Seed germination and seedling emergence in Amaranthus spp.
by David Morton Webb

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Agronomy
Montana State University

Abstract:
Grain amaranth has been investigated as a new crop in Montana since 1982. Little is known about amaranth seed germination and seedling emergence responses to the environment so several studies were conducted.

Amaranth seedling emergence was studied using constant temperatures between 15.3 and 45.6 C and seeding depths between 1.3 and 6.4 cm on a modified thermogradient plate and using alternating temperatures at 7-17, 10-20, and 13-23 C and seeding depths of 0.6, 1.9, and 3.2 cm in a growth chamber. Optimum constant temperatures for seedling emergence index (EI) ranged from 24.0 to 33.8 C and optimum seeding depth was 1.3 cm. Emergence index between 18.4 and 24.0 C and at 1.3 cm seeding depth may be acceptable if other conditions are favorable. EI was low from all depths at 7-17 C but was relatively high from 0.6 cm at 13-23 C. Emergence index at 10-20 C was intermediate tc EI's at the other temperatures. Recommended amaranth seeding would be at 0.6 cm and 13-23 C. Seedlot H83-438 had the largest seed and highest EI overall indicating larger seed may improve seedling emergence in cool temperatures.

White and black amaranth seed and pigweed (Amaranthus retroflexus L.) seed were germinated after different periods of overwintering from November to May. White seed decomposes in cool, moist soils resulting in poor germination. Consequently, white amaranth seed would not become a weed if escaped. Black seed germinated well through the test period and could become a weed if escaped. Also, white seed would be less likely to germinate and emerge if seeded into cool soils than would black seed. Black domestic seed expressed a primary dormancy similar to but not as pronounced as the phytochrome related dormancy of pigweed seed.

Genetically similar white and black amaranth seed were germinated at a range of constant temperatures on a thermogradient plate, 2 weeks, 11, and 16 months after harvest. Black seed expressed some dormancy at 2 weeks but not at 11 or 16 months from harvest. White seed did not express dormancy. Light was shown to inhibit amaranth germination at temperatures below about 24 C.

Amaranth remains a potential new crop in Montana below 1000 m elevation.

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ABSTRACT

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Amaranth seedling emergence was studied using constant temperatures between 15.3 and 45.6 C and seeding depths between 1.3 and 6.4 cm on a modified thermogradient plate and using alternating temperatures at 7-17, 10-20, and 13-23 C and seeding depths of 0.6, 1.9, and 3.2 cm in a growth chamber. Optimum constant temperatures for seedling emergence index (EI) ranged from 24.0 to 33.8 C and optimum seeding depth was 1.3 cm. Emergence index between 18.4 and 24.0 C and at 1.3 cm seeding depth may be acceptable if other conditions are favorable. EI was low from all depths at 7-17 C but was relatively high from 0.6 cm at 13-23 C. Emergence index at 10-20 C was intermediate to EI's at the other temperatures. Recommended amaranth seeding would be at 0.6 cm and 13-23 C. Seedlot H83-438 had the largest seed and highest EI overall indicating larger seed may improve seedling emergence in cool temperatures.

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Genetically similar white and black amaranth seed were germinated at a range of constant temperatures on a thermogradient plate, 2 weeks, 11, and 16 months after harvest. Black seed expressed some dormancy at 2 weeks but not at 11 or 16 months from harvest. White seed did not express dormancy. Light was shown to inhibit amaranth germination at temperatures below about 24 C.

Amaranth remains a potential new crop in Montana below 1000 m elevation.

CHAPTER 1

INTRODUCTION

Soil and Land Use Technology, Inc. (SaLUT) and the National Science Foundation identified amaranth (domesticated Amaranthus spp.) as one of ten plant types having the most potential as a new crop for low to moderate rainfall areas in the United States (Theisen et al., 1978), including Montana. Amaranth has a C-4 carbon fixation pathway enabling it to convert carbon dioxide to metabolic energy more efficiently than do C-3 plants. This efficiency may allow amaranth some drought tolerance after plants are established (Black et al., 1969). Amaranth produces large amounts of biomass and has high seed and leaf protein, giving it potential as silage. The U.S. market for amaranth grain is expanding as new products are being developed with amaranth as a nutritional ingredient. Therefore, amaranth is being investigated as a new crop in Montana.

As a new crop, little is known about amaranth's responses to the environment. Amaranth is native to and cultivated in tropical and subtropical climates where warm temperatures favor seed germination and plant development. Montana has relatively short growing seasons, so amaranth must be seeded early in cool soils to lengthen the growing season for it to mature before the first frost.

The objectives of this thesis were to study the effects of temperature, both constant and alternating, and seeding depth on

amaranth seedling emergence; and the effects of seed overwintering, seed age, and light on seed germination. This information can be useful in understanding amaranth field stand establishment in Montana.

CHAPTER 2

LITERATURE REVIEW

The literature review is divided into discussions of the background and relationships of the three grain amaranth species, the phytochrome control of amaranth seed germination, and the previous use of thermogradient plates in seed germination studies.

Grain Amaranth Species

Archaeological evidence of grain amaranth has been found in Mexico dated between 3500 and 2300 B.C. The pale (white) seed of Amaranthus cruentus and Amaranthus hypochondriacus found at these sites suggest that amaranth was cultivated and not gathered since pale seeded amaranth is not known to exist in the wild (Sauer, 1969).

Three species of grain amaranth are distinguished by having pale and black seed; Amaranthus hypochondriacus L., Amaranthus cruentus L., and Amaranthus caudatus L. Some taxonomists refer to a fourth grain amaranth species, Amaranthus edulis Speg., also known as Amaranthus mantegazzianus Pass., but it is otherwise considered a subspecies or variety of A. caudatus. The edulis type is known to have developed from A. caudatus and the two are very closely related (Coons, 1975 and 1982; Pal and Khoshoo, 1972 and 1973; Sauer, 1967). Morphological descriptions of the species have been published by Murray (1940), Sauer (1950 and 1967), Pal (1972), Cole (1979), and Coons (1975 and 1982). Taxonomic keys have been published by Sauer (1967) and Feine (1981).

Sauer (1950 and 1967) has given the most complete description of the ethnobotanical history and relationships of the grain amaranth species. Subsequent germ plasm expeditions to Mexico (Feine, 1980), Mexico, Guatemala, and South America (Coons, 1975; Hauptli et al., 1980), and India and Nepal (Jain et al., 1980) have contributed to the understanding of the extent of grain amaranth production and its cultural status in those regions.

The ethnobotanical studies show that, as grain crops, A. hypochondriacus is grown in northern and central Mexico, A. cruentus is grown in southern Mexico and Guatemala, and A. caudatus is grown in the Andes of South America, while all three species (but mostly A. hypochondriacus) are grown in India and Nepal (Feine, 1980; Hauptli et al., 1980; Jain et al., 1980; Nabhan, 1980; Sauer, 1957, 1967, and 1976). Amaranth is mostly grown by indigenous people, often in remote areas of Mexico, Central and South America and its production appears to have declined since 1950 because of the encroachment and influence of other cultures (Coons, 1975; Feine, 1980; Hauptli et al., 1980). However, production of grain amaranth in India is still expanding (Sauer, 1976).

It is generally accepted that all the grain amaranth species developed in North, Central, and South America. Domestic amaranths were introduced to Asia and have been recorded in India in the 18th century. Amaranth was probably introduced to Asia by Europeans, perhaps the Dutch colonists in Ceylon (Cole, 1979; Sauer, 1950, 1967, and 1976).

The evolutionary path of these three species is speculative with two hypotheses generally accepted. The oldest hypothesis proposes that the three species, A. hypochondriacus, A. cruentus, and A. caudatus, had parallel development from three different wild progenitors, A. powellii S. Wats., A. hybridus L., and A. quitensis H.B.K., respectively (Hauptli and Jain, 1984; Sauer, 1967). The more recent hypothesis is that the three species developed sequentially from a single progenitor and subsequent hybridizations with other wild species. According to the second hypothesis, A. cruentus arose from A. hybridus in Central America, moved northward hybridizing repeatedly with A. powellii to form A. hypochondriacus, and moved southward hybridizing repeatedly with A. quitensis to form A. caudatus (Hauptli and Jain, 1984; Sauer, 1967 and 1976). Efforts to prove or disprove either of the two hypotheses has produced a variety of sometimes conflicting evidence, none of which is conclusive.

Sauer (1950 and 1967) showed the three domestic species have distinct regions of cultivation in the New World. Each domesticate's region coincides with part of the habitat of its proposed progenitor or progenitors. A. hypochondriacus is cultivated in the southern area of the range for A. powellii in Mexico; A. caudatus is cultivated throughout the natural habitat of A. quitensis in the Andes; while all three domestic species are cultivated within the vast habitat of A. hybridus which ranges from eastern North America to northern South America. Coons (1975) reports A. powellii is also located in the Andes.

The chromosome numbers of the grain species and their progenitors are known. A. hypochondriacus, A. caudatus, A. hybridus, and A. quitensis have 2n=32, while A. cruentus and A. powellii have 2n=34 (Grant, 1959; Murray, 1940; Behera and Patnaik, 1974). Occasionally, both chromosome numbers are found in the same species (Grant, 1959; Pal et al., 1982). The chromosome numbers themselves neither indicate nor eliminate any particular species relationships.

Natural hybrids between some of these species have been reported (Coons, 1975 and 1982; Grant, 1959; Jain et al., 1980; Sauer, 1950 and 1967; Tucker and Sauer, 1958). However, attempts to hybridize these species have usually resulted in F_1 hybrid sterility and other malfunctions (Coons, 1982; Khoshoo and Pal, 1972; Murray, 1940; Pal and Khoshoo, 1972 and 1973). Interspecific crosses between A. cruentus and A. hypochondriacus (Kauffman, 1981), A. hybridus and A. cruentus (Hauptli and Jain, 1978; Kauffman, 1981), and A. hybridus and A. hypochondriacus (Kauffman, 1981; Pal and Khoshoo, 1972) resulted in some fertile hybrid populations.

Some effort has been made to compare the morphology of amaranth species to indicate relationships. Morphologically, A. hypochondriacus is similar to A. powellii and A. hybridus, A. caudatus is similar to A. quitensis, and A. cruentus is similar to Amaranthus dubius Mart. ex Thellung (Sauer, 1950). A. dubius is a weed of Central America and the West Indies (Sauer, 1950).

Hauptli and Jain (1978) compared 25 morphological characteristics of the three grain amaranth species, three weed species, A. retroflexus L., A. hybridus, and A. powellii, and a naturally occurring

hybrid between A. cruentus and A. hybridus. Combining 14 quantitative traits in a cluster analysis, the grain species sorted into one group while the three weed species sorted into another group. The hybrid was situated between the two groups but closer to the grain species. The three domestic species are similar morphologically but this could be as much a result of man's selection for favorable characteristics as it is to genetic relationship.

Some of the best evidence indicating species relationships is presented by Hauptli and Jain (1978 and 1984) in comparing allozyme variation among amaranth populations. They found certain enzymes to be representative of the species and representative of the crop and weed groups. Genetic distances between species based upon specific enzyme frequencies suggest the domestic species are more closely related to each other than they are to any of the weed species with the exception of A. caudatus to A. quitensis which had a genetic distance similar to the crop to crop distances. A. quitensis was also closer to the other two crop species than were any of the other weed species. A. hybridus had the next smallest genetic distance from the three crop species. The weed to weed genetic distances were greater than the crop to crop distances.

The morphological and allozyme studies by Hauptli and Jain (1978 and 1984) suggest the three domesticated grain species, being relatively closely related to each other, evolved from a single domestication event. Though A. quitensis is very closely related to A. caudatus and similar enzymatically to the other domestic species, the ethnobotanical, morphological, and allozyme evidence together indicate

A. hybridus to be the more likely common ancestor to the three grain species.

Phytochrome Control of Amaranth Seed Germination

Light effects on germination of Amaranthus spp. has been studied for Amaranthus retroflexus L. (Hendricks and Taylorson, 1978; Kadman-Zahavi, 1960; Taylorson and Hendricks, 1971 and 1972), Amaranthus arenicola I.M. Johnston (Hendricks et al., 1968), Amaranthus caudatus L. (Kendrick and Frankland, 1969a and 1969b; Kendrick et al., 1969), and Amaranthus albus L. (Chadoeuf-Hannel and Taylorson, 1985). Each of these species has been negatively photoblastic, showing the typical phytochrome red (Pr) and phytochrome far red (Pfr) reversal and Pfr promotion of germination. A few seconds of white or red (R) illumination promote germination while any amount of far red (FR) or prolonged white light inhibits germination. Inhibition by FR may be caused by photoconversion of Pfr while inhibition by white light is apparently a result of High Irradiance Response (HIR). The HIR occurs under prolonged irradiations at high fluence rates (such as sunlight) while the reversible Pr-Pfr photoresponse occurs under relatively short irradiations at low fluence rates (Borthwick et al., 1969; Hartmann, 1966; Hock, 1984; Mancinelli and Rabino, 1978; Rollin, 1966 and 1972; Toole, 1973).

