Characterization of foxtail (Setaria spp) seed production and giant foxtail (S faberi) seed dormancy at abscission

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Characterization of foxtail (*Setaria* spp.) seed production and giant foxtail (*S. faberi*) seed dormancy at abscission

by

Milton John Haar

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY

Major: Plant Physiology
Major Professor: Jack Dekker

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1998
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This is to certify that the Doctoral dissertation of
Milton John Haar
has met the dissertation requirements of Iowa State University

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For the Graduate College
To Friends
TABLE OF CONTENTS

CHAPTER 1. GENERAL INTRODUCTION 1
   Thesis Organization 1
   Biology of the Weedy Foxtails 1
   Seed Dormancy 18

CHAPTER 2. SEED PRODUCTION IN GIANT (S. FABERI),
GREEN (S. VIRIDIS) AND YELLOW (S. GLAUCALA) FOXTAIL 26
   Abstract 26
   Introduction 27
   Materials and Methods 31
   Results 33
   Discussion 43
   References 47

CHAPTER 3. VARIATION IN GIANT FOXTAIL (S. FABERI)
SEED DORMANCY AT ABSCISSION 51
   Abstract 51
   Introduction 53
   Materials and Methods 57
   Results 61
   Discussion 75
   References 81

CHAPTER 4. MICROGRAPHIC ANALYSIS OF GIANT FOXTAIL
(S. FABERI) SEED, CARYOPSIS AND EMBRYO GERMINATION 86
   Abstract 86
   Introduction 87
   Materials and Methods 90
   Results and Discussion 92
   References 105

CHAPTER 5. GENERAL CONCLUSIONS 108

GENERAL REFERENCES 111
ABSTRACT

The foxtails are cosmopolitan weeds and among the most troublesome in agriculture. High seed production and seed dormancy are important attributes contributing to the success of the foxtails as weeds. The amount and sources of germination variability among giant foxtail seed were evaluated. Seed from a single genetic line of giant foxtail was grown under field, greenhouse and growth chamber conditions. Germination assays were conducted at abscission and following stratification and seed dissection. Most giant foxtail seed were shed dormant. As the seed rain progressed, mean germination percentage and variability in the germination requirements among samples increased. Changes in seed dormancy were associated with biological and environmental parameters. Within an individual panicle, seed that developed later were more likely to germinate than those that developed earlier. Seed from panicles that developed relatively later on a plant were also more likely to germinate than seed from panicles that developed earlier. Seed grown in the field were less dormant than those grown in the greenhouse which were in turn less dormant than those from growth chamber conditions. It is possible that each seed has an individual germination requirement. Seed from giant, green and yellow foxtail panicles were collected throughout the reproductive period. A higher number of seed was found than has been generally reported. Although seed number per panicle, panicle length and seed density (seed number per unit panicle length) varied among foxtail species, panicles and sites, some consistent relationships were found. The relationship between seed number
and panicle length also varied among foxtail species, panicles and sites. The giant foxtail germination process was divided into three axis specific embryo growth states. Photographic evidence of each germination state is shown for both caryopses and seed. The germination state after eight to twelve days under germination conditions is believed to reveal the potential for germination possessed by the seed prior to germination.
CHAPTER 1. GENERAL INTRODUCTION

Dissertation Organization

This dissertation begins with a general introduction followed by three chapters based on independent research papers (to be submitted) and a general discussion. The general introduction includes a review of weedy foxtail (*Setaria spp.*) biology and ecology literature, comments on seed dormancy/germinability and overall experimental approach. Giant, green and yellow foxtail seed production is the subject of the first paper followed by papers on giant foxtail seed dormancy and germination. Individual papers have specific introduction, materials and methods, results, discussion and reference sections. References for the general introduction and discussion are listed following the general discussion.

Biology of the Weedy Foxtails

Taxonomy

The genus *Setaria* belongs to the tribe Paniceae, subfamily Panicoideae and family Poaceae (Pohl, 1978). One-hundred twenty-five species of *Setaria* make up the genus (Prasada-Roa et al., 1987; Rominger, 1962). The forty-three species of *Setaria* found in North America are divided into three subgenera: Ptychophyllum (6 species), Paurochaetium (10) and Setaria (27). Twenty-five of the North American species are indigenous, ten originated in South America, giant (*Setaria faberi* Herrm.) is from China, green (*S. viridis* (L.) Beauv.) and yellow (*S. glauca* (L.) Beauv.) are
from Europe (Rominger, 1962). The tetraploid foxtail species, giant and yellow, are thought to be derived from crosses between green and other unknown diploid foxtail species followed by a doubling of the chromosome number (Khosla and Sharma, 1973; Li et al., 1942 and 1945).

The genus *Setaria* includes crops such as foxtail millet which has been grown for thousands of years and remains an important crop in parts of Africa, China and India (Cheng, 1973; Gao and Chen 1988; Li et al., 1935; Prasada-Rao et al., 1987). Foxtail millet is thought to be a domesticated form of green foxtail (Stapf and Hubbard, 1930; Takahashi and Hoshino, 1934; Wang et al. 1995a; Willweber-Kishimoto, 1962). This genus also contains some of the worst agricultural weeds in the U.S. (Holm et al., 1977; Knake, 1977). For wildlife, however, the weedy foxtails are an important source of food (Martin et al., 1961).

**Distribution**

Members of the genus are found around the world in tropical, subtropical and temperate latitudes. The greatest number of *Setaria* species is found in tropic Africa, which has led to the hypothesis that this location is the center of origin for the genus (Rominger, 1962; Till-Bottraud et al., 1992). Giant foxtail was first described by Hermman in 1910 from a specimen collected in Szechwan, China, by Rev. Ernst Faber (Knake, 1977). Presently, giant foxtail is found in central Europe, Russia, the Middle East, East Asia, the north and central U.S., Canada and Mexico (Hafliger and Scholz, 1980). It is believed that giant foxtail was brought to the U.S. in the early 1930's with millet from China. (Knake, 1977; Musil, 1950). First reported in
Northern Virginia in 1936 (Allard, 1941), giant foxtail spread rapidly. Reports of early occurrence in other locations include: Illinois (Evers, 1949), eastern U.S. (Fernald, 1944), Iowa (Pohl, 1951; Read, 1951; Slife and Scott, 1951) and North Carolina (Wood, 1956). Approximately 30 years after introduction, giant foxtail was regarded as one of the worst weeds of the cornbelt (Morre and Fletchall, 1963). The introduction of 2,4-D, which controlled broadleaf weeds and reduced cultivation, may have contributed to the rapid spread of giant foxtail (Schreiber, 1977).

Green foxtail is one of the most common weeds of temperate regions; listed as a weed of 29 crops in 35 countries (Holm et al., 1977). Originating and widely distributed in Europe (Wilkenson and Jaques, 1979), green foxtail is now found in every state of the U.S., although it is rarer in the southeast (Pohl, 1978). Green foxtail is found in all Canadian provinces (Alex et al., 1972) and is the most abundant weed in Manitoba and Saskatchewan (Thomas and Wise, 1983, 1984). Green foxtail has also spread to Australia, and Argentina, Uruguay and Chile in South America (Holm et al., 1977).

Yellow foxtail is a common weed of cereal and row crops and waste places (Wilkenson and Jaques, 1979). Found throughout the world yellow foxtail is widely distributed in the U.S., Canada, Mexico, Africa, Asia, Australia, Europe and in South America, Argentina and Uruguay (Hafliger and Scholz, 1980; Holm et al., 1977).

Biotypes

Genetic diversity of the weedy foxtails is low in comparison with many other plant species (Wang et al., 1995a and 1995b). Giant foxtail genetic diversity was
especially low, nearly monomorphic (Wang et al., 1995b). Isozyme evidence of north and south biotypes among North American green foxtail has been found (Wang et al., 1995a). Variation in a number of plant characteristics such as height, leaf width, lodging, tiller number, rate of development, germination requirements and herbicide susceptibility have also been used as evidence for foxtail varieties or biotypes (Peters et al., 1963; Norris and Schoner, 1980; Santelmann and Meade, 1961; Schoner et al., 1978; Schreiber and Oliver, 1971). The foxtails to vary widely in plant size depending on the environment. Biotypes are one explanation for the variation in morphology and behavior observed within a species; phenotypic plasticity is another (Scheiner, 1993). Chapters two and three of this dissertation indicate that seed production and seed dormancy are both plastic characteristics in foxtail.

**Adaptation**

High seed production and seed dormancy are important attributes contributing to the success of the foxtails as weeds (Baker, 1974). The foxtails, like many weeds are adapted to colonizing recently disturbed sites, and producing many seeds enhances the likelihood of finding new sites (Cavers, 1987). By quickly reproducing, the foxtails are able to exploit the resources at a site (Baker, 1974). The foxtails are primarily self-fertilizing species; outcrossing rates ranged between 0 and 2.2% (Kawano and Miyake, 1983; Till-Bottraud et al., 1992); therefore a single individual is enough to establish the weed at a site. Another important weedy adaptation is seed dormancy. Dormancy distributes germination over time and allows periods of unfavorable growth conditions or control efforts to be avoided.
(Simpson, 1991). The formation of a seed bank from which weed communities regenerate and persist is made possible by dormant seed (Coleman et al., 1994; Grime, 1981; Silvertown, 1984).

Agriculture

Giant foxtail has been referred to as the most serious annual grass weed in the Midwest (Knake, 1977); a weed in corn (Nieto-Hatem and Staniforth, 1961), soybeans (Staniforth and Weber, 1956) sorghum (Feltner et al., 1969) and first-year alfalfa (Norris and Schoner, 1975). Green and yellow foxtails are weeds in many cereal, row and vegetable crops including wheat, oats, flax, barely, corn, rice, cotton, tomatoes and potatoes among others (Douglas et al., 1985; Holm et al., 1979).

Strategies for controlling foxtail populations rely predominately on herbicides and cultivation (Iowa State University, 1998). Resistance to the herbicide atrazine has been found in giant, green and yellow foxtails in the U. S., Canada and Western Europe (Heap, 1998). Giant foxtails resistant to fluazifop and dicofop, aryloxyphenoxy carboxylic acids, the sulfonylurea herbicide, nicosulfuron and trifluralin, a dinitroanaline, have also been found (Heap, 1998). Populations of yellow foxtail have shown resistance to imazapyr (imidazolinone).

Agronomic practices influence foxtail populations (Dawson and Burns, 1962; Dyer, 1995). Crop rotation can help control foxtails (Dyer, 1995). More giant foxtail seed was found in the soil from fields in continuous corn compared to corn-soybean or corn-soybean-wheat rotations (Schreiber, 1992). Tillage affects the number and distribution of foxtail seed in soil. No-till systems left more giant foxtail seed near
the surface compared to moldboard and chisel plowing (Schreiber, 1992), and no-till fields had more than eight times as many giant foxtail seedlings as did a conventional tilled plot (Buhler and Daniel, 1988).

Morphology

Mature plant

Giant, green and yellow foxtails are annual plants with simple erect to spreading culms with branches forming at the nodes (Holm et al., 1977). Plant size may vary widely depending on conditions (Whitson, 1991). Roots are fibrous and leaves flat and lanceolate (Holm et al., 1977). The genus *Setaria* is usually distinguished from the closely related genus, *Panicum*, by bristles below the spikelet (Pohl, 1978). Giant foxtail is distinguished from green foxtail by larger plant and panicle size, greater leaf width, nodding panicles and pubescence on upper leaf surface (Wilkenson and Jaques, 1979). Yellow foxtail is distinguished from giant foxtail and green foxtail by the presence of long hairs at the leaf base of an otherwise smooth leaf surface (Whitson, 1991). Yellow foxtail panicles also have less fascicle branching than giant or green foxtail and a yellowish tint to the bristles (King, 1952; Pohl, 1978).

Inflorescence

Foxtail inflorescences are dense panicles (Clark and Pohl, 1996). The terminal inflorescence of the main culm is referred to as the primary panicle; secondary tillers form from adventitious buds at nodes of the primary tiller, and tertiary tillers branch at the nodes of secondary tillers (Chapter 2, Figure 1, page 31). Panicles are
made up of fascicles that consist of spikelets and associated bristles (Rominger, 1962; Clark and Pohl, 1996). A bristle shoot, not individual bristles, represents a modified spikelet (Narayanaswami, 1956). Yellow foxtail fascicles have a single spikelet while fascicles of green and giant foxtails may have several (Clark and Pohl, 1996). The number of fascicles within a giant foxtail panicle is highest near the top and declines toward the base (Dekker et al., 1996). Flowering begins at the distal 30 to 40 percent of panicle length and advances both distally and proximally (Dekker et al., 1996).

**Spikelets**

Each spikelet contains two florets, the lower sterile and the upper fertile, subtended by two glumes (Li et al., 1935). The lemma and palea are borne immediately on the glumes (Willweber-Kishimoto, 1962). Both glumes and sterile lemma are thin and papery. The first glume covers the sterile lemma and about one third of the palea. The second glume covers the fertile lemma and is approximately two thirds the lemma's length. The sterile lemma covers and is as long as the fertile palea (Rost, 1975). The fertile lemma and palea, commonly referred to as the "hull", are hardened and the margins of the lemma curve around and surround the edges of the palea forming a tight seal which encloses and protects the caryopsis (Rominger, 1962; Morre and Fletchall, 1963). Near the base of the lemma a flap or doorlike structure known as the germination lid is found. The coleorhiza lifts this structure and extends from the seed during germination (Rost, 1975). Disarticulation occurs below the glumes and the dispersal unit, hereafter referred to as the "seed", although the term, spikelet, is more accurate (Hubbard, 1915; Morre
and Fletchall, 1963). The foxtails are prolific as the second chapter of this dissertation will show.

**Caryopsis**

Interior to the lemma and palea is the ripened ovary, which in grasses is a caryopsis (Clark and Pohl, 1996). The caryopsis consists of an embryo and endosperm surrounded by the caryopsis coat (Rost, 1973). The foxtail caryopsis has been described as elliptical in shape and dorsally compressed (Rominger, 1962). The endosperm consists mostly of stored starch and oils (Rost 1971; Rost and Lersten 1973). A single outer layer of endosperm cells is known as the aleurone layer and functions in reserve mobilization (Lehle et al., 1983; Rost, 1975).

