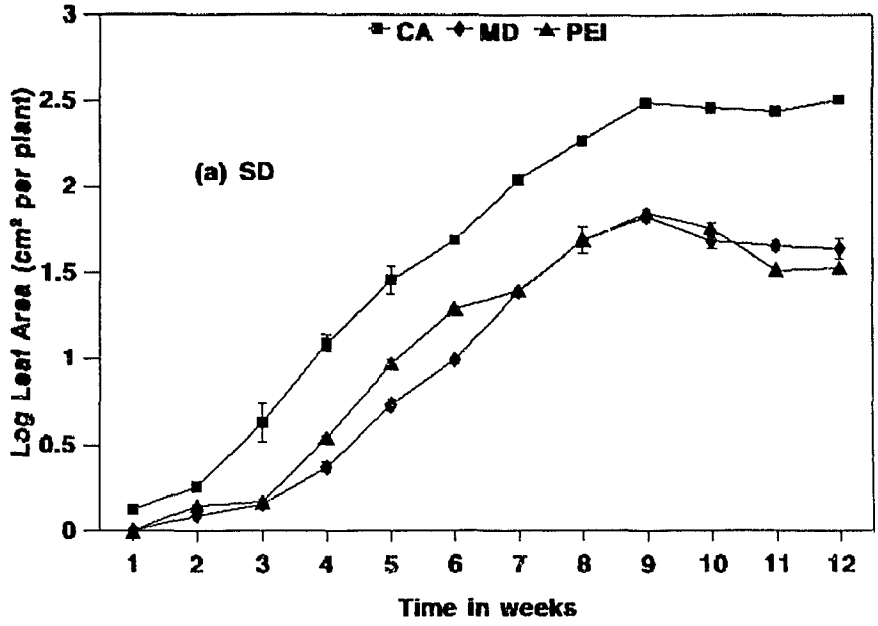
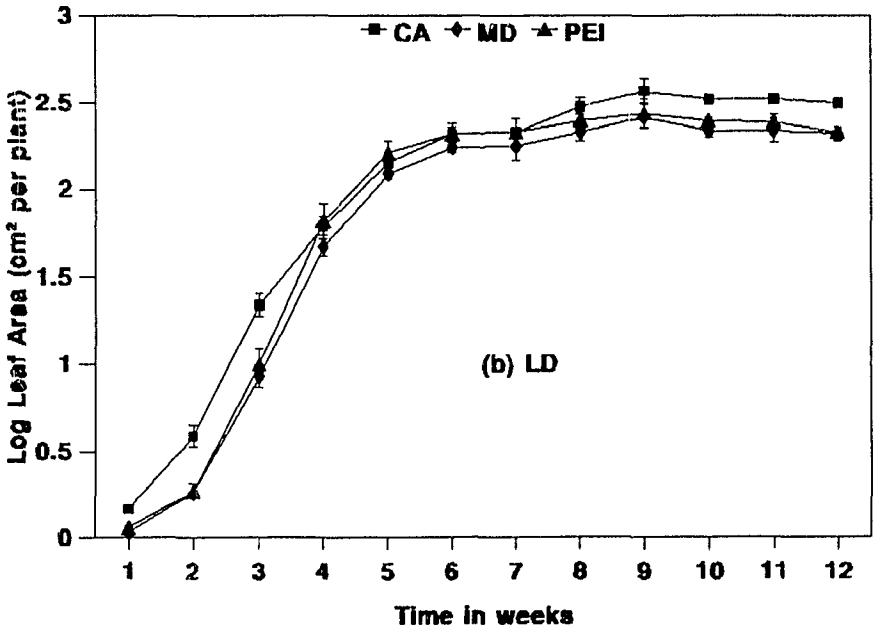


Fig. 6.4a, b. Effect of SD and LD on three barnyardgrass ecotype leaf area (data log transformed).



