The emergence capabilities of maize landraces

by

Jennifer McGuire Bousselot

A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Major: Sustainable Agriculture

Program of Study Committee:
Deborah Muenchrath, Major Professor
Lorna Michael Butler
Allen Knapp

Iowa State University

Ames, Iowa

2003

Graduate College
Iowa State University

This is to certify that the master's thesis of

Jennifer McGuire Bousselot

has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

Cold temperatures can interfere with maize (*Zea mays* L.) planting and yield potential is reduced when planting is delayed; spring frost and hail can also threaten early plantings. If producers could plant deeper and earlier in the spring, the planting season would be extended. When maize is planted deeply frost may be less damaging because the growing point stays insulated below the soil surface longer than if the seed (caryopsis) is planted at a shallow depth. Traditionally, Native Americans in the Southwestern United States (U.S.) have planted their open pollinated landraces of maize deeply. The capacity of 11 landraces and one Corn Belt check population to emerge from various depths, between 5 and 45 cm, was evaluated in a growth chamber study. A field study was performed comparing those landraces that successfully emerged ($\geq$75% success) from the 25 cm depth in the growth chamber to the check population. Results of the growth chamber and field experiments indicate that some landraces have a greater capacity to emerge from depth than the check population. Seedling dry matter partitioning and morphological characteristics were also examined. Emergence capacity is not related to initial seed weight. Mesocotyl elongation largely accounts for emergence success from the greater planting depths. The landraces partitioned relatively more dry matter to roots than shoots compared to the check population; these populations may therefore be useful for the development of maize varieties tolerant to some abiotic stresses such as drought.

INTRODUCTION

Farming systems in the Southwestern U.S. are examples of systems that have persisted, and therefore, may provide elements that could contribute toward sustainability. "Sustainable agriculture describes a food and fiber system that is economically viable, environmentally safe, and socially acceptable" and "sustainability denotes any system capable of persisting" (Robertson and Harwood 2001: 99). Studying their agricultural and social systems, including genetic resources, may provide information that will contribute to the development of a sustainable agronomic future.

A major topic in sustainable agriculture is the maintenance of genetic diversity both on the species and landscape levels. One helpful concept in maintaining genetic diversity in maize is conservation genetics; "conservation genetics is concerned with population genetic variation, population viability, and the future evolution of species" (Woodruff 2001: 811). Within species genetic diversity is important for the "future evolution" of that species; maintaining diversity also allows breeders to have more genetic stock to work with in the future (Harlan 1975). The characterization of plant genetic resources is needed to document potential traits available for crop improvement and to increase the genetic diversity of crops (Goodman 1990).

Today's Corn Belt commercial maize hybrids and their inbred parents resulted from intense human selection and controlled pollinations; these inbreds are homozygous and homogeneous and hybrids generated by mating inbred lines are therefore also homogeneous. The term homogeneous refers to an organism that is "composed of parts or elements that are all of the same kind" (Random House 1995: 642); this indicates that homogeneous organisms have a narrow genetic base. Although there are thousands of accessions of maize worldwide, most commercially available Corn Belt maize hybrids are derived from just a few, primarily from crosses between Iowa Stiff Stalk Synthetic (BSSS) populations and Lancaster Sure Crop (Smith 1988). Thus, Corn Belt maize has a narrow genetic base.

In contrast, landraces are not subjected to controlled pollinations, but instead, plants in a field are allowed to randomly mate or open pollinate; consequently, maize landraces are very heterogeneous. The term heterogeneous refers to an organism that is "composed of parts of different kinds; having widely dissimilar elements or constituents" (Random House 1995: 629); this indicates that heterogeneous organisms have a wide genetic base. A landrace is a population of cultivated plants which is adapted to its local native environment by natural and human selection pressures. Human selection pressure can be exerted by saving the seed of plants and ears that display characteristics considered desirable by the farmers. There are two types of human selection: "conscious" and "unconscious" selection. Conscious selection is choosing progeny based on desirable traits expressed in the parent plant; an example of unconscious selection is utilization of progeny that is most easily harvested (Venturieri 2001: 898). A landrace can also be described as "a group of related individuals with enough characteristics in common to permit their recognition as a group"; a race has to have "a significant number of genes in common" (Anderson and Cutler 1942: 71). The movement and trading between ethnic groups throughout history has influenced the genetic make-up of landraces (Harlan 1975).

Geographic isolation of landraces native to the Southwest U.S. has allowed the landraces to stay relatively uncontaminated by other maize producing regions in North America (Carter and Anderson 1945). The genetic diversity and heterogeneity of the landraces have contributed to the long-term success of Native American agriculture in the Southwest by providing a genetic buffer to the relatively harsh environment. As genetic diversity within a species increases heterogeneity also increases; increased heterogeneity improves the "fitness components (viability, growth rate, fecundity, mating success, and developmental success)" of a species, which can allow a species to survive in shifting environmental conditions (Nevo 2001: 211). Having a narrow genetic base (i.e. Corn Belt hybrids) can leave a species vulnerable to new or changing stresses. The greatest genetic yield gains are likely to result from improved stress tolerance (Tollenaar and Wu 1999). Producers frequently encounter abiotic stresses that threaten crops; some abiotic stresses include frost and drought.

Early growing season conditions in the Corn Belt often include wet field conditions and cold temperatures, which can prevent producers from timely planting or significantly delay germination and emergence. Spring days with good field and weather conditions are limited and farm size is increasing; producers are interested in planting early to spread their labor and equipment over more acres and still complete planting in a timely manner.

Planting date has a strong influence on yield; late planting dates reduce grain weight (Cirilo and Andrade 1994). In Iowa, maize yield potential is reduced about 1 bushel per acre per day of planting delay after May 10 (Farnham 2001). Optimally, maize would be planted early in the season and not emerge until after the frost-free date which is around May 10th in Iowa.

In industry there is work being performed on polymer seed coatings; these coatings are designed to suppress seed germination until soil temperatures are favorable for seedling development (Murua and Vyn 2002). An alternative strategy to seed coatings, which may be particularly useful for organic producers, would be to use varieties adapted to deeper planting. In modern commercial production, maize is customarily planted at 6 cm or less (Troyer 1997). Deeper planting may delay emergence of the growing point, extending the protection of the sensitive growing point from spring frost damage. If maize is planted deeper, then the planting window is expanded.

Some years, soil is too dry in the planting zone to obtain good germination and stand establishment. Soil tends to have more moisture at greater depths. Deep planting could also enable producers to place the seed in moist soil for better germination and emergence. For example, in semiarid eastern Kenya maize producers plant deeply in order to access moisture and to avoid problems associated with dry soil (Itabari et al. 1993). Planting maize deeply could be an important tool in lessening the annual springtime struggles of time availability and abiotic stresses that producers face.

In about the first half of 20th century, various studies were performed in the U.S. on the importance of planting depth and emergence in maize (Andrew 1953; Collins 1914a; Dungan 1950); since then, limited studies have been performed (Troyer 1997). These studies have shown that some maize cultivars can emerge from extraordinary depths, including the few maize landraces native to the U.S. Southwest examined in the studies.

Traditionally, Native Americans in the Southwestern U.S. plant their open-pollinated landraces of maize very deeply, 8 to 45 cm (Table 1). The main reason these Native American groups planted deeply was for moisture; other reasons for planting deeply are to protect from washouts and possibly from frost (Muenchrath and Salvador 1995).

Table 1: Planting depths of 11 Southwest landraces and a Corn Belt population.

Population	Traditional Planting Depth	Reference
	cm	
Havasupai, Grand Canyon	10 to 40	
Havasupai-Hopi	10 to 40	
Hopi	15 to 45	Brown et al. 1945; Collins 1914b
Hopi, Hotevilla	15 to 45	Brown et al. 1945; Collins 1914b
Hopi, Kokoma	15 to 45	Brown et al. 1945; Collins 1914b
Hopi, New Oraibi	15 to 45	Brown et al. 1945; Collins 1914b
Hopi, Shungopovi	15 to 45	Brown et al. 1945; Collins 1914b
Mojave	10 to 15	Stewart 1983
Navajo, Kayenta	15 to 45	Collins 1914b; Hill 1938
Tohono	10 to 15	Castetter and Bell 1942
Zuni	8 to 30	Muenchrath et al. 2002
BSSS-53 (Corn Belt)	≤ 6	Troyer 1997

Numerous ethnic groups of the Southwestern U.S. (Figure 1) developed and maintained their own sets of maize landraces adapted to their local environments and cultures. These environments can be separated into two major areas: the low desert of Arizona, and the higher elevation Colorado Plateau. In contrast to the arid and semiarid Southwest, the Corn Belt, which includes Iowa, has humid to subhumid climates (Table 2). Corn Belt and Colorado Plateau farmers, however, face similar spring frost risks and, in some years, dry soil conditions. There could be genes present in Southwest U.S. maize landraces that would be useful for improving Corn Belt varieties (Brown et al. 1952), specifically, genetics for capacity to emerge from great depths.

Hypothesis

Landraces of maize native to the U.S. Southwest can emerge from greater planting depths than Corn Belt maize.

Objectives

1. Identify maize populations that have the capacity to emerge from greater depths.
2. Examine relationships between maize seedling morphology and dry matter allocation and emergence capacity.
3. Examine the potential utility of landraces relative to issues in sustainable agriculture, specifically timely planting and maize genetic diversity.

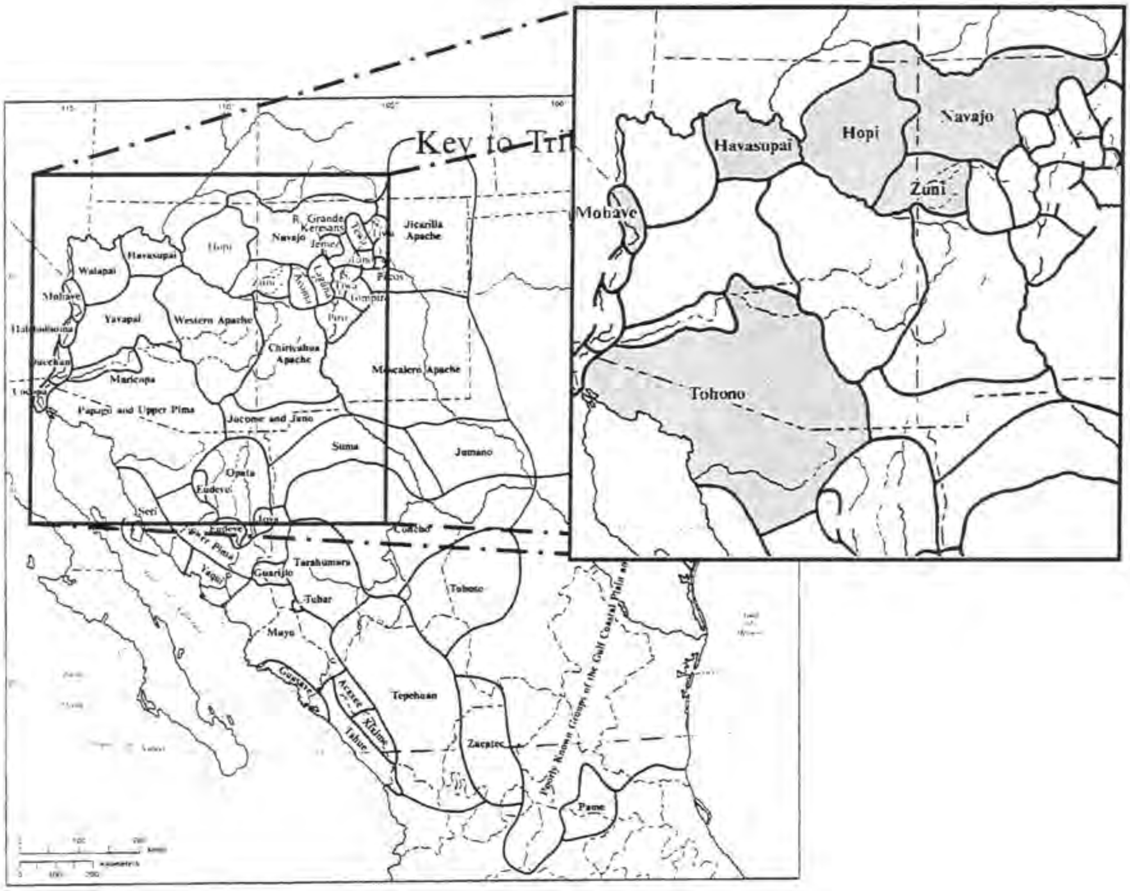

Figure 1: Map showing geographic distribution of Native American groups in the Southwest US. Inset highlights those ethnic groups associated with the landraces examined in this study. (Adapted from 1979 Ortiz, ed.).

Table 2: Climatic and geographic facts for the native areas of the maize populations tested in this study. Temperature and precipitation are reported as monthly averages.

Region	Populations	Elevation	Location	Month	Max temp	Min temp	Precipitation
		m			----------°C----------		mm
Colorado Plateau	Havasupai	978	Supai, AZ	May	29.9	11.0	10.4
				Jun	35.7	15.9	6.6
				Jul	37.6	18.9	31.4
				Aug	36.0	17.7	35.9
				Sep	32.4	13.9	16.4
	Hopi	1893	Keams Canyon, AZ	May	23.0	3.8	11.1
				Jun	29.4	8.4	8.3
				Jul	31.6	12.9	31.6
				Aug	29.6	12.6	41.7
				Sep	26.3	8.2	20.0
	Navajo	1731	Kayenta, AZ	May	24.9	7.0	9.9
				Jun	30.7	11.4	7.1
				Jul	33.0	15.5	29.9
				Aug	31.4	14.6	35.4
				Sep	27.9	10.0	19.0
	Zuni	1923	Zuni, NM	May	23.7	3.4	11.6
				Jun	29.4	8.0	10.6
				Jul	31.3	12.4	49.3
				Aug	29.6	12.1	56.4
				Sep	26.7	7.9	30.6
Sonoran Desert	Mojave	124	Parker, AZ	May	35.1	15.4	1.8
				Jun	40.0	20.1	0.8
				Jul	42.3	25.1	8.6
				Aug	41.4	24.8	15.7
				Sep	38.6	20.0	12.4
	Tohono	722	Sells, AZ	May	32.5	13.2	1.8
				Jun	37.7	18.6	5.1
				Jul	38.2	22.1	66.8
				Aug	36.9	21.1	66.8
				Sep	36.3	18.5	30.1
Corn Belt	BSSS	263	Cedar Rapids, IA	May	22.4	9.9	97.4
				Jun	27.6	15.1	113.1
				Jul	29.6	17.4	102.7
				Aug	28.2	16.1	107.0
				Sep	24.0	11.1	82.7

Southwest information adapted from: http://www.wrcc.dri.edu/inventory.html and http://www.wrcc.dri.edu/climsum.html
Corn Belt information adapted from: http://www.crairport.org/genav/aviators.htm and http://www.crh.noaa.gov/dvn/climate/CedarRapidsIowa.htm

LITERATURE REVIEW

The Value of Indigenous Knowledge

"This ecologic interaction between man and his plants is...all that ethnobotanical research is about." In this passage, Sarukhan (1985: 432) describes a phenomenon not always included in the scientific investigations of plants – ethnobotany. Research should not separate the "interaction" from the study of a plant; we need to learn about maize from the Native Americans in order to use it to its potential (Collins 1914b).

Throughout time, ethnic groups had to make the right decisions when it came to seeds, planting and other crop management or they would suffer dire consequences; this was a situation where research and learning were done efficiently because they had to be (Sarukhan 1985). The Native Americans, perhaps unknowingly, but efficiently performed experiments as they cultivated their maize landraces (Collins 1914b). The fact that these ethnic groups survived in the arid Southwest for centuries proves that they were successful experimenters.

Investigating what traits were selected for as a species was being domesticated and locally adapted provides information about those ethnic groups (Sarukhan 1985). Also, investigators can tell what purpose the plant was being used for and its role in the culture. Maize has been produced in the U.S. Southwest for at least 2000 years (Adams 1994; Cordell 1997). Maize was not only a staple crop, but also became central in the region's native cultures. Maize remains agriculturally and culturally significant in many Native American communities.