The caryopsis coat surrounds the aleurone and forms the caryopsis exterior. The outer layer of the caryopsis coat is a think cuticle (Rost, 1973). Other layers of the caryopsis coat are derived from pericarp, integuments, nucellus and ovary tissues (Rost, 1973), as the seed develops these layers are crushed and lose their cellular structure. The integuments are reduced to a thin dark band, dark because of silica content. This dark layer is suspected of having a role in seed dormancy (Rost, 1973; Narayanaswami, 1956). A reddish to brown oval region of the caryopsis coat, the placental pad, marks the location of the connection to the placental vascular bundle (Rost, 1975).

**Embryo**

The foxtail embryo is of the panicoid type (Rost, 1971). A coleoptile surrounds the embryonic leaves, and a coleorhiza covers the radicle. The scutellum lies beneath the embryo axis, between the embryo and the endosperm. The
scutellum secretes hormones and enzymes that aid mobilization of stored reserves (Bewley and Black, 1994).

**Plant Growth**

**Emergence date**

Foxtail emergence has been reported in reference to first Spring observation, peak time of emergence and duration. Emergence dates varied by location. Peak emergence for giant, green and yellow foxtail at Columbia, Missouri, was March 23rd, 1955 (Morre and Fletchall, 1963). Foxtail emerged between April 25th and May 20th over six years at Ames, Iowa (Martin, 1943). Waldron (1904) reported May 1st as the emergence date in North Dakota for green foxtail. Green foxtail first emerged between the 21st of May and 2nd of June over 5 years at Regina, Saskatchewan, and some were found to emerge as late as October (Banting et al., 1973). Later germination dates decreased the amount of tillering (Peters and Yokum, 1961; Peters et. al., 1963; Santelmann et al., 1963; Schreiber, 1965).

**Effects of light**

Daylength is an important factor in the timing of foxtail panicle formation. Short-day treatment stimulates panicle formation in yellow and giant foxtail (King, 1952; Peters and Yokum, 1961; Schreiber and Oliver, 1971). Continuous light or long day treatments reduced the number of yellow foxtail tillers, leaves and panicles (Peters et al., 1963; Santelmann et al., 1963) and inhibited flowering in giant foxtail (Schreiber and Oliver, 1971). Shade decreased plant growth, height and number of
tillers per plant for both giant and yellow foxtail (Bubar and Morrison, 1984; Knake, 1972; Lee and Cavers, 1981; Peters, et al., 1963; Santelmann et al., 1963; Van den Born, 1971).

Seed Germinability at Abscission

Freshly harvested foxtail seed has been found to be completely dormant (Dekker et al., 1996; Kollman, 1970; Nieto-Hatem, 1963; Peters and Yokum, 1961; Povilaitis, 1956; Rost, 1975; Sells, 1965) or near completely dormant (Chavarria, 1986; Stanway, 1971; Taylorson, 1986; Van den Born, 1971). Many factors have been shown to affect germination.

Germination

Emergence of the coleorhiza through the germination lid is usually the first evidence of seed germination. Soon after emergence, the coleorhiza becomes covered with trichomes (Rost, 1975; Rost and Lerston, 1973). Coleorhizal trichomes are thought to function in water absorption and or seedling anchoring (Northam et al., 1996). The next observable event in the germination process is often emergence of the radicle from the coleorhiza (Rost, 1975). At this time, or soon after, the coleoptile emerges by forcing apart the lemma and palea (Rost, 1971). Following a period of coleoptile elongation the first true leaf, cotyledon, emerges.
Germination conditions

The percentage and rate of foxtail seed germination is dependent on temperature. The optimum temperature range for green foxtail germination has been reported to be between 20 and 30°C (Blackshaw et al., 1981; Norris and Schoner, 1980) and for giant foxtail between 15 and 30°C (Morre and Fletchall, 1963). Green foxtail germination was higher than that of yellow foxtail at warmer temperatures (Manthey and Nalewaja, 1987).

Giant foxtail seed did not germinate in soil at 5°C (Mester and Buhler, 1991). At 10°C seed of giant, green and yellow foxtails failed to germinate (Banting et al., 1973; Norris and Schoner, 1980) or a reduction in emergence was observed (Mester and Buhler, 1991). Cooler temperatures, such as 15°C, slowed germination of green and yellow foxtail seed (Blackshaw et al., 1981; Manthey and Nalewaja, 1987).

Temperatures above the optimum range also reduced germination. Yellow foxtail seed did not germinate at or above 40°C and germination was reduced at 30°C (Norris and Schoner, 1980). The effect of temperature on yellow foxtail varied by biotype; a California biotype had greater germination at 35°C in comparison with biotypes from Eastern and Midwestern U. S. (Norris and Schoner, 1980).

Effects of moisture and temperature

Green foxtail flowered sooner, produced more seed and had greater leaf area and dry matter under a warmer regimes (Wall, 1993). Seed production per plant and dry weight were greater under higher moisture conditions (2.5 cm water per week compared to 0.3 and 0.6 cm per week) for both green foxtail and yellow foxtail (Nadeau and Morrison, 1986).
Germination Dormancy-Breaking Treatments

Foxtail seeds that do not germinate even under favorable conditions are considered dormant. Many treatments have been used to stimulate germination.

**Stratification**

Stratification, usually a cool, moist treatment, has been shown to be an effective method for releasing dormancy. Temperatures from 5 to 10°C for 2 to 12 weeks stimulate germination of foxtail seed (King, 1952; Kollman, 1970; Nieto-Hatem, 1963; Peters and Yokum, 1961; Stanway, 1971; Van den Born, 1971).

**Warm temperatures**

Exposure to hot water treatments, 24 hours at 54, 68, 78 or 92°C, inhibited yellow foxtail germination (Peters and Yokum, 1961). Treatment of dry seeds at 50°C for short periods of time, 3, 7 or 14 days, a process called accelerated afterripening, increased germination (Taylorson and Brown, 1977).

**Alternating temperatures**

Beneficial effects of alternating temperatures on germination have been reported in some studies (Fausey and Renner, 1997; King, 1952) but not all (Cross, 1931). Alternating wet freezing and thawing did not affect germination (Morre and Fletchall, 1963).

**Afterripening**

Foxtail seed eventually lose dormancy under dry conditions at room temperature. The time period is generally much greater than that required for stratification treatments. Dry storage for 17 weeks resulted in approximately 50
percent germination for 1 year's seed, but for a second year's harvest, no germination resulted after 14 months of dry storage (Povilaitis, 1956).

Light

Most evidence indicates that foxtail germination is light insensitive (Taylorson, 1982; Taylorson, 1986; Morre and Fletchall, 1963), although there are reports of light stimulation of germination of seeds of yellow foxtail (Povilaitis, 1956) and another foxtail species, *Setaria chevalieri* (ribbon bristle grass; Erasmus and Van Staden, 1982).

Mechanical damage

Removal of or damage to the foxtail hull has been shown to stimulate germination in several studies. Green foxtail (Martin, 1943), yellow foxtail (Biswas et al., 1970; Nieto-Hatem, 1963; Rost, 1975) and giant foxtail (Dekker et al., 1998) percentage seed germination increased, and the range of temperatures in which seed could germinate, expanded when hulls were removed (Povilaitis, 1956). Piercing the hull increased percentage germination of giant foxtail seed (Morre and Fletchall, 1963; Stanway, 1971). Location of puncture had an effect on germination; a pierce in the apical (distal to embryo) region resulted in the greatest increase (Morre and Fletchall, 1963).

Scarification with sandpaper or fuming sulfuric acid increased foxtail germination (King, 1952; Kollman and Staniforth, 1972; Peters et al., 1963). Morre and Fletchall (1963) found sulfuric acid treatment or abrasion with sandpaper ineffective for releasing seed dormancy; unfortunately, details for these treatments are not given; perhaps they were insufficient to weaken the hull, as most evidence
indicates the contrary result. Nieto-Hatem (1963) describes two levels of dormancy based on the germination response to hull removal: 1) hull imposed dormancy; for this type of dormancy, removal of the hull permits embryo germination. Embryos which did not germinate following hull removal were described as 2) caryopsis dormant. For seeds with this dormancy, stratification or another treatment was necessary to achieve germination.

Not only the hull, but other seed tissues may influence embryo germination; non-embryo caryopsis tissues have been shown to affect germination. Evidence implicating caryopsis coat or endosperm involvement in the germination process is found in studies of isolated embryo germination. Excised embryos from dormant and non-dormant caryopses germinated equally well, implying that the endosperm or caryopsis coat was responsible for the lack of germination in dormant seed (Rost, 1975). The case for a caryopsis coat influence is strong; simply removing the caryopsis coat adjacent to the embryo increased germination (Rost, 1975). Embryo dormancy also exists as chapter three shows with a large number of isolated embryos that did not germinate. There may also be different levels of dormancy among the tissues of an embryo. Foxtail germination has been observed in an axis-specific manner (Dekker et al., 1996).

Moisture

No difference in the amount or rate of imbibition of water was found between dormant and nondormant yellow foxtail seeds, implying that a simple moisture barrier is not responsible for foxtail seed dormancy (Nieto-Hatem, 1963). Temporary water stress treatments have been shown to stimulate giant foxtail and
green foxtail seed germination (Blackshaw et al., 1981; Manthey and Nalewaja, 1987), while continuous exposure to water stress has inhibited germination (Taylorson, 1986).

Inhibitors

The case for an endogenous inhibitor of foxtail germination is inconclusive. Leaching in cold water increased yellow foxtail seed germination; however, leachate did not prevent germination of non-dormant seed (Nieto-Hatem, 1963).

Plant hormones

Abscisic acid (1 x 10^{-5} to 10^{-4} M) inhibited germination of germinable yellow foxtail seeds and caryopses, while gibberellic acid (1 x 10^{-5} and 10^{-7} M) promoted caryopsis germination (Kollman and Staniforth, 1972). Van den Born (1971) however, found no effect of gibberellic acid (concentration not given) on green foxtail germination. Cytokinins were found to reverse abscisic acid inhibition (Kollman and Staniforth, 1972). Auxins did not increase germination of yellow foxtail seed (Peters and Yokum, 1961).

Allelopathy

Extracts of yellow foxtail and giant foxtail seeds inhibited growth of alfalfa (Peters et al., 1963) and wheat seedlings (Morre and Fletchall, 1963). Petroleum ether and ethanol extracts of giant foxtail did not have an effect on wheat seedling growth (Morre and Fletchall, 1963).

Inorganic chemicals

The effect of several inorganic chemicals on foxtail germination has been tested. Potassium nitrate (0.5, 1.0 and 2.0% volume:volume) ammonium nitrate (1
and 2%) with scarification (Peters and Yokum, 1961) and sodium thiocyanate without scarification greatly increased germination (King, 1952). Yellow foxtail seeds with and without a chilling treatment did not respond to 25 to 175 ppm nitrate or ammonium (Schimpf and Palmblad, 1980). Hydrogen peroxide treatments (3.0, 0.3 and 0.03% for 24 hours) did not affect germination of yellow foxtail (Peters and Yokum, 1961).

**Longevity**

A gradual decrease in green foxtail germination was found after the first 2 to 3 years of burial and was very low after 10 years. Less than 1% of giant foxtail seed survived more than 6 years of burial and none survived for 17 years (Burnside et al., 1981; Dawson and Burns, 1975; Thomas et al., 1986). In another study, green foxtail seed was capable of germination after 39 years buried in soil (Toole and Brown, 1946). Yellow foxtail seed has been observed to survive 13 (Dawson and Burns, 1975) and 30 years buried in the soil (Toole and Brown, 1946).

**Soil depth**

In general, foxtail germination decreased with soil depth (Mester and Buhler, 1991; Morre and Fletchall, 1963). Giant foxtail percentage seed emergence was greater near the surface, one to 2.5 cm (Dawson and Bruns, 1962; Fausey and Renner, 1997). Green foxtail seedlings readily emerged from 0.5 to 8 cm deep in soil (Van den Born, 1971); a maximum depth for emergence of 12 cm has been reported for giant foxtail in well aerated soil (King, 1952).
Time of seed maturity

Morre and Fletchall (1963) found that later-maturing giant foxtail seed was more germinable than earlier-maturing seed. Chapter three of this dissertation will investigate this thoroughly and correlate changes in germination with biological and environmental parameters. Seed that matures on later panicles and later within a panicle was less dormant.

Conclusion

The variety of treatments used to stimulate germination and differences in seed collection methods and storage make drawing conclusions regarding the mechanism of foxtail seed dormancy difficult. More than one seed dormancy mechanism is likely. A strong case is made for hull involvement in foxtail dormancy. The hull may be a barrier to oxygen or a physical restraint; it is less likely an obstacle to water absorption or the source of an inhibitor. An endogenous embryo dormancy is also evident and, again, the mechanism is not known. A metabolic block or a change in membrane properties are possibilities. Theories for the mechanism of hull or caryopsis coat imposed dormancy have focused on impermeability to gases and water or the presence of an inhibitor. There is some evidence of a role for oxygen. Inhibition of giant foxtail germination in soil aggregates was overcome by an enriched oxygen atmosphere (Pareja and Staniforth, 1985).
Seed Dormancy

There are several recent and excellent reviews on seed dormancy (Bewley and Black, 1994; Bradbeer, 1988; Dennis, 1994; Egley and Duke, 1985; Khan, 1982; Lang, 1987; Simpson, 1991; Taylorson and Hendrick, 1977; Tran and Cavanaugh, 1984), so no attempt to review the subject in general will be made in this dissertation. Background information believed to be helpful in understanding this dissertation, but thought to be inappropriate detail for the introduction of a specific papers has been included.

Terminology

Many definitions of dormancy can be found. Lang et al. (1987) identified 54 terms used to describe the phenomenon. No doubt, the number of terms reflect the lack of understanding and diversity of theories for the dormancy mechanism. A common element among the terms is a reference to an absence of plant growth; in the case of seed, as opposed to bud dormancy, the growth of interest is germination. Seed dormancy has been defined simply as a suspension of growth for example, “suspension of meristem growth” (Simpson, 1991), “the temporary suspension of visible growth of a meristem” (Lang, 1987) or “a condition in which germination is temporarily delayed by some internal control mechanism” (Amen, 1968). Roberts (1972) pointed out that the term dormancy is used in two senses: 1) in reference to seed that will not germinate under unfavorable conditions, e.g. dry storage and 2) a description of the lack of germination under conditions normally favorable for germination. A reference to the conditional as well as the temporary nature of the
lack of germination are both important aspects of a dormancy definition. Seed that
does not germinate under one set of conditions may do so in another or may
germinate under the same conditions after a period of time or a treatment. Dyer
(1995), Roberts, (1972) and Taylorson (1987) define dormancy in terms of both the
suspension of growth and "normal" germination, "a lack or prevention of
germination even under conditions normally favorable for germination." Under
unfavorable conditions, dormant and nondormant seed are indistinguishable. It is
only under conditions that normally permit germination that the term dormancy
becomes relevant. The lack of germination under normally favorable conditions is
the phenomenon of interest here and different from the prevention of germination
by unfavorable conditions. When describing results of germination-dormancy tests,
it is critical to describe the conditions under which tests were conducted.