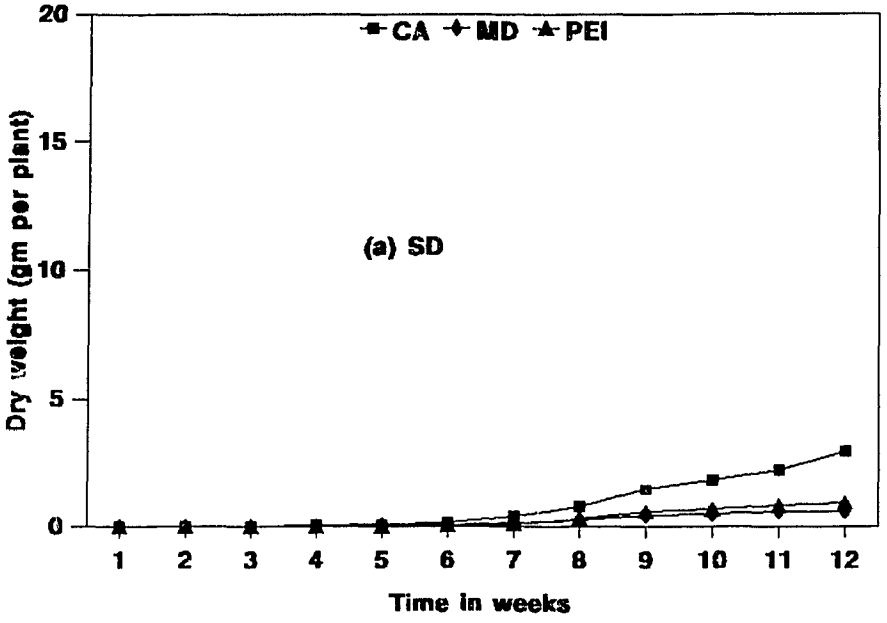
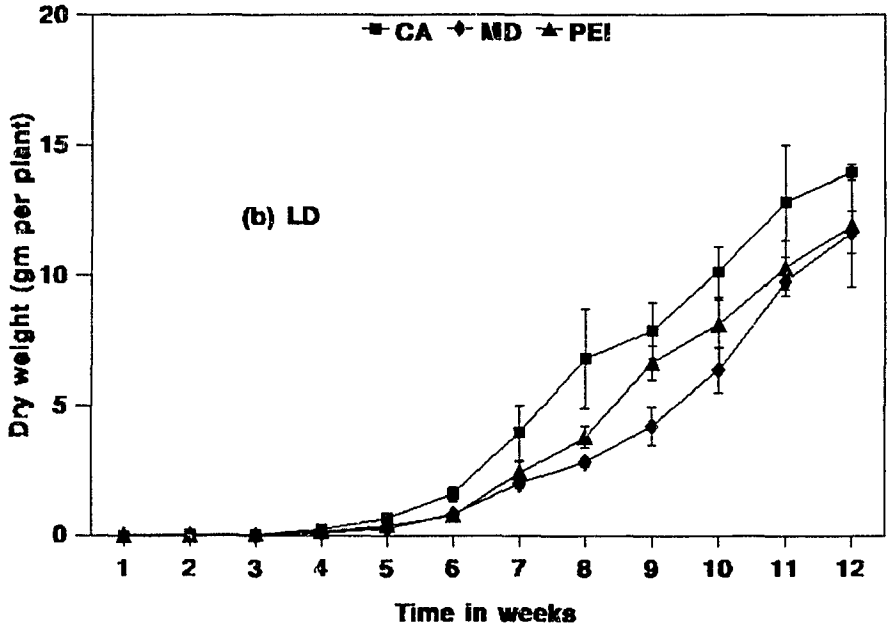


Fig. 6.5a, b. Effect of SD and LD on three barnyardgrass ecotype above ground dry weights.



Chapter 7

GENERAL DISCUSSION AND CONCLUSION

The experiment on longevity and germination pattern of buried seed shows that the CA ecotype response to burial is different from that of the MD and PEI ecotypes. Most of the CA seed exhumed during the initial four months of burial had either germinated, rotted or died in the field, such that subsequent retrieval yielded no data. This was attributed to lack of seed dormancy, and effect of ageing on the seed of the three ecotypes. The MD and PEI ecotypes, however, showed seed persistence in the soil and a seasonal cyclic pattern of germination, corresponding to rise and fall in soil temperatures. Their seed exhibited enforced dormancy during winter and late summer, but were stimulated to germinate in spring. It could be concluded that the CA ecotype is not adapted to persisting in the buried state, whereas the MD and PEI ecotypes do persist in a dormant state while buried during unfavourable seasons, common to their area of distribution.