Southwest Maize Culture

Corn is the center of life, the essence of life.
I still have a field. I still plant my corn.
Because why should I participate and pray for rain
if I don't have any plants for the rains to come and nourish?
Hopi man, Arizona.
(Trimble 1986)

For Hopi and other Southwestern Native Americans, not only is maize the central food source, but their cultures are so tied to maize that the history of their maize cannot be separated from the history of their cultures (Anderson 1954; Brown et al. 1952). Maize has been important to the Native Americans of the Southwest on many levels, "Indian people have perceived and used their traditions related to corn. They have seen it like the Tohono...and the Pueblo as mother ... like Navajo people as healer. ...corn is an enabler for things to happen." (Ortiz 1994: 544).

Each Southwestern culture had their own unique "corn songs" and rituals associated with or involving maize (Fussell 1992: 114):

- Havasupai maize harvest feasts and dances lasted several days; some surrounding ethnic groups (Navajo and Hopi) were invited (Schwartz 1983).
- A "corn-mother" is an ear of maize given to every Hopi child to protect and mother them through life (Brown et al. 1952:597).
- Navajo use maize pollen in healing ceremonies (Fussell 1992; Ortiz 1994).
- Tohono O'odham ceremony of singing up the corn is associated with the saguaro cactus fruit harvest and performed to bring the summer rains for maize production (Castetter and Bell 1942: 222).

- Zuni night dances are held to exchange seed; also, Zuni sing to their maize fields to encourage growth (Cushing 1974; Fussell 1992).

The maize of the Native Americans has also been described as a "gift of the gods" (Collins 1914b: 255).

Over generations, Southwestern Native Americans developed cultivars and management strategies to obtain reliable maize production despite their agriculturally challenging environments. Their maize cultivars yield comparably with other landraces and open pollinated Corn Belt varieties commonly produced before the widespread production of hybrids created by controlled pollinations (Troyer 1999). Southwestern Native American groups developed landraces and production practices suited to the specific resources and constraints of their particular environments.

Early Season Environmental Stresses

The 11 landraces native to the U.S. Southwest involved in this study are from arid to semiarid environments that are prone to drought and temperature extremes. In this region water availability is the main limiting factor for crop production at the lower elevations. High elevations receive more precipitation than lower elevations, but have a greater probability of frost, especially early in the growing season (Hendricks 1985; Tuan et al. 1973). Each ethnic group used planting times and depths that reduce potential risks associated with such early season environmental stresses in their area.

Planting Conditions and Timing

Throughout the Southwest, there is little or no precipitation during spring and early summer. People located in the lower deserts depend on floodwaters and summer rains to establish their crops. The Mojave planted their maize into the floodplains surrounding the Colorado River; as the spring floods subsided in June nutrients and sediment were deposited creating favorable growing conditions for maize (Stewart 1983). Tohono O'odham time maize planting with the onset of the summer rains, ordinarily in July. Tohono O'odham place fields on alluvial fans where the crop will receive storm runoff from adjacent upland areas or ephemeral waterways (Castetter and Bell 1942; Nabhan 1983; Hackenberg 1983). Both the Mojave and Tohono O'odham do not risk precious seed unless assured of adequate moisture to obtain germination and establishment.

In contrast to the early season conditions in the lower desert, the Hopi, along with other ethnic groups living on the Colorado Plateau (Havasupai, Navajo and Zuni), must balance their early growing season constraints of both limited moisture availability and cold temperatures (Hack 1942; Hill 1938; Muenchrath et al. 2002). Because the growing season length is limited by fall frost, they cannot delay planting until the summer rainy season. Instead, they rely on residual soil moisture from winter precipitation for germination and crop establishment during the dry spring and early summer. They use a long planting season, April through mid June, and plant more deeply to distribute risks of drought and frost (Schwartz 1983).

The Hopi's growing season begins in early April, when planting is done in order to harvest green maize in July (about 100 days after planting) (Hack 1942). The green maize is picked young and roasted for a religious ceremony and celebration, called *Nimankatcina.*

This ceremony involves traditional dances done to bring the summer rains needed to sustain the crop through flowering and grain fill. Green maize is planted early enough in the season that frost is a threat; therefore, the Hopi strategically plant these fields in more protected or enclosed areas, such as adjacent to mesa or canyon walls that retain heat to shield the maize from frost damage. The second wave of planting begins in mid-May and continues into mid-June to spread the risk of abiotic stress effects occurring at any one stage of maize development. The majority of this maize is planted for mature grain harvest in the fall (115 to 130 days after planting) (Bradfield 1971). In addition, the Hopi have a "crop insurance system" in which they hold a fall's harvest, rather than consume it, until the following year's yield is guaranteed (Brown et al. 1952: 599). The other Colorado Plateau groups use strategies similar to the Hopi ones (Muenchrath et al. 2002).

Planting Depth

Southwestern Native Americans traditionally plant maize by hand, opening the soil with a digging stick (Hill 1938; Schwartz 1983; Stewart 1983) and placing multiple seed together in each hole (Brown et al 1952; Castetter and Bell 1942; Cushing 1974). These plant clusters or "hills" are spaced equidistantly about 1 to 3 m apart; the spacing of the hills generally depends on the location's usual moisture availability over the growing season. The region's Native Americans tend to plant at the depth necessary to place the seed in moist soil, usually at the interface between a field's sandier and clay layers; the moisture held in the clay zone makes germination and early growth possible on the Colorado Plateau. Each ethnic group has a traditional range of planting depths that relates to the conditions at planting and early season risks (Table 1). Those groups that plant into moist soil, such as the Mojave and

Tohono O'odahm, plant more shallowly than those that plant under drier conditions or where early season frost is a common hazard. Sowing deeply and in hills also improves the standability of the plants and reduces washouts under storm runoff and flood conditions during the growing season.

Deeper planting may protect the seedling from spring frosts because the sensitive growing point may remain underground longer. When a maize plant is damaged by frost, the seedling will recover only if the growing point is not severely damaged or killed. Temperature extremes do not kill the plant if the growing point is protected (Blacklow 1972). When planted at depths of 6 cm or less, maize seedling growing points are ordinarily protected from frost below ground until about the V7 vegetative stage (Elmore and Doupnik 1995).

In dry growing regions, planting maize deeply may allow the seed to be placed in moist soil. In a 1961 trial performed in North Dakota, a 2.5 cm planting depth was very unsuccessful and slow at emerging; the researchers indicated that "germination was severely retarded by a soil water deficit" (Alessi and Power 1971:718). In a Kenyan study testing planting depth of maize it was found that the deeper plantings (7.5 and 12.5 cm) had better germination and emergence success than the shallower planting depth (2.5 cm); after investigating the failure of the 2.5 cm planting depth, scientists concluded that lack of soil moisture was the cause (Itabari et al. 1993).

Corn Belt maize is typically planted up to 6 cm deep (Troyer 1997). Because of how deep the Native Americans traditionally plant their maize, studies have been performed on the emergence capacity of some Southwest landraces. Navajo maize emergence was compared with a Chinese maize line and a Boone County (Corn Belt) maize line (Collins

1914a). The Navajo maize emerged from the deepest planting depth (30 cm), the Chinese came up from 10 cm deep, and the Boone maize emerged from 20 cm deep. In a similar study, a line of Navajo maize was compared to a Corn Belt variety common at the time, called U.S. Hybrid 13. The Navajo maize was superior to the U.S. 13 maize in emerging from depth; the planting depths ranged from 5 to 30 cm deep (Dungan 1950). More recently, Troyer (1997) located genes responsible for long mesocotyl length from Hopi-Kokoma genetics. The results of these studies indicate that there at least a few landraces native to the Southwest that have the capacity to emerge from relatively great depths.

Emergence from Depth

The mesocotyl is the organ that pushes the shoot (plumule) to the soil surface during the emergence process (Kiesselbach 1949) (Figure 2). The tender shoot is protected by the coleoptile on the way to the surface. The coleoptile ordinarily sheaths the shoot until it breaks the surface of the soil, where exposure to light slows or stops the coleoptile's growth, allowing the shoot to emerge from the coleoptile (Blacklow 1972). If the shoot opens in soil 2 or more cm from the soil surface, the tender seedling tends not to have the ability to make it to the surface (Collins 1914a). In another planting depth study, prematurely opened seedlings grew laterally when the coleoptile opened underground (Andrew 1953).

The mesocotyl is credited as the organ that allows emergence of Southwest landraces from their traditional planting depths of 8 to 45 cm (Collins 1914a; Troyer 1997). Consistent with traditional planting depths, Hopi maize has mesocotyls up to 36 cm long (Troyer 1997); Navajo maize has been shown to have mesocotyls of 30 cm (Collins 1914a). Mesocotyl lengths of Corn Belt maize, customarily planted up to 6 cm deep, only reached 10

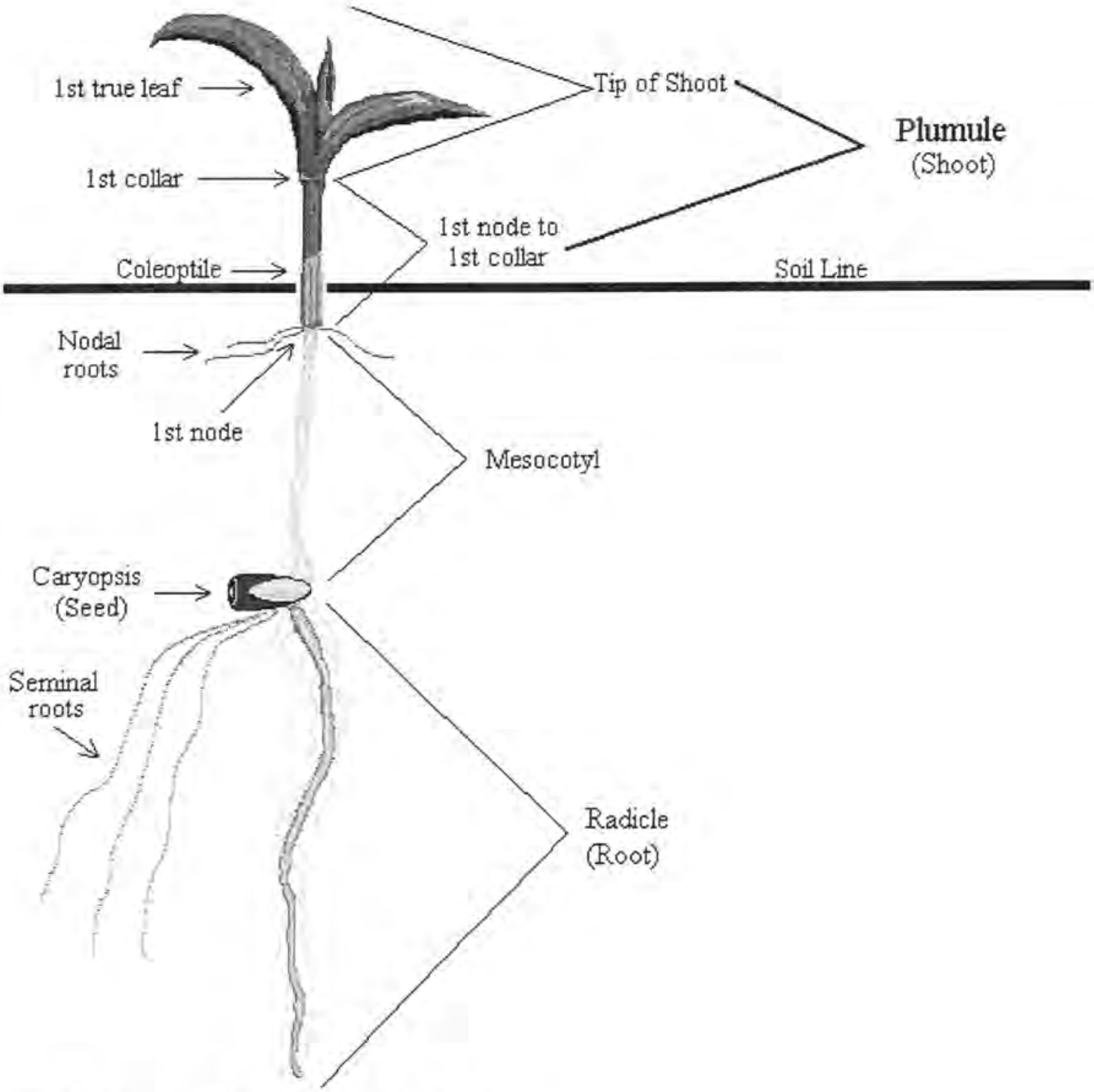

Figure 2: Diagram of maize seedling parts.

cm length. Greater understanding of the emergence capacity of Southwest maize could benefit Corn Belt and worldwide maize cultivation (Collins 1914b) especially drought prone areas. In a study on planting depth and emergence, mesocotyl length was not limited by seed reserves. Based on a study involving a single Southwest cultivar, Hopi-Kokoma, Troyer (1997) recommends incorporating long mesocotyl genetics of Southwest populations into

Corn Belt yellow dent varieties by backcrossing. The previous studies performed on emergence from deep planting each involved only one or two of the Southwest landraces; the present study tests 11 landraces for emergence capacity from depth.

MATERIALS AND METHODS

Genetic Materials

Eleven open pollinated maize landraces, native to the Southwestern U. S. and associated with Native American groups who customarily plant maize deeply, were evaluated for their capacity to emerge from various depths (Table 3). Hopi cultivars, originally collected in different villages, were specifically included because of their reputed capacity to emerge from extraordinary depths (Collins 1914a; Bradfield 1971; Brown 1952; GRIN 2002; Hack 1942).

Table 3: Treatment depths included in each experiment.

	Depth				
Experiment	5 cm	15 cm	25 cm	35 cm	45 cm
1	*	*	*		
2	*			*	*
3			*		
4	*	*	*		

Because the Southwest cultivars are heterogeneous populations, an improved heterogeneous modern maize population, BSSS-53 (Cycle 0) was used as the check. Iowa Stiff Stalk Synthetic (BSSS), generated at Iowa State University beginning in the 1930s, was originally derived from Reid's Yellow Dent and other lines adapted to the Midwest (Troyer 1999). Many of today's Corn Belt commercial varieties were derived, in part, from BSSS populations. Thus, a BSSS population was used as an analogue to estimate the relative emergence capacity of the landraces and modern Corn Belt commercial varieties.

Landrace seed stock was obtained primarily from the USDA North Central Regional Plant Introduction Station (NCRPIS), Ames, IA (Table 4). To increase seed, the landraces and check population were grown at the Iowa State University Bruner Research Farm, located approximately 4 km west of Ames, Iowa, on Nicolett loam and Canisteo silty clay loam soils (Fine-loamy, mixed, mesic Aquic Hapludolls; and Fine-loamy, mixed (calcareous), mesic Typic Haplaquolls, respectively) (Soil Survey Staff 1979). Seed of each population was increased in 2001 by controlled pollinations. To maintain the genetic diversity within each population, more than 200 plants of each population were grown and at least 100 ears of each population were pollinated using a chain-cross mating system to prevent self-pollinations and reciprocal crosses. In the chain-cross mating system, pollination began at the same corner of the plot every day, with each bagged and shedding tassel used to pollinate the next available silked ear in the sequence of plants (Figure 3). At maturity, ears were harvested, dried in circulating air at 32°C for 4 days, and shelled.

Table 4: NCRPIS numbers, seed sources, endosperm type and experiment inclusion for the 11 landraces and the check population.