Seed dormancy can not be measured directly because the mechanism is
unknown, but is inferred from germination tests. The results of germination studies
may be more literally described in terms of a seed's (embryo's) capacity to germinate
(germinability) defined by Dekker et al. (1996) as "[the degree or level of] the
capacity of an embryo to germinate under some set of conditions." Vegis (1964) also
describes dormancy/germinability in degrees or levels by referring to "the range of
conditions within which an embryo will germinate." This definition is based on the
range of conditions instead of a range of embryo germination capacity. In both cases
a completely dormant (low germinability) seed will not germinate under any
conditions and a highly germinable (low dormancy) seed will germinate under a
wide range of conditions. Both concepts provide a spectrum or range to the concept
of dormancy/germinability, something missing from earlier concepts that perceived dormancy as a simple "on or off" switch.

Another interesting perspective regarding the nature of dormancy is found in Vleeshowers et al. (1995); here seed dormancy is defined as "a characteristic, the degree of which defines what conditions should be met to make the seed germinate." Seed dormancy, as described by Vleeshowers et al. (1995) appears less a definition of dormancy than it is method for measuring dormancy/germinability and assigning units to the different levels, degrees or states. For example, a seed that germinates following 2 weeks of stratification is less dormant or more germinable than one that requires 4 weeks of the same treatment.

Types of Seed Dormancy

Dormancy has been classified on the basis of timing and source. Harper (1977) recognized three types of dormancy: innate, enforced and induced, based on time in the plant life cycle. Innate dormancy is that possessed by the seed when it leaves the parent plant, and enforced dormancy is the lack of germination under unfavorable conditions. After innate dormancy has passed, conditions may be unfavorable for germination, and the seed may become dormancy again. This type of dormancy is thought to be brought on by environmental conditions and so is called induced. Karssen et al. (1989) also classified dormancy based on time. Primary dormancy corresponds to Harper's (1977) innate, and secondary dormancy is analogous to induced, while the enforced dormancy category is excluded. Lang (1987) and Lang et al. (1987) proposed three terms to describe dormancy based on
source of control. Control within the seed structure (endodormancy), control within
the plant, but outside the seed (paradormancy) and control by the environment
(ecodormancy). The concepts of ecdormancy and enforced dormancy are similar
and refer to seeds that do not germinate under unfavorable conditions. Dormancy
classified on source of control is a good idea, but only in rare cases is this known.
Dormancy based on time is, at present, more useful.

Secondary dormancy

Both dry and hydrated giant foxtail seeds have been induced into secondary
(induced) dormancy by treatments of 35°C and darkness for more than 24 hours
(Taylorson, 1987). Anesthetics (ethanol and methanol) prevented the induction of
secondary dormancy (Taylorson, 1982). Forcella et al. (1997) report that when soil
temperature, 5 to 10 cm below the surface, reaches 16°C and above; conditions are
right for secondary dormancy induction for giant foxtail seeds.

Variation in Seed Dormancy

Germination for an individual seed is an all or nothing event, but among a
population of seed there is variation (Taylorson, 1987). Variation in germination
was noted as far back as Theophrastus (371-287 B.C.) who wrote, “about beet; the
seed does not germinate at once, but some even in the next or third year” (Evanari,
80/81). A treatment applied to a population of seeds rarely results in complete
germination; sequentially applied treatments are necessary for maximum
germination (Silvertown, 1984). Dormancy is a quantitative characteristic or
behavior. A spectrum of levels for dormancy exists, not a single level or state
(Dennis, 1994). Each seed or embryo may have its own intensity of dormancy (Come, 1980/81). Once established, seed dormancy is not static; but continues to change under the influence of the environment (Treweyas, 1987).

**Phenotype Plasticity**

The variation in phenotypic expression of a genotype that occurs in response to environment is referred to as phenotype plasticity (Sultan, 1987; Scheiner, 1993). Although phenotype plasticity is usually associated with physical characteristics such as color or size (Silvertown, 1984); in the case of dormancy, a behavior, there are also changes in response to the environment. Some species rely on genetic diversity, while others depend on phenotypic plasticity for adapting to varying environments (Simpson, 1991). For primarily self pollinating species such as the foxtails, a highly flexible phenotype plasticity is selectively maintained (Jain, 1982; Sultan, 1987; Simpson, 1991). Phenotype plasticity may be a product of numerous environmentally responsive traits (Via, 1993), or there may be regulatory genes that coordinate responses that can be considered plasticity genes (Schlichting and Piglencci, 1993).

**Ecological Advantage/Evolutionary Significance**

Seed dormancy is a valuable characteristic for a weed. The forty most widespread serious weeds in the world all have seed dormancy (Simpson, 1991). Baker (1974) in his review article on the evolution of weeds, lists as the first two of ten ideal weed characteristics: 1) germination requirements fulfilled in many
environments and 2) discontinuous germination and great longevity of seed; both traits rely on seed dormancy. Dormancy prevents premature germination (vivipary), allows time for dispersal, and extends germination over time. Staggered weed emergence allows control measures and unfavorable growth conditions to be avoided, or, as Vleeshouwers et al. (1995) point out, the brief periods of favorable growth followed by unfavorable conditions that are to be avoided. Seed dormancy, especially variable seed dormancy, is a strategy for heterogeneous environments (Jain, 1982). The germination requirements of some seeds will be met under a wide range of environments (Simpson, 1991). The addition of dormant seed to the soil forms a seedbank that is the source of regeneration for weed communities and serves as a "genetic memory" for a plant community (Cavers, 1987). Natural selection favors individuals possessing dormancy in heterogeneous environments (Jain, 1982; Silvertown, 1984). Diversity offers a means of survival in stressful, variable environments (Sultan, 1987), and, generally, colonizers of disturbed habitats such as weeds encounter more environmental heterogeneity than many other plant species (Levins, 1963).

**Importance of Information**

If a goal of weed science is less reliance on the conventional weed control methods of cultivation and herbicides for weed management, then a better understanding of basic weed biology, particularly the important characteristics of seed dormancy and production, is needed. Seed production and dormancy affect the composition and density of weed communities and therefore have implications
for control methods (Blackshaw et al., 1981; Dyer, 1995). Economic models are currently being developed to assist weed management. These models attempt to predict crop yield loss based on weed competition, then recommend management strategies. Information on seed production and dormancy would be useful for these models, especially models which consider the impact of weed populations for more than the present season (Bauer and Mortensen, 1992; Swinton and King, 1994; Wiles et al., 1996).

**Experimental Approach**

Seed dormancy, like many other biological phenomena, is complex. Simpson (1991) proposed a systems approach to studying and understanding seed dormancy. This system is organized as a hierarchy of influential factors. He writes, "the behavior at one level is explained in terms of the levels below and the significance of a level is found in the level above." The factors examined in this work include: 1) genotype, 2) environment and 3) the processes associated with plant development. These factors are interactive and difficult to separate. In the seed dormancy study, chapter 3, we attempt to control some factors, genotype and environment, to evaluate the influence of plant development, or compare seed from the same levels of plant maturity and evaluate the influence of environment. By studying the influence of a factor or factors, the behavior of seed dormancy can be understood. The significance of seed dormancy can be found at higher levels of organization such as seed emergence or seedbank dynamics. The changes in mean dormancy or the variation in dormancy among seed there are two basic approaches:
1) to subject seed from the same sample to different treatments and evaluate the responses or 2) subjecting different samples to the same treatment then evaluating the differences in response. The later approach was followed in these studies. Seeds were grouped in reference to time of harvest and plant growth so that inferences about the influence of the environment and development could be made.

Care was taken in these studies to described the foxtail genetics, seed development condition, collection methods and storage condition. Seed was collected and analyzed with reference to plant and panicle development. It is hoped that these techniques will make the germination data more interpretable and comparable than has often been the case with weed seed germination studies.
CHAPTER 2. SEED PRODUCTION IN GIANT (S. FABERI), GREEN (S. VIRIDIS) AND YELLOW (S. GLAUCa) FOXTAIL

A paper for submission to the journal Weed Science

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Abstract

Seed from giant, green and yellow foxtail panicles was collected throughout the reproductive period to obtain an accurate measure of seed production. A higher number of seed was found than has been generally reported for the foxtails. Seed number per panicle, panicle length and seed number per unit panicle length (seed density) varied among foxtail species, panicle types and sites. Some consistent observations were made. Giant foxtail had longer panicles than did green foxtail. Green foxtail panicles had a greater number of seed and higher seed density than did yellow foxtail. Earlier developing panicle types were always greater than or similar to the later developing panicle type for each of the parameters measured. Differences in seed production were found among sites. A linear model best described the relationship between panicle length and seed number or seed density. This relationship varied among foxtail species, panicle types and sites. The degree
of variation observed may indicate the range and limit for the plasticity of these reproductive characteristics.

**Nomenclature:** Giant foxtail, *Setaria faberi* Herrm. SETFA; green foxtail, *Setaria viridis* (L.) Beauv. SETVI; yellow foxtail, *Setaria glauca* (L.) Beauv. SETLU.

**Key words:** fecundity, tillering, SETFA, SETLU, SETVI.

**Introduction**

The success of the foxtails (*Setaria spp.*) as weeds is due, in part to an ability to produce seed under a wide range of environments and to high reproductive output under favorable conditions. Annual weeds such as the foxtails rely on seed for dispersal, and a large number of seed increases the likelihood of finding new sites (Cavers, 1983). The production of many dormant seed helps disperse germination over time (Grime, 1981). A large seedbank allows the foxtails to persist at a site. The seedbank serves as a "genetic memory" and source of regeneration (Cavers, 1983).

For self-pollinating species such as the foxtails, introduction of a single seed is sufficient to exploit the available resources (Baker, 1974; Mulligan and Findlay, 1970). An accurate measure of seed production will improve the understanding of foxtail population dynamics and assist in the development of more efficient weed management systems.

The values reported for seed production may not be reliable in non-identical situations. Genetic diversity and environment affect seed production. The weedy
foxtail species contain a low degree of genetic variation, but there is evidence for biotypes of green and yellow foxtail which may have different seed production characteristics (Hubbard, 1915; Norris and Schoner, 1980; Santelmann and Mead, 1961; Schoner et al., 1978; Schreiber and Oliver, 1971; Wang et al., 1995a; Wang et al., 1995b).

The environment affects plant growth and seed production (Lee and Cavers, 1981; Nadeau and Morrison, 1986; Santelmann and Meade, 1961; Santelmann et al., 1963; Schreiber, 1965; Van den Born, 1971). The three weedy foxtail species included in this study frequently exist together; the relative presence and proportion of the individual foxtail species varies by site (Wang et al., 1995a; Wang et al., 1995b). Although foxtail panicles and seeds develop over a period of time, it is common to find reports of seed production based on a single or periodic harvests (Biniak and Aldrich, 1986; Defelice et al., 1989; Fausey et al., 1997; Kawano and Miyake, 1983; Knake, 1972; Nadeau and Morrison, 1986; Santelmann and Meade, 1961; Schreiber, 1965; Wall, 1993). Values determined by such methods represent only a fraction of total seed production. There is also little consistency in the degree of maturity of plants from which seed is harvested or the units of measure for foxtail seed production. Seed production has been reported on per panicle (Biniak and Aldrich, 1986; Santelmann et al., 1963), per panicle length (Fausey et al., 1997), per plant (Kawano and Miyake, 1983; Nadeau and Morrison, 1986; Schreiber, 1965; Wall, 1993) or per area basis (Defelice et al., 1989).

The relationship between seed number and panicle length has been described for a species as stable across environments (Barbour and Forcella, 1996) and has
been used to estimate foxtail seed production (Defelice et al., 1989; Fausey et al., 1997). We have made this relationship between seed number and panicle length the subject of further investigation, in particular its strength and consistency among foxtail species, panicle types and environments.

Foxtail panicles can be categorized developmentally by branching pattern. Designation of panicle types follows that described by Norris (1992) for barnyardgrass. Panicles that develop at the end of the main shoot are referred to as primary panicles (Figure 1). Secondary panicles arise at the nodes of the primary tiller, and tertiary panicles are those that branch laterally from secondary tillers. Developmentally, primary panicles are the first to flower on a plant followed by secondary then tertiary.

Within Setaria spp., panicles are composed of fascicles, which consist of spikelets and associated setae. The number of fascicles within each giant or green foxtail panicle is variable (Clark and Pohl, 1996). Longer, earlier developing giant or green foxtail panicles may have the most extensive fascicle branching and more spikelets per fascicle. Environment may affect the number of spikelets that fully mature and alter the seed number per panicle length (seed density). Under favorable conditions, more spikelets may develop into seeds, while under unfavorable conditions, some spikelets may be aborted. Yellow foxtail panicle morphology is different from that of giant or green foxtail. Only a single spikelet is found in each yellow foxtail fascicle (Clark and Pohl, 1996). The degree of change in seed number is more limited for yellow foxtail by the constant number of spikelets per fascicle.
Figure 1. Giant foxtail branching pattern.
The first objective of this study was to provide an accurate measure of foxtail seed production by collecting the entire seed output of individual panicles throughout the seed rain period. Secondly, seed production and panicle length were compared among the three foxtail species, developmental types of panicles and sites. We hypothesized that although differences in seed production and panicle length may exist among foxtail species, panicle types and sites, the relationship between seed number and panicle length would be stable across environments. Evaluating this hypothesis was the third objective. If the relationship between seed number and panicle length proves to be stable, measurement of panicle length would be a simple and useful tool for estimating seed production in the field.