The temperature effect experiment showed that the CA ecotype had more than 95% germination over the range of 10-40 °C. The MD and PEI ecotypes on the other hand, showed above 80% germination between 15 and 20 °C, and decreasing germination at temperatures below 15 and above 30 °C. Their optimum temperature for germination was at 20 °C. It is apparent in this study that the CA, MD and PEI ecotypes respond differently to temperature levels, hence might suggest their adaptability to their provenance. Keeley et al. (90), for example, pointed out that germination of a higher percentage of barnyardgrass seeds under a controlled temperature regime of

15/10 °C, accounts for its early emergence in California in March when air and soil temperatures do not exceed 14 and 17 °C, respectively. It is concluded that the CA ecotype is adapted to areas experiencing warm temperatures during most seasons of the year, whereas the MD and PEI ecotypes are adapted to areas of cool temperatures.

Temperature by nitrate interactive effects showed that the CA ecotype had more than 95% germination either imbibed in water or KNO_3, ranging from 5 to 30 mM and at 10 to 40 °C. This indicates that KNO_3 is not a factor influencing its germination. The MD and PEI ecotype germination, however, was enhanced by the addition of KNO_3, especially at low (10 °C) and high (40 °C) temperatures. The PEI ecotype, however, showed a decline in germination at 25 mM and at 10 °C; 15 to 30 mM at 30 and 40 °C. This might suggest that the PEI ecotype has an optimum germination limit with temperature by nitrate interaction. It is concluded therefore that in a field situation, besides other interacting factors within the soil environment, addition of nitrate fertilizers enhances the MD germination, and PEI germination with some limitation, whereas the CA ecotype might germinate with high percentages, with or without nitrate application. Also, that the CA ecotype might do well in areas of low soil nitrate level. It is assumed that the response of the three ecotypes to the addition of nitrate might indicate the nature of their habitats, hence the MD and PEI ecotypes may be weeds that have adapted to arable conditions, whereas the CA ecotype may be a weed of transient conditions. Overall, the KNO_3 stimulation on seed of the MD and PEI ecotypes may be beneficial in that greater seed production will be ploughed back into their seed banks, thus

increasing the seed bank reserve. These seed will be induced to dormancy and remain buried in the soil until they are exposed to favourable environmental conditions.

The temperature by water potential interactive effect showed that at high water potential of 0 and -2 MPa and temperature ranging from 20 to 30 °C, the ecotypes displayed more than 95 and 85% germination, respectively. However, increasing temperature and declining water potential from -4 to -10 MPa led to decrease in germination. The MD and PEI ecotypes were affected more at 30 °C by decreasing water potential from -6 to -10 MPa. Additionally, the CA, MD and PEI shoot and root lengths were progressively reduced by decreasing water potential. The shoot and root lengths at 30 °C and high water potential were generally longer than those at 20 °C. Decreasing water potential at high temperature, however, inhibits shoot lengths, whereas the root lengths appeared unaffected. It is concluded that the CA ecotype was better adapted to decreasing water potential and increasing temperatures, compared to the MD and PEI ecotypes. This observation implies that the CA ecotype is probably adapted to areas experiencing high temperatures and low water potential; whereas, the MD and PEI ecotypes have adapted to areas that maintain lower temperatures and higher soil moisture. This might explain barnyardgrass distribution world wide, and especially for the latter two ecotypes, being a major problem in periodically flooded or irrigated fields.

The seed depths effect on the emergence of ecotype seed indicated that the highest percent emergence (more than 75 to 95%) was obtained at 1 and 2.5 cm depths, suggesting that seeds proximal to the soil surface have a greater chance of emergence, and least percentage (less than 20%) at 7.5 and 10 cm depths. Seedling emergence on

the surface was in flushes and variable, most likely due to the uncertain environment on the surface to which the seed were exposed. Rate of emergence and total percent emergence for all ecotypes decreased with increasing depths. The CA ecotype was better able to emerge from greater depths, than the MD and PEI ecotypes, likely due to larger versus smaller seed size. Additionally, emergence from greater depths suggests that light is not a factor influencing germination.