Population	Abbreviation	NCRPIS	Seed Source	Endosperm	Experiment
Havasupai	Hav	PI 317675	PI Station	floury	1,3
Havasupai-Hopi	Hav-Hopi	PI 476870	PI Station	floury	1
Hopi	Hopi	PI 213735	PI Station	floury	1,3
Hopi, Hotevilla	Hopi-H	PI 213734	PI Station	floury	1
Hopi, Kokoma	Hopi-K	PI 213733	PI Station	floury	1,3
Hopi, New Oraibi	Hopi-NO	PI 476869	PI Station	flint/floury	1,2,3,4
Hopi, Shungopovi	Hopi-Sh	PI 420250	PI Station	flint/floury	1,3
Mojave	Mojave	PI 218186	PI Station	floury	1,2,3,4
Navajo, Kayenta	Navajo	PI 311229	PI Station	flint/floury	1
Tohono	Tohono		Native Seeds, Tucson	floury	1
Zuni	Zuni		D. Muenchrath, ISU	flint/floury	1,2,3,4
BSSS 53	BSSS		A. Hallauer, ISU	dent	1,2,3,4

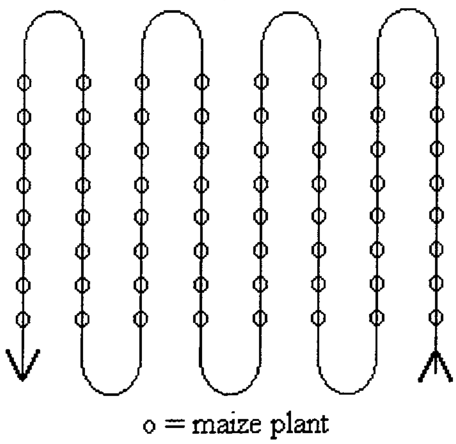

Figure 3: Diagram of chain-cross mating system.

Seed Quality

To assess seed quality, seed germination tests of the landraces and the check population were performed following the guidelines established by the Association of Official Seed Analysts (AOSA 2001). Germination percentage of each population was calculated by the ratio of normal seedlings to total number of seed used in the trial (i.e. 50 normal/50 seed used = 100%); normal seedlings are those seedlings that are not dead or abnormal as defined by AOSA (2001).

Seed was screened through a series of sieves to exclude unusually small and large seed from the study to block potential effects due to size differences. Seeds that fit through a 24/64 inch sieve, but not through a 20/64 inch one, were retained for use in the experiments.

One hundred seed from each of the 11 landraces and check population were counted out and weighed from screened stock to determine the 100-seed weight. Each seed used in the experiment was randomly drawn from the screened seed stock that met the size qualification. Initial seed weight of each kernel was determined before planting.

Emergence Capacity Tests

Emergence capacity was evaluated in a sequence of three controlled environment experiments (Experiments 1, 2, and 3) and one field test (Experiment 4).

- Experiment 1 – Each landrace and check was planted at each of three treatment depths, 5, 15 and 25 cm.
- Experiment 2 – Each landrace that consistently emerged from 25 cm in Experiment 1 (75% emergence), plus the check population, was planted at 5 (control), 35 and 45 cm depths.
- Experiment 3 – Those landraces that exhibited greater than 50% emergence from 25 cm depth in Experiment 1, plus the check, were tested for emergence from 25 cm depth in a replicated study.
- Experiment 4 – The landraces and check tested in Experiment 2 were similarly tested for emergence from 5, 15 and 25 cm under field conditions.

Seedling characteristics were examined in conjunction with the first two controlled environment experiments.

Controlled Environment Studies

Experiments 1, 2 and 3, were conducted under controlled conditions in a 2.74 x 1.22 m growth chamber (Conviron Model CMP 3244 Growth Chamber, Pembina, ND). The chamber control panel was programmed to maintain optimal light and temperature conditions at 12-h of 125 $\mu E\ m^{-2}\ s^{-1}$ light per 24-hr period and 25 °C constant ambient temperature.

The bank of lights was placed about 1 m above the top of the planting containers. A HOBO® H8 Pro RH/Temperature Logger (Onset Computer Co., Bourne, MA) was placed in the chamber to monitor its environmental conditions.

Planting Container

In Experiments 1, 2 and 3, seed were planted in 60 x 10.2 cm polyvinylchloride (PVC) pipes. Each PVC pipe was cut longitudinally with a bandsaw to facilitate seedling retrieval at the end of each experiment. Two hose clamps were used to fasten the pipe halves together. One clamp was fastened approximately 20 cm from the top of the PVC pipe. The other clamp was fastened 2 cm from the pipe base and secured a 16.5 x 16.5 cm piece of Weed-X® commercial grade porous landscape fabric (Dalen Products Inc., Knoxville TN) on the bottom of the pipe. The landscape cloth allowed drainage while retaining the sand medium. This PVC pipe apparatus was used as a container to grow the maize seedlings (Figure 4).

Planting

Controlled Environment (Experiments 1, 2 and 3)

Industrial coarse quartz sand (Table 5), obtained from Unimin Co., LeSueur, MN, was autoclaved before each trial to prevent disease problems. Damp sand was placed in the PVC pipe apparatus up to the desired planting depth. For each population, kernels were

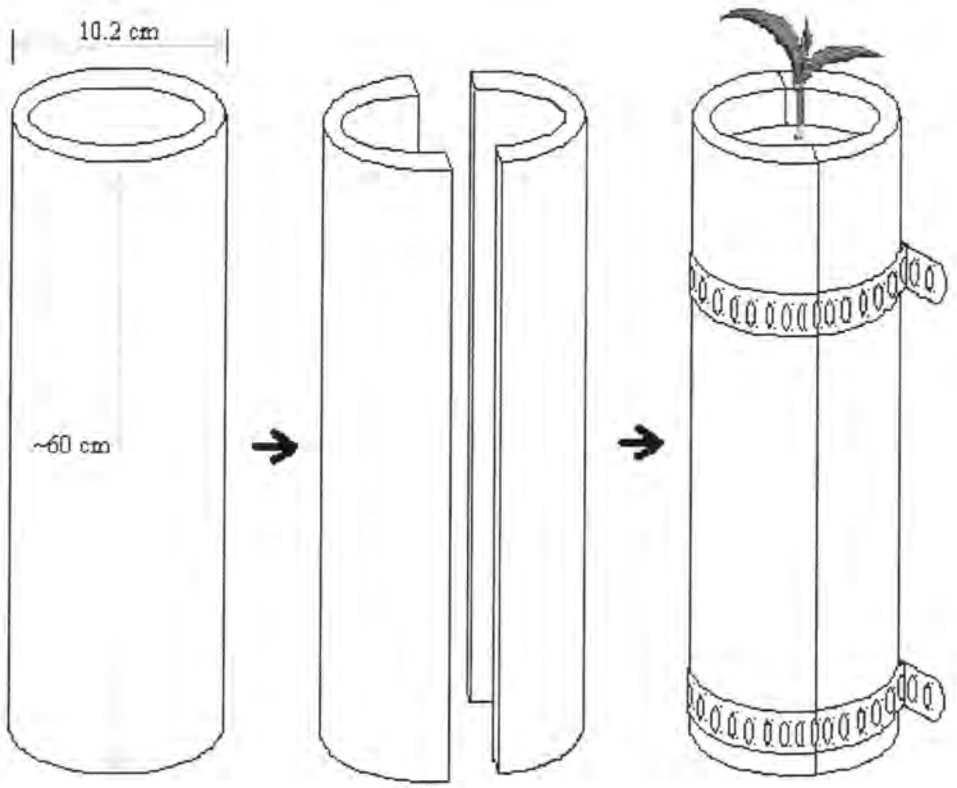

Figure 4: Diagram of PVC pipe apparatus.

Table 5: Sand medium particle size analysis.

Soil Texture	%
Very Coarse Sand	6
Coarse Sand	85
Medium Sand	9

drawn blindly and at random from a cloth bag containing the screened seed of similar size, and individual kernel weight determined before planting.

- Experiment 1 – In total, twelve seeds of each of the 11 landraces and check population were planted at each of three treatment depths, 5, 15, and 25 cm.

- Experiment 2 – In total, twelve seeds of the three landraces that qualified and check population were planted at depths of 5, 35 and 45 cm.
- Experiment 3 – In total, forty seeds of each of the seven qualified landraces and check population were planted at 25 cm deep.

One seed was centered in each pipe on the sand surface and the remaining pipe volume filled with more damp sand to 2 cm from the top of the pipe. Pipes were placed in the growth chamber for 14 d. Each pipe was watered with 250 ml distilled water every 48 hr. Each pipe was covered with aluminum foil to reduce moisture loss and prevent seedling exposure to light until emergence. In preliminary trials, seedlings tended to open their shoots below ground level when pipes were not covered with foil to exclude light; light can encourage the shoot to open below ground (Collins 1914a). Similar to most domesticated crops, maize does not need light to germinate (Gardner et al. 1985). Once emerged, a small hole was punctured in the foil to allow the seedling to grow into the light while minimizing evaporation from the sand.

Field Experiment (Experiment 4)

Experiment 4 was planted 2 August 2002 at the Iowa State University Bruner Research Farm in Clarion loam soil (Fine-loamy, mixed, mesic Typic Hapludolls) (Soil Survey Staff 1979). The maize was planted following the oat crop harvested in July 2002. Ten kernels of each population were spaced approximately 25 cm apart within the row, with approximately 76 cm between rows in each replication; within the experiment, a total of 30 seed were planted from each population at each depth. Two methods of planting were used to attain the desired treatment depths. Hand-held punch planters (Almaco, Nevada, IA) were set to place the seed at 5 cm for the shallowest treatment depth. Because the punch planter cannot reach depths of 15 and 25 cm, narrow blade spades were marked at the appropriate depths (15 or 25 cm) and inserted into the ground to the marked depth; the spade handle was pushed forward and pulled back several times to create a slot reaching down to the desired planting depth. With the tip of the spade visible, a kernel was dropped to the bottom of the opening. To keep the seed at the desired depth, a stick was used to hold it in place while the spade was removed. The slot was filled and the soil surface leveled over the planted seed.

Soil bulk density and particle size analyses were measured from samples taken at 5 and 20 cm deep. For each depth, four random samples were taken using a bulb planter. These soil samples were oven dried at 105°C to constant weight; soil bulk density was determined by dividing the dry weight of the soil sample by the bulk volume of the bulb planter used to sample, 517 cm^3. Particle size analyses were performed by the ISU Agronomy Pedometrics Laboratory using a modification of the pipette method (USDA-NRCS-NSSC 1996; Konen 1999) with samples pretreated with 30% hydrogen peroxide reagent for digestion of organic matter and a sodium hexametaphosphate solution for clay dispersion.

Data Collection

Controlled Environment Studies

Beginning two days after planting, the pipes were checked for seedling emergence at 24 hr intervals. In Experiments 1 and 2 only, the PVC pipes were removed from the growth chamber 14 days after planting and seedlings harvested. To retrieve intact seedlings, each pipe apparatus was disassembled and the sand gently removed from around the seedling. General observations and ultimate seed depth were noted. Tissue lengths were also determined (Figure 2):

- Radicle length,
- Mesocotyl length (seed to the first node),
- First node to the first leaf collar, and
- First collar to the longest leaf tip for the remainder of the shoot.

Each extracted seedling was rinsed in distilled water to remove remaining sand. Seedlings from each of the three depths in replications 5 through 10 of Experiment 1 were carefully spread out on a flat surface and photographed to document seedling phenotype and root architectures. For comparison, each landrace seedling was photographed side by side with a check population seedling and a meter stick for scale; a string was placed to depict the soil surface.

Each seedling was then partitioned into shoot (from the top of the seed upwards), seed, and roots (Figure 2). The partitioned seedling was placed in labeled paper envelopes and dried in an oven for 48 hr at 70°C. and weighed. Dry weights were obtained from each of the partitioned seedling parts.

Field Experiment

Emergence was monitored daily beginning four days after planting and continuing until 30 Aug 2002. The date of VE was recorded for each seedling. No other data were collected on the seedlings. Soil temperature and moisture at 10 cm was collected by an automated system located about 100 m from the field site. The system also collected weather data, including air temperature and precipitation.

Experimental Design

Experiments 1 and 2

Experiments 1 and 2 were two-factor randomized block designs with replications as blocks, and maize population and planting depth as factors. Experiment 1 had 36 population x depth combinations (12 populations at three planting depths). Experiment 2 had 12 population x depth combinations (4 populations at three depths). Twelve individuals of each population were tested for emergence capacity from each of the three depth treatments. Each experiment and replication included BSSS as the check population and the 5 cm planting depth as the control depth.

Because of time and growth chamber space constraints, each replication consisted of a total of 36 pipes. Each replication in Experiment 1 tested one seed per population at each of the three depths. Each replication in Experiment 2 tested three seed per population at each of the three depths. At the beginning of each replication, pipes were randomly assigned a code number from 1 to 36 to prevent any bias. Once the pipes were labeled and planted, they were randomly placed within the replication block.

Only two full replications fit in the growth chamber at once, for a total of 72 pipes in the chamber. In order to keep the work manageable and the chamber conditions consistent across replications, one replication was initiated and another ended each week. For the first and final replications of each experiment, the other half of the chamber was filled with 36 'filler' pipes planted in a similar manner as in the replications, but no data were collected from the filler pipes. At the end of the first week after replication 1 was initiated, the filler pipes were removed and replaced with replication 2; the following week, replication 1 was removed, data collected, and replication 3 initiated; and so forth (Figure 5).

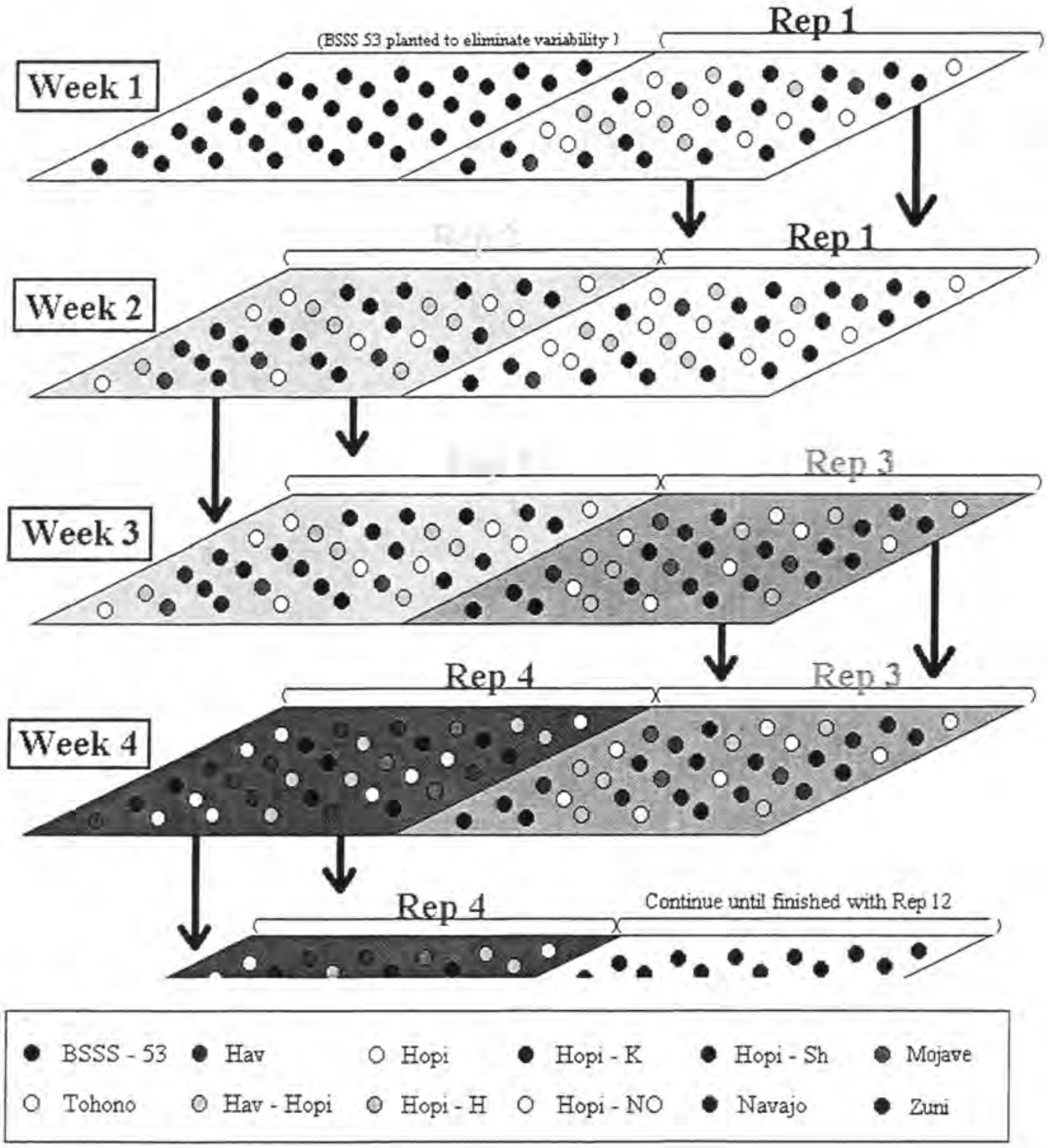

Figure 5: Flow diagram of chamber set up. This is an example of the random placement.