Methods and Materials

Sites

Giant, green and yellow foxtails were selected at three sites near Ames, Iowa, in 1995. The first site (A) was a soybean field chemically untreated for weed control with all three foxtail species (277 to 2,903 foxtail plants per m²). A corn field having yellow foxtail and a soybean field with giant foxtail were found at the second site (B). No green foxtail was found at site B. Both fields at site B had been cultivated for weed control and had a low number of foxtail. The third site (C) was a corn field, also cultivated for weed control, with a low number of all three foxtail species. The effects of both differences in genotype among the plants of a population at a site
and differences in the conditions (environment, resource availability, weed competitors, cropping system) at each site are included in comparisons among sites.

Seed Collection

At anthesis, panicles were covered with mesh pollination bags\(^1\) that were held in place with wire. Panicle type was determined at this time. Panicles were bagged between July 25 and September 8, 1995. No more than two bags were attached to a plant. Panicles were harvested on October 10 and 12, 1995. A killing frost occurred on September 21 and prevented a few late tertiary yellow foxtail panicles from maturing.

Data Collection

Panicles and seed were removed from bags after harvest, and panicle length was determined by measuring from the panicle tip to the point of attachment for the most basal fascicle. Seed that remained attached to the panicle was removed. Seed was cleaned with an air flow cleaner to remove empty spikelets and debris, weighed, and then counted with an electronic seed counter.

Statistical Analysis

Means were calculated for seed number per panicle, panicle length and seed density (seed number per unit panicle length) for foxtail species, individual panicle

\(^1\) 3 by 10 inch bags, Delnet non-woven fabrics, Applied Extrusion Technologies Inc. Middletown, DE 19899.
types and sites. Paired t-tests ($\alpha=0.05$) were used to separate means and slopes for all parameters among panicle types within a species and site, among sites within a species and panicle type, among species within a site and among sites within a species. Linear models best described (highest $R^2$ value) the relationship between seed number or seed density and panicle length. Analysis was done using the linear regression procedure of SAS (1989).

Results

Foxtail Species

giant foxtail

Giant foxtail seed number, length and seed density was usually greater for primary panicles than for tertiary, with a single exception in seed density at a site A (Tables 1, 2, 3; comparison 1). For all parameters, secondary panicles were either similar to or greater than tertiary. When differences occurred among sites for a panicle type, seed number, panicle length and seed density were greater at site B than at the other sites, with the exception of tertiary panicles, which usually did not differ among sites (Tables 1, 2, 3; comparison 2). Averaged over all giant foxtail panicle types, seed number, panicle length and seed density were usually similar at all sites, with a single exception in which seed density was greater at site B than C (Tables 1, 2 and 3; comparison 4).
Table 1. Mean seed number and standard error for foxtail species, panicle types and sites (A, B and C).

<table>
<thead>
<tr>
<th>species</th>
<th>panicle type</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>site and comparison</th>
</tr>
</thead>
<tbody>
<tr>
<td>giant</td>
<td>1°</td>
<td>725 (133) a B 14</td>
<td>2127 (110) a A 22</td>
<td>427 (54) a B 7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2°</td>
<td>578 (58) ab B 22</td>
<td>1063 (123) b A 29</td>
<td>330 (61) a B 9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3°</td>
<td>317 (57) b AB 4</td>
<td>365 (37) c A 31</td>
<td>165 (20) b B 8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>540 (119) a A 3</td>
<td>1185 (512) a A 3</td>
<td>355 (37) ab A 3</td>
<td></td>
</tr>
<tr>
<td>green</td>
<td>1°</td>
<td>725 (105) a A 16</td>
<td></td>
<td>685 (69) a A 13</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2°</td>
<td>592 (71) a A 9</td>
<td></td>
<td>413 (58) b A 11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3°</td>
<td>172 (56) b A 7</td>
<td></td>
<td>144 (24) c A 19</td>
<td></td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>496 (167) a A 3</td>
<td></td>
<td>414 (156) a A 3</td>
<td></td>
</tr>
<tr>
<td>yellow</td>
<td>1°</td>
<td>105 (16) a B 9</td>
<td>213 (17) a A 11</td>
<td>139 (35) a B 5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2°</td>
<td>63 (11) b B 15</td>
<td>167 (12) b A 26</td>
<td>147 (13) a A 3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3°</td>
<td>0</td>
<td>54 (9) c A 20</td>
<td>64 (12) a A 3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>84 (17) b B 2</td>
<td>145 (47) a A 3</td>
<td>117 (26) b AB 3</td>
<td></td>
</tr>
</tbody>
</table>

* comparisons: 1 = mean panicle length among panicle types within a species and site, 2 = mean panicle length among sites within a species and panicle type, 3 = mean panicle length among species within a site, 4 = mean panicle length among sites within a species. Means within a column (1 and 3) and within a row (2 and 4) followed by the same letter are not significantly different (P=0.05) as determined by t-tests.
Table 2. Mean panicle length and standard error for foxtail species, panicle types and sites (A, B and C).

<table>
<thead>
<tr>
<th>species</th>
<th>panicle type</th>
<th>site and comparison</th>
<th>site</th>
<th>site</th>
<th>site</th>
<th>site</th>
<th>site</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>A 1(a) 2 3 4 n</td>
<td>B 1 2 3 4 n</td>
<td>C 1 2 3 4 n</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>giant</td>
<td></td>
<td>cm (s.e.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1°</td>
<td>13.3 (0.5) a B</td>
<td>14</td>
<td>16.3 (0.2) a A</td>
<td>22</td>
<td>12.6 (0.7) a B</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>2°</td>
<td>12.0 (0.6) a A</td>
<td>22</td>
<td>12.0 (0.7) b A</td>
<td>29</td>
<td>11.6 (1.1) a A</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>3°</td>
<td>7.9 (0.7) b A</td>
<td>4</td>
<td>7.3 (0.4) c A</td>
<td>31</td>
<td>7.6 (0.9) b A</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>mean</td>
<td>11.1 (1.6) a A</td>
<td>3</td>
<td>11.9 (2.6) a A</td>
<td>3</td>
<td>10.6 (1.5) a A</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>green</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1°</td>
<td>9.9 (0.5) a A</td>
<td>16</td>
<td>10.0 (0.4) a A</td>
<td>13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2°</td>
<td>9.1 (0.5) a A</td>
<td>9</td>
<td>7.5 (0.6) b A</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3°</td>
<td>4.6 (0.7) b A</td>
<td>7</td>
<td>5.3 (0.4) c A</td>
<td>19</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean</td>
<td>7.9 (1.7) b A</td>
<td>3</td>
<td>7.6 (1.4) b A</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>yellow</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1°</td>
<td>6.4 (0.5) a B</td>
<td>9</td>
<td>10.9 (0.8) a A</td>
<td>11</td>
<td>7.8 (1.0) a AB</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>2°</td>
<td>5.6 (0.3) a B</td>
<td>15</td>
<td>8.9 (0.4) b A</td>
<td>26</td>
<td>7.3 (0.6) ab AB</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>3°</td>
<td>5.6 (0.3) a B</td>
<td>0</td>
<td>5.5 (0.3) c A</td>
<td>20</td>
<td>4.5 (0.5) b A</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>mean</td>
<td>6.0 (0.4) c B</td>
<td>2</td>
<td>8.4 (1.6) a A</td>
<td>3</td>
<td>6.5 (1.0) b B</td>
<td>3</td>
<td></td>
</tr>
</tbody>
</table>

\(a\) comparisons: 1 = mean panicle length among panicle types within a species and site, 2 = mean panicle length among sites within a species and panicle type, 3 = mean panicle length among species within a site, 4 = mean panicle length among sites within a species. Means within a column (1 and 3) and within a row (2 and 4) followed by the same letter are not significantly different (P=0.05) as determined by t-tests.
Table 3. Mean seed number per panicle length (seed density) and standard error for foxtail species, panicle types and site and comparison

<table>
<thead>
<tr>
<th>species</th>
<th>panicle type</th>
<th>site and comparison</th>
<th>seed number per panicle length (s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>A 1(^a) 2 3 4 n</td>
<td>B 1 2 3 4 n C 1 2 3 4 n</td>
</tr>
<tr>
<td>giant</td>
<td>1(^o)</td>
<td>55 (9) a B</td>
<td>14 130 (6) a A 22 33 (3) a B</td>
</tr>
<tr>
<td></td>
<td>2(^o)</td>
<td>48 (4) a B</td>
<td>22 80 (6) b A 29 28 (4) ab C</td>
</tr>
<tr>
<td></td>
<td>3(^o)</td>
<td>40 (4) a A</td>
<td>4 46 (3) c A 31 23 (3) b B</td>
</tr>
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<td></td>
<td>mean</td>
<td>48 (4) a AB</td>
<td>3 85 (24) a A 3 28 (3) ab B</td>
</tr>
<tr>
<td>green</td>
<td>1(^o)</td>
<td>69 (8) a A</td>
<td>16 69 (6) a A</td>
</tr>
<tr>
<td></td>
<td>2(^o)</td>
<td>64 (6) a A</td>
<td>9 54 (6) b A</td>
</tr>
<tr>
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<td>3(^o)</td>
<td>31 (7) b A</td>
<td>7 26 (3) c A</td>
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<td></td>
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<td>3 50 (13) a A</td>
</tr>
<tr>
<td>yellow</td>
<td>1(^o)</td>
<td>16 (2) a A</td>
<td>9 20 (1) a A 11 17 (3) a A</td>
</tr>
<tr>
<td></td>
<td>2(^o)</td>
<td>11 (1) b B</td>
<td>15 19 (1) a A 26 20 (2) a A</td>
</tr>
<tr>
<td></td>
<td>3(^o)</td>
<td>0 (1) b A</td>
<td>10 (1) b A 26 20 (2) a A</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>14 (3) b A</td>
<td>2 16 (4) b A 3 17 (2) b A</td>
</tr>
</tbody>
</table>

\(^a\) comparisons: 1 = mean panicle length among panicle types within a species and site, 2 = mean panicle length among sites within a species and panicle type, 3 = mean panicle length among species within a site, 4 = mean panicle length among sites within a species. Means within a column (1 and 3) and within a row (2 and 4) followed by the same letter are not significantly different (P=0.05) as determined by t-tests.
The value of the linear model to describe the relationship \((R^2)\) varied widely among sites and panicle types. The change in seed number with panicle length was greater in secondary panicles than that observed for tertiary panicles at two of the three sites (Table 4, comparison 1). The secondary and tertiary panicles at site C did not show a change in seed number with panicle length. No difference in the relationship between seed number and panicle length was observed between primary and secondary panicle types at any of the three sites. Differences were not found among panicle types for the seed density panicle length relationship at any site.

Comparisons within individual giant foxtail panicle types between sites revealed that the differences were largely due to changes in secondary and tertiary but not primary panicles (Table 4, comparison 2). Changes in seed number and seed density with panicle length were similar in primary tillers at all three locations. For secondary panicles. Changes in secondary giant foxtail seed number and seed density with panicle length were greater at site B compared to both other sites. Changes in tertiary giant foxtail seed number and seed density with panicle length were greater at site B compared to site C.

When averaged over all three panicle types (Table 4, total) giant foxtail seed number per panicle was correlated with panicle length. Greater change in seed number with changes in panicle length were observed at site B compared to the other two sites (Table 4, comparison 3). A linear model best explained the change at site B. Site B also revealed a greater change in seed density with panicle length.
Table 4. Slopes (± s.e.) and coefficients of determination describing the relationship between seed number or seed density to panicle length.

<table>
<thead>
<tr>
<th>species</th>
<th>population</th>
<th>panicle type</th>
<th>seed number per panicle length (cm)</th>
<th>seed density per panicle length (cm)</th>
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<tr>
<td></td>
<td>site</td>
<td></td>
<td>slope</td>
<td>s.e.</td>
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<tr>
<td>giant</td>
<td>A</td>
<td>1°</td>
<td>38.7</td>
<td>95.0</td>
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<tr>
<td></td>
<td></td>
<td>2°</td>
<td>48.2</td>
<td>19.7</td>
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<td>75.9</td>
<td>23.9</td>
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<tr>
<td></td>
<td>total</td>
<td></td>
<td>56.8</td>
<td>20.4</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>1°</td>
<td>149.7</td>
<td>113.8</td>
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<td></td>
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<td>153.4</td>
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<td>86.4</td>
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<td>total</td>
<td></td>
<td>172.3</td>
<td>8.6</td>
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<tr>
<td></td>
<td>C</td>
<td>1°</td>
<td>64.6</td>
<td>15.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2°</td>
<td>33.8</td>
<td>17.8</td>
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<td></td>
<td></td>
<td>3°</td>
<td>12.5</td>
<td>8.3</td>
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<tr>
<td></td>
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<td>7.2</td>
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<tr>
<td>green</td>
<td>A</td>
<td>1°</td>
<td>163.3</td>
<td>33.2</td>
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<td></td>
<td></td>
<td>2°</td>
<td>121.9</td>
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<td>3°</td>
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<tr>
<td></td>
<td>total</td>
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<td>118.5</td>
<td>13.5</td>
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Table 4. (continued)

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<th>species</th>
<th>population</th>
<th>panicle type</th>
<th>seed number panicle length (cm)</th>
<th>seed density panicle length (cm)</th>
</tr>
</thead>
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<td>site</td>
<td></td>
<td>slope</td>
<td>s.e.</td>
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<tr>
<td>green</td>
<td>C</td>
<td>1°</td>
<td>49.8</td>
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<td></td>
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<td>total</td>
<td>92.0</td>
<td>10.1</td>
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<td></td>
<td>2°</td>
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<td></td>
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</tr>
<tr>
<td></td>
<td>2°</td>
<td>22.9</td>
<td>3.9</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>3°</td>
<td>13.6</td>
<td>7.2</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>total</td>
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<td>2.1</td>
<td>a</td>
</tr>
<tr>
<td>C</td>
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<td>24.0</td>
<td>14.4</td>
<td>a</td>
</tr>
<tr>
<td></td>
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<td>10.1</td>
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<td>a</td>
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<td></td>
<td>total</td>
<td>22.8</td>
<td>6.2</td>
<td>a</td>
</tr>
</tbody>
</table>

*a* comparisons: 1 = slopes among panicle types within a species and site, 2 = slopes among sites within a species and panicle type and 3 = slopes for total panicle types among sites within a species.
Unlike at sites A and C, giant foxtail seed density at site B increased as panicle length increased.

**Green Foxtail**

Primary panicles were greater in seed number, panicle length and seed density than tertiary tillers at both sites; secondary panicles were either greater or similar to tertiary panicles (Tables 1, 2, and 3; comparison 1). Whether averaged over all panicle tiller types or compared by individual tiller type, seed number, panicle length and seed density in green foxtail were similar at both sites (Tables 1, 2, 3; comparisons 2 and 4).