Photoperiod and temperature effect on the growth and development of the ecotypes showed that ecotypes under LD had vigorous vegetative growth, greater heights, larger leaf area, greater fresh and dry weights, whereas the ecotypes under SD, especially the MD and PEI, were inhibited in their growth. In addition, the ecotypes under LD showed comparable morphological growth characteristics. The MD and PEI ecotypes flowered and matured fast under SD, compared to the CA ecotype. It might be concluded that all these ecotypes are able to adapt to a wide range of photoperiods and temperatures. This ability would be advantageous and help to explain their wide distribution globally.

The overall conclusion that may be drawn from this set of experiments is that barnyardgrass ecotypes appear to have undergone an evolutionary tradeoff. The CA ecotype appears to have lost its seed dormancy qualities and in the process has adapted to a high range of temperatures, hence adapting successfully to areas experiencing warm temperatures. It is also possible that this tradeoff is advantageous for this ecotype under California conditions. Its lack of dormancy leads to inability to persist in buried

conditions of continental climate of the Atlantic regions, for long durations. This observation, however, may not be a problem in California.

Comparatively, the MD and PEI ecotypes ability for seed to undergo dormancy during unfavourable environmental conditions would likely be essential in both locations. This enables these ecotypes to adapt successfully to areas with harsh winter conditions. Experimentally, it was possible to continue retrieving viable but dormant seed over twenty-four months of seed burial.

The CA ecotype's ability to grow at high temperatures and decreasing water potential might be a positive adaptive strategy, especially in areas experiencing moisture stress during part of its life cycle. The MD and PEI ecotypes on the hand appear adapted to areas of higher water potential (irrigated or flooded conditions) and they may be similar to the ecotype of barnyardgrass infesting rice fields.

The CA ecotype ability to emerge better from greater depths might be advantageous in that germination and emergence at these depths need not be influenced by light; besides, seedlings could easily exploit soil moisture found at deeper levels. Large seed size of the CA ecotype would seem to be an advantageous factor, whereby this ecotype has enough food reserve to nurture its seedlings before emergence. The MD and PEI ecotypes appeared to lack the above qualities. Emergence from greater depths will result in delayed emergence, hence may confer some advantage on seedlings, such as avoidance of pre- and post-emergence herbicide treatments and possibly tillage.

The ability of the CA ecotype to prosper under both SD and LD conditions may

also be an advantage in its area of adaptation. California conditions during winter months when the SD prevails may be adequate to enable plants to reach maturity and form seed. This may be a disadvantage in some years when its maturity is delayed such that it might not shed mature seed on time before autumn frost.

Finally, photoperiod and temperature response, as noted for the CA ecotype, might be a compromise tradeoff. The MD and PEI ecotypes, however, appeared to have an "avoidance strategy" for their survival. Such a strategy allows them to mature and set seed before frost. Compared to the CA ecotype, adaptation to a wide range of photoperiod and temperature, allows them the advantage of global distribution.

APPENDIX 1

DESCRIPTION OF TAXONOMIC STATUS, MORPHOLOGY, ECONOMIC AND GEOGRAPHICAL DISTRIBUTION OF BARNYARDGRASS *ECHINOCHLOA CRUS-GALLI* [L.] BEAUV.

NAME. *Echinochloa crus-galli* (L.) Beauv. (4) - Barnyardgrass, Echinochloa pied-de-coq (4, 63).

Other common names. Summergrass, watergrass, cockspur grass, cock's foot, junglerice (a confusion with *E. colonum*) (64, 80), barnyard millet (10).

Family. Poaceae (Gramineae, grass family) (80, 115).

Taxonomic history. Barnyardgrass was named *Panicum crus-galli*, by Carolus Linnaeus (dated from 1707-1778) in volume 56 of his *Species Plantarum* (dated 1753). *Panicum*, a genus in which he placed many grasses, is a word meaning "millet" in Latin, and is related to *panis*, Latin for bread (191), while *crus* is Latin for leg (191); *galli* is the possessive form of *gallus*, Latin for cock (183).

Ambroise Marie Francois Joseph Laisot de Beauvois (1752-1820) placed barnyardgrass in a new genus in response to the enormous number of *Panicum* species. *Echinochloa* is a composite word - *Echinos*, from both Latin and Greek (183) means "prickly" or "spiny" and *Chloa* is Greek for grass or young herbage (191).

Though the genus *Echinochloa* was not universally accepted at first, Brewer (32) recognized *E. crus-galli* as a synonym for *P. crus-galli* in 1876.