Experiment 3

Experiment 3 was a randomized complete block design with replications as blocks and population as the single variable. In each replication, 10 individuals of each of 8 maize populations were tested at the 25 cm planting depth. This experiment was replicated 4 times.

One replication, consisting of 80 pipes, occupied the entire growth chamber. At the beginning of each replication, pipes were randomly assigned a code number from 1 to 80, and that label was used instead of maize type to prevent bias. Once the pipes were labeled and planted, they were randomly placed in the chamber.

Experiment 4

This experiment was also a randomized complete block design with replications as blocks; the experiment was replicated three times. Ten individuals of 4 maize populations were tested at each of 3 planting depths (5, 15 and 25 cm) in each replication. Each maize population x planting depth treatment combination was randomly arranged within each replication.

Data Analyses

Descriptive statistics and correlations were calculated in Excel™ (Microsoft Corporation, 2000). The generalized linear model analysis (GLM) procedure of SAS, version 8.1 (SAS Institute, 1999-2000, Cary NC), was used for the analyses of variance; means were separated using Tukey's LSD at the 0.05 probability level. There were no significant interactions in any of the experiments and therefore, only main effects are reported. Data reported as mean and + or – standard deviation (sd).

For Experiments 1 and 2, the mean emergence data of all the landraces was compared to the check population using the GLM procedure; individual population comparisons were also performed. GLM was also used to test for significant differences of seedling attributes, including tissue lengths and dry weights. These data were used to examine dry matter allocation among seedling tissues and utilization of seed storage reserves; the relationships among these factors to emergence capacity were tested by correlation. The GLM procedure was also performed on data from Experiments 3 and 4; the fraction of emerged seedlings from each of the treatment depths was the response variable.

RESULTS AND DISCUSSION

Seed Quality

Germination tests, performed under AOSA guidelines (2001), were used as an indicator of seed quality. Seedlings that exhibit abnormalities, according to the AOSA guidelines, are excluded in the calculation of germination percentage; abnormal seedlings are albino, or have damaged or missing shoot or root tissue. Abnormal seedlings are excluded from the calculation because they have a limited probability of success under field conditions in the spring (Allen Knapp, Iowa State University, personal communication, 2002). The check population had 93% germination success and the landraces had a mean of 88% (sd 5) germination success (Table 6). The industry standard for quality seed is approximately 90% germination success; therefore, the seed in this study has acceptable quality. In Experiments 1, 2, and 3, all seeds of each population germinated with the exception of one Mojave seed in Experiment 1. Actual germination was not determined in the field study, Experiment 4.

Table 6: Germination test results of the 11 landraces and the check population.

Population	Germinated	Normal	Dead	Abnormal	Germination
	--------------number of individuals--------------				%
Hav	49	42	1	7	83
Hav-Hopi	48	39	2	9	78
Hopi	49	41	1	8	83
Hopi-H	49	45	1	4	91
Hopi-K	50	44	0	6	89
Hopi-NO	49	44	1	5	88
Hopi-Sh	48	43	2	5	86
Mojave	50	47	0	3	94
Navajo	50	45	1	4	91
Tohono	49	47	1	2	95
Zuni	49	46	1	4	91
Landraces Mean	49	44	1	5	88
BSSS	49	47	1	3	93

To compare seeds of similar physical size, seed was passed through a series of sieves. All populations had the largest proportion of their seed in the 20/64 to 24/64 inch class; actual proportions were not quantified. The industry standard accepts seed sizes between 16/64 and 26/64 inch screens (Sayers 2002).

The 100-seed weight was measured to verify that population seed used in this study had weights consistent with those of NCRPIS and were representative of the seed lot (Table 7). The 100-seed weight was taken after sieving; the weight of the check population differed significantly from the landraces (P <0.001). Differences in 100-seed weight of the landraces and check are attributed to endosperm type (Table 4). BSSS is a dent type of maize, whereas the landraces are flint and floury types (GRIN 2002); endosperms of dent maize are denser than flint and floury types, and therefore, dent seed tends to be about 10 to 12% heavier more than flint and floury seed (Glover and Metz 1987).

Experiment 1

Chamber Conditions

Throughout Experiment 1, chamber temperature averaged 25.1°C (sd 0.1) and relative humidity was maintained at 60% (Figure 19, Appendix A). Lights provided 12 h of 125 μE m^{-2} s^{-1} light per 24 hr period.

Emergence

After planting and watering, sand and seeds tended to shift slightly. Seed depth, determined at harvest, did not differ significantly from planting depth among populations (Table 8). All populations exhibited 100% emergence success from 5 cm depth, and 80 to

Table 7: Initial kernel weight of seed used in Experiment 1, seed weight derived from 100-seed weight, and seed weight reported by GRIN (2002). Different lowercase letters indicate significant differences at the 0.05 probability level by Tukey's LSD test.

Population	Mean Initial Kernel Weight 5 cm	15 cm	25 cm	Mean	Seed Weight[1]	GRIN Seed[2]
	g					
Hav	0.25 (0.04) bc	0.27 (0.03) b	0.25 (0.03) bcd	0.26	0.24	nd
Hav-Hopi	0.27 (0.03) b	0.27 (0.03) b	0.29 (0.04) b	0.28	0.27	0.29
Hopi	0.27 (0.03) b	0.27 (0.03) bc	0.26 (0.03) bcd	0.27	0.26	0.26
Hopi-H	0.22 (0.03) de	0.22 (0.02) d	0.24 (0.03) cd	0.23	0.20	nd
Hopi-K	0.22 (0.01) e	0.22 (0.01) d	0.22 (0.02) d	0.22	0.21	nd
Hopi-NO	0.23 (0.02) cde	0.23 (0.02) cd	0.23 (0.01) d	0.23	0.22	0.20
Hopi-Sh	0.23 (0.03) cde	0.25 (0.02) bcd	0.23 (0.04) d	0.23	0.21	0.24
Mojave	0.27 (0.02) b	0.27 (0.04) b	0.27 (0.03) bc	0.27	0.26	0.27
Navajo	0.26 (0.03) bc	0.27 (0.02) b	0.26 (0.03) bcd	0.26	0.25	0.24
Tohono	0.24 (0.02) bcde	0.24 (0.04) bcd	0.25 (0.02) bcd	0.24	0.24	nd
Zuni	0.25 (0.04) bcd	0.25 (0.03) bcd	0.26 (0.03) bcd	0.25	0.25	nd
Landraces Mean	0.25 (0.02)	0.25 (0.02)	0.25 (0.02)	0.25	0.24	0.25
BSSS	0.33 (0.02) a	0.35 (0.02) a	0.33 (0.05) a	0.34	0.32	nd

[1] Derived from 100-seed weight of screened seed.
[2] GRIN (2002) data. nd indicates no data reported.

Table 8: Mean and standard deviation of actual seed depth and emergence percentage in Experiment 1; no significant differences.

Population	Mean seed depth* 5 cm	15 cm	25 cm	Emergence 5 cm	15 cm	25 cm
	cm			%		
Hav	5.50 (0.77)	15.25 (0.50)	25.58 (0.63)	100	90	58
Hav-Hopi	5.38 (0.48)	15.42 (0.63)	25.17 (0.62)	100	100	50
Hopi	5.54 (0.50)	15.33 (0.91)	25.33 (0.89)	100	100	58
Hopi-H	5.17 (0.62)	15.38 (0.93)	25.21 (0.84)	100	80	50
Hopi-K	5.42 (0.67)	15.58 (0.67)	25.38 (1.05)	100	90	58
Hopi-NO	5.75 (0.45)	15.25 (0.72)	25.29 (0.69)	100	80	75
Hopi-Sh	5.75 (0.78)	15.38 (0.61)	25.21 (0.40)	100	90	58
Mojave	5.54 (0.69)	15.54 (0.50)	25.38 (1.07)	100	90	75
Navajo	5.29 (0.78)	15.29 (1.05)	25.96 (1.86)	100	90	50
Tohono	5.63 (0.64)	15.33 (0.75)	26.08 (1.38)	100	80	50
Zuni	5.38 (0.80)	15.29 (0.92)	25.33 (0.78)	100	100	75
Landrace Mean	5.48 (0.65)	15.37 (0.75)	25.45 (0.93)	100	90	60
BSSS	5.50 (0.48)	15.33 (0.49)	25.25 (0.75)	100	80	42

*at harvest, seed depth from surface was measured to determine extent of post-planting settling.

100% success from 15 cm. Although the landraces tended to emerge more frequently from 25 cm, emergence success did not differ significantly among populations in this screening; the check population had 42% (sd 0.51) emergence success and the mean emergence success of the landraces was 60% (0.45). These preliminary findings suggest that further study of emergence from 25 cm was warranted (Experiment 3).

This experiment was 14 days long; running the experiment longer should not have significantly changed the emergence success. Of those seedlings that emerged, the days to emergence at the deepest depth of 25 cm for the mean of the landraces and the check population were 8.4 d (sd 1.4) and 9.0 d (sd 0.7), respectively (Table 9); these data suggest that more time would not have changed the emergence success. Also, the retrieved seedlings appeared unable to emerge with more time; for example, some seedlings prematurely opened their coleoptile and the shoot was doubled over below the surface, or seedlings had rotted shoots.

Table 9: Population mean days to emergence and standard deviation in Experiment 1.

	Mean Days to Emergence		
Population	5 cm	15 cm	25 cm
	---------------days---------------		
Hav	4.5 (0.5)	6.2 (1.1)	8.9 (1.4)
Hav-Hopi	4.8 (0.6)	7.0 (1.0)	8.8 (1.0)
Hopi	4.3 (0.6)	6.3 (1.2)	8.7 (1.4)
Hopi-H	4.3 (0.6)	6.9 (0.9)	8.2 (1.2)
Hopi-K	4.9 (0.5)	7.0 (1.7)	8.9 (1.7)
Hopi-NO	4.8 (1.7)	6.4 (1.1)	9.0 (2.4)
Hopi-Sh	4.4 (0.5)	6.2 (1.2)	7.7 (0.5)
Mojave	4.2 (0.4)	5.6 (0.8)	7.9 (1.2)
Navajo	4.2 (0.4)	6.4 (0.5)	8.5 (2.7)
Tohono	4.1 (0.3)	5.4 (0.5)	8.3 (1.6)
Zuni	4.3 (0.5)	6.3 (0.6)	7.8 (0.7)
Landraces Mean	4.4 (0.6)	6.3 (1.0)	8.4 (1.4)
BSSS	4.6 (0.7)	6.7 (0.7)	9.0 (0.7)

Seedling Morphology

When a seed germinates, the radicle protrudes from the seed (Kiesselbach 1949). Subsequently, the shoot emerges from the seed; mesocotyl tissue elongates until the coleoptile encounters light. Then the mesocotyl growth slows and the coleoptile extends through to the soil surface (Figure 2). Maize seminal roots emerge and elongate.

Although foil over the tops of the PVC pipes excluded light, mesocotyls of numerous seedlings apparently ceased growth before reaching the soil surface, and their shoots prematurely grew out of the coleoptiles (Figure 6). The prematurely opened shoots of some of the seedlings doubled over as they continued growth through the sand; few of these seedlings successfully emerged from 15 or 25 cm depth. Collins (1914a) noted a similar observation of those seedlings that opened their shoots below the soil surface; most seedlings that opened their shoot $\geq$ 2 cm from the soil surface failed. The seedlings that did emerge had folded shoots that apparently provided sufficient strength to push through the sand to the surface. Those landraces that most consistently emerged from 25 cm (Zuni, Hopi-NO, and Mojave), however, rarely opened shoots prematurely. Several of the seedlings rotted or just quit growing. Some seedlings curled their mesocotyls around the seed but still emerged; some of these seedlings had a longer mesocotyl length than planting depth.

Mesocotyl length increased with planting depth (Figure 7) and was related to emergence capacity. Mesocotyl length had a strong positive correlation ($r = 0.81$) with actual planting depth and differed significantly among planting depths ($P < 0.0001$); this indicates that mesocotyl length increased as planting depth increased. These findings are consistent with earlier studies that included one or two Southwest landraces and attributed emergence success from extraordinary depths to elongated mesocotyls (Collins 1914a; Troyer 1997).

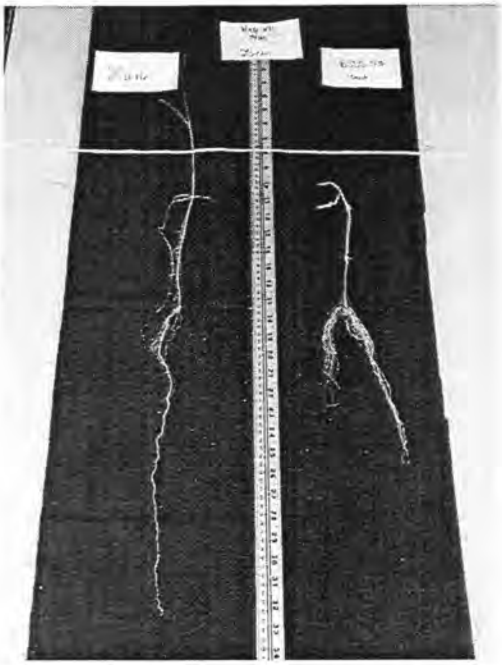

Figure 6: The check population seedling on the right opened its coleoptile before reaching the soil surface.

Mesocotyl length also differed significantly among populations ($P < 0.0001$); the check population had the shortest mean mesocotyl length of all the populations at each depth (Figure 7). Differences between the landraces and check may be explained by differences in their customary planting depths; the landraces are typically planted at least 10 cm deep, whereas the check is planted at 6 cm or less. Differences among the landraces, however, cannot be explained by differences in their customary planting depths or native environments.