Kendrick et al. (1969) found little or no photoreversible absorption changes attributable to phytochrome (P) in dry seed of A. caudatus indicating phytochrome was in a stable dehydrated state. Upon imbibition in the dark, phytochrome became detectable in two phases, one immediately after sowing and another beginning after about 8 hours.

They explained the first phase as rehydration of existing phytochrome and the second phase as phytochrome synthesis. The rate of phytochrome rehydration doubled for A. retroflexus with each 10 C rise in temperature between 10 and 35 C (Taylorson and Hendricks, 1972).

Phytochrome synthesis in A. caudatus was temperature and light dependent but apparently unrelated to germination (Kendrick and Frankland, 1969a). Synthesis during dark imbibition did not occur at 0 C but was significant at 25 C. Surprisingly, phytochrome synthesis under FR, which totally inhibited germination, was almost as great as that in darkness, but synthesis under R, which promoted germination, did not occur. The Pfr/P ratio, rather than the absolute concentration of Pfr may be the factor controlling germination.

High irradiance photoinhibition is temperature dependent as shown in A. caudatus by Kendrick and Frankland (1969a). Below 25 C, final germination percentage was reduced and delayed under FR or white light. Above 25 C, ultimate germination percentages were the same in light and dark, but white light delayed germination. The higher the temperature, the less important Pfr is for germination. Mancinelli et al. (1967) suggested an alternative temperature-dependent germination control system takes over and by-passes the phytochrome system or that seed may require lower Pfr levels because of faster reaction rates at higher temperatures. Hendricks and Taylorson (1976, 1978 and 1979) associated the function of Pfr in seed germination with the phase condition of membranes. At warmer temperatures, membranes undergo structural changes and have greater permeability and as a result the role of Pfr in activating seed germination somehow becomes less important.

Phytochrome required for seed germination results in a form of dormancy when that requirement is not met. In Amaranthus spp. the required P is generally adequate in darkness for germination to proceed, but in Amaranthus retroflexus (Baskin and Baskin, 1977; Crocker, 1916; Evans, 1922; Kadman-Zahavi, 1960; Kigel, et al., 1977 and 1979; McWilliams et al., 1968; Schonbeck and Egley, 1980, 1981a and 1981b) and Amaranthus albus (Hendricks and Taylorson, 1974 and 1975), both weed species, a primary seed dormancy occurs even in the dark. Dormancy in A. retroflexus is a result of the inability of expanding seed contents to rupture the testa during imbibition (Crocker, 1916; Evans, 1922). If the seed coat barrier is physically removed by scarification or other means, the embryo will begin rapid growth (Crocker, 1916; Evans, 1922). The dormancy can be gradually overcome with time as the testa looses elastic strength. Some seed harvested from green plants of A. retroflexus will germinate at 40 C; the minimum temperature for germination decreases as after-ripening progresses (Crocker, 1916). Crocker (1916) and Evans (1922) observed that A. retroflexus seed was inhibited by light even when seedcoat restrictions were removed by scarification, indicating the seedcoat induced dormancy is a separate phenomenon from the embryo-light induced dormancy.

Stratification is known to break seed dormancy of many species but how it functions is not known. Prechilling A. retroflexus seed at 10 C for 28 days resulted in 80% germination at 35 C in the dark, breaking the seed coat imposed dormancy (Taylorson and Hendricks, 1969). Without prechilling, only about 5% of the seed germinated. Five minutes of R after 24 hours of prechilling shortened the prechilling

necessary to achieve 80% germination at 35 C from 28 days to under six days. It appears that Pfr was involved in loosening the seed coat for germination. Taylorson and Hendricks (1969) speculated that at low temperatures during prechilling the pre-existing Pfr was preserved long enough to perform its function on the seed coat so subsequent germination at higher temperatures occurred. At warm imbibing temperatures (>20 C) Pfr underwent thermal inactivation and dormancy was maintained. If this is correct, then the Pfr may act to loosen the restrictive seed coat as well as promoting embryonic root cell elongation. The addition of R would create a greater Pfr/P photoequilibrium, providing more Pfr molecules to accomplish the same function in less time.

Amaranthus spp., such as A. caudatus, that do not have the seedcoat induced dormancy still require Pfr but do not require prechilling to germinate.

Thermogradient Plate Uses

A thermogradient plate was used by Halldal and French (1958) with a cross gradient of light to study temperature and light effects on algal growth. Elliott and French (1959) modified the same apparatus to show that a thermogradient plate could be used to study temperature effects on seed germination. Designs for the construction of thermogradient plates were published by Larsen (1965, 1971), Barbour and Racine (1967), Wagner (1967), Chatterton and Kadish (1969), Evans et al. (1970), and Clegg and Eastin (1978). Thermogradient plates have been used to evaluate the effects of temperature on the germination of lettuce (Lactuca sativa L. var. Grand Rapids) (Elliott and French,

1959), alfalfa (Medicago sativa L.) (Larsen, 1965), various herbs (Wagner, 1967), a desert shrub (Larrea divaricata Cav.) (Barbour, 1968), crambe (Crambe abyssinica Hochst. ex R. E. Fries) (Larsen and Skaggs, 1969), sweet corn (Zea mays L.) (Cole, 1972), rescuegrass (Bromus catharticus Vahl.) (Larsen et al., 1973), dandelion (Taraxacum officinale Weber) (Mezynski and Cole, 1974), sorghum [Sorghum bicolor (L.) Moench] and corn (Clegg and Eastin, 1978), and amaranth (Amaranthus hypochondriacus L.) (Webb et al., 1985). Thompson (1970) used a "thermogradient bar" to relate temperature effects on seed germination with adaptibility of wild plant species to their native environments. Hendricks and Taylorson (1976) used a thermogradient plate to study amino acid leakage through cell membranes in relationship to seed germinability over a range of temperatures. The value of a thermogradient plate for testing seed germination across a range of temperatures is well accepted.

Modifications of thermogradient plates have been made to study temperature effects on seedling growth. Barbour and Racine (1967) added an aluminum V-shaped trough, filled with soil, to a thermogradient plate but did not describe any experiment utilizing this technique. Clegg and Eastin (1978) covered their thermogradient plate with 10 cm of quartz sand to support centrifuge tubes in which seed were rolled up in moist paper towels. They removed the tubes and obtained oven dry weights of the seedlings as a measure of relative growth rate at each temperature. They maintained near constant temperatures at all depths of any given tube location by utilizing a very good heating and cooling design and insulating well.

CHAPTER 3

TEMPERATURE AND SEEDING DEPTH EFFECTS ON AMARANTH SEEDLING EMERGENCE

Amaranth exhibits slow and low percentage seedling emergence in cool soils. Seed of warm season plants, such as amaranth, must be seeded shallower in cool soils than in warm soils to obtain similar seedling emergence (Grabe and Metzer, 1969; Martin et al., 1935). If seeded too shallow, there is an increased risk of germinated seed or emerging seedlings desiccating in dry weather. Amaranth seed should be seeded as deep as its food reserves and soil conditions allow for adequate seedling emergence. Therefore, an understanding of temperature and seeding depth effects on amaranth seedling emergence is important for its successful field establishment.

Temperature and seeding depth effects on amaranth seedling emergence were assessed in two experiments using constant temperatures on a thermogradient plate (experiment 1) and alternating temperatures in a growth chamber (experiment 2). Several seed characteristics were observed for their influence on amaranth seedling emergence at the various seeding depths and temperatures; ie. seed color in experiment one and seed color, seed size, and seed age in experiment two. Also in experiment two, Amaranthus domestic and weed species were compared for emergence.

Experiment One: Constant Temperature and Seeding Depth Effects

Materials and Methods

Two seedlots tested in this experiment were H83-382W (white seed) and H83-382B (black seed). Each was a bulk collection from 60 high yielding, early maturing, phenotypically similar plants, selected from a heterogeneous population of Amaranthus hypochondriacus L., accession RRC-382 (Rodale Research Center number), at the Southern Agricultural Research Center near Huntley, MT in September 1983. The seed was dried and stored at 10 C. Seedlot 1000-seed weights were not significantly different and both had 99% viability according to tetrazolium test results.

A one-way thermogradient plate was modified for this experiment to provide numerous constant temperatures and seeding depths; a new application for a thermogradient plate. The plate was covered with two thicknesses of blue germination blotter paper which extended beyond the hot end of the plate into a reservoir filled daily with 1.2 L distilled water. Water moved uniformly across the plate by capillary action maintaining blotter paper saturation. The blotter paper was covered with a sheet of clear acrylic 12.7 mm thick in which had been milled a 12 x 10 matrix of 50 mm diameter holes. Each of the 10 columns of 12 holes was oriented perpendicular to the temperature gradient so each column was at the same temperature (isotherm) (Fig. 1). White PVC pipe, 50 mm in diameter, cut to 1.27, 2.54, 3.81, 5.08, and 6.35 cm lengths, were placed into the holes in the acrylic (Fig. 2). The cylinders were filled with a 1:2 peat sand medium (by volume).

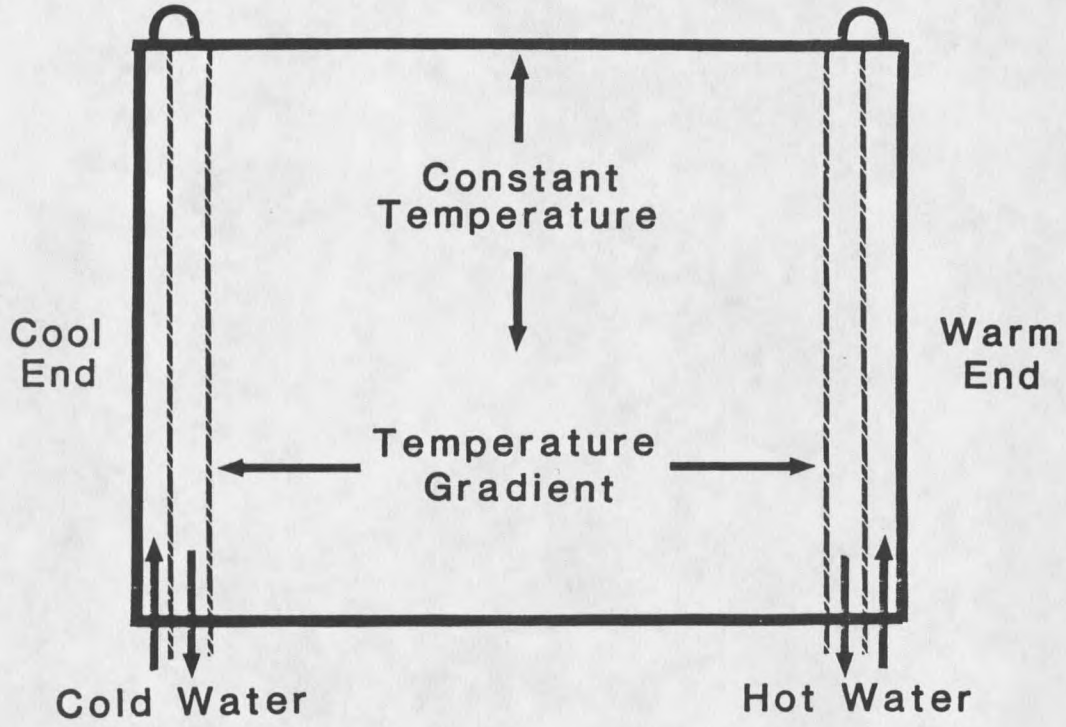

Figure 1. Top view of a thermogradient plate.