Changes in seed density with panicle length were similar for all panicle types (Table 4 comparison 1) at site C, but lower for tertiary panicles at site A. Comparisons within individual green foxtail panicle types between sites revealed differences for tertiary panicles, but not primary or secondary panicles (Table 4, comparison 2). The change in seed number or density with tertiary panicle length was greater for site A than site C. Green foxtail seed number and seed density changed with panicle length at both sites when averaged over all three panicle types (Table 4, comparison 3). These rates of increases (slopes) were similar at both sites for either the seed density or seed number to panicle length relationship.

**Yellow Foxtail**

Seed number, panicle length and seed density in primary yellow foxtail tillers were either greater than or similar to those in secondary tillers, depending on the
site in which the comparison was made (Tables 1, 2, and 3; comparison 1).
Differences between primary and secondary panicles were not observed in yellow
foxtail at site C. For all three parameters, primary and secondary panicles at site B
were either greater than or similar to comparable types at the other sites. Tertiary
yellow foxtail panicles, however, were similar for all parameters at all sites in which
they were sampled (Tables 1, 2, and 3; comparison 2). Inferences about yellow
foxtail were compromised because no tertiary panicles occurred at site A. High
plant density is thought to be responsible for the absence of yellow foxtail tertiary
panicles. When averaged over panicle types, the seed number, panicle length and
seed density for yellow foxtail at site B were either similar or greater than those at
the other sites (Tables 1, 2, and 3; comparison 4).

Comparisons among sites for individual yellow foxtail panicle types revealed
no differences in terms of changes in seed number or density with changes in length
(Table 4, comparisons 1 and 2). Seed number did not change with changes in
panicle length in primary yellow foxtail panicles at sites B and C, in secondary at site
C, or in tertiary at either site (Table 4). The only change in seed density with
changes in panicle length occurred in secondary panicles at site A. When averaged
over all three panicle types, the number of yellow foxtail seed per panicle increased
with panicle length at all three sites, while seed density increased at two sites, (Table
4 comparison 3). The degree of change was similar at all three sites for both
parameters.
Foxtail Species-Group

Relative differences in mean panicle length, seed number per panicle and seed density between species often changed among sites. When averaged over panicle types, variation is large; however, some differences can be found.

**giant and yellow foxtail**

Giant foxtail was greater than or similar to yellow foxtail for all three parameters at the different sites (Tables 1, 2 and 3; comparison 3). Giant foxtail was greater than yellow for all parameters at site A, for seed density at site B and for panicle length at site C. Giant and yellow foxtail were similar in seed number at sites B and C, in panicle length at site B and seed density at site C.

**green and yellow foxtail**

Green foxtail was usually greater than yellow for all three measured parameters for the two sites at which they were comparable (Tables 1, 2 and 3; comparison 3). Green foxtail was greater than yellow foxtail for all parameters at site A and for seed number and density at site C. An exception was found at site C, where panicle lengths were similar in these two species.

**giant and green foxtail**

Giant foxtail panicle length was greater than that of green at both sites evaluated (Tables 1, 2 and 3; comparison 3). Giant foxtail and green foxtail seed number and density; however, were similar.
Discussion

Seed Number

We found a higher number of seed per panicle at each site (Table 1) compared to that reported for giant foxtail, 207 (Biniak and Aldrich, 1986), 110 to 280 (Defelice et al., 1989); seeds per panicle for green foxtail, 437 to 577 (Wall, 1993) or 350 to 500 seed per panicle (Van den Born, 1971). The mean number of giant foxtail seed per panicle in this study is above that found for entire giant (220, 730 and 2,423 seeds per plant), green (234) or yellow (199) foxtail plants in two studies by Kawano and Miyake (1983). Differences in collection technique and the amount of time over which seed was gathered may be responsible for the disagreements in seed number.

Plasticity and Stability in Foxtail Seed Production

A phenotype results from the interaction of the environment with the plant genome during plant development (Scheiner, 1993). Environment includes competition from neighbors, weather and climate conditions, resource availability and cropping system influences. The adaptive value plasticity is that it allowed individual plants to adjust their phenotype to fit a particular environment. In this study all observed seed production parameters were plastic. This variability may indicate that different factors influenced different parameters, in a dynamic way. While selection over many generations has resulted in a degree of phenotype stability, trait plasticity is also advantageous and preserved (Sultan, 1987).
Plasticity at Different Levels of Plant Organization

The plasticity of seed production at the level of the foxtail species was expressed in differences between the three foxtail species evaluated. The plasticity of seed production responses of individual foxtail species depended on whether observations were made at the species level (averaged over panicle types), the individual tiller type or intra-panicle level of plant organization.

Responses to conditions were observed in seed production parameters of individual panicle types among sites. Giant and yellow foxtail seed production usually was greater at site B within individual panicle types. The productivity of individual green foxtail panicle types was similar at both sites in which it was evaluated, but this stability could be an artifact of not having evaluated this species at site B. Earlier-maturing panicle types usually were more productive than later maturing panicles.

Within individual panicles of any type, seed production plasticity was expressed in two ways. At the first level, seed number per panicle could change with changing panicle length (Table 4, seed number per panicle length). At the second level, seed density could change with changing panicle length (Table 4, seed density per panicle length). These two types of intra-panicle plasticity played a role in the three foxtail species in different ways.

For giant foxtail, intra-panicle plasticity among sites in the form of differences in slope was observed in secondary and tertiary panicles expressed as both seed number and density changes with length. For green foxtail, intra-panicle plasticity was observed in only tertiary panicles, for both number and density changes with
panicle length. Differences were observed less often among primary giant and green foxtail panicles either because of greater stability among sites or more variable (plasticity) within sites.

Yellow foxtail intra-panicle seed productivity was relatively stable, compared to the plasticity observed in giant and green foxtail. Yellow foxtail was much less plastic in changes in seed number with panicle length and even less plastic in changes in seed density than green or giant foxtail. These species differences may be a function of differences in panicle branching and fascicle organization (Narayanaswami, 1956). Yellow foxtail panicle morphology allows much less spikelet flexibility in response to changing environmental conditions. Yellow foxtail stability also occurs at the level of panicle type. No differences between primary, secondary or tertiary panicles were observed within a site in changes in seed number and density with panicle length. The differences in panicle morphology among foxtail species and panicle types may also have consequences for spikelet microenvironment. Conditions such as light and temperature may change with seed density and influence embryogenesis and dormancy induction, resulting in a variety of seed phenotypes (Dekker et al., 1996).

Green and giant foxtail seed productivity was usually similar at all sites evaluated indicating that seed production is a relatively stable (non-plastic) characteristic when averaged over all three panicle types. Yellow foxtail exhibited plasticity at the whole-plant level, and unlike the other two species, seed production parameters were usually greater at site B when averaged over types.
This study indicates that foxtail traits such as seed number per panicle, panicle length, and seed density possess both stable and variable attributes. These traits were plastic, but there was a range within which plastic responses occur. The relative differences in panicle length among species, population-sites and panicle types revealed limits to plasticity. Although characteristics were variable, some consistent observations occurred. Giant foxtail had longer panicles than green foxtail. Green foxtail panicles had a greater number of seed and higher seed density than yellow. Earlier-developing panicle types were always greater than or similar to the later developing panicle type for each of the parameters measured. Where a difference among sites was found, the values from site B were always the greatest. All other comparisons varied.

The correlation between seed number and panicle length is not constant across environments or panicle types. It is evident that estimates of seed production based on the panicle length must be population and panicle-type specific for giant foxtail and perhaps for green foxtail, while comparatively little change in seed density for yellow foxtail was observed. The observed degree of variation among these characteristics calls into question the accuracy of estimating seed production based on panicle length for giant or green foxtail as proposed by some (Barbour and Forcella, 1993; Fausey et al., 1997).

Acknowledgment

The authors would like to thank Dr. Doug Buhler of the National Soil Tilth Laboratory for his technical assistance.
References


CHAPTER 3. VARIATION IN S. FABERI (POACEAE)

SEED DORMANCY AT ABSCISSION

A paper for submission to the American Journal of Botany

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Abstract

The amount and sources of variation in germination among seed shed from giant foxtail (Setaria faberi) plants during their annual seed rain were evaluated. Seed from a single genetic line of giant foxtail was grown under field, greenhouse and controlled environment growth chamber conditions. Seeds were collected as they abscised sorted by plant and panicle development. Germination assays were conducted immediately. Stratification treatments and dissection were used to characterize seed dormancy further. Germination data were grouped in several different ways to examine the influence of panicle tiller type, relative time of abscission within an individual panicle (seed position) and abscission date. At abscission, a small fraction of giant foxtail seed germinated under favorable conditions. Differences in germination were found among environmental and biological categories. As the seed rain season progressed the mean percentage seed germination, as well as the variability among samples increased. Seed produced on tillers that developed earlier (primary) were more likely to be dormant than seed
from later-developing tillers (secondary or tertiary). An important correlation with changes in seed dormancy was the relative time of development within a panicle. Seed that developed later in a panicle were more likely to germinate than seed that developed earlier on the same panicle. Evidence provided in these studies supports the hypothesis that seed grown in different environments differs in the degree of dormancy. The more variable environmental conditions during seed development resulted in greater percentage germination and more variation in percentage germination among samples. These results suggest that the dormancy induction mechanism(s) that operate in giant foxtail are sensitive to environment. This sensitivity may be an inherent biological or genetic trait that acts either independently of, or in conjunction with, individual spikelet microenvironment. Support for an endogenous, developmental control of dormancy induction is provided by growth chamber experiments. The variation in percentage germination among samples and the response to stratification and dissection indicated that the foxtail seed rain consists of individuals, each with different germination requirements. The production of seed with a variety of germination requirements confers a selective advantage on giant foxtail. Dormancy heterogeneity among seed in the soil seed bank permits germination under a wide range of conditions and over an extended period of time; thus increasing the likelihood of some plants avoiding unfavorable conditions and producing seed.
The foxtails (*Setaria* spp.) are among the worst weeds in U.S. agriculture (Knake, 1977). The success of the foxtails as weeds is due in large part to seed dormancy. Seed dormancy prevents premature germination (vivipary), allows time for seed dispersal and staggers germination over time (Coleman et al., 1994; Silvertown, 1984; Sultan, 1987). Seed dormancy, especially variable seed dormancy, is a strategy for survival in heterogeneous environments (Jain, 1982). The distribution of germination over time allows periods of unfavorable growth conditions and control efforts to be avoided (Simpson, 1990). The addition of dormant seed to the soil creates a seedbank that provides a source of re-establishment and a "genetic memory" for foxtail communities (Cavers, 1983; Grime, 1981). Seed dormancy has implications for the density and species composition of weed communities that affect weed management (Dyer, 1995).

At abscission, giant, green (*S. viridis*) and yellow (*S. glauca*) foxtail seed are either completely (Kollman, 1970; Nieto-Hatem, 1963; Peters and Yokum, 1961; Povilaitis, 1956; Rost, 1975; Sells, 1965) or nearly completely dormant (Chavarria, 1986; Stanway, 1971; Taylorson, 1986; Van den Born, 1971). Several foxtail germination studies indicated that within a group of seeds a single level of dormancy does not exist, but diversity in the requirements for germination are the rule (Banting et al., 1973; Blackshaw et al., 1981; Chavarria, 1986; Dekker et al., 1996; King, 1952; Manthey and Nalewaja, 1987; Martin, 1943; Morre and Fletchall, 1963; Norris and Schoner, 1980; Stanway, 1971; Taylorson, 1986; Taylorson, 1987; Van den Born, 1971). Interpretation and comparison of foxtail seed dormancy and germination studies are made difficult by the lack of consistency in methods of collection, storage and testing.
The sources of variation in seed dormancy phenotypes can be assigned to three categories: genotype, environment and development (Scheiner, 1993). These sources of variation interact to produce a heterogeneity of seed dormancy. At the species and subspecies levels, foxtail genotypes potentially shed sets of seed that differ in proportion and range of requirements for germination (Norris and Schoner, 1980; Schreiber and Oliver, 1971; Schoner et al., 1978). The environment experienced by the parent plant and the developing seed also influences seed dormancy in many species (Fenner, 1991; Gutterman, 1992), including the foxtails (Biniak and Aldrich, 1986; Chavarria, 1986; Lee and Cavers, 1981). The third source of variation is due to random events during development that result in different phenotypes. This is sometimes referred to as “developmental noise” and describes the differences found among phenotypes of the same genotype grown under identical conditions (Scheiner, 1993).

Seed structures affect giant foxtail seed dormancy. Removal of or damage to the hull has stimulated germination (Biswas et al., 1970; Dekker et al., 1996; Kollman, 1970; Martin, 1943; Nieto-Hatem, 1963; Peters and Yokum, 1961; Povilaitis, 1956; Rost, 1971; Stanway, 1971). The non-embryo caryopsis tissues also to inhibit yellow foxtail embryo germination (Dekker et al., 1996; Nieto-Hatem, 1963; Rost, 1975) and foxtail embryos themselves possess dormancy (Nieto-Hatem, 1963). Embryo dormancy has been localized in either shoot or root axis, or both (axis specific germination, Dekker et al., 1996).

The interpretation of seed dormancy phenotype in reference to the sources of variation must be made by comparing equivalent levels of plant development and not simply age, because plants may grow at different rates and many phenotypic traits change over the course of development (Coleman et al., 1994). In this study,
anthesis and abscission provided easily identifiable markers of plant and seed development.

Developmental and environmental sources of variation in seed dormancy are experimentally difficult to separate. This difficulty can be overcome to some degree by harvesting seed in a regular and frequent manner during plant development and with controlled-environment conditions. The influence of plant development on seed dormancy was evaluated at the level of panicle tiller types (e.g. primary, secondary, tertiary) (Haar and Dekker, 1998) and seed position within an individual panicle. The influence of environment was evaluated over two time scales: 1) that of individual giant foxtail seed development, which is the period from fertilization to abscission; eight to twelve days (Dekker et al., 1996), and 2) the time over which all the seed on a panicle matures (one to two months; data not reported).