Origin. Barnyardgrass is thought to have originated from Eurasia (13, 80, 173).

DESCRIPTION.

Morphology and cytology. The following descriptive account on morphology and cytology is taken from Maun *et al.* (105) and is based on the work of Dore *et al.* (50) Holm *et al.* (80) and Rahn *et al.* (134).

> "Barnyardgrass is an annual, tufted, robust grass with fibrous roots, which reproduce by caryopses. Culm is glabrous, stout, often branching and rooting from a decumbent base (Fig. 7.1a) up to 1.5 m tall; leaves glabrous and rolled at emergence, blades elongated with smooth or scabrous margins, 5-50 cm long, 5-20 mm wide with parallel hyaline veins and often a prominent and sharp midrib, leaf sheaths often with conspicuous anthocyanin (red pigmentation; sheaths glabrous, compressed, keeled, split with overlapping hyaline margins, ligules and auricles absent (Fig. 7.1b); collar glabrous, broad, continuous; panicles erect or nodding, green or purple-tinged, 10-20 cm long; racemes many, 2-4 cm long, spreading, ascending or appressed, lower ones more distant than appear (Fig. 7.1c); spikelets 3-4 mm long crowded in 2-4 rows on each side of rachis (Fig. 7.1c); awns when present are variable, 0-10 mm long, sometimes as much as 30 mm long, oval unequal pointed and bristly glumes, first glume almost half as long as the spikelet (Fig. 7.1d), second glume and sterile lemma equal in length; spikelet contains one perfect and one sterile floret (Fig. 7.1d); fertile floret plano-convex; sterile lemma often drawn out into a long coarse awn; fertile lemma with a dull coloured

and wrinkled tip marked off rather abruptly from the shiny body, minute setae present on the shiny portion of the fertile lemma just below the wrinkled tip; caryopses strongly convex on one side (Fig. 7.1e), flat on the other, broad below, narrow towards apex, (though not so with all ecotypes, for example, California ecotype used in this project), orange yellow to buckthorn brown, 2.5-3.5 mm long, obscurely three-veined.

The chromosome number of *E. crus-galli* is 2n=54. This number was reported for Canadian specimens by Mulligan (114). The species is hexaploid with the basic chromosome number of the genus n=9".

The above chromosome number was further confirmed by Crompton (1990 personal communication), for the three ecotypes used in this project

GROWTH AND DEVELOPMENT.

Morphology. This descriptive account on morphology is taken from Maun *et al.* (105) and Rahn *et al.* (134), and some sections from Dawson (42) and Kacperska-Palacz *et al.* (84).

"The developmental morphology of barnyardgrass has been described in three phases: (a) the embryonic phase consisting of primary root ensheathed by a coleoptile and root cap while the plumule is enclosed with the coleoptile; (b) the ensuing vegetative phase, which initiates and matures the photosynthetic leaves, axillary shoots (tillers) and permanent root system, but no internodal elongation of the stem; and (c) the

reproductive phase, signalled by internodal elongation and the transformation of the growing point into an inflorescence primordium (84). The vegetative tillers (up to 15) arise in the axils of leaves by periclinal divisions in the third layer of cells of the embryonic internode just above the leaf primordium. As the primordium further enlarges, the apex turns upwards between the inner surface of the leaf sheath and the stem forms an intravaginal shoots whose further development repeats the pattern of the parent axis (134). The root system of the mature barnyardgrass plant consists chiefly of fibrous or adventitious roots. The primary root supports the young seedling only for the first few days following germination. The first adventitious roots arise from the segment between the scutellum and coleoptile known as the mesocotyl, at the time of seedling emergence. The secondary root primordia originates from the pericycle. The stele is polyarch and the roots are white in colour (84). The root system of barnyardgrass may extend down to 116 cm in depth and 106 cm in lateral diameter in porous well aerated soils (42, 134)".

Distinguishing features. Barnyardgrass can be distinguished from other genera of Canadian weeds by the absence of a ligule (105).

Propagation. Like many other problematic weeds, barnyardgrass is a prolific seed producer, growing rapidly, and flowering throughout the year in the field (13). Seed of

barnyardgrass is contained in spikelets that consist of caryopses with associated palea, lemmae, and glumes. At maturity the surviving outer layer of the caryopsis forms a hard covering (caryopsis coat) (159). The caryopses are dormant when mature and require an after-ripening period of at least one to two months before they will germinate (9, 24).