Additionally, mesocotyl length of emerged seedlings was greater than that of failed seedlings in the 25 cm treatment (Figure 8). Mesocotyl length had a weak positive correlation with emergence success ($r = 0.47$) in the 25 cm treatment; this means seedlings

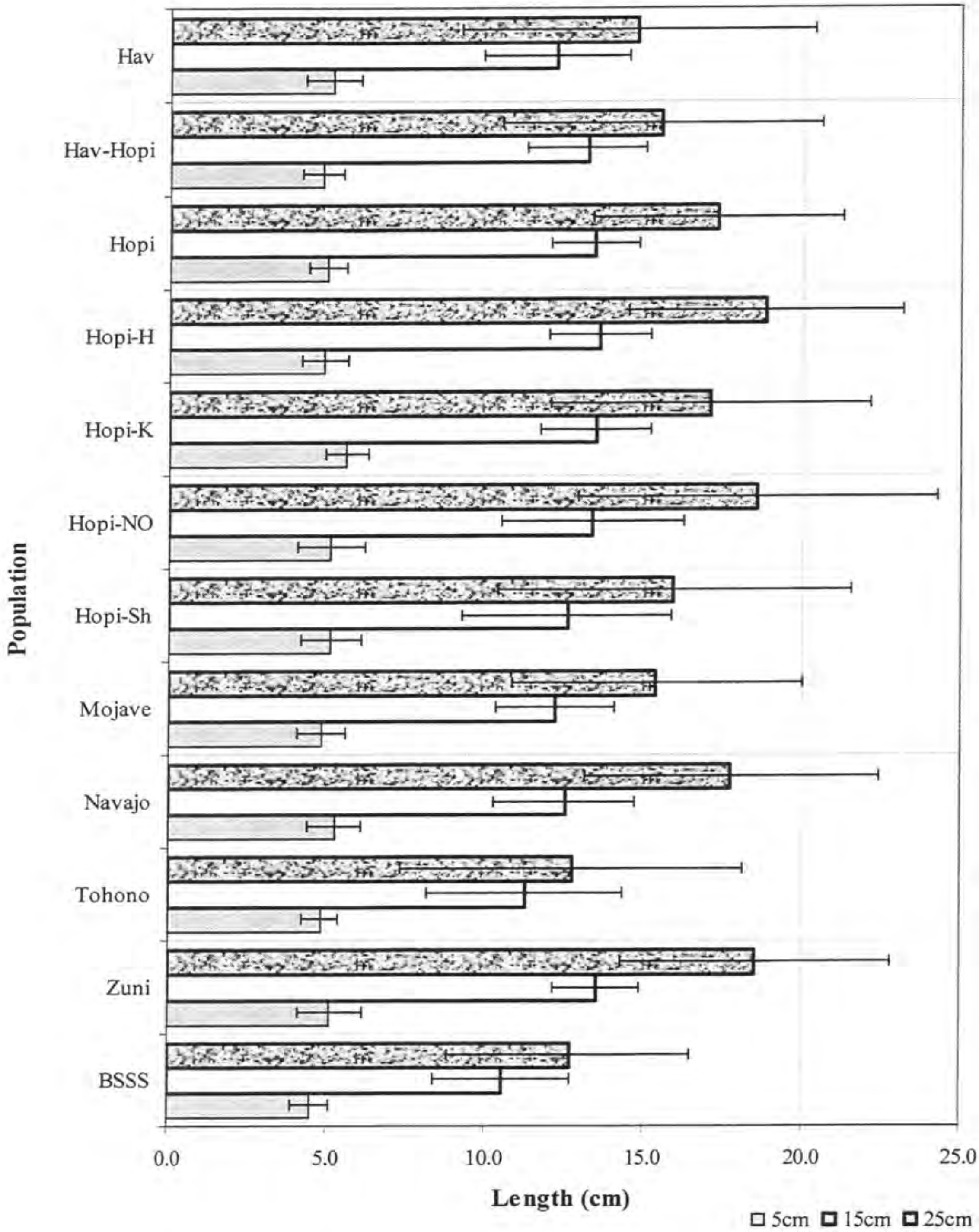

Figure 7: Mean and standard deviation of mesocotyl length of each population at each planting depth for Experiment 1 (for significant statistical differences see Table 16 in Appendix B).

with longer mesocotyls tended to emerge successfully. Mesocotyl length largely explains emergence success from deep planting.

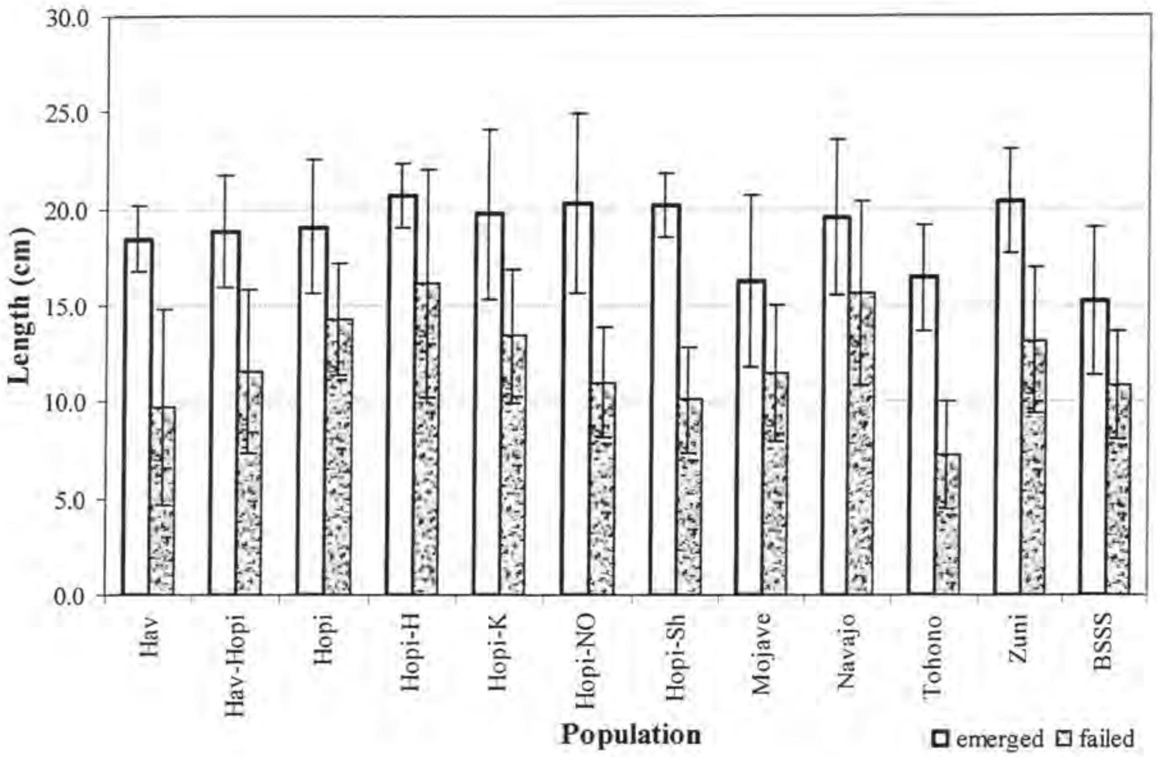

Figure 8: Mean and standard deviation mesocotyl length of emerged and failed seedlings from 25 cm in Experiment 1 (data in Appendix B, Table 17).

As expected, mesocotyl length accounted for a greater proportion of total shoot length with increasing planting depth; mesocotyl growth slows or ceases when the coleoptile is exposed to light (Kiesselbach 1949). Mesocotyl length averaged 48% (sd 0.07) of total shoot length ('mesocotyl' plus 'to 1st collar') of seedlings planted at 5 cm, and 68% (sd 0.06) and 71% (sd 0.08) for those planted at 15 and 25 cm, respectively. As planting depth increased, the length of 'to 1st collar' also increased, apparently to make up for the mesocotyl halting before reaching the sand surface (Table 10; Figure 9). Emergence success had a slightly

Table 10: Population means and standard deviations of length to first collar of seedlings grown in Experiment 1.

Population	Mean Length to First Collar		
	5 cm	15 cm	25 cm
	-----------------cm-----------------		
Hav	5.00 (0.71)	5.64 (0.71)	5.89 (1.08)
Hav-Hopi	5.25 (0.84)	5.46 (1.10)	7.50 (0.96)
Hopi	5.83 (0.62)	6.42 (1.20)	7.21 (1.29)
Hopi-H	5.75 (1.31)	5.91 (1.39)	6.07 (1.34)
Hopi-K	5.13 (0.74)	5.36 (0.81)	6.64 (1.60)
Hopi-NO	5.00 (0.60)	5.30 (1.27)	6.61 (0.96)
Hopi-Sh	5.42 (0.93)	5.68 (0.84)	6.93 (1.10)
Mojave	6.21 (1.05)	7.14 (1.03)	8.83 (1.41)
Navajo	5.13 (0.68)	5.91 (0.80)	7.67 (1.69)
Tohono	5.71 (0.84)	7.25 (0.82)	8.08 (0.66)
Zuni	5.25 (1.16)	6.00 (1.80)	8.11 (1.88)
Landraces Mean	5.43 (0.40)	6.01 (0.67)	7.23 (0.91)
BSSS	4.88 (0.88)	6.50 (1.29)	8.50 (2.33)

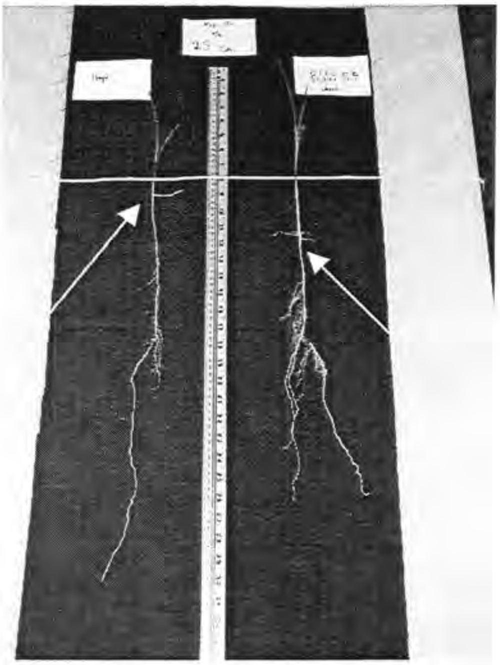

Figure 9: The mesocotyl ends where the nodal roots appear (white arrows); mesocotyl lengths of a Hopi seedling (left) and the check (right) are 22 cm and 16 cm, respectively.

stronger positive correlation with total shoot length (r = 0.54) than with mesocotyl length alone (r = 0.47) in the 25 cm treatment.

The radicle may influence emergence capacity because it competes with the shoot for seed resources. Radicle length differed significantly among planting depths across populations ($P < 0.0001$); this indicates that radicle length decreased as planting depth increased (Figure 10). Radicle length also differed significantly among populations across planting depths ($P < 0.0001$). Although competition with the mesocotyl for seed stored compounds to support growth may have limited radicle length, it appears that reduced radicle length in the deeper plantings is at least partially an artifact of having less sand volume below the seed. Seedlings planted at 25 cm depth had radicles that curled and thickened at the point of contact with the landscape cloth.

Early in the development of maize seedlings, the radicle and seminal roots together form the dominant root system (Figure 2). These roots arise from initials in the embryo with the lateral seminal roots forming adventitiously from the scutellar node (Kiesselbach 1949). After about the V3 stage, these roots stop growing. Dent maize seedlings usually have several lateral seminal roots, but some flint varieties may have none and only the radicle (Kiesselbach 1949). Collins' (1914a) study indicates that radicles were strongly developed, rarely having seminal roots present, in the Hopi, Navajo and Zuni populations investigated. These observations support this study's findings that seminal roots occur rarely or as relatively minor parts of the primary root system on many of the landraces in the early developmental stages (Figure 11). The seedlings in this study were harvested at or before the V2 leaf stage, so the radicle and seminal roots were still dominant.

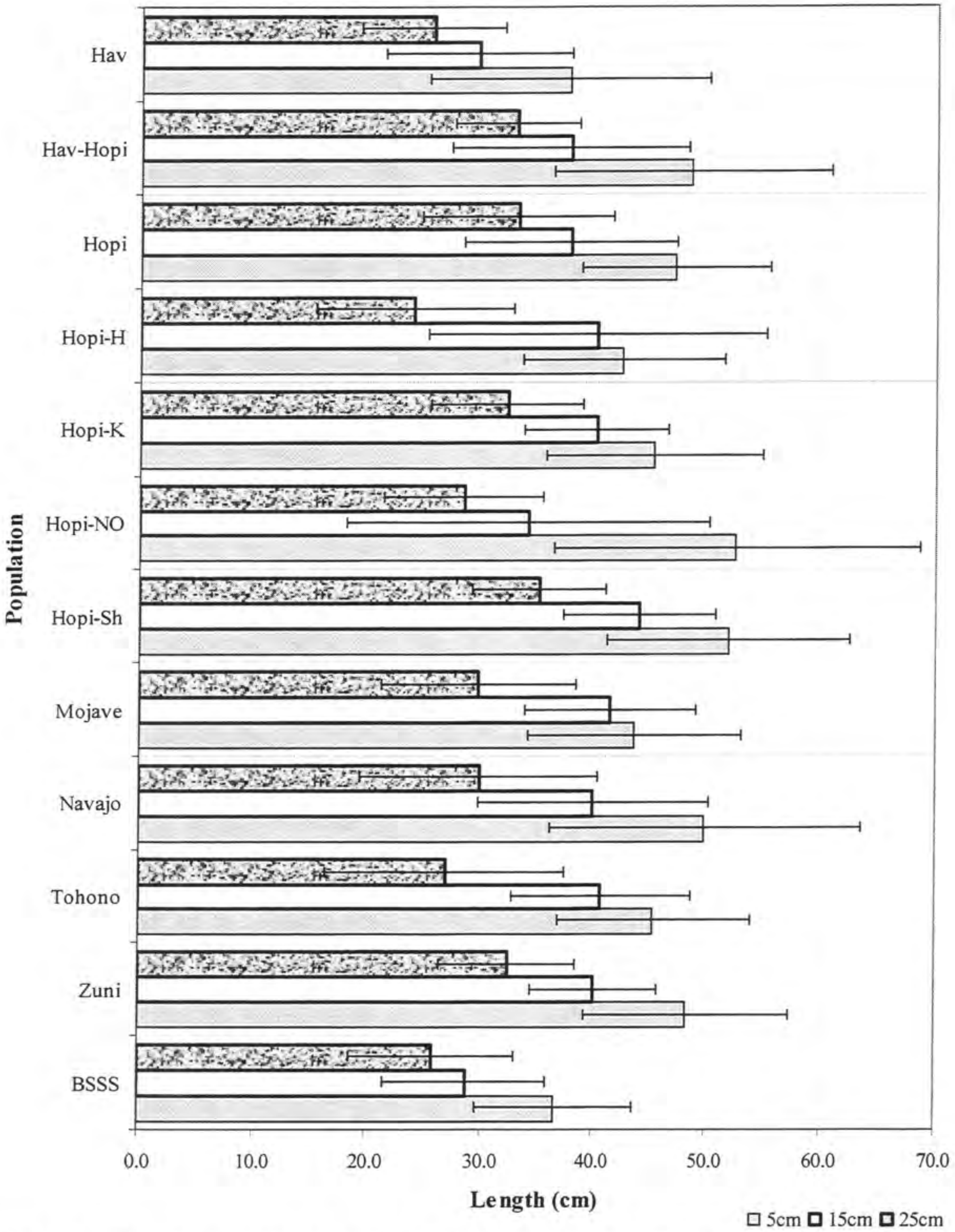

Figure 10: Mean and standard deviation of radicle length of each population at each planting depth in Experiment 1 (for significant statistical differences see Table 18 in Appendix B).

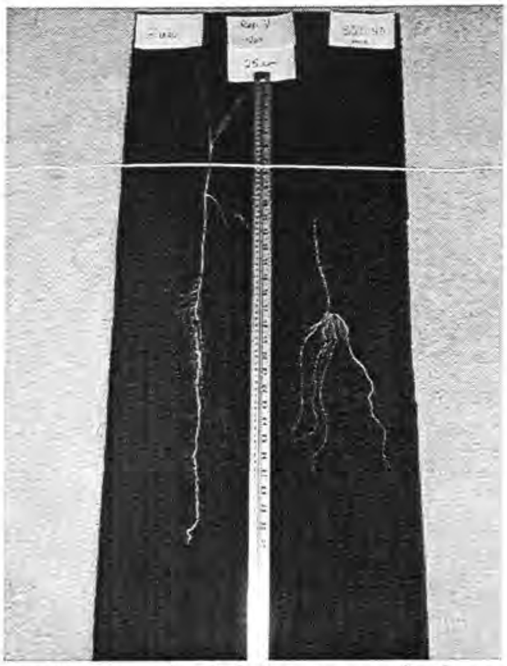

Figure 11: The flint/floury seedling on the left has no seminal roots; the dent seedling on the right has three seminal roots.

Generally, maize nodal roots (also called adventitious or crown roots, or the secondary root system) usually appear at the VE stage of development; by V6 the nodal roots become the main suppliers of water and nutrients (Ritchie et al. 1997). Nodal roots form about 2.5 to 3.8 cm below the soil surface, regardless of planting depth, and arise from stem tissue, beginning at the first node at the base of the coleoptile. Seedling root architecture and development differed between the landraces and check population. The check population commonly had nodal roots. Some landrace seedlings exhibited no nodal root development by the time of seedling harvest.