It was our goal to describe and compare differences and variation in giant foxtail germination for seed from a single genetic line grown under several conditions. Conditions ranged from controlled to highly variable: growth chamber, greenhouse and field. We hypothesized that germination would differ among seed grown in different environments and that an increase in the degree of variation in the environmental conditions would result in greater diversity in the germination requirements of the seed rain. We also hypothesized that changes in the amount and variability of giant foxtail seed germination would be correlated with plant development and environment.
Methods and Materials

Plant Material

Although giant foxtail possesses relatively low genetic diversity and is almost exclusively a self-pollinated species (Li et al., 1935; Till-Boutraud et al., 1992; Wang et al., 1995a; Wang et al., 1995b), care was taken to minimize effects that could result from different genotypes. All plants used in these experiments were grown from seeds of a single self-pollinated plant (lot 1816; Dekker et al., 1996). The original plant was grown from a seed collected at Iowa State University's Curtiss Farm, Ames, Iowa. Seeds used in germination tests are the self-pollinated progeny of experimental plants.

Growth Conditions

Controlled-environment experiments were conducted in a growth chamber set at 16:8 h light:dark and constant temperature (26°C). Radiation was provided with both fluorescent and incandescent bulbs with an intensity of 450±50 μmoles m⁻² s⁻¹ at approximate panicle level (40 cm from floor of growth chamber). Seeds were started in a growth chamber in a 1:2:2 mixture by volume of soil, peat moss and perlite1. Ten days after sowing, seedlings were transplanted to 15 cm diameter plastic pots filled with the same soil mixture. Thirty plants were used per experiment. Plants were watered as needed (approximately every other day) and fertilized every two weeks with 30 mg N. Greenhouse-grown giant foxtail plants were started in soil (same mixture as above), transferred ten days after planting to 10

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1 Silbrico Corp. 6300 River Road Hodgkins, IL 60525
cm diameter clay pots then at the five to six leaf stage, transplanted to 20 cm diameter clay pots. Fifteen ml Osmocote fertilizer was applied at second transplant and again 60 days later. Seeds were planted for the greenhouse experiment on January 10 and flowering began March 16. Only natural lighting was used. Plants for the field experiment were started in the greenhouse and transplanted to the field at the five to six leaf stage (June 1).

Seed Collection

The word "seed" used in this paper refers to the giant foxtail dispersal unit, although spikelet is a more accurate term (Narayanaswami, 1956; Rost, 1975). At the first sign of anthesis panicles, were covered with a plastic mesh bag and secured with a wire twist tie. The bags collected seed as it abscised and prevented cross pollination. Seed was harvested every three to five days by gently shaking the panicle then removing the plastic mesh bag. Harvests occurred from the time shattering began until seed was completely shed from a panicle. The giant foxtail seed rain in the field typically occurs from late July until killing frost (October to November) in the Midwestern U.S.

Developmental and Environmental Categories

Because panicles flower along a pattern, the panicle position of a seed can be estimated by the length of time abscission follows the first anthesis on a panicle. Seed collected with reference to the time abscission followed first anthesis are referred to as PDP (panicle developmental position) cohorts. Seed within a PDP

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2 Osmocote 19-6-12 Grace-Sierra Horticultural Products Co. 1001 Yosemite Drive Milpitas, CA 95035
3 7.6x25 cm delnet bags, Applied Extrusion Technologies Inc. Middletown, DE
cohort came from similar levels of panicle maturity or positions within panicles (e.g. the first, from the distal 30 to 40 percent of panicle axis; Dekker et al., 1996).

Comparison of percentage germination among PDP cohorts measures the influence of seed position and panicle maturity on seed dormancy. Because first anthesis began at different days for different panicles, seed within a PDP cohort developed under different environmental conditions, which may contribute to the variation within these cohorts (Figure 1).

Seed collected on a single harvest date were referred to as CD (calendar date) cohorts. If harvesting is frequent, an assumption can be made that the environment during seed development was similar. Changes in germination among CD cohorts are attributed to differences in environment during seed development. Seed within a CD cohort abscised at a similar time, but differed in the level of panicle maturity (position) from which they originated.

A group of panicles for which first anthesis appeared on the same day was another observational category, referred to as a DAFF (days after first flower) cohort. The first anthesis on a panicle was used as a morphological marker of physiological development, and panicles with the same anthesis date were considered physiologically and developmentally equivalent. The percentage germination of a DAFF cohort is the average of all the seed collected from the group of panicles. Comparisons between DAFF cohorts permitted inferences about individual whole panicle sources of variation, as well as how germination requirements change with seasonal environment.

The pattern of tiller branching also allowed comparison of seed germination to be made. Panicles were designated as primary, secondary or tertiary as described in Haar and Dekker, (1998). Designation of panicle types was done for growth chamber studies only.
Figure 1. Schematic description of giant foxtail observational categories. Each small circle represents a seed harvest and subsequent germination test. Seed was harvested every three to five days. Panicles that began to flower on the same day were considered a group, DAFF (days after first flower) cohort. Seed was grouped with reference to the time it abscised within a panicle, PDP (panicle developmental position) cohorts. Seed collected on the same date were considered CD (calendar date) cohorts.
Germination Tests

Germination tests were conducted immediately following harvest. Only dark brown mature seeds were used. For controlled environment experiments, germination of isolated caryopses and embryos was also tested. Seeds were dissected under a microscope by using forceps and a scalpel. Before embryos were excised, caryopses were allowed to imbibe for two to four hours under germination conditions. Care was taken to remove the caryopsis coat from over isolated embryos. Ten to twenty seeds or their dissected components were then put on moist (two ml distilled water) blue blotter germination paper\(^4\) in five-cm-diameter glass petri dishes sealed with parafilm and placed in a germination cabinet\(^5\) at 26°C and constant light PPFD 640 \(\mu\text{moles m}^{-2} \text{s}^{-1}\). Germination was recorded after ten days. The criterion for seed germination was emergence of the coleorhiza or coleoptile. Evidence of embryo growth qualified as germination for the dissected components (Dekker et al., 1996). Seed from field and greenhouse experiments were not dissected and germination tests differed in the following manner: seeds were placed on filter paper\(^6\) in 100-by-15 mm plastic petri dishes and placed in darkness at 20°C.

Stratification

Seed not tested for germination at harvest were stratified in petri dishes with moist sand (one ml water per six g sand), double wrapped in Aluminum foil and kept at 4°C for various lengths of time (2, 4, 6, 8 or 16 weeks). Following stratification, a sample was removed from sand under green light and germination tested as described above. Seed not tested for a treatment was left in petri dish, rewrapped in foil and returned to stratification conditions.

\(^4\) Anchor 5 cm diameter
\(^5\) Hoffman SG 30 Hoffman Man. Co., Albany OR
\(^6\) Whatman no. 1
Statistics

Data were arranged to examine the influence of biological and environmental events in association with changes in germination for each experiment. Treatment differences refer to either stratification or the observational categories PDP, CD and DAFF, which represent the environmental or biological causes of variation in this study. The degree of variation associated with these categories was determined with analysis of variance by using the ANOVA procedure of SAS (1989). DAFF and CD cohort categories were highly correlated so two separate analysis of variances were conducted. Correlation occurs because DAFF cohorts were selected in part by date. A low correlation between PDP and other variables was found.

Results

Germination at Abscission

At abscission, percentage germination of field- and greenhouse-grown seed was 8.9 and 4.9, respectively (Table 1). No seed germination at abscission was observed in any controlled environment experiment. The presence of surrounding caryopsis and hull tissues inhibited embryo germination. Removal of the hull increased percentage germination (Table 1). Caryopsis germination was low (about one percent), but greater than seed germination at that time. Isolated embryos had the greatest percentage germination at abscission, between 20.1 and 40.5. The foxtail embryo itself can be dormant as indicated by the many isolated embryos that did not initially germinate.
Table 1. Percentage germination (± s.e.) of giant foxtail seed, caryopses or embryos in response to stratification. Seed developed under different types of environmental conditions: growth chamber, greenhouse or field. Growth chamber data are from three experiments: GC 1, GC 2 and GC 3.

<table>
<thead>
<tr>
<th>Weeks of Stratification</th>
<th>% Germination (±s.e.)&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Environment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>GC 1 n&lt;sup&gt;2&lt;/sup&gt;</td>
<td>GC 2 n</td>
</tr>
<tr>
<td>Seed</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0.0 (0.0) a 31</td>
<td>0.0 (0.0) a 109</td>
</tr>
<tr>
<td>2</td>
<td>0.2 (0.2) a 25</td>
<td>0.0 (0.0) a 52</td>
</tr>
<tr>
<td>4</td>
<td>1.7 (0.7) a 70</td>
<td>0.0 (0.0) a 112</td>
</tr>
<tr>
<td>8</td>
<td>5.8 (1.8) b 21</td>
<td>64.8 (3.9)&lt;sup&gt;3&lt;/sup&gt; b 44</td>
</tr>
<tr>
<td>Caryopsis</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0.5 (0.3) a 32</td>
<td>0.3 (0.2) a 111</td>
</tr>
<tr>
<td>2</td>
<td>5.1 (1.6) a 25</td>
<td>14.3 (2.4) b 51</td>
</tr>
<tr>
<td>4</td>
<td>49.2 (3.2) c 72</td>
<td>9.5 (1.4) b 111</td>
</tr>
<tr>
<td>8</td>
<td>65.8 (6.0) b 21</td>
<td>78.2 (0.0) d 43</td>
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<tr>
<td>Embryo</td>
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<td></td>
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<td>20.1 (1.8) a 152</td>
</tr>
<tr>
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<td>80.1 (3.7) b 25</td>
<td>83.4 (2.9) b 67</td>
</tr>
<tr>
<td>4</td>
<td>96.9 (1.3) c 105</td>
<td>94.2 (1.8) c 111</td>
</tr>
<tr>
<td>8</td>
<td>98.3 (0.6) c 21</td>
<td>98.9 (0.1) c 46</td>
</tr>
</tbody>
</table>

<sup>1</sup>Means within columns for a compartment followed by the same letter are not different at p=0.05 according to paired t-tests.

<sup>2</sup>n = number of germination tests (petri dishes).

<sup>3</sup>In the second growth chamber experiment, germination tests following eight weeks of stratification used seed from secondary and tertiary panicles only.
Effect of Stratification

Stratification treatments increased percentage seed, caryopsis and embryo germination in each experiment (Table 1). The magnitude of response varied by seed tissue, environment and experiment. Seed or its components from the field experiment was the most responsive to stratification followed by those from greenhouse and growth chambers. Two or four week stratification treatments increased germination of seed grown in field or greenhouse, but had no effect on seed in growth chamber experiments. An eight week stratification treatment increased seed germination in all experiments. Caryopses percentage germination increased more than that for seed with the same stratification treatments within an experiment. Embryo percentage germination increased between two to four fold with stratification depending on the experiment. After four weeks of stratification, isolated embryos were essentially all germinable.

Panicle Tiller Types

For comparisons in which a difference in germination occurred among seed or their dissected components, samples from later-developing panicles had the higher percentage germination. In controlled environment conditions, tiller development was a sequential process with a consistent pattern and duration (Figure 2); which was highly correlated with CD and DAFF cohorts \( r = 0.90 \) to 0.96. Tiller panicle development began with the emergence of the primary \( (1^\circ) \) panicle at the terminal end of the main culm; followed by branches forming at the nodes of the main culm, these tillers were referred to as secondary \( (2^\circ) \). Tertiary \( (3^\circ) \) tillers arose at nodes of the secondary tillers. Development of secondary and tertiary tillers began with lower nodes.
Figure 2. Anthesis period and seed rain duration for panicle tiller types. Time is expressed in days after the first observation of anthesis on a plant. Data are from two growth chambers experiments: GC1 and GC2. Open symbols represent the beginning and end points of initial anthesis for a panicle type. Closed symbols represent the beginning and end of the seed rain.
No differences were observed in the germination of seed or caryopses among panicle types in the second growth chamber experiment (GC2), primarily because these tissues were very dormant (Table 2). In the third controlled environment experiment (GC3), percentage seed germination from primary panicles was less than that from secondary or tertiary panicle after eight weeks of stratification. Other stratification treatments in GC3 did not stimulate seed germination in any panicle type, again primarily because these seed were very dormant. At harvest in GC3, caryopsis germination was greater when taken from secondary compared to primary panicles, while the same tissues from tertiary compared to primary panicles had a higher percentage germination after four and eight weeks of stratification.

Embryos from secondary panicles had higher percentage germination than those from primary panicles in GC3 at harvest and after two and four weeks stratification. Embryos from tertiary panicles had greater germination percentage than those from primary panicles after two weeks stratification in GC2, and at harvest and after four weeks of stratification in GC3. Following eight weeks of stratification, embryo percentage germination from all panicles types was above 90 percent.

**Panicle Development Position Cohort (PDP)**

Percentage germination differed among PDP cohorts of field- and greenhouse-grown seeds (Tables 3 and 4). No changes were found among PDP cohorts for seed or caryopsis percentage germination in any controlled environment experiment, but there were differences among PDP cohorts for embryo germination (GC3). Seed and embryo percentage germination and variation among samples increased as panicle development (PDP cohort) progressed in cases where differences were observed (Figure 3). These differences among seed that developed
Table 2. Percentage germination (± s.e.) of seed, caryopsis and embryos from 1°, 2° or 3° panicles in response to stratification. Data are from two growth chamber experiments: GC2 and GC3.

<table>
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<th>Panicle type</th>
<th>Weeks of Stratification</th>
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<td>0.0 (0.0) a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2°</td>
<td>0.0 (0.0) a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3°</td>
<td>0.0 (0.0) a</td>
</tr>
<tr>
<td></td>
<td>GC3</td>
<td>1°</td>
<td>0.0 (0.0) a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2°</td>
<td>0.0 (0.0) a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3°</td>
<td>0.0 (0.0) a</td>
</tr>
<tr>
<td>Caryopsis</td>
<td>GC2</td>
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</tr>
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<td>2°</td>
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</tr>
<tr>
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<td>3°</td>
<td>0.0 (0.0) a</td>
</tr>
<tr>
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</tr>
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</tr>
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<td></td>
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<td></td>
<td>3°</td>
<td>43.2 (5.3) b</td>
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Table 2. (continued)

1 Means within columns for a compartment and experiment followed by the same letter are not different at P=0.05 according to paired t-tests.
2 n = number of germination tests (petri dishes).
Table 3. Analysis of variance for parameters describing the biological and environmental influences during seed development on percentage germination. Data are from five experiments: three growth chamber (GC 1, GC 2 and GC 3), field and greenhouse conditions. Calendar date (cd) refers to seed that matured on the same date. Panicle developmental position (pdp) is the relative location within a panicle where a seed developed.