ECONOMIC IMPORTANCE. Most of the following descriptive account on detrimental effects is taken from Maun et al. (105), based on the accounts of various authors (24, 25, 80, 93, 134, 142, 154, 160 and 174) whereas part of the account of beneficial effects was taken from Mitich (114).

(i) *Detrimental. E. crus-galli* is a cosmopolitan weed in both temperate and tropical regions and is reported as a weed in 36 different crops in 61 countries (80). In North America, it is a troublesome weed in rice fields, grain crops, row crops, root crops, open disturbed habitats (25. "In Atlantic regions, this weed is found in potato fields, grain crops, most cultivated fields and well-manured soils (Sampson personal comm.)". Vengris (174) in Connecticut, found that as a weed, barnyardgrass ranked first in potato fields, second in tobacco, third in onion and eighth in corn fields. According to Vengris (174), seedling mortality of alfalfa was 80% if barnyardgrass emerged within the first two weeks of its life cycle. Barnyardgrass causes considerable yield decrease of potatoes (24), snap beans (134), sugar beets, green peas and melons (142). Heavy

barnyardgrass infestations make mechanical harvesting difficult for row crops, increase labour costs in separating potatoes from barnyardgrass clumps, and cause considerable breakage of machinery during lima and snap bean harvesting (134). Experimental studies indicate that heavy stands of barnyardgrass may remove 60 to 80% of nitrogen from the soil (80), and considerable amounts of other macronutrients (105). Fertilizer application favours the weed over rice (80). Barnyardgrass is a host to many viruses of rice and other grass crops (80). It is a host to *Striga asiatica*, which infests sorghum, corn, millet, sugarcane, rice, and tobacco in India, Africa, and the United States (93). Under heavy competition, tillering in rice is reduced by 50%, and a drastic reduction in number of panicles, plant height, weight of grains and number of grains per plant (80). It has been shown that one to five plants of barnyardgrass per 900 cm^{-2} may reduce rice yields by 18 to 35% (160) and 9 plants m^{-2} could reduce yield of low density rice by 57% (154).

(ii). *Beneficial.* In North America some barnyardgrass varieties were recommended for forage; var. *frumentaceae* was advertised by seedsmen as "billion-dollar grass" for this purpose. Barnyardgrass has some forage value but requires considerable water to produce well and is too succulent for hay (78 In: 114). However, barnyardgrass have been used for sheep in Australian drought mitigation programs (105). In tropical Asia and Africa, it is cultivated for its seed which are eaten (78 In: 114).

GEOGRAPHICAL DISTRIBUTION.

The following account of geographical distribution is taken from Maun et al. (105) and is based on work by various authors (25, 30, 34, 64 and 115); part of this account is taken from Mitich (114) and Potvin (132).

> "Phytogeographic studies have shown that the distribution of C_3 and C_4 grass species is directly related to climate. Plants with the C_4 photosynthetic pathway are associated consistently with hot dry regions (166 In: 132). Only a few C_4 species are distributed as far north as the 53° latitude (99 In: 132). Barnyardgrass, a C_4 grass (132, 183), is a major weed problem throughout the world; its distribution ranges from latitude 50 °N to 40 °S (78, 105) (Fig. 7.2). In Canada, it has been recorded above 50 °N latitude, for example Saskatoon (52° 07' N), Prince Albert (53° -12' N), Edmonton (53° -12' N) and several other localities. It occurs in all provinces of Canada, but not in the Northern Territories. Herbarium information, floras and published accounts suggest that barnyardgrass is abundant in Ontario, Quebec and the Maritime provinces (105). Erskine (56) reported its distribution throughout Prince Edward Island. Boivin (30) reported it being found on roadsides and fields in Newfoundland, and the French islands of St. Pierre and Miquelon (Fig. 7.3). Generally, it is rare in Saskatchewan and Alberta but abundant in eastern Manitoba and British Columbia (25, 34, 64, 115)".