Dry weights

Based on the 100-seed weights taken prior to the experiment, each kernel in the experiment should weigh close to the average kernel weight of the 100 seeds used to find the

100-seed weight. But, there were differences between the two weights; generally, seeds used in the experiment were slightly heavier than the average kernel weight derived from the 100-seed weight (Figure 12). Differences can be attributed to the exclusion of broken, sprouted, or severely diseased seed from the experiment; these damaged seed, included in the 100-seed weight, tended to be slightly lighter.

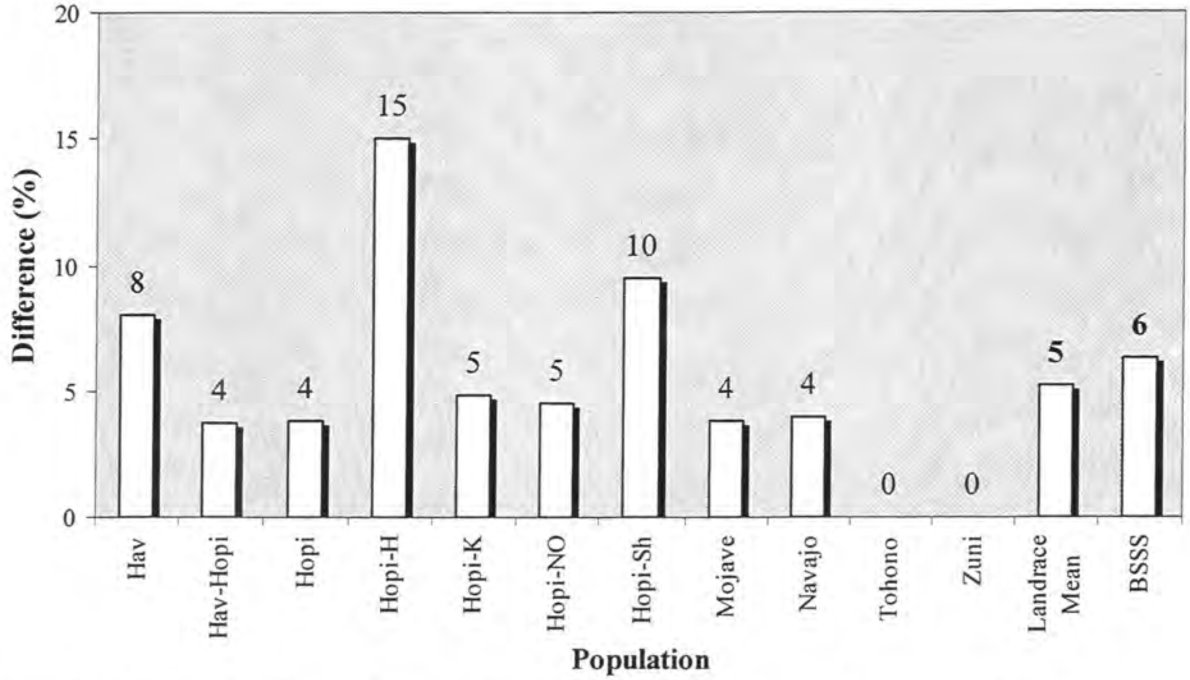

Figure 12: Percent difference in initial seed weight in Experiment 1 compared to average kernel weight derived from 100-seed weight.

For Experiment 1, mean seed weight of the check was significantly greater (36%) than that of the landraces (Table 7), because seed weight of flint and floury types is typically at least 10 to 12% lower than dents (Glover and Mertz 1987). Seed weight was not correlated with emergence success (r = -0.20), and therefore, seed weight cannot be used as an indicator of emergence success. In a study comparing emergence capacity of a Navajo landrace and a Corn Belt maize line (U.S. 13) it was found that even though the average

Navajo kernel was 20% smaller than the average U.S. 13 kernel, it had better emergence capacity; other observations stated that the Navajo line efficiently utilized seed assimilates while the U.S. 13 maize consistently failed to emerge and still had dry weight remaining in the seed (Dungan 1950).

In a maize seed the main food storage structure is the endosperm (Ingle et al. 1964; Gardner et al. 1985). When a seed germinates, food storage compounds, including starches and proteins, break down into other compounds, such as sugars and amino acids, and are metabolized to provide energy and assimilate for tissue growth and elongation; this means that maize seedlings are heterotrophic. Seedlings utilize energy from seed reserves early in their development and about 10 days after germination they begin to transition into being autotrophic (Cooper and MacDonald 1970; Deleens et al. 1984). When seedlings are grown in the dark, they cannot photosynthesize, and therefore, must use seed reserves for energy to grow; as these seedlings metabolize, they respire and therefore, lose weight. In a study performed on non-photosynthetic maize seedlings, the results state that smaller seeds did not grow for as long as larger seeds (Derwyn et al. 1966).

Total seedling dry weight was compared to initial seed weight (Figure 13). In the 5 cm depth treatment, total seedling dry weight was greater than initial seed weight. The greater seedling dry weight can be attributed to carbon gained from photosynthesis; at harvest, these seedlings were at a more advanced leaf stage because they emerged earlier than those from deeper depths. The findings that these seedlings showed an increase in seedling dry weight corroborate the results reported by Deleens et al. (1984). For the 15 cm depth seedlings, the initial seed and total seedling weights were similar; any differences are attributed to either photosynthetic accumulation (when total dry weight exceeded initial seed weight) or respiration (when total dry weight was less than initial seed weight). Finally, dry weights of the 25 cm total seedlings were consistently lower than initial seed weights with the exception of Mojave, which showed little difference between initial seed and total seedling weights. The difference between total seedling dry weight and initial seed weight is attributed to seedling respiration during emergence from the greater depth.

Seed utilization, defined as [(initial seed weight – seed weight remaining at harvest) x initial seed weight^{-1}] x 100, did not differ significantly among planting depths across populations. Regardless of depth, seed utilization remained relatively constant within each population (Figure 14).

Seedling dry weight allocation among shoot, root, and remaining seed varied among depths and populations (Figure 15). The landraces generally partitioned more dry matter to roots than shoots. The results from a study about temperature effects on maize germination suggest that development of roots and shoots are not limited by seed reserves (Blacklow 1972).

Seedling root-to-shoot ratios were significantly different among populations across depths ($P = 0.0023$) (Figure 16). The mean root-to-shoot ratio was greater in the landraces than the check across depths, averaging 1.26 (sd 0.25) and 0.67 (sd 0.07), respectively. In a study on inbred maize seedling root morphology, lines with high root-to-shoot ratios had more root tissue and those lines with fewer seminal roots had greater total root dry matter (Andrew and Solanki 1966). The results of the present study support the results of Andrew and Solanki (1966); not only do the landraces have greater root-to-shoot ratios, but also fewer seminal roots than the check population. Root-to-shoot ratios do not explain emergence capacity; the ratios did not correlate with emergence success at 25 cm ($r = -0.23$).

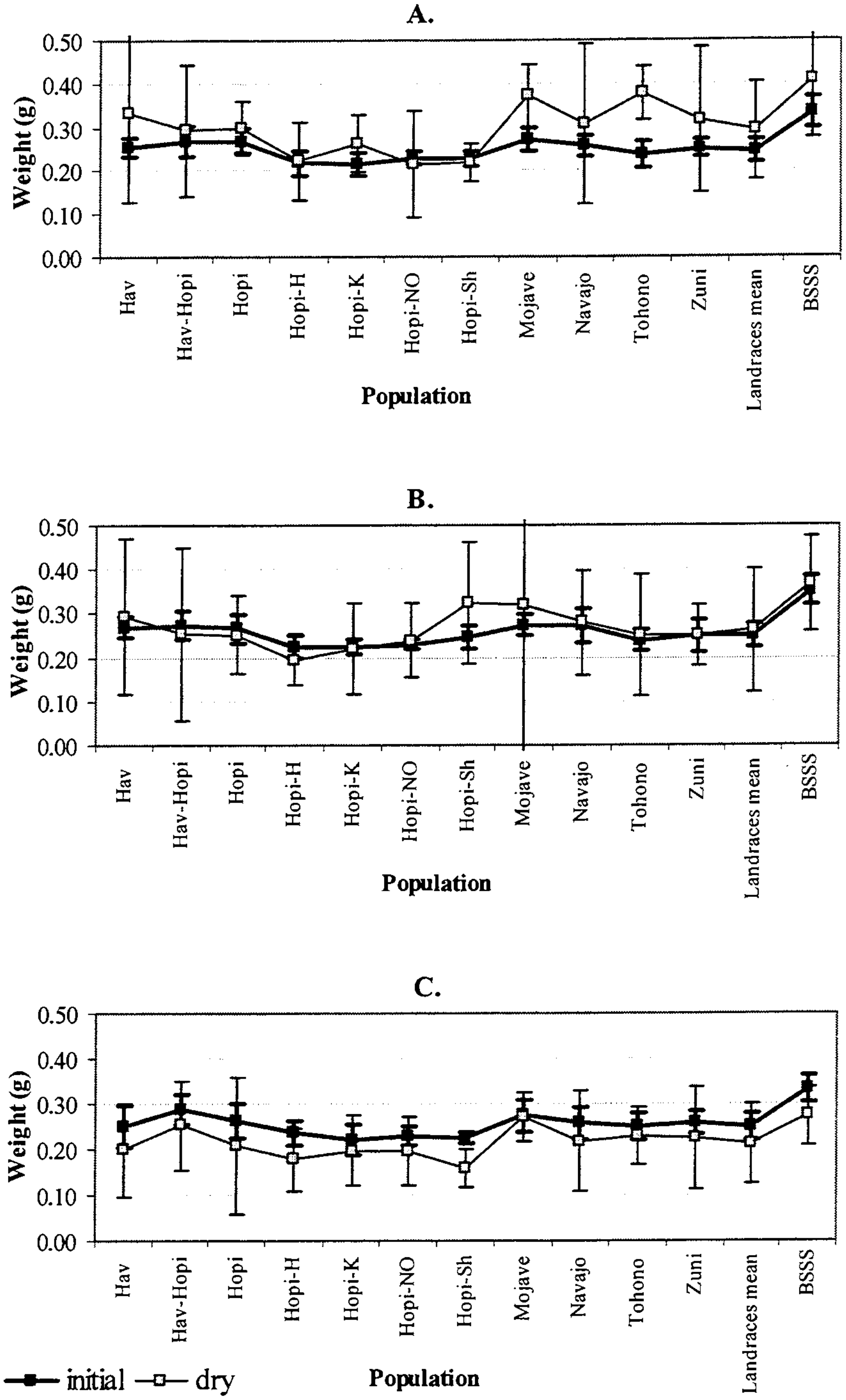

Figure 13: Mean and standard deviation of initial seed weight and total seedling dry weight in Experiment 1 for each depth: A, 5 cm; B, 15 cm; C, 25 cm. (data in Appendix B, Table 19).

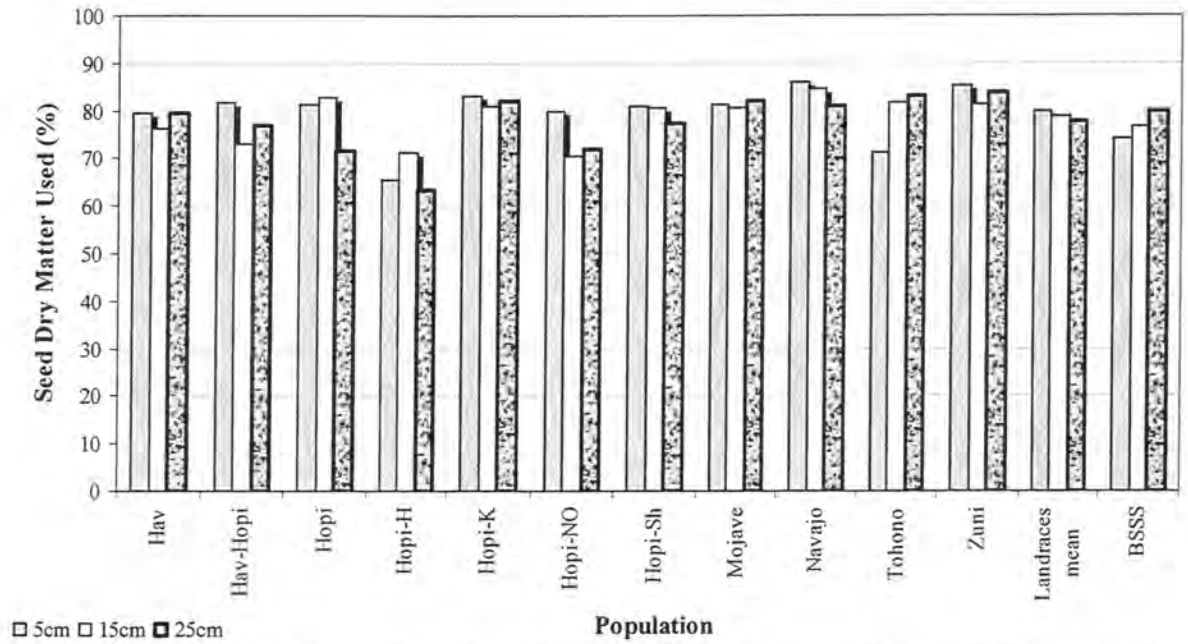

Figure 14: Mean initial seed weight utilization in Experiment 1 (data in Appendix B, Table 20).

The greater relative allocation of dry matter to roots among landraces may contribute to adaptation to their native arid and semiarid environments. Varieties of drought tolerant sorghum (*Sorghum bicolor* (L.) Moench) exhibit greater root-to-shoot ratios than susceptible varieties (Jordan and Miller 1980). Plants that grow roots at the expense of shoot tissue tend to have a better chance of survival when water is limited (Passioura 1986).

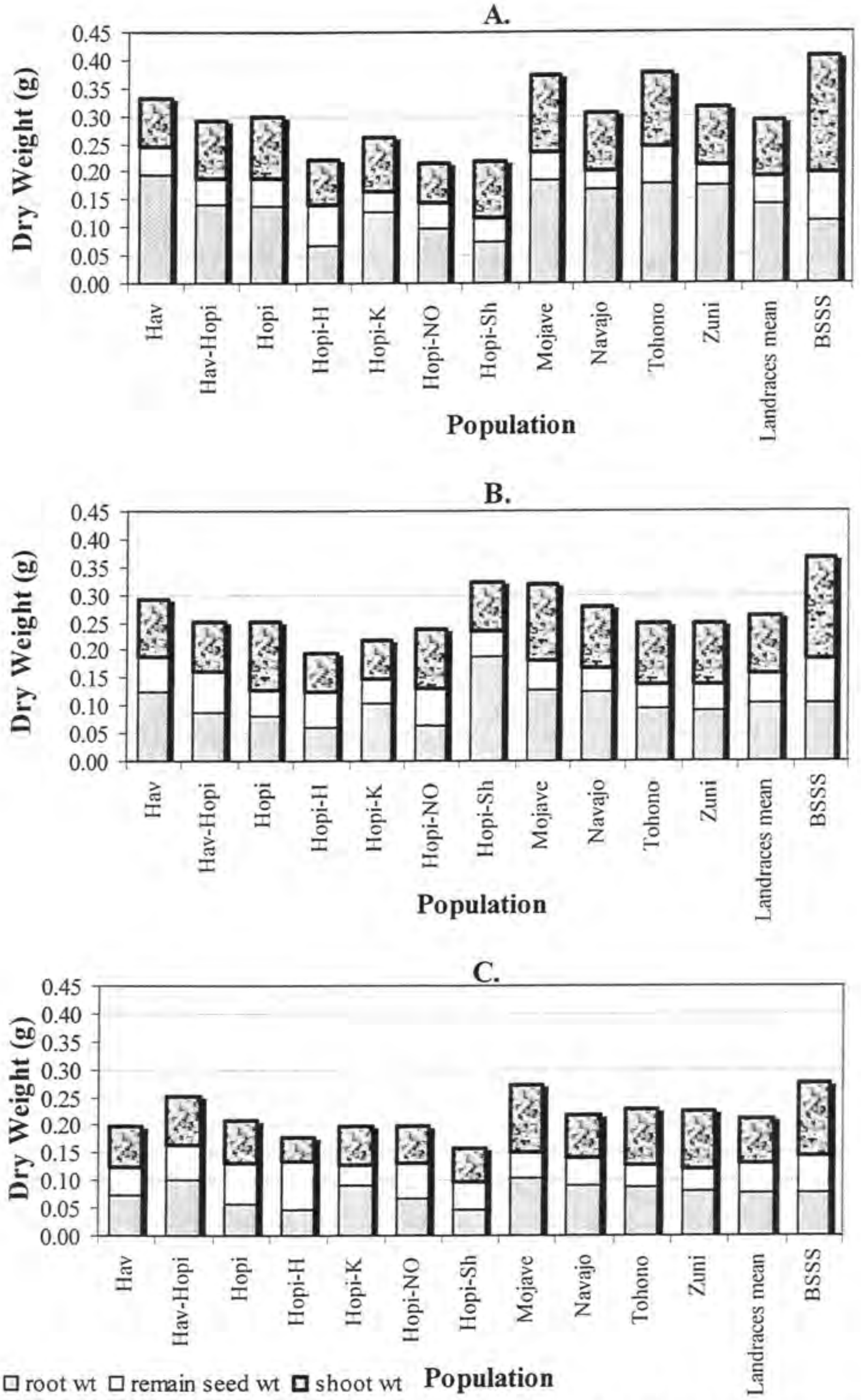

Figure 15: Mean seedling dry weight allocation for each depth in Experiment 1: A, 5 cm; B, 15 cm; C, 25 cm (data in Appendix B, Table 21).