Figure 2. Thermogradient plate modified for seedling emergence studies at different seeding depths.

Temperatures on the blotter paper surface were automatically recorded at each end of each isotherm every four hours using copper-constantan thermocouples and an Omega Engineering OM-205, 24 channel data logger. The temperature gradient ranged from 15.3 to 45.6 C, with isotherms at about 3 C intervals. Soil temperature in cylinders approached room temperature with distance above the blotter paper, but remained uniform at the blotter paper surface under all depths within each isotherm (from preliminary measurements). Isotherm temperatures recorded during the growth periods were averaged.

Fifty seed were placed on the moistened blotter paper at each location, covered with the appropriate depth of autoclaved peat-sand mixture, lightly packed, and watered from above to settle the medium. Additional medium was added after watering to compensate for settling. The medium was subsequently watered from above if emerging seedlings began to lift the medium. Continuous illumination was provided at 8 to 10 uE sec-1 m-2. Emerged seedlings were counted and removed twice daily for the first three days and once daily for the remainder of the 21 day growth period. A seedling was considered emerged when any part of the hypocotyl or cotyledons was seen. Because of the large number of treatments, the experiment was replicated in time.

Emergence index (EI) was calculated using the following equation (Maluf and Tigchelaar, 1980).

$$EI = \frac{\Sigma(TD + 1 - D)(E_D)}{PLS}$$

TD is the number of days in the experiment, D is the day number for each count (0.5 to 21), E_D is the number of seedlings emerged on day D

(since the previous count), and PLS is the number of pure live seed (50) per experimental unit.

Analysis of variance was used to examine the main effects and interactions of seed color, temperature, and seeding depth for EI and percentage emergence. Regression methods were used to quantify the relation between the response variables, EI and percentage emergence, and temperature and seeding depth. Optimum temperature ranges for amaranth EI and percentage emergence were determined by Tukey's multiple comparison test at the .05 probability level.

Results

The thermogradient plate provided uniform temperatures throughout the three replications. Standard errors for the ten mean temperatures ranged from 0.006 to 0.05 C (252 recordings per mean).

No seedlings emerged at 45.6 C (highest temperature) or from 6.4 cm (deepest depth) so these levels of temperature and depth were excluded from the statistical analyses. Differences in EI and percentage emergence due to seed color were not significant but differences in EI and percentage emergence due to temperature, seeding depth, and temperature by depth interaction were significant (Table 1).

EI, combined for the two seedlots, increased at all seeding depths as temperature increased from 15.3 to 24.0 C, remained optimal from 24.0 to 33.8 C, and decreased as temperature increased from 33.8 to 41.2 C (Fig. 3). A large reduction in EI occurred due to increased seeding depth from 2.5 to 3.8 cm. The temperature by depth interaction was evident as the temperature range for emergence narrowed with increased seeding depth.

Table 1. Three factor analysis of variance for amaranth emergence index and percentage emergence at constant temperatures.

Source	df	Mean square Emergence Index		Mean square Percentage Emergence	
Replications	2	95.99		4112.00	
Seed Color (C)	1	0.40		26.74	
Temperature (T)	8	252.20	**	8082.00	**
Depth (D)	3	1848.00	**	64670.00	**
C x T	8	1.51		65.32	
C x D	3	1.04		73.90	
T x D	24	45.79	**	1442.00	**
C x T x D	24	2.26		85.10	
Residual	142	3.81		179.20	

** Significant at the 0.01 probability level.

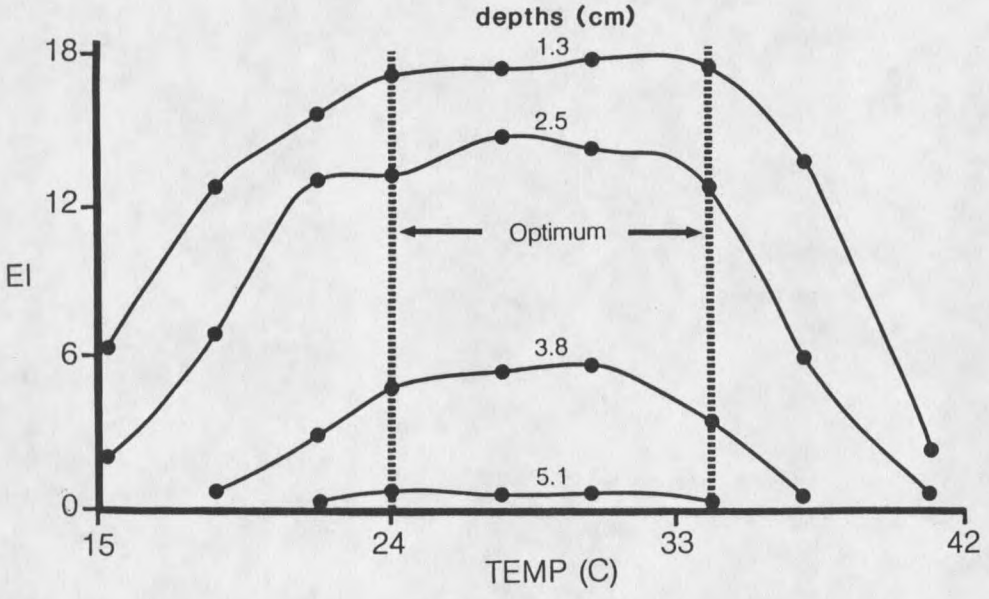

Figure 3. Amaranth emergence index (EI) based on combined seedlot means plotted against temperature at four seeding depths. Optimum temperature range based on EI means over all depths.

Final percentage seedling emergence was assessed in the same manner as EI (Fig. 4). The optimum temperature range over all depths for percentage emergence was broader (21.3-33.8 C) than for EI (24.0-33.8 C), but the large reduction in percentage emergence was similar to

that in EI as seeding depth increased from 2.5 to 3.8 cm. Percentage emergence increased as temperature increased from 15.3 to 21.3 C, and decreased as temperature increased from 33.8 to 41.2 C.

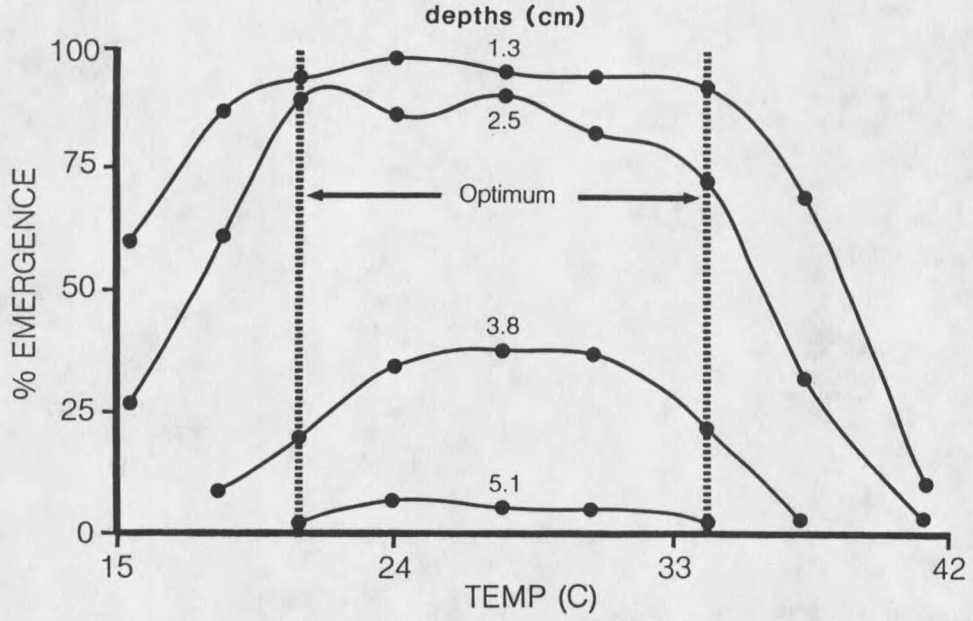

Figure 4. Amaranth percentage emergence (%) based on combined seedlot means plotted against temperature at four seeding depths. Optimum temperature range based on percentage emergence means over all depths.

The EI values for both seed colors were combined for use in the multiple regression analysis because the differences in EI associated with seed color were nonsignificant. Treatments yielding no emergence were excluded from the regression to avoid predicting negative emergence values. The F test for regression of EI was highly significant with depth (D), temperature (T), and temperature-squared (T^2) as independent variables. A highly correlated regression equation describes the predictive response surface (Fig. 5). The calculated temperature for maximum amaranth EI from all depths was 27.7 C.

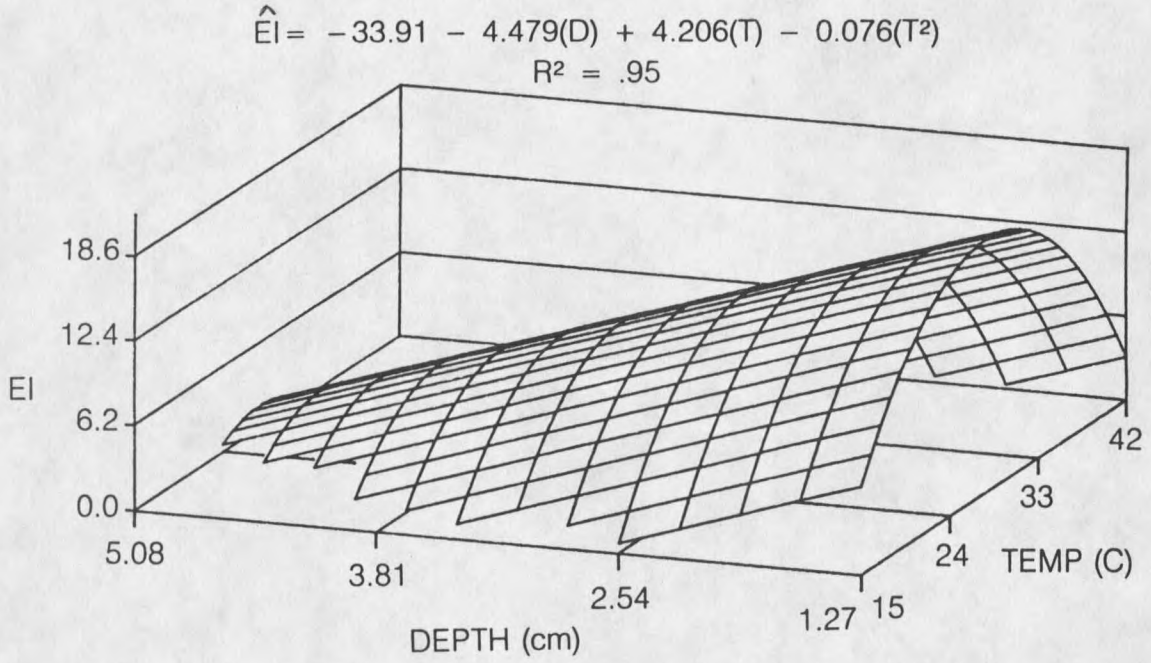

Figure 5. Predictive response surface for amaranth emergence, expressed as emergence index (EI), at a range of seeding depths and temperatures.

Discussion

Domesticated amaranth, native to the tropics and subtropics, is a warm season crop. In temperate climates, amaranth must be seeded as early as possible in the spring to increase the likelihood of adequate moisture for seed germination and seedling emergence and to extend the growing season for crop maturity. The risk of seeding amaranth too early in spring is that cool temperatures will delay seedling emergence and promote seed decay. Based on growers' experience, Weber et al. (1985) recommended seeding amaranth when spring soil temperatures range from 18 to 24 C. The data in this study corroborate that recommendation. Percentage emergence and EI were 85% and 12.3, respectively, at 18.4 C and were 95% and 16.7, respectively, at 24.0 C. The loss and delay in emergence from 18.4 to 24.0 C is probably not

enough to necessitate seeding in warmer temperatures, risking drier weather and shorter growing season.

Amaranth's small seed has limited food reserves to support germination and seedling emergence prior to the seedling becoming photosynthetically active. This limitation restricts the depth from which an amaranth seedling can emerge. Data from this experiment show that even with favorable soil texture and moisture, seeding amaranth deeper than 1.3 cm delayed and decreased emergence. Soil crusting or lack of moisture could have even more adversely affected seedling emergence with increasing seeding depth. Seeding deeper than 1.3 cm may be needed to obtain adequate soil moisture for amaranth germination in dryland areas. Seeding as deep as 2.5 cm may be practical in friable soils if seeding rates are adjusted to compensate for reduced emergence associated with depth.

