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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A thesis submitted in partial fulfillment
of the requirements for the degree

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Master of Science

in

Agronomy

MONTANA STATE UNIVERSITY
Bozeman, Montana

November 1985

APPROVAL

of a thesis submitted by

David Morton Webb

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ACKNOWLEDGMENTS

I sincerely thank my co-advisers, Drs. J. R. Schaeffer and C. W. Smith, and committee members, Drs. L. E. Wiesner, G. A. Taylor, and C. F. McGuire for their guidance throughout this three year effort. I am also grateful to many other faculty members for sharing their expertise with me and to Dr. D. G. Miller, department head, for his continuous support and funding. Thanks also to my fellow graduate students for sharing this arduous experience.

Paramount to my completion of this project has been the love, encouragement, and companionship of my best friend, Laura.

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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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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).

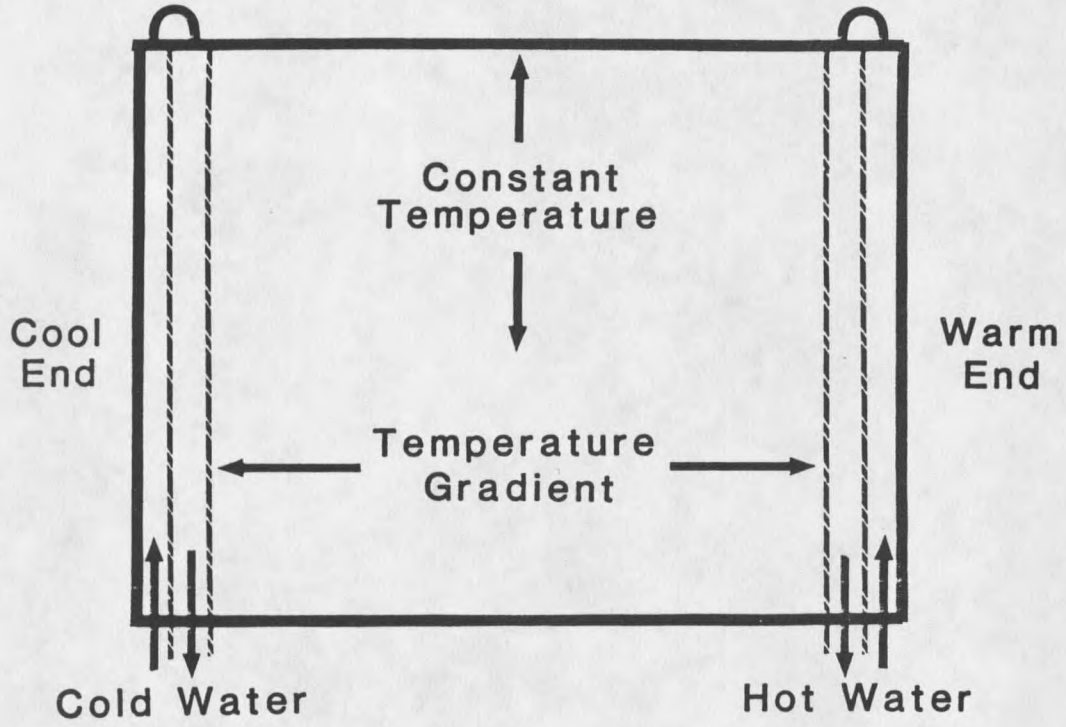

Figure 1. Top view of a thermogradient plate.

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.