<table>
<thead>
<tr>
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<th>Source of Variation</th>
<th>GC 1</th>
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<th>GC 3</th>
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<th>Greenhouse</th>
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<td>0.94</td>
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<tr>
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<td>NS</td>
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<tr>
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1 Degree of significance: NS P>0.05, * P <0.05, ** P <0.01 *** P <0.001, **** P <0.0001.
Table 4. Analysis of variance for parameters describing the biological and environmental influences during seed development on percentage germination. Data are from five experiments: three growth chamber (GC 1, GC 2 and GC 3), field and greenhouse conditions. Days after first flower (daff) is the time of seed maturity as measured from the first anthesis for a plant. Panicle developmental position (pdp) is the relative location within a panicle where a seed developed.

<table>
<thead>
<tr>
<th>Compartment</th>
<th>Source of Variation</th>
<th>GC 1</th>
<th>GC 2</th>
<th>GC 3</th>
<th>Field</th>
<th>Greenhouse</th>
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<td>NS</td>
<td>*</td>
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</tr>
<tr>
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<td>NS</td>
<td>*</td>
<td>NS</td>
<td>****</td>
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</tr>
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¹ Degree of significance: NS P>0.05, * P <0.05, ** P <0.01 *** P <0.001, **** P <0.0001.
Figure 3. Relationship between germination and PDP (panicle developmental cohorts) at abscission; a) field b) greenhouse c) third growth chamber study. A PDP cohort consists of seed that abscised the same number of days after first anthesis on a panicle. Bars represent standard errors of the mean and are not shown when less than marker size.
on different parts of the panicle (PDP cohorts) were most apparent at harvest, then decreased with stratification until all cohorts had high germination, above 90 percent (data not reported).

Calendar Date Cohorts (CD)

Seed germination differed among CD cohorts as the seed rain proceeded for field- and greenhouse-grown foxtail plants (Table 3). No differences in seed or caryopsis germination were found among CD cohorts for controlled environment experiments. Embryo germination in GC2 was the only instance of a difference in germination among CD cohorts grown in that environment. As the season progressed, seed germination and variation within sample dates increased within CD cohorts harvested from the field and greenhouse experiments (Figures 4a and 4b). This seasonal pattern was not observed for embryo germination in GC2, although the highest embryo germination occurred in a later CD cohort (Figure 4c).

Anthesis Date Cohort (DAFF)

Germination differed among DAFF panicle cohorts of field and greenhouse grown seeds, but not in growth chamber experiments (Table 4). Differences in caryopsis germination were found among DAFF cohorts in GC2, and among DAFF panicle cohorts for embryo germination in GC2 and GC3. No consistent pattern for changes in seed or embryo germination was observed (Figures 5 and 6). Most differences were obscured by the high variability caused by grouping all the seed from a panicle together into DAFF cohorts. Despite this, embryo germination in the later developing panicles (DAFF) of GC3 was greater than that observed in the first DAFF panicles (Figure 6b). Additionally, seed germination in the last two DAFF
Figure 4. Relationship between germination and CD (calendar date) cohorts at abscission; a) field b) greenhouse c) growth chamber study. A CD cohort consists of seed harvested on the same date. Bars represent standard errors of the mean and are not shown when less than marker size.
Figure 5. Relationship between germination and DAFF (days after first flower) cohort at abscission; a) field b) greenhouse experiments. A DAFF cohort consists of seed harvested from panicles that began to flower on the same date. Bars represent standard errors of the mean and are not shown when less than marker size.
Figure 6. Relationship between caryopsis or embryo germination and DAFF (days after first flower) cohort after four weeks of stratification; a) growth chamber experiment 2 (GC2) b) growth chamber experiment 3 (GC3). A DAFF cohort consists of seed harvested from panicles that began to flower on the same date. Bars represent standard errors of the mean and are not shown when less than marker size.
cohorts was greater than that in the first two cohorts grown in the greenhouse (Figure 5b).

**Interactions among Cohorts and Stratification**

When grown in the field or greenhouse, the germination of giant foxtail seed developing early on panicles (PDP cohorts) was in most instances less than that for seed developing later on the same panicles (Figure 3, Table 5). Seed developing in the same environment early in the seed rain season (CD cohorts) usually had lower germination than seed developing later (Figure 4, Table 5). In general, the earliest-to-develop seeds on panicles maturing early in the season had lower germination than did seeds developing later on panicles and later in the season (Tables 3, 5). This pattern was apparent in both field- and greenhouse-grown seed. Higher germination in later-developing seed in later-maturing panicles also was observed in PDP by DAFF interactions involving field- and greenhouse-grown seed, as well as embryos in GC3 (Table 4).

**Discussion**

Germination tests at abscission, stratification treatments and seed dissection were used to evaluate seed dormancy. Stratification was effective in promoting germination of giant foxtail seed or their dissected components in each experiment, and provided important information about dormancy and germinability states not revealed in germination assays conducted at abscission. Comparison of isolated embryo germination with caryopses or whole seed germination indicated that tissues surrounding the embryo inhibit its germination. This is consistent with previous studies indicating whole giant foxtail seed dormancy is controlled by its several component parts (Dekker et al., 1996).
Table 5. Germination (percentage ± s.e.) of giant foxtail from CD (calendar date) and PDP (panicle developmental position) cohorts at harvest. Seed grown under field (A) or greenhouse (B) conditions.

Table 5A, Field.

<table>
<thead>
<tr>
<th>Panicle Development Position</th>
<th>% Seed Germination (±s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CD (calendar date) cohorts</td>
</tr>
<tr>
<td></td>
<td>0-19</td>
</tr>
<tr>
<td>15-26</td>
<td>0.74 (0.53)</td>
</tr>
<tr>
<td>27-36</td>
<td>2.00 (0.88)</td>
</tr>
<tr>
<td>37-48</td>
<td>..... 1</td>
</tr>
<tr>
<td>49-64</td>
<td>.....</td>
</tr>
</tbody>
</table>

Table 5B, Greenhouse.

<table>
<thead>
<tr>
<th>Panicle Development Position</th>
<th>% Seed Germination (±s.e.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CD (calendar date) cohorts</td>
</tr>
<tr>
<td></td>
<td>0-25</td>
</tr>
<tr>
<td>13-22</td>
<td>0.04 (0.04)</td>
</tr>
<tr>
<td>23-37</td>
<td>0.24 (0.14)</td>
</tr>
<tr>
<td>38-52</td>
<td>.....</td>
</tr>
<tr>
<td>55-67</td>
<td>.....</td>
</tr>
</tbody>
</table>

1 These combinations do not exist.
Dormancy Induction and Environment

Giant foxtail seed grown in different environments have the potential to vary considerably in their germination. Results support the hypothesis that seed grown in different environments would vary in degree of dormancy: large differences in germination were found among the experimental regimens. No seed germinated at harvest from plants grown in growth chambers, while low numbers of seed germinated at harvest from field- and greenhouse-grown plants. Stratification revealed greater germination (less dormancy) in greenhouse-grown plants compared to those grown in the field.

Giant foxtail seed grown under apparently equivalent conditions also varied in percentage germination. Stratification revealed a high degree of latent variation in germination not apparent at harvest in growth chamber grown seed. Over ten-fold differences in seed germination were found among the several growth chamber experiments (e.g. Table 1, eight week stratification). Four to five-fold differences in caryopsis germination between growth chamber experiments not apparent at harvest were also revealed by stratification (e.g. Table 1, 4, 8 week stratification). Finally, two-fold differences in germination between embryos from different growth chamber experiments were observed at harvest.

These results suggest that the dormancy induction mechanism(s) that operate during embryogenesis and seed development (caryopsis and hull dormancy) are sensitive to environmental conditions. This sensitivity may be an inherent developmental or genetic trait that acts either independently of, or in conjunction with individual spikelet microenvironment. Support for endogenous, developmental control of dormancy induction is provided by comparing the large differences in seed, caryopsis and embryo dormancy among the growth cabinet experiments (Table 1) with the consistent panicle development sequence for the
plants that produced those seeds (Figure 2). These results are also very compelling considering the large numbers of seed (1604 petri dish tests), caryopses (764 petri dish tests) and embryos (881 petri dish tests) evaluated to reach these conclusions (Table 1).

**Tiller Development and Dormancy**

The tiller type on which a giant foxtail seed develops is an important source of seed, caryopsis and embryo dormancy heterogeneity. Under controlled environmental conditions, subtle differences in germination among seed from different panicle tiller types was revealed. In general, seed from panicles on earlier-emerging (primary) tillers was more dormant than seed from later-emerging secondary and tertiary tiller panicles (Table 2). Germination of seed from primary panicles was less than germination of seed from secondary and tertiary tillers (e.g., Table 1, GC3: eight week stratification). Germination of caryopses from primary panicles was less than that from secondary (e.g., GC3: at harvest) or tertiary (e.g., GC3 four, eight week stratification). Embryos from primary panicles were more dormant compared to those from secondary (e.g., GC3: at harvest; two, four week stratification) or tertiary panicles (e.g. GC2: two week stratification; GC3: at harvest, four week stratification).

Calendar date cohorts provided an indirect indication of the influence tiller type has on heterogeneous seed dormancy phenotypes. As the seed rain season progressed, seed and embryo germination and variability increased (Figure 3; Table 5). This decrease in dormancy with time was probably not due to changes in the environment, as it occurred under controlled growth chamber conditions. A more likely explanation is that increased germination was correlated with plant and
panicle development from the more dormant primary to the less dormant tertiary panicles.

The time of development (DAFF cohorts) provided a less sensitive indication of the influence tiller panicle type has on germination variation at abscission. Although DAFF cohorts were highly correlated with tiller development, sensitivity to differences in germination associated with DAFF cohort was less because these cohort groups bulk seed from all parts of the panicle in a single mean. No consistent pattern of change in germination with DAFF cohorts was observed, but when differences were found, the later-developing seed and embryos were less dormant than those maturing earlier (Figure 4b, 5b).

**Seed Position in the Panicle and Dormancy**

The relative time of development (PDP), or panicle position, of a seed within an individual panicle is another important influence of seed dormancy in giant foxtail. Seed developing earlier in an individual panicle were more dormant than those maturing later in the same panicle. The later maturing seed were also more variable in germination than earlier, more dormant seed. This contribution of development time within a panicle to germination variability occurred in giant foxtail plants grown in the field, greenhouse and growth chamber. The effect of panicle position had a much larger influence on seed germination than did tiller type.

**Cumulative Influences of Development, Morphology and Environment on Dormancy**

Seed shed from giant foxtail plants during the seed rain of one season are mostly dormant at abscission, with only a small fraction capable of germination
immediately under favorable conditions. As the seed rain season progresses the percentage germination, as well as the variability in germination requirements of those seeds, increases. The sources of seed dormancy heterogeneity are both environmental and biological. The more variable environmental conditions resulted in greater seed heterogeneity. Biological sources of germination variability are associated with morphology and development. The panicle type, relative position within the panicle, and the interaction of seed parts with differing amounts dormancy, are all factors which contribute to a heterogeneous seed rain.

**Weedy Adaptation and Seed Dormancy Heterogeneity**

Observations of seed dormancy provided here are not adequately explained by concepts of seed dormancy as a single state with a “trigger” mechanism that releases dormant seed to a second state, germination. The variation in dormancy observed at abscission, and the differences in response to stratification, indicate that giant foxtail produces individual seeds, each with a different germinability state (Trevewas, 1987). These dormancy states arise during development as a function of each seed’s structural and physiological components as modified by parental influences and environment (Come 1980/81; Dekker et al., 1996; Silvertown, 1984). The production of seed with a variety of germination requirements is an advantage to giant foxtail. Dormancy heterogeneity among seed in the soil seed bank permits some germination to occur over an extended period of time or under a wide range of environmental conditions. This increases the likelihood of some giant foxtail plants avoiding unfavorable environmental conditions to produce seed.
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CHAPTER 4. MICROGRAPHIC ANALYSIS OF GIANT FOXTAIL (S. FABERI) SEED, CARYOPSIS AND EMBRYO GERMINATION

A paper for submission to the American Journal of Botany

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Abstract

Giant foxtail (Setaria faberi) seeds differ in requirements for germination. Variable germinability arises during seed development under the influence of genotype, environment and parent plant. Giant foxtail seed germination has been shown to be regulated by independent asynchronous or dependent synchronous action of seed structures. To gain better insight into the process, germination was divided into axis specific embryo growth categories or states. Three states were defined for each embryonic axis. The degree of embryo growth (germination state) after eight to twelve days under germination conditions is believed to reveal the germinability state (potential for germination) possessed by the seed before germination. The embryo axes behave independently, which allows any combination of germination states to occur. In general, the greater the difference in
germination between the axes, the less likely the combination of states will occur. Photographic evidence of each germination state is shown for caryopses and seed. Seed with a variety of germinability states is a strategy for surviving variable environments.

**Introduction**

Giant foxtail is a major weed of the U. S. (Holm et al., 1977; Knake, 1977) and seed dormancy is one of the primary factors responsible for the success of foxtails as weeds (Simpson, 1990). Shedding seed with different germinability states is a strategy for survival in highly variable environments (Silvertown, 1984). The addition of dormant seed to the seedbank serves to disperse foxtail germination over time and enables the species to survive unfavorable environmental conditions or control efforts (Cavers, 1983; Grime, 1981). The annual seed rain of a foxtail plant consists of individuals with different germination requirements; each seed shed from the parent plant has, potentially, a different germinability state (Dekker et al., 1996; Treveswas, 1987). Germinability states are believed to arise during seed development under the influence of the parent plant and the environment (Bewley and Black, 1994; Simpson, 1990). Tiller type, fascicle branching, spikelet position and seed tissues have been shown to influence the diversity of germinability phenotype (Dekker et al., 1996; Haar and Dekker 1998). Germinability is not fixed after induction but may change in response to environmental conditions throughout the seed phase of the plant life cycle (Treveswas, 1987).
Embryo germination in foxtail species is influenced by other seed structures. The dispersal unit for giant foxtail is referred to as a seed, although the term, spikelet is more accurate. Each seed consists of a single fertile floret subtended by a sterile lemma and two glumes (Narayanaswami, 1956; Rost, 1975). A lemma and palea surround the caryopsis and together form a hard protective covering commonly referred to as the hull (Gould, 1968; Rost, 1975). Physical removal of the hull has been observed to stimulate germination of foxtail caryopses (Biswas et al., 1970; Haar and Dekker, 1998; Kollman, 1970; Martin, 1943; Nieto-Hatem, 1963; Povilaitis, 1956; Rost, 1975). Hull-damaging treatments such as scarification or piercing increased germination (King, 1952; Kollman and Staniforth, 1972; Peters et al., 1963; Stanway, 1971).