The regression equation and response surface describing amaranth EI may be used to estimate seedling emergence at many constant temperatures and seeding depths. The high coefficient of multiple determination (0.95) indicates that the variable EI was a useful parameter for establishing a predictive equation for amaranth and may work as well for other species.

Experiment Two: Alternating Temperature and Seeding Depth Effects

Materials and Methods

Six seedlots from two domestic species and one weed species of Amaranthus, were tested in this experiment (Table 2). Four of the seedlots, H83-382W, H83-382B, H83-438 and H83-1041, were produced in 1983 at the Southern Agricultural Research Center near Huntley, MT. One seedlot, B84-382B, was collected from an evenly spaced stand of volunteer domestic amaranth plants in 1984 at the Arthur H. Post Research Farm, near Bozeman, MT. The sixth seedlot, B84-WEED, was collected in 1984 from wild pigweed plants at the Post Research Farm. Two of the seedlots, H83-382W and H83-382B, were also tested in experiment one and can be used for comparison of results. All seed were dried and stored at 10 C and low humidity until their use in this experiment conducted January through March 1985.

Table 2. Seedlot descriptions.

ID	Year Produced	Accession RRC No.	Species	Seed Color	50-Seed wt (mg)
H83-382W	1983	382	A. hypochondriacus	white	3.12 bc[#]
H83-382B	1983	382	A. hypochondriacus	black	3.06 b
B84-382B	1984	382	A. hypochondriacus	black	3.20 c
H83-438	1983	438	A. cruentus	black	4.33 e
H83-1041	1983	1041	A. cruentus	white	3.96 d
B84-WEED	1984	---	A. retroflexus	black	2.27 a

[#] Means followed by the same letter are not significantly different, using Tukey's mean separations at the 0.01 probability level.

A Percival E-57 growth chamber provided the controlled environment for the experiment. Three alternating (16:8 hours cycle) temperature

regimes, 7 and 17 C (7-17 C), 10 and 20 C (10-20 C), and 13 and 23 C (13-23 C), simulated daily minimum and maximum soil temperatures such as occurred in 1983 and 1984 at the Post Farm near Bozeman, MT in the last week of May, first week of June, and middle of June, respectively, when poor amaranth seedling emergence was experienced. Alternating dark and light periods followed the same cycle. Each temperature regime was a separate 21 day growth period. Maximum and minimum temperatures were recorded at least once every two days with two maximum/minimum thermometers. The maximum and minimum values for each interval never deviated more than one degree from the temperature settings and the temperatures on the two growth chamber shelves never differed from each other by more than one degree.

Six plastic planting trays held the 1:1 peat sand medium (by volume). Each shelf accommodated three trays. Each tray had a single seeding depth and was divided to represent two replications of that depth. Two trays were required for four replications of each seeding depth.

Seeding depths of 0.6, 1.9, and 3.2 cm (0.25, 0.75, and 1.25 inches, respectively) were accurately established by placing a wire grid across the top of each tray and frequently measuring from the wire to the soil surface as the moistened soil was placed. The soil was thoroughly wetted and additional soil carefully placed as needed before the final depth was confirmed.

The experimental unit was 50 seed spaced evenly in a straight line. Each 50-seed unit was weighed and average seedlot weights recorded in Table 2. After all seed were carefully placed on the soil

surface, the tray was gradually filled with medium up to the wire grid, by alternately adding and wetting the medium until it was firmly and uniformly placed. Care was taken not to wash the small seed from their original positions. The medium was kept moist throughout each growth period.

Emerged seedlings were counted every two days from day five to day twenty-one. Emergence index (EI) for each experimental unit was calculated as described for experiment one.

Temperature, seeding depth, and seedlot were analyzed for EI and percentage emergence as a 3 x 3 x 6 factorial experiment, random complete block design, with four replications. It was not necessary to analyze the experiment as a split-split plot design because of the high degree of uniformity within the growth chamber and control of experimental conditions.

Results

Overall, highly significant differences in EI and percentage emergence occurred due to temperature, seeding depth, seedlot, and all the possible interactions (Table 3). Emergence index and percentage emergence increased as temperature became warmer and seeding depth became shallower (Table 4).

There was no emergence from 1.9 and 3.2 cm depths at 7-17 C. Percentage emergence from 0.6 cm at 7-17 C and 3.2 cm at 10-20 C was slight (0 to 11.5%) and not significantly different among seedlots. Significant differences in seedlot emergence occurred at all other depth and temperature combinations. Mean percentage emergence and EI values are shown in Table 4.

Table 3. Three factor analysis of variance for Amaranthus emergence index and percentage emergence at alternating temperatures.

Source	df	Mean square Emergence Index		Mean square Percentage Emergence	
Replications	3	4.92		61.25	
Temperature (T)	2	994.70	**	16670.00	**
Depth (D)	2	515.30	**	6489.00	**
T x D	4	138.20	**	1630.00	**
Seedlot (S)	5	33.97	**	480.40	**
T x S	10	10.92	**	118.40	**
D x S	10	17.18	**	222.50	**
T x D x S	20	5.11	**	81.54	**
Residual	159	0.68		18.71	

** Significant at the 0.01 probability level.

Differences in seedlot EI and percentage emergence, over the three depths at 10-20 C and 13-23 C, are shown in Figure 6 and Figure 7, respectively. Note that the loss of emergence as depth increased from 0.6 to 1.9 cm was much greater at 10-20 C than it was at 13-23 C. At 0.6 cm, white-seeded H83-382W and H83-1041 emergence levels were not significantly different from those of black-seeded H83-438 and H83-382B, but the white-seeded seedlots had a much greater decline in emergence than did black-seeded seedlots as depth increased. The same trend occurred for EI but was not as great as percentage.

A summary of the six seedlot performances at the two higher temperature regimes is as follows. Seedlot H83-438 consistently emerged better than the other seedlots, especially at the cooler (10-20 C) temperature regime. However, at 13-23 C, H83-382B performed almost as well as H83-438. The two white-seeded seedlots, H83-382W and H83-1041, were not significantly different from each other in EI and percentage emergence at all temperatures and seeding depths. Seedlot B84-382B had poorer emergence than did the other domestic seedlots.

Table 4. Percentage (%) emergence and emergence index (EI) for six Amaranthus seedlots from three seeding depths and three temperature regimes.

	% Emergence			EI		
Seedlot	7-17 C	10-20 C	13-23 C	7-17 C	10-20 C	13-23 C
			0.6 cm			
H83-382W	4.5a[#]	84.5 c	86.0 c	0.14a	9.65 cd	12.59 c
H83-382B	6.0a	81.0 c	96.0 c	0.12a	8.30 c	14.07 c
B84-382B	3.5a	56.5 b	66.5 b	0.14a	4.96 b	9.12 b
H83-438	8.5a	93.5 c	95.0 c	0.33a	10.93 d	14.10 c
H83-1041	1.0a	82.0 c	88.5 c	0.02a	9.15 cd	13.05 c
B84-WEED	0.0a	36.5a	52.0a	0.00a	1.81a	6.74a
			1.9 cm			
H83-382W	0	16.5a	58.5a	0	0.98a	6.21a
H83-382B	0	38.0ab	84.0 bc	0	1.86a	9.69 b
B84-382B	0	31.0a	55.0a	0	1.60a	5.78a
H83-438	0	62.5 b	85.0 c	0	3.62 b	10.20 b
H83-1041	0	25.0a	67.5ab	0	1.05a	7.04a
B84-WEED	0	21.5a	62.5a	0	0.53a	6.90a
			3.2 cm			
H83-382W	0	8.5a	17.5ab	0	0.46a	1.52ab
H83-382B	0	8.0a	48.0 c	0	0.29a	4.32 c
B84-382B	0	6.0a	42.5 bc	0	0.13a	3.74 bc
H83-438	0	6.0a	50.5 c	0	0.18a	4.57 c
H83-1041	0	1.5a	14.0a	0	0.04a	1.00a
B84-WEED	0	11.5a	44.0 bc	0	0.40a	3.28abc

[#] Means followed by the same letter are not significantly different using Tukey's mean separations at the 0.05 probability level.

The only weed seedlot, B84-WEED, had poor emergence compared to the other seedlots except at 3.2 cm depth where its emergence was similar (11.5 and 44% at 10-20 and 13-23 C, respectively). The weed seedlot did not have as great a variability due to varying depth as did the domestic seedlots.

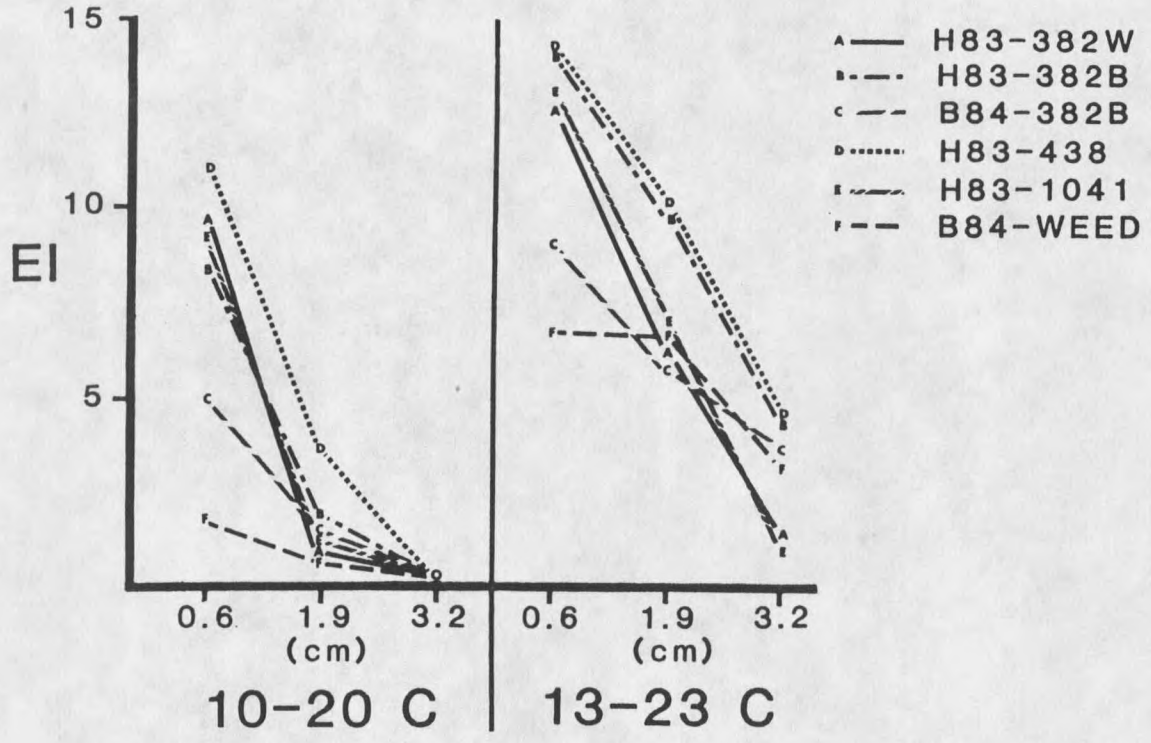

Figure 6. Emergence index (EI) for six Amaranthus seedlots at three seeding depths and two temperature regimes.

Discussion

The 7-17 C temperature regime was near the lower limit for amaranth seed germination and seedling emergence from a shallow seeding and would not provide for adequate stand establishment. Seeding when soil temperatures reached 10-20 C should allow reasonable emergence from a shallow depth for some accessions; but 13-23 C appears to be the lowest temperature regime at which adequate emergence may occur from seeding depths as deep as 2 cm.