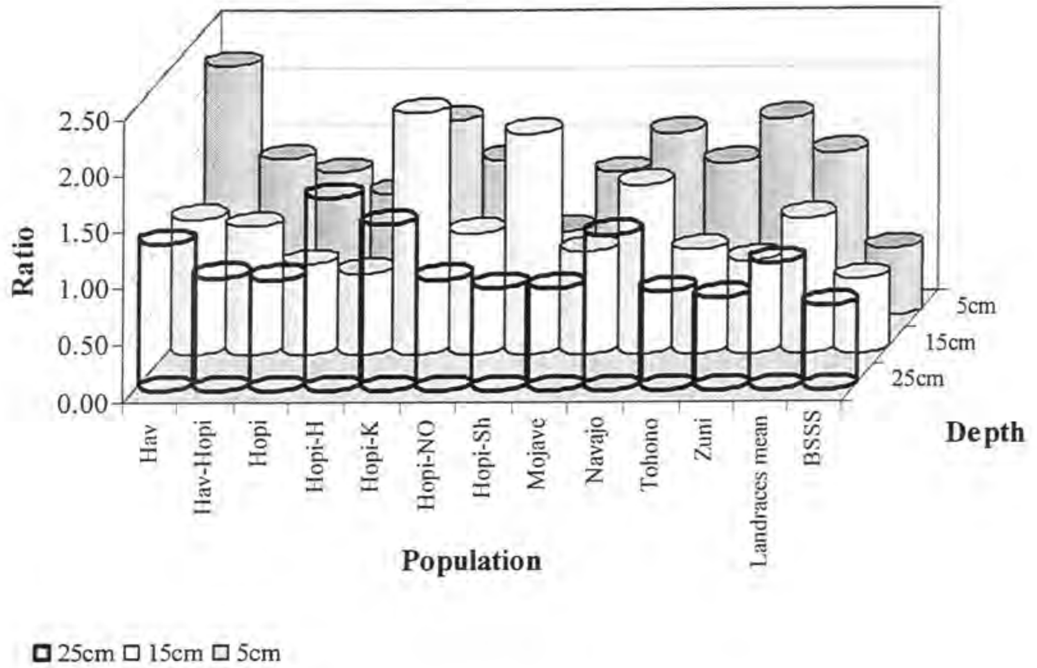

Figure 16: Mean dry weight root-to-shoot ratios in Experiment 1 (for significant statistical differences see Table 22 in Appendix B).

Experiment 2

Throughout Experiment 2, chamber temperature averaged 25.0°C (sd 0.2) and relative humidity was maintained at 77% (Figure 19, Appendix A). Lights provided 12 h of 125 μE m^{-2} s^{-1} light per 24 hr period.

This experiment tested emergence capacity from 35 and 45 cm deep because ethnographic information reports traditional planting depths of some landraces are up to 45 cm deep (Table 1). This experiment tested those landraces that demonstrated 75% emergence success from 25 cm in Experiment 1, plus the check population (Table 8).

In this experiment, emergence from the control depth of 5 cm was 100% for all four populations. The check population had 0% emergence success from 35 and 45 cm depths.

The emergence success of landraces from 35 cm averaged 14%; no significant differences among landraces were detected (Table 11). None of the landraces emerged from 45 cm.

Table 11: Emergence percentage and population mean days to emergence and standard deviation of seedlings that emerged in Experiment 2; no significant differences at any depth.

Population	Emergence			Mean Days to Emergence (sd)	
	5 cm	35 cm	45 cm	5 cm	35 cm
	------------%------------			------------days------------	
Hopi-NO	100	17	0	4.3 (0.9)	10.0 (0.0)
Mojave	100	8	0	4.3 (0.6)	13.0 (0.0)
Zuni	100	17	0	4.1 (1.2)	11.5 (2.1)
Landraces Mean	100	14	0	4.2 (0.9)	11.5 (0.7)
BSSS	100	0	0	4.8 (0.3)	-- (--)

This experiment was 14 days long; running the experiment longer should not have significantly changed the emergence success. Similar to the results from Experiment 1, the retrieved seedlings appeared unable to emerge with more time; for example, some seedlings prematurely opened their coleoptile and the shoot was doubled over below the surface, or seedlings had rotted shoots.

Based on these results, emergence capacity was somewhat consistent with traditional planting depths. Both Hopi-NO and Zuni maize exhibited 17% emergence success from 35 cm; Hopi and Zuni customarily plant at 10 to 45 cm and 8 to 30 cm, respectively (Table 1). In contrast, Mojave maize (8%) is usually planted at 10 to 15 cm and the check (0%) planted at 6 cm. In addition to deep planting, Southwest landraces are traditionally planted in clusters or 'hills' of multiple plants, rather than singly as done in this experiment. Planting several seed in the same hole may contribute to emergence success from greater depths under native conditions. In a New Mexico field study, Tohono maize emerged more rapidly when multiple seed were planted together than when planted singly (Muenchrath and Salvador

1995); seedlings emerging together may increase mechanical loosening of the soil and facilitate emergence from depth. Ethnographic information on traditional planting depths is indicative of potential emergence capacity, but other factors may also be involved in emergence success.

Experiment 3

Throughout Experiment 3, chamber temperature averaged 25.3°C (sd 0.3) and relative humidity was maintained at 71% (Figure 19, Appendix A). Lights provided 12 h of 125 μE m^{-2} s^{-1} light per 24 hr period.

Because the 25 cm depth was the only depth in Experiment 1 that exhibited any differences in emergence success, those populations that had greater than 50% emergence were further tested in this experiment (Table 8). This experiment was designed to allow for greater sample size per replication to better detect differences among populations.

For Experiment 3, emergence percentage for BSSS, the check population, from 25 cm was 10% (sd 0.08); the mean emergence for the landraces was 53% (sd 0.13) (Figure 17). The mean emergence success of the landraces was significantly different from the check population ($P < 0.0001$). Also, there were significant differences among all populations in emergence success ($P < 0.0001$). The results of this replicated experiment indicate that the landraces native to the Southwestern U.S. tend to have greater capacity to emerge from 25 cm than the check population. The general trend of the landraces able to emerge from 25 cm is similar in Experiment 3 as in Experiment 1.

This experiment was 14 days long; running the experiment longer should not have significantly changed the emergence success. Of those seedlings that emerged, the days to emergence for the mean of the landraces and the check population were 8.5 d (sd 1.7) and 10.8 d (sd 2.6), respectively (Table 12); these data suggest that more time would not have changed the emergence success. Also, similar to the previous experiments, the failed seedlings appeared unable to emerge with more time; for example, some seedlings prematurely opened their coleoptile and the shoot was doubled over below the surface, or seedlings had rotted shoots.

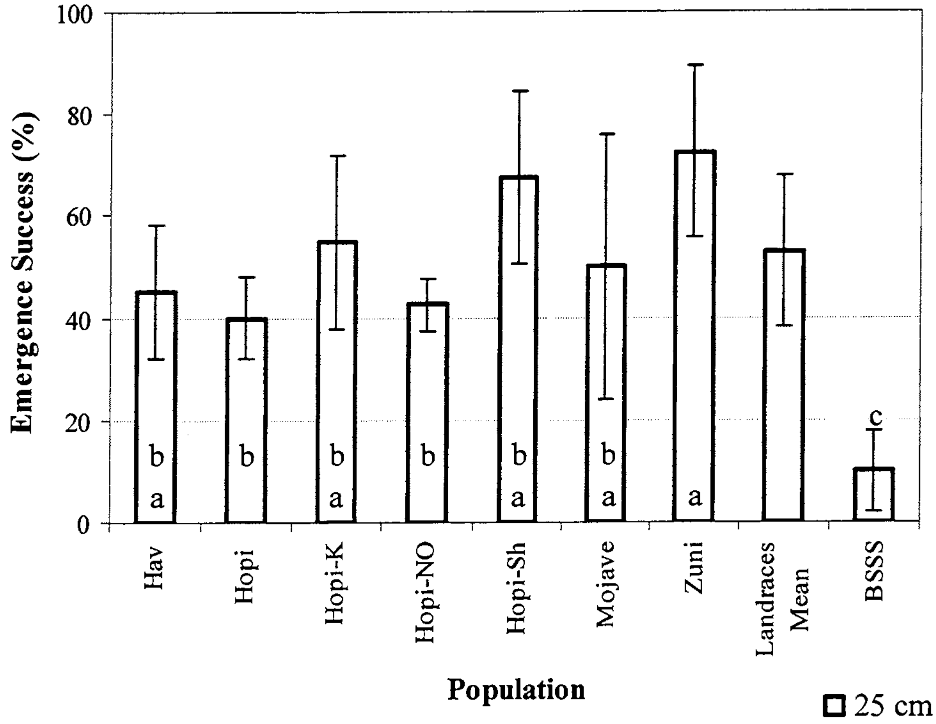

Figure 17: Mean and standard deviation of emergence success from 25 cm in Experiment 3. Different lowercase letters indicate significant differences among populations at the 0.05 probability level by Tukey's LSD test (data in Table 23, Appendix B).

Table 12: Population mean days to emergence and standard deviation in Experiment 3.

Population	Mean Days to Emergence (sd)
	days
Hav	8.6 (2.0)
Hopi	8.6 (1.3)
Hopi-K	9.0 (1.5)
Hopi-NO	8.4 (2.3)
Hopi-Sh	8.3 (1.5)
Mojave	8.7 (1.8)
Zuni	7.8 (1.8)
Landraces Mean	8.5 (1.7)
BSSS	10.8 (2.6)

Based on the results, emergence capacity was somewhat consistent with traditional planting depths. In this experiment four landraces, Hopi-K, Hopi-Sh, Mojave and Zuni, emerged ≥ 50% from 25 cm; Hopi and Zuni customarily plant at 10 to 45 cm and 8 to 30 cm, respectively (Table 1). In contrast, Mojave maize emerged from 25 cm deep 50% of the time; this landrace appears to be able to emerge from greater depths than its traditional planting depth of 10 to 15 cm. The remaining landraces (Hav, Hopi and Hopi-NO) did not reflect traditional planting depth. The check had poor emergence success (10%) which can be explained by its typical planting depth (6 cm).

Experiment 4

This experiment was performed to evaluate emergence capabilities of the populations under field conditions. To avoid confounding effects of wet and cool conditions, that often accompany spring planting, this study was conducted in early August when soil temperatures and moisture were conducive to germination and emergence.

A weather station located on the Bruner Farm near the experiment recorded environmental conditions, including soil and air temperatures, soil moisture, and rainfall

(Figures 20 and 21, Appendix A). The total precipitation for the period during Experiment 4 was 170.27 mm. Mean soil temperature and soil moisture at 20 cm depth were 19.3°C (sd 0.17) and 39% (sd 0.22); soil temperature and soil moisture ranged between 17.8 and 20.5°C, and 34 and 40%, respectively. The mean soil temperature for the field experiment (19.3°C) was 5.9°C cooler than the temperature in the growth chamber studies.

Particle size analyses were performed on field soil samples taken at 5 and 20 cm depths, as well as the medium used in the growth chamber experiments. Results indicate differing particle sizes between the sand used in the growth chamber and the loamy field soils (Table 13). Only 35% of the soil from the field is classified as sand, whereas 100% of the soil used in the growth chamber was sandy, with most of this classified as coarse sand.

Table 13: Particle size analysis measured from soil samples taken at the site of Experiment 4 compared to medium used in the growth chamber.

	Particle Size Distribution		
	Field Soil		Sand Medium
Soil Texture	5 cm	20 cm	
	%		
Total Clay	20	21	0
Total Silt	44	46	0
Total Sand	36	34	100
Very Coarse Sand			6
Coarse Sand			85
Medium Sand			9

The field experiment plot was tilled with one pass of a field cultivator prior to planting (Michael Fiscus, Agronomy Farm, Iowa State University, personal communication, 2002). Tillage operations can compact soil and influence emergence; bulk density is a measure of compaction. Bulk density is the mass of a unit volume of soil. A bulk density analysis was performed on soil samples taken at 5 and 20 cm depths (Table 14). Bulk density in Iowa soils is typically 1.3 g cm^{-3}; therefore the soil for the field test is representative (mean 1.29 g cm^{-3}). Bulk density tends to be greater in sandy than loamy soils (Brady and Weil 2002). In addition, the mechanical resistance (soil particle-particle locking) is greater in sandy than loamy soil; mechanical resistance, rather than bulk density, is assumed to have greater influence on emergence capacity.

Table 14: Bulk density (g cm^{-3}) measured from soil samples taken at the field location of Experiment 4.

Depth	Bulk Density
	g cm^{-3}
5 cm	1.34
20 cm	1.24

Emergence data shows significant differences in emergence capacity across planting depths among populations ($P < 0.0001$) (Figure 18). Similar to the growth chamber study results, emergence success generally decreased with increasing planting depth. Among populations, emergence success is not significantly different at the 5 or 15 cm depths. From the 25 cm depth, however, there were significant differences between some populations; as in Experiment 3 (Figure 17), Zuni maize exhibited the greatest emergence capacity from 25 cm in this field study. The other landraces did not emerge significantly better from 25 cm than the check population under these field conditions.

Emergence was monitored for 29 days after planting. No seedlings emerged after 15 days past the planting date (Table 15); any seed not emerged at 29 days was considered dead or not successful. Unsuccessful seeds/seedlings could have been preyed upon by arthropods or plant pathogens in the soil. Mesocotyls of other unsuccessful seedlings could have ceased growth before reaching the soil surface similar to the phenomena noted in the growth chamber; the shoots of these seedlings may have prematurely opened and doubled over under the soil surface.