Attempts to explain the mechanism by which hulls affect germinability have focused on three hypotheses: 1) physical restraint of the hull on the embryo 2) presence of an inhibitory substance and 3) impermeability to water and gases. Hulls do not appear to impede water absorption significantly in the foxtail species. Germinable and dormant seeds were found to imbibe similar amounts of water (Kollman, 1970; Nieto-Hatem, 1963). Evidence for an inhibitor is inconclusive. Leaching increased percentage germination of intact and damaged seeds of yellow foxtail, however hull leachate failed to inhibit caryopses germination (Kollman, 1970; Nieto-Hatem, 1963). Nieto-Hatem (1963) described two levels of yellow foxtail seed dormancy: hull and caryopsis. Removal of the hull allowed some caryopses to germinate; these seeds were defined as having hull dormancy. Other caryopses did not germinate when hulls were removed and were regarded as having caryopsis dormancy.
dormancy. A stratification or another treatment was required before caryopsis dormant embryos would germinate.

Interior to the hull is the caryopsis, composed of the embryo, endosperm and caryopsis coat. A layer 3-10 μm thick known as the caryopsis coat forms the surface of the caryopsis (Rost, 1973). The caryopsis coat has been implicated in affecting seed germinability, usually as an impediment to gas or water movement. Disruption of the caryopsis coat has stimulated yellow foxtail embryos to germinate (Rost, 1973). Excision of embryos from germinable seeds also stimulates germination, implying an inhibitory role for caryopses coat or endosperm (Dekker et al., 1996; Rost, 1971 and 1975).

A previous paper in this series of articles on foxtail species weed adaptation provided evidence for a complex model of germinability regulation based on the independent, asynchronous actions of the embryo, caryopsis and hull compartments, as well as on their dependent, synchronous action (Dekker et al., 1996). Embryo germination can be axis specific and take place in either or both axes (coleoptile, shoot; coleorhiza, root). The germinability of isolated embryos is not necessarily an indication of their germinability when enclosed in the caryopsis or hull, often surrounding envelopes inhibit germination (Dekker et al., 1996; Haar and Dekker, 1998).

The germination states as previously described were those attained after the eight to twelve days of the germination assay (Dekker et al., 1996; Haar and Dekker 1998). Typically the terminal germination state was reached within four or five days and little change occurred thereafter. We concluded from these observations that
the terminal germination state revealed during the four to twelve days of the assay was the germinability state possessed by the seed before germination. If this were not the situation, we would have expected to observe continuous germination over the entire eight to twelve day period, i.e. the assay conditions would have been an after-ripening treatment themselves.

The goal of this study was to provide photographic evidence of the several morphological germination states of giant foxtail quantitatively described previously (Dekker et al., 1996). We provide herein a micrographic presentation of the continuous nature of giant foxtail embryo germination process, as well as a systematic classification system for seed, caryopsis and embryo germination states. The germination process for this study was broadly defined, and divided into categories or states based on continuous embryo growth. It is believed that more insight into the behavior of seed germination can be gained by using several quantitative states of embryo growth. It may also provide additional insights into the nature of foxtail species seed dormancy and seed bank dynamics.

Materials and Methods

Plant Material

To reduce variation among observations due to differences in genotype, seed used in this study were the self-pollinated progeny of a single plant (single seed descent propagation scheme; seed lot number 1816; Dekker et al., 1996). Seed was harvested in 1991 and stored dry at 4 to 6°C in darkness. Only dark brown seeds
were used in this study. Germination was greater than 90 percent at the time this study took place. The hull was removed with a scalpel and forceps under a dissecting microscope for caryopsis observations.

Germination

Before germination seed was surface sterilized by immersion in a 10% commercial bleach solution (five percent sodium hypochlorite) for 15 minutes then rinsed with distilled water. Seeds or caryopses were placed in 5.5-cm-diameter glass petri dishes on two five-cm diameter filter paper discs moistened with 1.5 ml distilled water. Petri dishes were sealed with Parafilm M then placed in a controlled environment chamber at 25°C and constant PAR of 290 μmoles m⁻² s⁻¹ provided with fluorescent bulbs.

Electron microscopy

Seeds or caryopses were observed at various stages of germination under one of two electron microscopes at the Wageningen Agricultural University, Wageningen, The Netherlands. For observations under field scanning electron microscope Specimens were mounted using tissue tech, frozen in supercooled liquid Nitrogen, then warmed to -85°C at 7 torr. Samples were then sputter coated with gold palladium.

1 No. 595; Schleicher and Schuell, Dassel, Germany
2 American National Can, Neenah, WI 54956
3 JSM 6300 F, Jeol
Other specimens were fixed in four percent formalin in a phosphate buffer solution (pH 7.4) followed by dehydration in an ethanol series. Specimens were then critical point dried in carbon dioxide, mounted on Aluminum studs with double sided tape and sputter coated with gold palladium for two minutes. Observations were made using a scanning electron microscope.

Results and Discussion

The process of germination for seeds and caryopses consists of a continuous chain of events that we have for descriptive and comparative purposes divided into several discrete stages (Figure 1). Three germination states were defined for each embryonic axis. An example of each state is shown.

Caryopsis and Embryo Germination

Isolated caryopses permit observation of the early embryo germination events that in seed are covered by the hull. The embryo is approximately one half the caryopsis length and is found near the surface of the caryopsis covered only by the caryopsis coat. The embryo scutellum surrounds the embryonic axis below and along the margins, forming a cuplike structure in which the axis lies (Rost, 1973). Before imbibition the caryopsis is dry, the caryopsis coat wrinkled and the embryo sunken within the endosperm. This germination state is referred to as N (no germination; Figures 1a and 2). As the caryopsis imbibes water the embryo swells and longitudinal cracks begin to appear in the caryopses coat over the middle of the embryo axis (Figure 3). The cracking of the caryopsis coat due to growth defines the
Figure 1. Giant foxtail germination states. Germination states are embryo axis specific and defined by growth: a) N, no germination; b) S1R0, first shoot (S1) growth state, embryo swells and cracks appear in caryopsis coat; c) S2R0, coleoptile extends and rises above caryopsis; d) S3R0, cotyledon emerges from coleoptile; e) first root axis growth state (R1), coleorhiza expands; f) S0R2, trichomes form on coleorhiza; g) S0R3, radicle emerges from coleorhiza.
Figure 2. The dry shrunken embryo axis (ea) within the endosperm of a giant foxtail caryopsis. Magnification = X80
Figure 3. S1R1 germination state. Giant foxtail caryopsis with swollen embryo. Longitudinal cracks (arrows) in the caryopsis coat appear above the embryo. Magnification = X50.
S1 state in caryopses (S for shoot apex; Figure 1b). Interpretation of the S1 state in isolated embryos was categorized by extension of the coleoptile beyond the scuttelum. It is possible, if S1 was the final germination state the individual seed reached, that the state could be due to water imbibition alone. Only cellular or molecular analyses may reveal whether S1 caryopsis coat cracking was due to germination growth or imbibition. In most observations cracking and embryo swelling in shoot tissues of S1’s were sufficient to eliminate imbibition as the sole explanation for the increase in embryo size and caryopsis coat cracking. It was also noted that occasionally upon dissection of intact ungerminated seed, arrested S1 caryopses were found within.

After imbibition, growth begins in germinable caryopses and the embryo increases in length. The second stage of germination for the shoot apex, S2, is determined by the upward bending of the coleoptile (Figures 1c and 4) followed by the emergence of the first true leaf, the cotyledon, from the coleoptile, which is the third stage, S3, in shoot germination (Figures 1d and 5).

The growth of the coleorhiza is the first germination event to occur for the root axis. When the coleorhiza has extended beyond the scuttelar cup, the R1 (R for root axis) germination stage has been achieved (Figures 1e and 6). Initiation of trichomes on the coleorhiza advances germination to stage R2 (Figure 7). Trichomes begin to appear at the coleorhiza margins then expand to cover the coleorhiza (Figure 4). The observed degree of trichome growth was variable and in some cases absent. Water absorption and seedling anchoring are thought to be trichome
Figure 4. S2R3 germination state. The coleoptile (cp) is curving upward while the coleorhiza is covered with trichomes (t) and the radicle (r) has emerged. Magnification = X35.
Figure 5. S3 germination state. First true leaf, cotyledon (ct), emerges from coleoptile (cp). Magnification = X50.
Figure 6. S1R1 germination state. Coleorhiza (cr) and coleoptile (cp) expanding. Arrows point out crack in caryopsis coat. Magnification = X 65.
Figure 7. S1R2 caryopsis germination state. Trichomes are found at the margins of the coleorhiza. Magnification = X100.
functions (Northam et al., 1996). The third and final embryo germination state for the root axis, R3, is emergence of the radicle from the coleorhiza (Figures 1f; 4).

**Seed Germination**

A door or lid-like structure known as the germination lid is found at the proximal end of the lemma. It is through this structure that the coleorhiza exits the hull during germination (Rost, 1975). The hull exists in one of two states depending on whether the germination lid is open or closed (Dekker et al., 1995). The germination lid is attached hinged to the lemma on one side; the other sides abut against the lemma. We observed in these investigations that the three unhinged sides lack any physical connection to the adjacent lemma. The hinge provides the only resistance to the opening of the germination lid which implies a physical mechanism for hull dormancy.

The first evidence of foxtail seed germination is usually protrusion of the coleorhiza through the germination lid (germination state R1 for seed, Figure 8). Other root axis states are the same as those described for caryopsis germination. Concurrent with coleorhiza and radicle growth is growth of the other embryo axis. Opening of the lemma and palea at the apical end of the seed is the first indication of shoot growth, followed by the emergence of the coleoptile (germination state S2 for seed; Figure 9). Initially the direction of coleoptile growth is controlled by the shape of the lemma, but soon orientation is upward. After a period of growth the first true leaf emerges from the coleoptile and the S3 state is achieved.
Figure 8. Side view of germination lid (gl) slightly open and the colerhiza (cr) emerging. Magnification = X150.
Figure 9. The emergence of the coleoptile (cp) from the distal end of the seed. The lemma (le) is above and the palea (pa) below. Magnification = X100.
Relative Sequence of Events

Both axes must follow a sequential pattern of development, i.e. R3 can not precede R1. The most typical germination state of giant foxtail seed is when germination takes place in both axes so that a seed, caryopsis or embryo is described by the germination stage of both its root and shoot, e.g. S1R2. Typically in excised caryopses and embryos the shoot axes will germinate somewhat sooner than the root axis, although there is considerable variation in the relative timing of axis specific germination among embryos. In seed, evidence of germination is first apparent by the coleorhiza emergence through the germination lid; only rarely does the emergence of the coleoptile at the distal end occur first.

The two axes behave independently of one another, and this independent axis growth makes possible several combinations of embryo germination: coleoptile only, coleorhiza only, both axes, an absence of germination (Dekker et al., 1996). Some combinations occur more frequently than others. In general, the greater the difference in germination between the axes, the less likely the combinations will occur. It is thought that the variety of embryo axis combinations of growth patterns are the result of differences in the amount of dormancy induced in axis tissues during embryogenesis, and maintained in those tissues subsequent to abscission. This axis-specific germinability may be an important contribution to the production of heterogeneous seed (Haar and Dekker, 1998) and heterogeneous behavior of that seed in the soil bank (Forcella et al., 1992; 1997). Variable seed germinability allows a plant to disperse seed through time. The behavior of individual seeds in response
to stimuli differs, allowing the population to respond to a heterogeneous environment (Skelly, 1996; Trevewas, 1987).

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CHAPTER 5. GENERAL CONCLUSIONS

The foxtails (*Setaria spp.*) are among the most troublesome weeds in the world. Current management strategies rely heavily on herbicides and tillage, both of which have harmful environmental consequences. If a goal of weed science is to move away from conventional weed control toward more sustainable systems, a better understanding of weed biology is necessary. Studies of fundamental weed population biology, physiology and adaptation are important first steps toward this goal. Through the work described in this dissertation, I investigated both the quantity and dormancy quality of seed, both of which are significant features of foxtail population biology.

Evolutionary success of an organism can be measured by reproductive output, area of the earth's surface covered, range of habitats or number of offspring (Baker, 1974). With regard to reproductive output, the foxtails are successful; under favorable conditions foxtails are prolific. A large number of offspring increases the likelihood of some individuals surviving to another generation and of these individuals locating new habitats. The addition of a large number of seed to the soil creates a seedbank which ensures that the species will persist at a site.

Quantity of seed is an important aspect in seed bank dynamics as is the seed dormancy quality. My work indicates that dormancy is variable, which gives the foxtails the ability to disperse germination over time and, under a
range of conditions, increases the chances of at least a few individuals escaping unfavorable conditions including weed control methods to reproduce.

This dissertation describes dormancy at a specific time in the plant life cycle, abscission. Characterization of seed dormancy at abscission permits evaluation of the influences of environment and plant development during seed development and dormancy induction. The environment continues to influence seed dormancy, but abscission allows evaluation before after-ripening and provides a good reference point for comparison between experiments. The degree of control in these studies is unusual for the topic of weed seed germination. The history of the seed was well known including, genotype, and developmental environment. Seeds were collected frequently at known stages of plant growth. In consideration of this, the degree of variation among samples, especially those grown under very controlled conditions, is revealing. It is apparent that a large amount of genetic diversity or environmental fluctuation is not required for a variable seed rain, but is an inherent characteristic of the foxtails.

It is believed that the degree of growth over a set period of time (rate) reflects the amount of seed dormancy. Seedlings that grow less or slower are more dormant/less germinable. To investigate the process of seed germination was observed and recorded in great detail by using electron microscopy. A connection between seed dormancy and seed vigor may exist because both are measured in terms of growth. The combined influences of both high seed production and variable dormancy allow foxtails to explore, colonize and persist
in a wide range of habitats. The success of this strategy can be shown by the current worldwide distribution of the foxtails as weeds.
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