Seedlot H83-438 was superior in emergence compared to the other seedlots. Its superiority could be a result of its significantly larger seed (Table 2) providing greater stored energy necessary to overcome temperature imposed stress. Its superiority was most evident

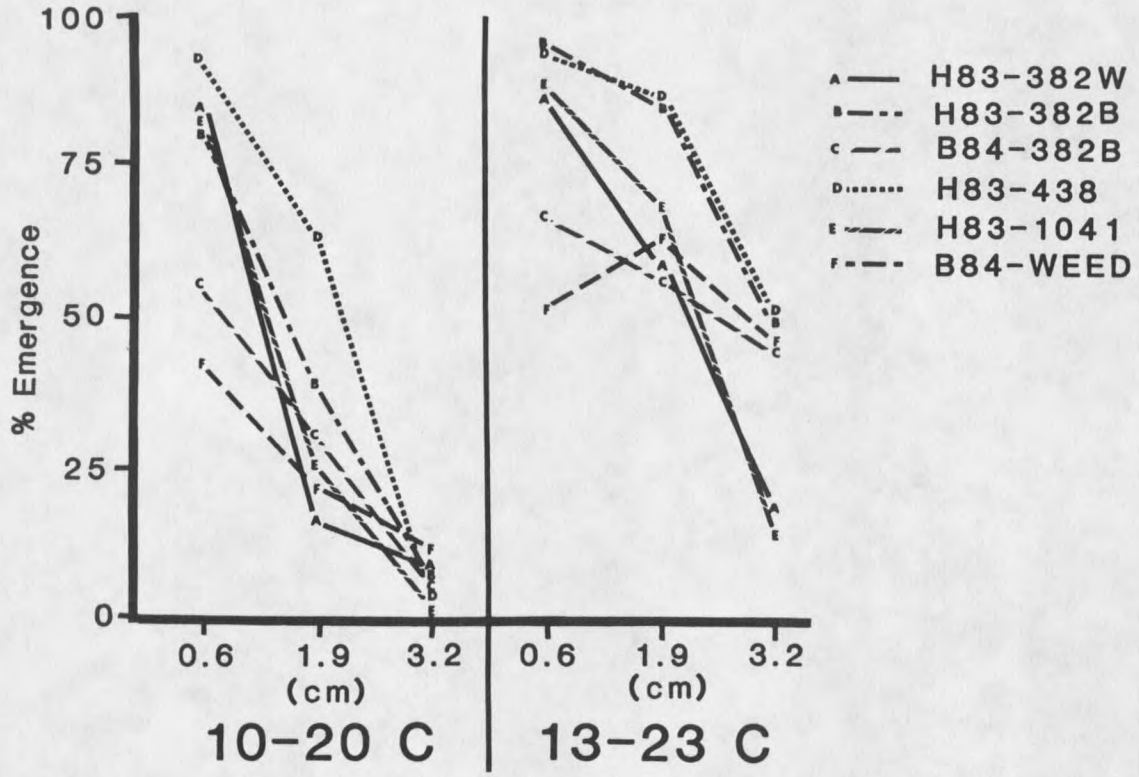

Figure 7. Percentage (%) emergence for six Amaranthus seedlots at three seeding depths and two temperature regimes.

at the cooler temperature regime of 10-20 C (Fig. 6 and 7) where seed vigor would be more important for emergence than at 13-23 C. Seed sizes of the other seedlots did not correlate with their relative performances; perhaps because of interacting factors such as seed color and seed age or because the size differences among them were not great enough. Seed size does vary among amaranth populations and could be an important characteristic to select for in breeding.

Seed color could be another important characteristic affecting amaranth seedling emergence under stress. Temperature did not seem to affect emergence of white-seeded seedlots as much as did seeding depth. The large reduction in white-seedlot emergence due to depth cannot be explained by seed size since the white seed of H83-1041 was heavier

than that of the other seedlots, except H83-438, and the seed weights of white-seeded H83-382W and black-seeded H83-382B were not significantly different from each other. The poorer emergence of white seed could be associated with a reduction in seed vigor during storage when the properties of a black seed coat could protect seed from deterioration (aging) better than those of a white seed coat.

In this study, H83-382B emerged significantly better than H83-382W, but this difference did not occur in the concurrent constant-temperature study (experiment 1). Both seedlots were from the same population. The different results could be due to the cooler temperature in the alternating temperature regimes having a more adverse affect on the white seed than it did on the black seed. Another possibility is black seed germination and seedling emergence may be slightly promoted by alternating temperatures. Seedling emergence was generally faster but percentage emergence lower for white-seeded seedlots than for black-seeded seedlots; thus the difference between H83-382W and H83-382B was greater for percentage emergence than it was for EI. The same situation occurred between black-seeded H83-438 and white-seeded H83-1041; different accessions but both Amaranthus cruentus, indicating seed color effect on emergence may be a genus-wide characteristic.

Dormancy also seems to be a factor affecting seedling emergence in this experiment. Seed dormancy in A. retroflexus is well known (Kadman-Zahavi, 1960; McWilliams et al., 1967; Taylorson and Hendricks, 1969 and 1971). Consistent with that, was the low emergence of B84-WEED in this experiment. However, there have been no studies reported

concerning seed coat promoted dormancy in any of the domestic amaranth species.

The emergence of B84-382B was poor compared to the other domestic seedlots but was significantly better than B84-WEED from the 0.6 cm depth (Fig. 6 and 7). The seedlots B84-382B and B84-WEED were produced in the same growing season at the same location and B84-382B is closely related to the other two seedlots in accession RRC-382. The poor seedling emergence of B84-382B may be due to a seed coat induced dormancy similar to, but not as pronounced as, that of B84-WEED (A. retroflexus). The good seedling emergence of H83-382B, a year older than B84-382B, could be a result of its having overcome dormancy with time in storage. Because domestic white seed have germinated so rapidly and domestic black seed were delayed in the amaranth germination studies (Chapters 4 and 5), there is no evidence that white seed have the same seed coat promoted dormancy as may black seed.

CHAPTER 4

OVERWINTER EFFECTS ON AMARANTH SEED GERMINATION

If amaranth seed successfully overwinters, fall-seeding amaranth as a summer crop may be feasible and domestic amaranth may have weed potential if escaped. Seed of accession RRC-382, A. hypochondriacus, survived the winter of 1983-1984 and became established as volunteer plants the following summer at Bozeman, MT. It was not known whether both black and white seed would overwinter equally well nor whether seed of domestic species would overwinter as does A. retroflexus (redroot pigweed).

The objectives of this experiment were to compare overwinter effects on germination of pigweed seed and white and black domestic amaranth seed of several ages, and to compare germination of overwintered seed with stored seed at the end of winter.

Materials and Methods

Four seedlots, H83-382W, H83-382B, B84-382B, and B84-WEED, were used in this experiment. H83-382W and H83-382B were collected from the same population of A. hypochondriacus, accession RRC-382, grown at the Southern Agricultural Research Center near Huntley, MT in 1983. B84-382B was collected from a uniform stand of volunteer plants, also of accession 382, at the Arthur H. Post Research Farm near Bozeman, MT in 1984. B84-WEED was collected in 1984 from wild pigweed plants at the

same farm in 1984. H83-382W had white seed while the other three seedlots had black seed. All seed were dried and stored at 10 C and low humidity until their use in this experiment.

Six metal flats, filled with moist loam soil and containing seed from the four seedlots, were buried at the Arthur H. Post Research Farm near Bozeman, MT on 9 November 1984. The top of each flat was even with the ground surface. Each flat contained four replications of 150 seeds of each seedlot in a randomized complete block design. Each 150-seeds was placed in a nylon mesh bag and buried 1 cm below the soil surface.

One flat was removed from the field on each of the following dates: 16 November, 9 January, 9 February, 9 March, 9 April, and 9 May. When a flat was removed from the field, the seed packets were removed from the soil, rinsed, and placed in a plastic germination box with enough moisture for seeds to imbibe. The germination box was kept in a refrigerator at 1 C for 8 to 9 hours. In May, a control group of seed (kept in dry storage) from each seedlot was placed on moist germination blotter paper in germination boxes and placed in the refrigerator at the same time as the seed from the field. The refrigeration time allowed all seed to imbibe and be ready to germinate. Seed were removed from the refrigerator and 100 seed were randomly selected from each seedlot and placed on two layers of moist germination blotter paper in a plastic germination box. The covered boxes were placed in a germinator at a constant 35 C and continuous darkness. The high temperature promoted germinations and minimized the effect of light on germination (Kendrick and Frankland, 1969a). The temperature was

monitored daily using a maximum/minimum thermometer. Daily fluctuations were no more than 1 C. The blotter papers were moistened with distilled water. Germinated seed were counted and removed twice daily for the first two days and once daily for the remainder of the 21 day germination period.

Twenty-one day germination indices (GI) were calculated as described for emergence index in Chapter 3. Separate analyses of variance were conducted on GI for each population over time, and mean separations were determined by Tukey's Studentized Range Test.

Results

Overwintering duration and seedlot differences resulted in significant changes in GI and percentage germination (Table 5). Significant differences in GI due to time overwinter occurred within each seedlot (Table 6), but the four seedlots responded in three different ways. H83-382W (white seed) GI was not significantly different from November to April and as a control (GI=15.28 to 19.86) but its GI in May was significantly lower (7.21). The white seed that did germinate in May lacked vigor. The black seed of H83-382B and B84-

Table 5. Two factor analysis of variance for Amaranthus germination index and percentage germination after overwintering.

Source	df	Mean square Germination Index		Mean square Percentage Germination	
Replications	3	2.69		36.73	
Time (T)	5	18.24	**	941.70	**
Seedlot (S)	3	7.90	**	1182.00	**
T x S	15	42.31	**	512.10	**
Residual	69	2.59		37.52	

** Significant at the 0.01 probability level.

382B germinated much the same as each other. Their lowest GI occurred in November (15.98 and 15.01, respectively), while significantly higher GI occurred from January to May and as controls. The black-seeded control of B84-WEED had a low GI (6.90) while the seed from the field had its highest GI in May (20.86).

Table 6. Germination index after 21 days at 35 C for four Amaranthus seedlots at different overwintering times.

Month	H83-382W	H83-382B	B84-382B	B84-WEED
November	19.86 b[#]	15.98a	15.01a	13.60 b
January	19.56 b	19.02 b	18.58 c	18.02 bc
February	15.28 b	19.01 b	17.13 bc	17.59 bc
March	19.31 b	18.06ab	15.97ab	15.50 bc
April	18.01 b	16.85ab	17.02 bc	12.84 b
May	7.21a	17.07ab	18.58 c	20.86 c
May control	18.86 b	19.00 b	17.77 c	6.90a

[#] Means followed by the same letter are not significantly different using Tukey's mean separations at the 0.01 probability level.

Differences in GI's were apparent in the first eight days, so germination curves as described by Nichols and Heydecker (1968) were drawn for November, April, and May for each seedlot (Fig. 8). GI's from January to April were similar (Table 6) so April is shown as representative of those months. Figure 9 shows seedlot eight-day germination curves for May and the controls (also germinated in May).

The germination curves reveal differences between white and black seed, and differences between black domestic and weed seed. About 80% of the white seed germinated within two days in November, April, and as the control, while only 35% germinated within eight days in May. Though less than 15% of the black seed (domestic and weed) germinated after 4 days in November, all black-seeded seedlots had at least 75%

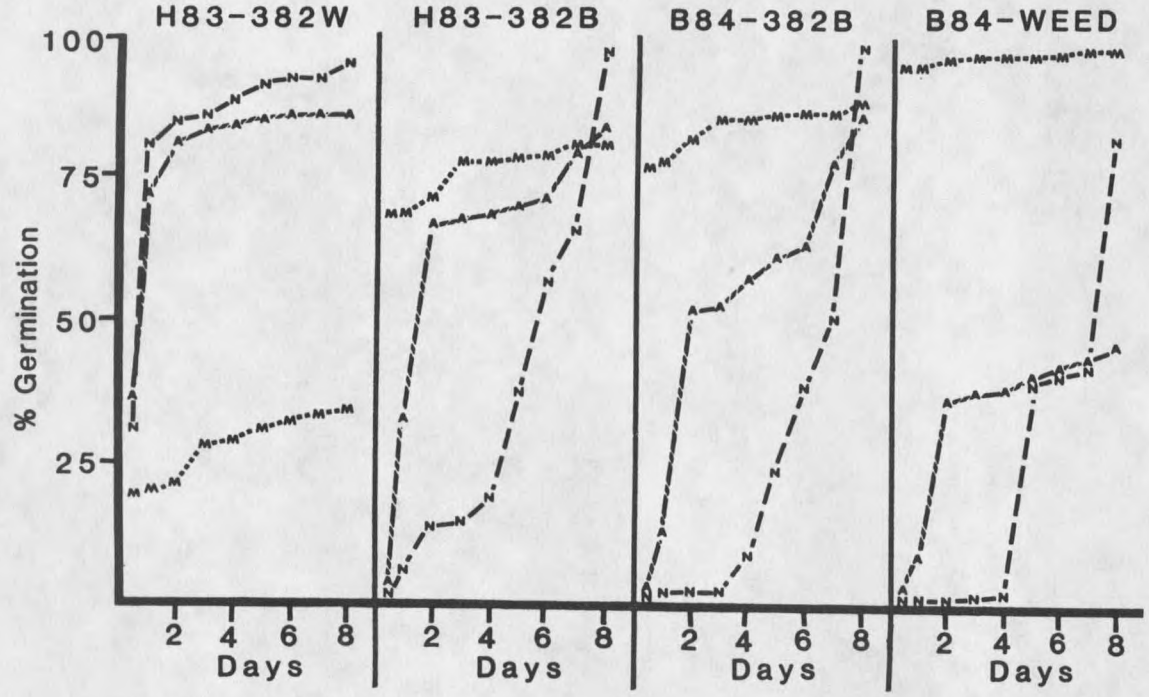

Figure 8. Eight-day germination curves for four Amaranthus seedlots in Nov. (N), Apr. (A), and May (M) after overwintering.