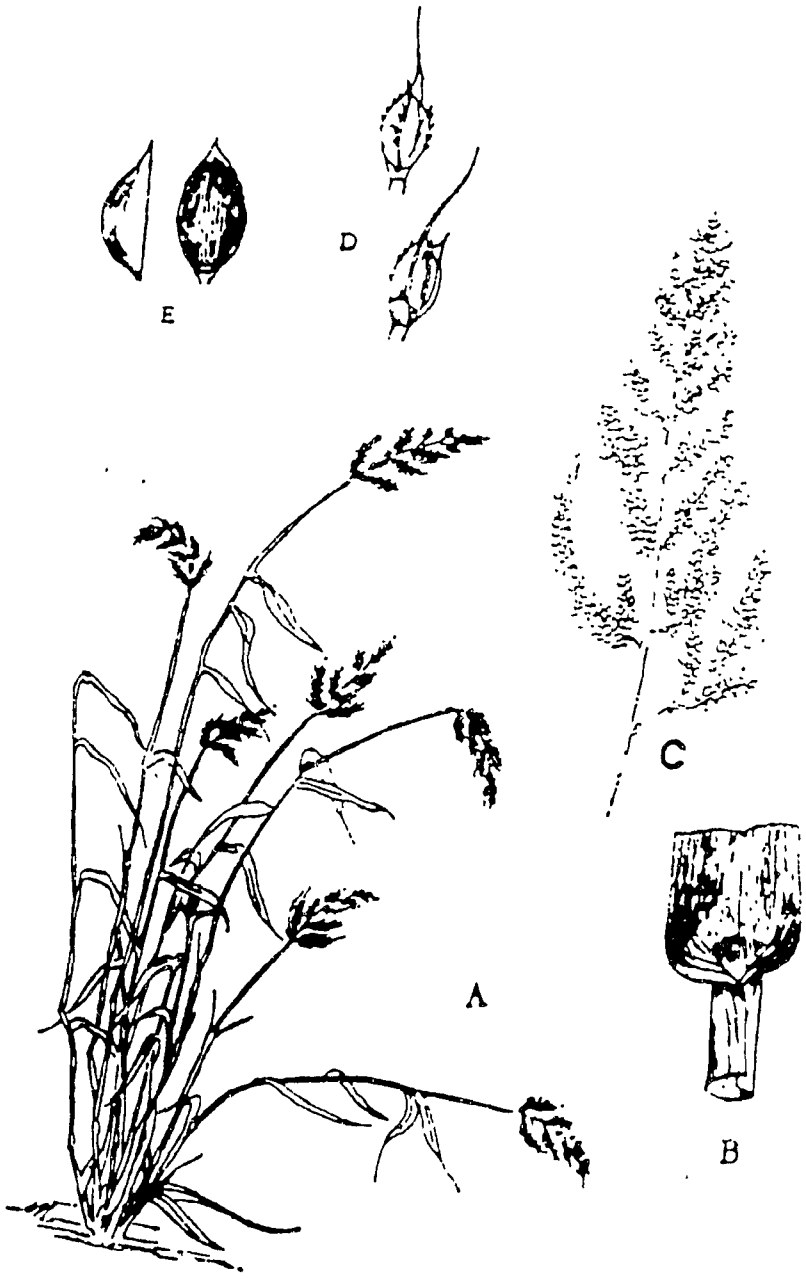


Fig. 7.1. (a) Mature barnyardgrass plant (b) leaf base collar (c) close-up of part of panicle (d) spikelet (e) seed (Adapted from Bayer, 1965. *In*: Rahn *et al.* 1968) and Alex, 1992).