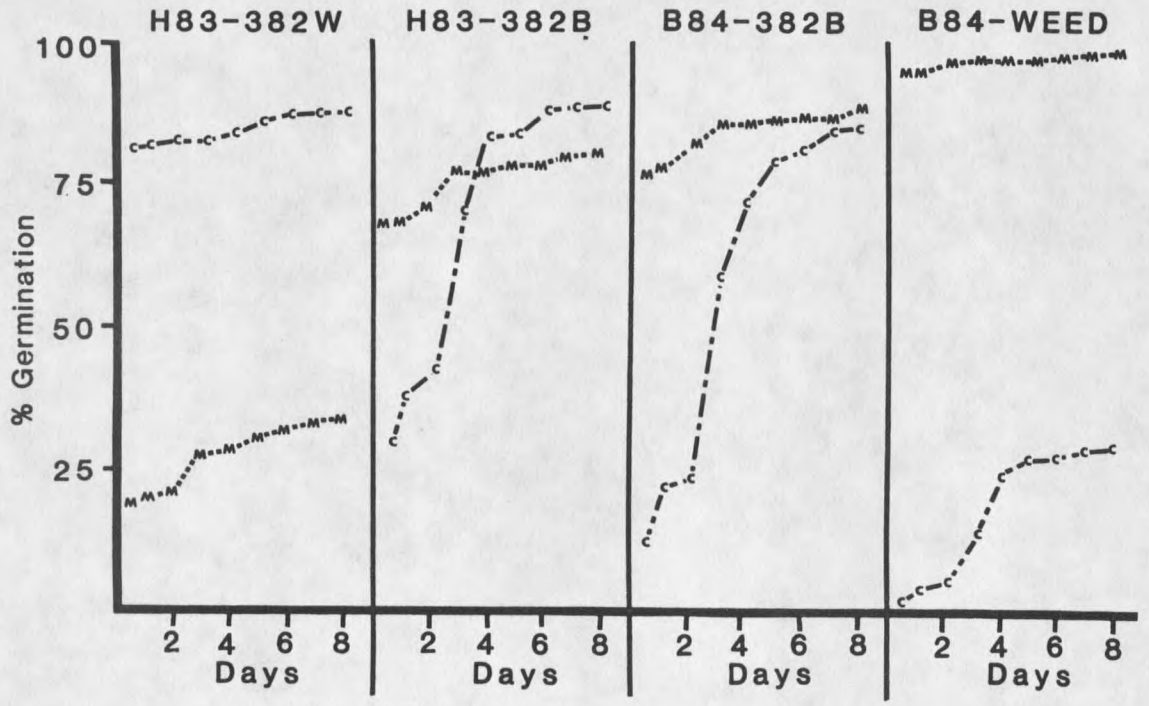

Figure 9. Eight-day germination curves for four Amaranthus seedlots after the same time overwintering (M) and in storage (C).

germination within the first half day in May. The two domestic black-seeded seedlots did not differ as much in May from their respective controls as did the black-seeded weed from its control. The black-seeded domestic seedlots also had about 10% less germination than did the weed after eight days.

Discussion

The overwintering ability of Amaranthus seed is greatly affected by seed color. The white seed of accession H83-382W did not overwinter well while the black seed of the other seedlots did. The critical time determining overwintering ability was between 9 April and 9 May. This was a period when the soil was thawed but temperatures were too cold for seed germination. The white seed removed from the field on 9 May showed signs of decomposition and loss of vigor, possibly the result of pathogens. Mold grew rapidly on these seed. White-seeded amaranths appear unlikely to become weeds in any climate that has a month or longer of cold, wet soil conditions. Black seed, however, retained a high degree of vigor, indicating that domestic black-seeded amaranths could be a weed threat if allowed to escape.

Fall-seeding amaranth appears to only be feasible for a black-seeded crop. The only use for black seed may be as animal food, for which fall-seeding might be further investigated.

Seed age did not significantly affect the overwintering ability between H83-382B and B84-382B, which germinated similarly.

Seed of A. retroflexus has a primary dormancy which can be overcome by stratification. Taylorson and Hendricks (1969) prechilled A. retroflexus seed at 10 C for 28 days and subsequently found 80%

germination after three days at 35 C. We found 98% germination of overwintered A. retroflexus seed in May after only a half day at 35 C. The difference between the two germination percentages may be because prechilling in this experiment was longer and at colder temperatures than in the 1969 experiment. Phytochrome, which in the Pfr form is responsible for breaking the primary seed dormancy in A. retroflexus (Taylorson and Hendricks 1969), must be hydrated to function (Kendrick et al. 1969). Therefore, it would seem likely that phytochrome would not function if frozen. Taylorson and Hendricks (1969) also found that at imbibition temperatures above 20 C, Pfr underwent thermal inactivation and dormancy was maintained. For prechilling to be effective in breaking seed dormancy temperatures must be above freezing and below 20 C for an extended period of time.

The black domestic amaranth seed survived the winter well, presumably because of the nature of their black seed coats. They germinated faster after prechilling than before prechilling (April-May), but a comparison of H83-382B and B84-382B control seed germination with that of B84-WEED control seed shows the domestic seed germinates better without prechilling than does the weed seed. Therefore, it seems that the domestic black seed have a primary dormancy similar to that of the weed seed but to a lesser degree. Dormancy in the black-seeded amaranths would have been selected against during domestication when they no longer needed the competitive advantage of dormancy for their species' survival.

CHAPTER 5

TEMPERATURE, LIGHT, AND SEED AGE EFFECTS ON AMARANTH SEED GERMINATION

Three separate experiments assess temperature and seed color effects on amaranth seed germination. The experiments were not designed for direct comparison of results, so comparisons made are intended only to indicate trends in amaranth germination with time from harvest and should not be considered conclusive. Light effect on amaranth seed germination was not realized until the final germination test when germination in light was directly compared with seedling emergence from 1.3 cm depth of soil (dark germination).

Materials and Methods

Three germination tests were conducted at varying temperatures on a one-way thermogradient plate using seedlots H83-382W (white seed) and H83-382B (black seed), collected from the same A. hypochondriacus population on 13 September 1983 at the Southern Agricultural Research Center near Huntley, MT. The seed were dried and stored at 10 C and low humidity.

Seed were placed on germination blotter paper, kept moist, and covered with a clear plastic lid to minimize drying in each test. Temperatures on the blotter paper surface were recorded manually at random within each isotherm for the first two tests and automatically at two consistent points within each isotherm for the third test. Both

methods utilized thermocouples and digital thermometers. Seed were considered germinated when the radicle emerged. Germinated seed were counted and removed twice daily for the first three days and once daily for the remainder of each 14 day test period. Germination index (GI) was calculated using the formula described in Chapter 3 for emergence index. Additional details of the three tests are given in Table 7.

Table 7. Details of three amaranth germination tests conducted on thermogradient plates.

	First	Second	Third
test date	Oct. 1983	Aug. 1984	Jan. 1985
time from harvest	2 weeks	11 months	16 months
germination period	14 days	14 days	14 days
experimental unit	50 seeds	50 seeds	50 seeds
no. temperatures	10	6	10
no. replications	7	4	3
temperature range (C)	10.5-37.0	15.5-33.0	15.3-45.6
light source	fluorescent	fluorescent	mercury vapor
photoperiod	15 hours	15 hours	continuous

Analysis of variance was used to obtain the degrees of freedom and mean square error for each test so mean separation by Least Significant Difference (LSD) could be determined between the black and white seed at each temperature. Germination indices for the three tests were plotted to show the effect of amaranth seed age on seed germination.

The third germination test was conducted in conjunction with the amaranth seedling emergence test on the thermogradient plate (Chapter 3) so that germination could be compared with seedling emergence from 1.3 cm depth. The comparison was presented graphically.

Results

Germination Tests. Temperatures on the blotter paper surface fluctuated in each experiment by no more than 1.5 C above and below each mean. Black-seed GI was lower than white seed GI at every temperature in each test indicating black seed germinated more slowly than did white seed (Table 8). Differences between black- and white-seed GI diminished in each subsequent experiment so that significant differences between seed colors in the 16 month test occurred only above 41 C (Table 8). Average number of days taken for each seed color to reach 50% germination at each temperature in each experiment also shows white seed germinated more rapidly than did black seed (Table 8).

Minimum temperatures for germination varied between 15.5 and 21.3 C for black seed and 14.0 and 18.4 C for white seed. Differences in minimum temperatures among the experiments could be due to the effects of temperature fluctuations within isotherms. Maximum temperature for germination of black and white seed was near 45.6 C in the 16 month test. Germinated seed at this temperature were "mushy" and broke apart when handled.

Black-seed GI increased considerably over the range of temperatures from two weeks to 11 months after harvest but increased less from 11 months to 16 months after harvest (Fig. 10). The decrease in GI from 28 to 33 C in the 11 month test does not fit the pattern of the other curves and could be a result of drying at the warmest temperature, although the same discrepancy does not occur with white seed. White-seed GI increased overall between two weeks and 11 months from harvest but did not increase from 11 to 16 months (Fig. 10).

Table 8. Days to 50% germination and germination index for white and black amaranth seed, at various temperatures and times.

Temperature (C)	No. Days to 50% Germination		Germination Index after 14 Days	
	Black Seed	White Seed	Black Seed	White Seed
2 Weeks After Harvest.				
10.5	--	--	0.00	0.00
14.0	--	--	0.00	0.04
15.5	--	--	0.03	0.20
18.5	--	--	0.14	0.55
21.5	--	--	0.66	1.36
26.0	10	6	3.93	7.02 **
29.0	6	1	6.98	11.29 **
31.5	4	1	8.00	12.14 **
34.5	4	1	8.84	12.38 **
37.0	13	1.5	3.33	11.63 **
** Significant for GI at the 0.01 probability level (LSD = 1.23).				
11 Months After Harvest				
15.5	--	--	0.00	0.04
19.0	--	--	0.04	1.05
20.0	--	7	0.67	4.28 **
24.0	2.5	1.5	9.93	11.98 **
28.0	4	1.5	10.06	12.03 *
33.0	7	1	7.08	12.89 **
* Significant for GI at the 0.05 probability level (LSD = 1.47).				
** Significant for GI at the 0.01 probability level (LSD = 1.97).				
16 Months After Harvest				
15.3	--	--	0.00	0.00
18.4	--	--	0.00	1.03
21.3	--	--	2.36	4.11
24.0	3	1.5	10.53	12.01
27.5	1	1.5	11.59	11.95
30.4	1	1	12.30	13.75
33.8	1	0.5	13.25	13.63
37.2	1	0.5	12.12	13.69
41.2	5	0.5	7.30	12.18 **
45.6	--	--	0.40	3.39 **
** Significant for GI at the 0.01 probability level (LSD = 2.86).				

-- Less than 50% of the seed germinated within 14 days.

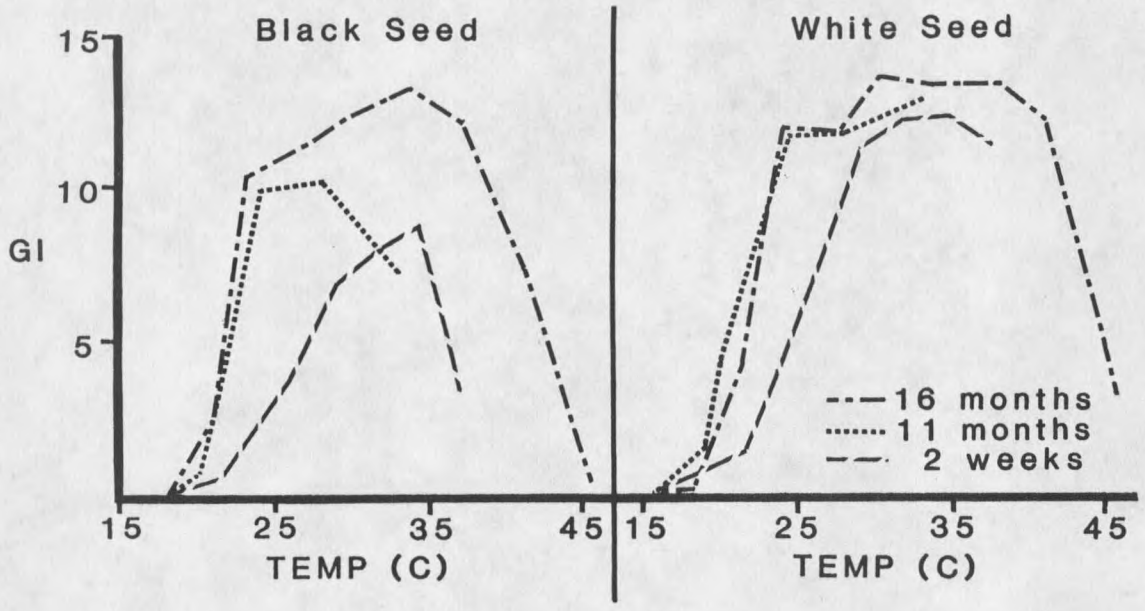

Figure 10. White and black amaranth seed germination index (GI) at various temperatures, 2 weeks, 11 months, and 16 months after harvest.

Seed germination and seedling emergence. Percentage seedling emergence from 1.3 cm depth exceeded percentage seed germination for both black and white seed between 15.3 and 24.0 C (Fig. 11). Above 24.0 C, percentage germination is nearly as high or higher than emergence.

Discussion

The higher percentage seedling emergence than percentage seed germination at temperatures below 24 C (Fig. 11) shows germination in light does not represent amaranth germination in soil. Photoinhibition of seed germination is a result of phytochrome action in a High Irradiance Response. Kendrick and Frankland (1969a) found continuous white light reduced A. caudatus germination percentage at temperatures below 25 C. This coincides with these results using A. hypochondriacus

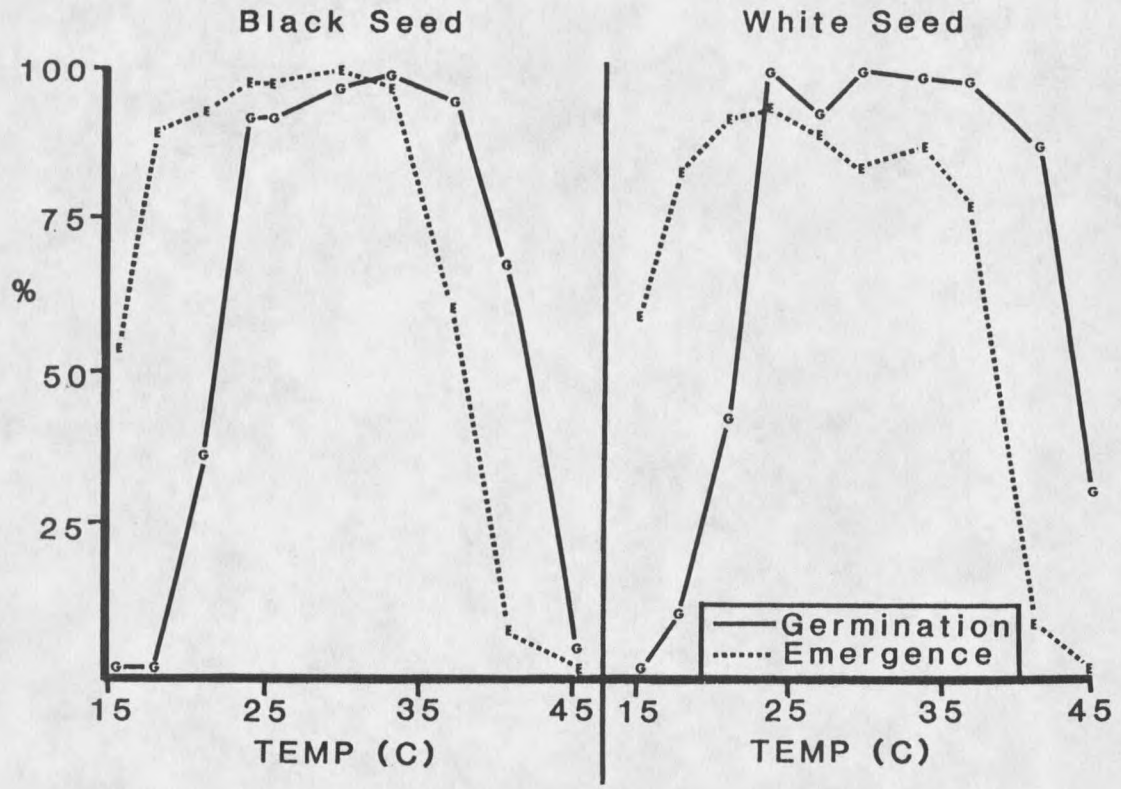

Figure 11. White and black amaranth seed percentage germination in light compared to percentage emergence from 1.3 cm seeding depth, at various temperatures.

indicating this response could be widespread among the genus Amaranthus. Kendrick and Frankland also found that above 25 C, light delayed A. caudatus germination and as temperature increased, the germination delay decreased. It was not possible to assess germination delays in this experiment by comparing speeds of germination and seedling emergence as was done by comparing percentages of germination and emergence. We may assume, however, that since germination percentage was affected by light then germination speed was also affected.

The dramatic increase in black-seed GI from two weeks to 16 months after harvest may be due to the breaking of primary dormancy during

that time. Black-seed GI was significantly different from white-seed GI between 26.0 and 37.0 C at two weeks from harvest while there were no significant differences in GI between these temperatures due to seed color at 16 months from harvest. White-seed GI was only slightly less at two weeks than at 16 months from harvest, indicating that there may have been little if any primary dormancy. Primary dormancy in black seed may be associated with properties of the black seed coat. These findings are consistent with those of the other experiments (Chapters 3 and 4).

The black-seed dormancy at two weeks from harvest may or may not be associated with photoinhibition of germination. This may have been clarified if a dark germination or seedling emergence test had been performed at that time. A primary seed dormancy occurs even in darkness for A. retroflexus and A. albus, both weed species with black seed coats (see Literature Review), so the same cause of dormancy may occur with black-seeded A. hypochondriacus. The mechanism of dormancy in black-seeded grain amaranth warrants further investigation.

CHAPTER 6

SUMMARY AND CONCLUSION

Amaranth seedling emergence. Amaranth seedling emergence at constant temperatures between 15.3 and 45.6 C and seeding depths between 1.3 and 6.4 cm was investigated using a modified thermogradient plate. Seedling EI was maximum between 24.0 and 33.8 C while percentage emergence was maximum between 21.3 and 33.8 C over all seeding depths. EI between 18.4 and 24.0 C may be acceptable from 1.3 cm seeding depth if other conditions are favorable. Seedling EI and percentage emergence decreased with increasing seeding depth but may be acceptable down to 2.5 cm, again if temperature and other conditions are favorable.

Amaranth seedling emergence at 7-17, 10-20, and 13-23 C alternating temperature regimes and 0.6, 1.9, and 3.2 cm seeding depths was investigated using a growth chamber. EI and percentage emergence were very low at 7-17 C and increased with increasing temperature to their highest values at 13-23 C and 0.6 cm seeding depth. Again, seedling EI and percentage emergence decreased with increasing seeding depth. Seeding deeper than 0.6 cm may not result in acceptable emergence in the field at any of these cool temperatures. H83-438 had the largest seed of the six seedlots and had the best emergence at the cooler temperatures. Black domestic amaranth seed produced in 1984 emerged less and slower than did black domestic seed produced in 1983,

indicating that the black seed has a primary seed dormancy that can be overcome with time.

Seed color effect on amaranth seedling emergence was different in each of the two experiments. At constant temperatures between 15.3 and 41.2 C, no difference in emergence was evident between 16 month old white (H83-382W) and black (H83-382B) seed. When seed was compared at alternating temperatures, black seed emerged significantly better than did white seed. The low temperature in the alternating temperature regimes in the growth chamber was lower than any constant temperature on the thermogradient plate. Black seed may be less adversely affected by cold temperatures than white seed.

Amaranth overwintering. White and black domestic amaranth seed were compared with local pigweed seed for their ability to germinate after different periods of overwintering. White amaranth seed decomposed in the field between April 9 and May 9 resulting in very poor germination. Escaped white-seeded amaranth would have little weed potential. Also, seeding white amaranth seed in cold soils could later reduce its germination and seedling emergence when soils warmed.

Black amaranth seed survived the winter very well. Pigweed seed germinated best in May after a sufficient period of prechilling in cool, moist soil. Primary dormancy was more pronounced in the weed seed than it was in the domestic black seed. Domestic black seed germinated equally well between January and May after germinating slightly less in November. Black-seeded domestic amaranth could have high weed potential if escaped and could possibly be seeded in cold soils without consequently reducing germination and seedling emergence.

Amaranth seed germination. Temperature, light, and seed age effects on amaranth seed germination were investigated on black and white seed in three experiments on a thermogradient plate. Black seed germinated noticeably better at 11 months than it did at two weeks from harvest but not much different between 11 and 16 months. White seed germinated better at 11 months than at 2 weeks from harvest but the difference was not as great as with black seed. White seed germinated much the same at 16 months as it did at 11 months. This is another indication that amaranth seed has a primary seed dormancy, which is expressed in black seed but not at all or very little in white seed.

Amaranth seed germination in light was compared with amaranth seedling emergence at temperatures between 15.3 and 45.0 C on a thermogradient plate. Percentage seedling emergence was greater than germination at temperatures below 24 C. Light inhibited germination by inactivating phytochrome far red in a High Irradiance Response. At temperatures above 24 C, germination may have been only delayed. The higher the temperature, the less important phytochrome is in the promotion of amaranth seed germination.

Amaranth research needs and recommendations. Selections can be made for early maturity, high yields, short stature, white seed, large seed, and drydown using existing germ plasm. Contact and cooperation should be maintained with the Rodale Research Center where an active breeding program is underway. Genotypes from their program could be screened annually in Montana and selections made in Montana could be sent to Rodale Research for breeding. Cooperation should also be maintained with the USDA Plant Introduction Station at Ames, Iowa where

an extensive and well described amaranth germ plasm collection is being developed to distribute to researchers around the world.

Management practices for amaranth production and processing have been worked out by numerous U.S. growers over the past decade. These practices should be adopted in Montana before research in amaranth management is conducted.

Amaranth should be studied for its potential as a silage because of its nutritional quality and biomass capability. Silage use would help bring amaranth into general acceptance, give more farmers experience in its production, and eliminate transportation and seed marketing problems particular to Montana.

Amaranth in Montana. Amaranth remains a potential new crop in Montana below about 1000 m elevation. Irrigation and friable soil may be necessary to obtain reliable seedling emergence. The economic potential for amaranth grown in Montana remains uncertain and promotion of amaranth should proceed with caution.

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APPENDICES

APPENDIX A

EXPLORATORY FIELD TESTING OF AMARANTH IN MONTANA (1982-1984)

Montana has diverse climates due to elevations ranging from 550 to 3,900 m and latitudes between 45° and 49° north. The potential for amaranth growth and seed production in Montana was investigated; providing field production experience and indicating inferior and superior species, types, and accessions.