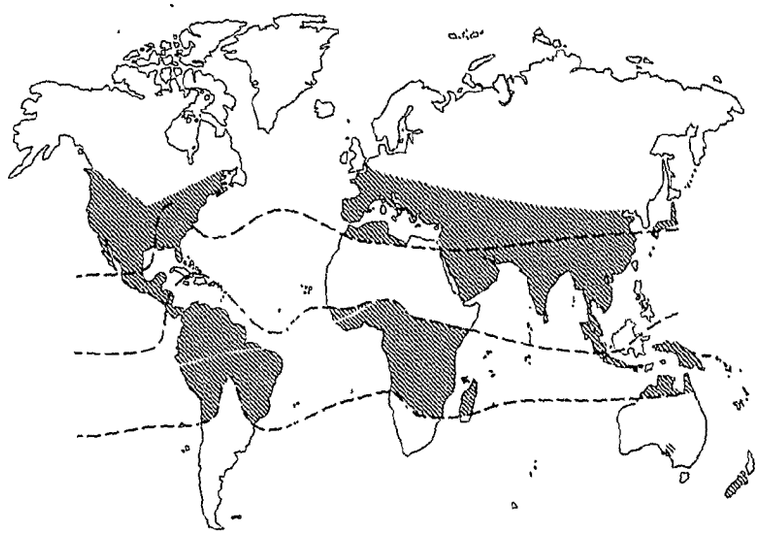


Fig. 7.2. Distribution (grey hatched area) of *Echinochloa crus-galli*. This species is not confine to temperate zone but is generally distributed throughout much of the world (Adapted from Holm *et al.* [80]).

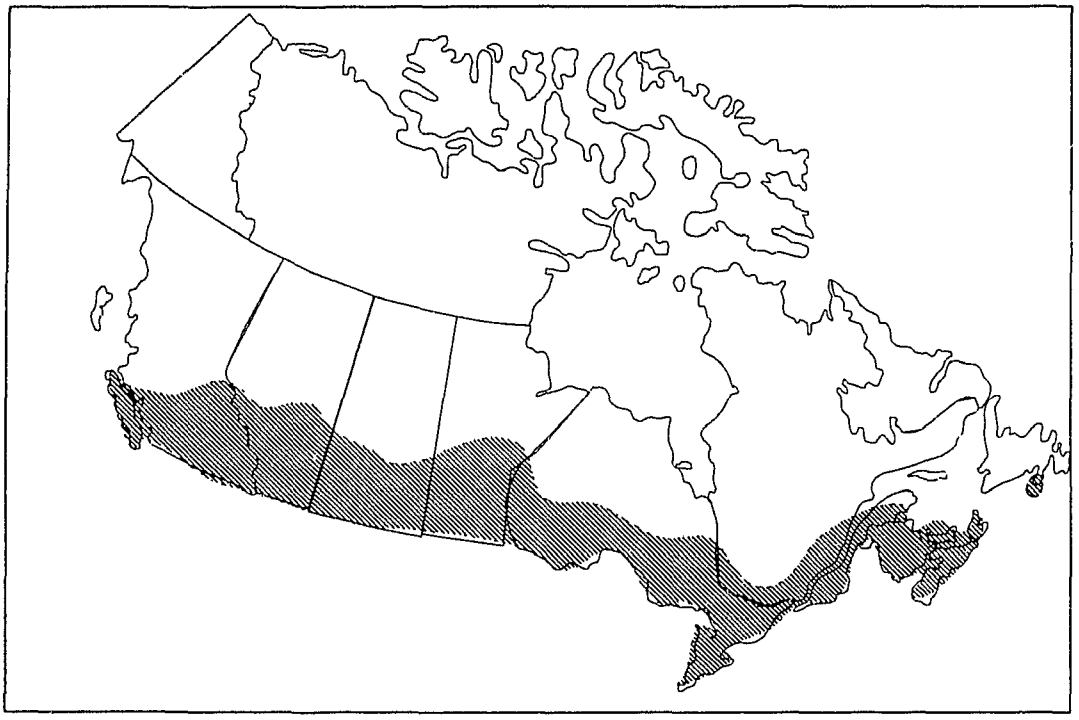


Fig. 7.3. Distribution (grey hatched area) of *Echinochloa crus-galli* (L.) Beauv. in Canada from specimens in the Plant Industry Laboratory, Alberta Agriculture, Edmonton and the following herbaria: UAC, DAS, USAS, TRT, MTJB, CAN, SASK (Herbarium abbreviations as in Holmgren *et al.* [1981]). Adapted from Maun *et al.* (105).

APPENDIX II

Seedling emergence of three barnyardgrass ecotypes under short (SD) and long (LD) day photoperiod

Ecotype	Number of seed per pot	Photoperiod	Percent seedlings emergence
CA	10	LD	98
MD	10		95
PEI	10		93
CA	10	SD	96
MD	10		88
PEI	10		89

APPENDIX III

Seed production by three barnyardgrass ecotypes under long (LD) and short (SD) day photoperiods.

Ecotypes	Total plants	Photoperiod	Seed per plant
CA	36	LD	1511
MD	36		3682
PEI	36		3448
CA	36	SD	97
MD	36		130
PEI	36		141

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