Materials and Methods

Two sites were used for the field tests during the three years; the Arthur H. Post Research Farm near Bozeman, MT and the Southern Agricultural Research Center near Huntley, MT. The two sites are similar in latitude but differ in elevation (Table 9). Growing Degree Days (GDD) were used to indicate the average amount of heat present throughout the growing season (Table 9).

1982 Field Trials. Eighteen early maturing grain amaranth accessions from the 1981 Rodale Amaranth Germ Plasm Collection (Kauffman and Reider, 1981) were hand-seeded shallowly in unreplicated three-row plots on 15 and 16 June at Huntley and Bozeman, respectively. The rows were 76 cm apart, 4.3 m long with about 28 plants per row. The plots were sprinkler irrigated and hand-weeded, and the mature seed heads were hand-harvested from live plants in September. The seed heads were dried and threshed and the seed yields calculated.

Table 9. Comparison of test sites at Bozeman and Huntley, MT.

	Bozeman	Huntley
Latitude	45° 40' N	45° 55' N
Elevation	1455 m	911 m
Years	1882-1976	1911-1981
Avg. last freeze	May 31	May 17
Avg. first freeze	Sept. 15	Sept. 21
Avg. freeze-free season	107 days	127 days
Years	1917-1971	1911-1971
Avg. accumulative growing degree days# (corn model) June 1 - Sept. 15	1509.2	1779.0

$$\#_{GDD} = \frac{\text{daily max. temp. (86°F)} + \text{daily min. temp. (50°F)}}{2} - 50$$

1983 Field Trials. Two hundred thirteen accessions representing a cross section of the 1983 Rodale Amaranth Germ Plasm Collection (Kauffman and Reider, 1983) were machine-seeded 1.3 cm deep in single-row, unreplicated plots on 27 and 30 May at Huntley and Bozeman, respectively. The rows were 6 meters long, 61 cm apart at Bozeman and 56 cm apart at Huntley, with 200 seed per row. The Bozeman trial was sprinkler irrigated regularly through the end of July while the Huntley trial was flood irrigated on 27 June and 29 July. The Huntley trial received only 5 mm of rain in June. The plots at both sites were hand-weeded. Mature seed heads were hand-harvested from live plants at Huntley on 13 September, 109 days after planting. The heads were dried and threshed and the seed yields calculated. No seed was harvested at Bozeman because little seed matured before the season's first hard freeze on 18 September.

1984 Field Trials. Six accessions were machine-seeded 1.3 cm deep in three-row plots, replicated four times, on 17 May, 2 June, and 14 June at Huntley and 24 May at Bozeman. Nine accessions were seeded on 27 June at Bozeman. The accessions were selected for their good yields at Huntley in 1983. Rows were 4.5 m long by 61 cm apart at Bozeman and 3 m long by 76 cm apart at Huntley, with 100 seed per row at both sites. Each 100 seed was scarified for three to five seconds using a Forsberg seed scarifier. Abundant rain fell at Bozeman during June, preventing a mid-June seeding, and sprinkler irrigation began regularly on 2 July. The trials at Huntley were flood irrigated on 18 May, 4 June, and 29 June and only a trace of rain fell during this period. Weeds were controlled at both sites by cultivation and hand-weeding and one application of Roundup herbicide was applied at Bozeman to control Canada thistle. No seed harvests were made at either location from these plantings, but some seed heads were hand harvested from volunteer plants at Bozeman.

Results

Differences in plant development were observed between the Bozeman and Huntley sites presumably because of differences in climates (temperature and moisture) due to elevation.

1982 Field Trials. Only accession RRC-382 (A. hypochondriacus) matured at Bozeman, the cooler of the two sites, while thirteen accessions matured at Huntley (Table 10). Estimated grain (clean seed) yields for accession RRC-382 at Bozeman and Huntley were 411 kg/ha and 1070 kg/ha, respectively.

Table 10. 1982 amaranth seed yields at Huntley, MT.

Accession RRC No.	Species	Type	Yield Kg/Plot	Est. Yield Kg/Ha
399	A. caudatus	Edulis	0.0	0
572	A. caudatus	S. American	0.0	0
104	A. cruentus	Mexican	0.7	704
158	A. cruentus	Mexican x African	0.0	0
390	A. cruentus	Mexican	1.2	1256
438	A. cruentus	Guatemala	2.8	2830
1034	A. cruentus	African	0.7	687
1035	A. cruentus	African	0.2	253
1040	A. cruentus	African	0.8	794
1041	A. cruentus	Mexican	1.9	1926
385	A. hybridus	Prima	0.2	232
386	A. hybridus	Prima	1.1	1078
1004	A. hybridus	Prima	0.6	615
1044	A. hybridus	Prima	0.2	157
382	A. hypochondriacus	Spike	1.0	1070
51	A. hypochondriacus	Nepal	0.0	0
126	A. hypochondriacus	Nepal	0.2	189
159	A. hypochondriacus	Nepal	0.0	0

1983 Field Trials. Cool temperatures and soil crusting seemed to substantially reduce seedling emergence at Bozeman while drought seemed to be the primary cause for poor emergence at Huntley. Despite these unfavorable conditions, some plants from most accessions at both sites did emerge, allowing observation of individual characteristics.

Flowering initiated around 25 July for many accessions of A. cruentus and A. hypochondriacus at both locations. Accessions of A. caudatus did not flower during the season.

The plants at Bozeman were 0.5 to 1.5 m tall at the end of the growing season but no seed was harvested. Many volunteer plants emerged at the site the following year between 20 and 27 June. Some volunteers were identified as accessions 382 and 674 and others less specifically as A. hypochondriacus, Nepal type. These volunteer plants

were significant in three ways; a few accessions produced mature seed in a short (110 days), cool growing season; their seed overwintered with soil temperatures reaching -18 C; and the seedlings emerged when temperatures reached about 21 C in moist soil.

The plants at Huntley were 0.5 to 3 m tall at the end of the growing season and 54 accessions matured (Table 11). The highest yielding type was A. cruentus, Mexican (Table 12). Six individual plants, all A. cruentus, Mexican type, had dried-down after developing mature seed. Seed shattering was prevalent. A. caudatus plants were the shortest in the plot and none matured.

Table 11. Number of amaranth accessions by species and type matured at Huntley, MT, 1983.

Species[#]	Type	No. of Accessions Seeded	No. of Accessions Matured
A. cruentus	African	13	2
	Mexican	48	30
	Guatemalan	12	8
	Nepal	1	0
	Unknown	1	1
A. hypochondriacus	Nepal	38	4
	Aztec	20	0
	Spike	3	2
	Mercado	15	0
	Unknown	12	2
A. caudatus	S. American	21	0
	Edulis	3	0
	Nepal	1	0
A. hybridus	Prima	5	2
	Sangorache	3	0
	Vegetable	1	0
	Unknown	2	0
A. tricolor	Weedy	1	0
A. blitum	Horsetooth	1	0
A. unknown	Unknown	12	3
	Total	213	54

[#]Species and type as registered in the 1983 Rodale Amaranth Germ Plasm Collection.

Table 12. Highest yielding amaranth accessions in 1983 at Huntley, MT, based on yield/plant.

Accession RRC No.	Species	Type	Average Grams Seed/Plant	No. Plants Harvested
429	A. cruentus	Mexican	169.2	5
443	A. cruentus	Mexican	150.6	3
419	A. cruentus	Mexican	140.9	1
423	A. cruentus	Mexican	131.1	5
424	A. cruentus	Mexican	106.1	7
1026	A. cruentus	Mexican	100.4	3
400	A. hybridus	Prima	100.0	3
432	A. cruentus	Mexican	93.7	10
444	A. cruentus	Mexican	93.7	1
438	A. cruentus	Guatemalan	85.0	11

1984 Field Trials. Seedling emergence at Huntley was so poor from all three seedings that the plot was abandoned in early August. No seedlings emerged from the first seeding (24 May) at Bozeman but emergence was good from the second seeding (27 June). The second seeding was late in the season so mature seed was not produced.

Discussion

Seedling emergence. In 1982, small plots were hand-seeded and carefully watered resulting in good seedling emergence. Seedling emergence was poor in 1983 and 1984 when plots were larger, machine-seeded, and watered less. The small size of amaranth seed necessitates favorable environmental conditions for good seedling emergence and stand establishment. In 1983, soil crusting and cool temperatures seemed to cause poor amaranth seedling emergence at Bozeman while insufficient soil moisture seemed to cause poor emergence at Huntley.

In 1984, a serious mistake was made when the seed were briefly scarified before seeding (see Appendix B). The scarification reduced

seed vigor and consequently seedling emergence. Of the five seedings in 1984, only the last resulted in significant emergence because it was irrigated well and the soil was warm. Emerging seedlings in the final seeding experienced less stress so the loss of seed vigor due to scarification was less manifested.

Site differences. The difference in amaranth maturity between the Bozeman and Huntley sites can be attributed to the sites' respective accummulative Growing Degree Days, since seeding and harvesting at both sites occurred at approximately the same dates. Huntley's warmer freeze-free season allows amaranth to develop faster than does Bozeman's cooler freeze-free season and consequently many accessions matured at Huntley while very few matured at Bozeman. Because only two of 213 accessions matured at Bozeman, it appears that Bozeman's climate is near the limit for any amaranth maturity. Amaranth seems to develop normally, though slowly, at Bozeman, showing no obvious signs of deformities or dysfunction. Flower induction occurs about the same time at Bozeman and Huntley though the plants at Bozeman are shorter, indicating floral initiation is more a factor of plant age than plant size. Maturity is possible at Bozeman but the smaller plants yield less seed. Accession RRC-382 yielded only half as much seed at Bozeman as it did at Huntley in 1982.

Species differences. A. caudatus is a short-day species (Zabka, 1961; Kohli and Sawhney, 1979) as is A. retroflexus (Anderson and Salisbury, 1977) but the literature contains nothing concerning a floral photoperiod response for A. cruentus or A. hypochondriacus. Zabka (1961) found A. caudatus required about 4 weeks to reach

"ripeness to respond" at which time only two inductive short-days (9 hours) were needed for floral initiation. A. caudatus also flowered in long-days (18 hours) after about 60 days but the inflorescences did not develop normally. This did not correspond with our observations in the greenhouse where A. caudatus accessions flowered after 139 short- and long-days (March-August) and in the field where they did not flower at all by 110 long-days (June-September). Photoperiods at this latitude are on 3 June, 15 hours 24 minutes, and on 15 September, 12 hours 6 minutes. One point is clear, A. caudatus accessions have not matured in Montana while numerous accessions of the other two domestic species have.

A. hypochondriacus Nepal and Spike types were the earliest maturing and best adapted types to the short, cool growing season at Bozeman. These accessions are the result of several hundred years of selective adaptation by farmers in the Himalaya Mountains of India and Nepal where growing seasons can also be short and cool. Though yield data was based on few plants, A. cruentus Mexican type seemed the highest seed-yielding type at Huntley where the freeze-free season was warm. Breeding for early maturity and high yields in Montana is conceivable using these populations.

APPENDIX B

SEED SCARIFICATION EFFECT ON AMARANTH SEED GERMINATION AND SEEDLING EMERGENCE

Seed scarification improved amaranth seed germination at cool temperatures but reduced seed and seedling vigor. An eight-day seed germination test (1000 seeds per treatment) showed seed scarification can increase amaranth germination at alternating 7 and 17 C (12:12 hours) (Table 13).

Table 13. Number of germinated white and black amaranth seed (H83-382W and H83-382B, respectively) unscarified and scarified for 5, 10, 15, and 60 seconds.

		Scarified							
Unscarified		5 sec.		10 sec.		15 sec.		60 sec.	
White	Black	White	Black	White	Black	White	Black	White	Black
1	0	63	5	60	8	5	2	1	0

The 1984 amaranth field trials used scarified seed. Seedling emergence was almost nonexistent (see Appendix A) due to loss of seed vigor from seed scarification, except for the final seeding. Good emergence occurred in the final seeding because of warm temperatures and abundant moisture. Seed scarification was confirmed as a cause of poor field emergence when 53% of unscarified seed and 0% scarified seed from the same seedlot of accession 382 emerged from 1.3 cm depth at alternating 7-21 C after 14 days in a growth chamber.