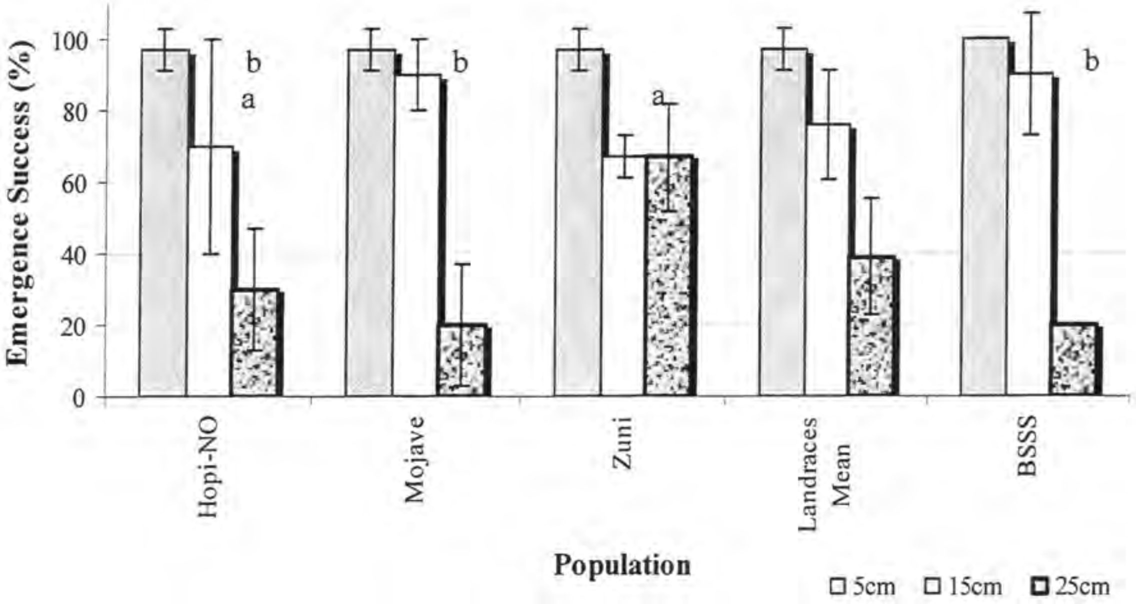

Figure 18: Mean and standard deviation of emergence success of all populations and depths in Experiment 4. Different lowercase letters indicate significant differences at the 0.05 probability level by Tukey's LSD test. (data in Table 24, Appendix B).

Table 15: Population mean days to emergence and standard deviation in Experiment 4.

	Mean Days to Emergence		
Population	5 cm (sd)	15 cm (sd)	25 cm (sd)
	------------------days------------------		
Hopi-NO	5.2 (0.9)	7.9 (2.6)	8.7 (2.0)
Mojave	5.1 (1.2)	7.5 (1.4)	8.5 (1.0)
Zuni	5.1 (0.9)	7.3 (1.0)	9.1 (1.3)
Landraces Mean	5.1 (1.0)	7.5 (1.7)	8.8 (1.5)
BSSS	5.3 (0.7)	8.3 (1.3)	7.7 (1.0)

CONCLUSIONS

Maize landraces native to the U.S. Southwest are traditionally planted more deeply, 8 to 45 cm (Table 1), than modern Corn Belt varieties, which are usually planted up to 6 cm depth. This study tested the hypothesis that these landraces have a greater capacity to emerge from deeper planting depths than a population representative of Corn Belt varieties.

The landraces and the check population have similar emergence capacities from 5 and 15 cm planting depths. From 25 cm, however, the Southwest maize landraces tested had greater emergence capacity (60%, sd 0.45) than the check population (42%, sd 0.51) in Experiment 1. Results from the replicated study Experiment 3 show a significant difference between the emergence success of the landraces (53%, sd 0.14) and the check population (10%, sd 0.08). Emergence was poor from greater depths. From the 35 cm depth, the three landraces tested emerged (14%), and the check population failed entirely. None of the landraces, or the check, emerged from 45 cm depth.

Customary planting depths of a landrace are not a reliable indicator of potential emergence capacity under the conditions tested. For example, the Hopi landraces are reputed for extraordinarily deep planting (10 to 45 cm), but these landraces were not consistently better at emerging from greater depths than landraces traditionally planted more shallowly, such as the Mojave and Tohono landraces, usually planted at 10 to15 cm.

In addition to testing the hypothesis, the first objective was to identify landraces capable of emerging from depth as potential genetic resources for transfer of this trait into other varieties. Zuni maize exhibited the greatest and most consistent capacity, about 75% success, to emerge from 25 cm under both controlled and field conditions. These results suggest that of the landraces tested, Zuni maize has the greatest potential to contribute genes that confer emergence capacity.

The second objective of this study was to characterize potential traits, such as morphological and dry matter partitioning characteristics, which could contribute to emergence capacity. The characterization of plant genetic resources is needed to document potential traits available for crop improvement (Goodman 1990).

Successful emergence from depth is attributed to mesocotyl elongation capacity, consistent with the findings of Collins (1914a) and Troyer (1997). Mesocotyl length increases with increasing planting depth, and mesocotyl lengths of seedlings that failed to emerge are consistently shorter than those of successful seedlings.

Differences in seed size and utilization of seed reserves do not explain differences in emergence capacity among populations. The check population had 36% greater initial seed weight than the mean seed weight of the landraces, but poorer emergence capacity from 25 cm. No significant differences were observed in percent seed weight utilized among populations within depths or across depths; the overall mean was 78% (sd 0.06).

Landraces allocated a greater proportion of dry matter to roots than shoots compared to the check population. Given the generally greater emergence capacity of the landraces, and the relationship between emergence success and mesocotyl length ($r = 0.47$), the greater allocation of dry matter to roots was unexpected. The greater root-to-shoot ratio of the landraces may reflect their adaptation to environments where water is often limiting. High root-to-shoot ratios of sorghum are associated with drought tolerance (Jordan and Miller 1980). Also, root architectures of some landraces differ from that of the check population.

The third objective was to evaluate characteristics of these landraces in terms of potential contributions to agricultural sustainability. Altieri (1995: 93) outlines several "objectives" of sustainable agricultural systems; the three most relevant "objectives" to this study are:

- "Productive" – Systems have the ability to provide sufficiently for the producer.
- "Dynamically stable" – Although systems are dynamic, they remain in relative balance over time.
- "Conservation and regeneration" – The resource base is not used up, but rather, is continually replenished or improved; genetic resources provide a gene pool to improve crops.

Genetic resources, such as the landraces evaluated in this study, could be used to broaden the genetic base of commercial varieties. Genetic diversity can contribute to sustainability by improving yield stability. Heterogeneity, or genetic variability, present in a population or among populations can buffer against environmental fluctuations. Specifically, genetic variability improves the chances that sufficient individual plants within a population will be capable of withstanding unusual conditions, and thus, maintain overall productivity at a relatively stable level regardless of conditions. Greater stability means more reliable maize productivity under variable conditions, fostering economic and social stability for producers and consumers alike, and for greater basic food security for society. Expanding crop genetic diversity, similar to biodiversity in less managed ecosystems, is an important factor to support the long-term productivity, stability, conservation and regeneration of the system as envisioned by the concept of sustainability.

Traits observed in these landraces indicate that these genetic resources have potential to contribute genes for characteristics to improve abiotic stress tolerance. Those landraces that exhibit high root-to-shoot ratios, for example, may improve tolerance to water deficits. Given the relatively precarious and harsh conditions of the native environments of these landraces, it is likely that these landraces possess genes for tolerance to such conditions as limited and unreliable moisture availability, temperature extremes, and nutrient limitations. Information about genetic resources that can potentially provide genes to improve abiotic stress tolerance of crops is important to long-term agricultural sustainability.

Several of the landraces evaluated in this study exhibit capacity to emerge from extraordinary depth. This trait may allow timelier planting and/or planting under conditions that would otherwise be unfavorable. Drought prone areas may be interested in incorporating these genetics so maize can be planted deeply to access valuable moisture reserves. In regions where wet, cold springs are prevalent, these genetics could enable producers to plant deeply and earlier with fewer complications from frost damage that often threaten early, shallowly planted maize. These landraces could provide the genes to enable producers to adjust planting depth to better accommodate the specific conditions at planting to improve the likelihood of good emergence and stand establishment. Potentially, this could also reduce the need and associated expense of replanting, as well as reduce yield loss due to delayed planting, and thus, contribute to the economic viability of agriculture.

The greatest future genetic yield gains are likely to be obtained from better tolerance to abiotic stresses (Tollenaar and Wu 1999). These landraces provide a reservoir of genetic traits that may confer stress tolerance. Their useful traits should be identified and transferred to into commercial varieties. Introgressing landrace genetics into Corn Belt varieties would expand the general genetic base of commercial maize, promoting agricultural sustainability.

Recommendations

In order to better understand the characteristics identified in this study and their mechanisms, additional research is needed; specifically, investigations of root architecture and tolerances of drought and frost. Also, further characterization of these landraces could identify other beneficial traits that could be useful in breeding efforts or to increase the genetic diversity of maize.

The dry matter partitioning and root architecture differences between the landraces and check suggest that future studies should be performed to investigate these characteristics, particularly as they may relate to adaptations to abiotic stresses. One recommendation for studying dry matter partitioning would be to perform experiments in the dark to prevent photosynthesis; in the present study, the seedlings from the 5 cm depth in Experiment 1 showed an increase in total seedling weight compared to initial seed weight, apparently because they accumulated carbon through photosynthesis.

The landraces involved in this study are not only traditionally planted deeply, but also native to drought and frost prone areas of the Southwest. The relatively high root-to-shoot ratios are suggestive of drought tolerance; the unusual root architectures may also be related to drought tolerance. Experiments should be conducted to specifically examine root-to-shoot ratios and root architectures. Additional studies should be conducted to determine if deep planting delays emergence of the growing point in the landraces, as well as the check population; if so, deep planting may be a useful strategy for extending protection from spring frost. Various water treatments and cold tolerance tests would indicate relative drought and cold tolerance compared to a check population. A growth chamber study could provide the conditions for testing these two variables, because water and light can be controlled efficiently and effectively. Responses under field conditions also should be examined.

These Southwest landraces and other genetic resources should be further characterized to identify useful traits. Populations cultivated for hundreds or thousands of years undoubtedly persisted through changing environments. These types of genetic resources may aid in the journey toward a more sustainable agriculture by incorporating useful traits of the past.

REFERENCES CITED

Adams, K.R. 1994. A regional synthesis of *Zea mays* in the prehistoric American Southwest. p. 273-302. *In* S. Johannessen and C. A. Hastorf (ed.) Corn and culture in the prehistoric new world. Westview Press, Boulder, CO.

Alessi, J., and J.F. Power 1971. Corn emergence in relation to soil temperature and seeding depth. Agron. J. 63:717-719.

Altieri, M.A. 1975. Agroecology the science of sustainable agriculture. Westview Press, Boulder, CO.

Anderson, E. 1954. Maize of the southwest. Landscape 3(2):26-27.

Anderson, E., and H.C. Cutler 1942. Races of *Zea mays*: I. their recognition and classification. Annals of the Missouri Botanical Garden 29:69-89.

Andrew, R.H. 1953. Short first internode in maize. J. of Heredity 49:146-148.

Andrew, R.H., and S S. Solanki 1966. Comparative root morphology for inbred lines of corn as related to performance. Agron. J. 58:415-418.

AOSA. 2001. Rules for testing seeds protocol.

Blacklow, W.M. 1972. Influence of temperature on germination and elongation of the radicle and shoot of corn (*Zea mays* L.). Crop Sci. 12:647-650.

Bradfield, R.M. 1973. An interpretation of Hopi culture. Duffield, Derbyshire.

Brady, N.C., and R.R. Weil 2002. The nature and property of soils. Prentice Hall, Upper Saddle River, NJ.

Brown, W., E. Anderson, and R. Tuchawena. 1952. Observations on three varieties of Hopi maize. Am. J. of Botany 39:597-608.

Carter, G.F., and E. Anderson 1945. A preliminary survey of maize in the Southwestern United States. Annals of the Missouri Botanical Garden 32:297-323.

Castetter, E.F., and W.H. Bell 1942. Pima and Papago Indian agriculture. The University of New Mexico Press, Albuquerque, NM.

Cirilo, A.G., and F.H. Andrade 1994. Sowing date and maize productivity: I. crop growth and dry matter partitioning. Crop Sci. 34:1039-1043.

Collins, G.N. 1914a. A drought-resisting adaptation in seedlings of Hopi maize. J. of Agric. Res. 1(4):293-307.

Collins, G.N. 1914b. Pueblo Indian maize breeding. J. of Heredity 5:255-268.

Cooper, C.S. and P.W. MacDonald. 1970. Energetics of early seedling growth in corn (*Zea mays* L.). Crop Sci. 10:136-139.

Cordell, L. 1997. Archeology of the southwest. Academic Press, San Diego.

Cushing, F. 1974. Zuni breadstuff. AMS Press, New York.

Deleens, E., N. Gregory, and R. Bourdu 1984. Transition between seed reserve use and photosynthetic supply during development of maize seedlings. Plant Science Letters (Ireland) 37:35-39.

Derwyn, R., B. Whalley, C.M. McKell, and L.R. Green 1966. Seedling vigor and the early nonphotosynthetic stage of seedling growth in grasses. Crop Sci. 6:147-150.

Dungan, G.H. 1950. Response of corn to extremely deep planting. Agron. J. 42:256-257.

Elmore, R.W., and B.J. Doupnik 1995. Corn recovery from early-season frost. J. Prod. Agri. 8:199-203. (Available online at http://screc.unl.edu/Hotline/Frost/frost.htm).

Farnham, D. 2001. Corn planting guide. Iowa State University, Ames, IA.

Fussell, B. 1992. The story of corn. North Point Press, New York.

Gardner, F.P., R.B. Pearce, R.L. Mitchell 1985. Seeds and Germination. p. 209-245. *In* Physiology of crop plants. Iowa State University Press, Ames, IA.

Glover, D.V., and E.T. Mertz 1987. Corn. p. 184-307. *In* R.A. Olson and K.J. Frey. (ed.) Nutritional quality of cereal grains: genetic and agronomic improvement. American Society of Agronomy, Inc., Madison, Wisconsin.

Goodman, M.M. 1990. Genetic and germ plasm stocks worth conserving. J. of Heredity 81:11-16.

Hack, J.T. 1942. The changing physical environment of the Hopi Indians of Arizona. Peabody Museum of American Archaeology and Ethnology, Harvard University, Cambridge, Mass.

Hackenberg, R.A. 1983. Pima and Papago Ecological Adaptations. Smithsonian Institution, Washington DC.

Harlan, J.R. 1975. Our vanishing genetic resources. Science 188:618-621.

Hendricks, D.M. 1985. Arizona Soils. University of Arizona, Tucson, AZ.

Hill, W.W. 1938. The agriculture and hunting methods of the Navaho Indians. Yale University Publications in Anthropology, New Haven.

Ingle, J., L. Beevers, and R.H. Hageman 1964. Metabolic changes associated with the germination of corn I. Changes in weight and metabolites and their redistribution in the embryo axis, scutellum, and endosperm. Plant Physiol. 39:735-740

Itabari, J.K., P.J. Gregory, and R.K. Jones 1993. Effects of temperature, soil water status and depth of planting on germination and emergence of maize (*Zea mays*) adapted to semi-arid eastern Kenya. Expl. Agric. 29:351-364.

Jordan, W.R., and F.R. Miller 1980. Genetic variability in sorghum root systems: Implications for drought tolerance. p. 383-399 *In* P.J. Kramer, N.C. Turner (ed.) Adaptation of Plants to Water and High Temperature Stress. Wiley-Interscience, New York.

Kiesselbach, T.A. 1949. The structure and reproduction of corn. University of Nebraska Press, Lincoln, NE.

Konen, M. 1999. Human impacts on soils and geomorphic processes on the Des Moines Lobe, Iowa. Iowa State University, Ames, IA.

Muenchrath, D., and R.J. Salvador 1995. Maize productivity and agroecology: effects of environment and agricultural practices on the biology of maize. p. 303-327. *In* H.W. Toll (ed.) Soil, water, biology, and belief in prehistoric and traditional southwestern agriculture. New Mexico Archaeological Council, Albuquerque, NM.

Muenchrath, D., M. Kuratomi, J.A. Sandor, and J.A. Homburg 2002. Observational study of maize production systems of Zuni farmers in semiarid New Mexico. [In press]. J. of Ethnobotony.

Murua, M., and T.J. Vyn 2002. Polymer seed coatings and risk reduction for early plant corn. *In* Agronomy abstracts [CD-ROM] ASA, Madison, WI.

Nabhan, G. 1984. Soil Fertility Renewal and Water Harvesting in Sonoran Desert Agriculture: The Papago Example. Arid Land Newsletter (University of Arizona, Office of Arid Lands Studies) 20:20-28.

National Genetic Resources Program. 2002. [Online]. www.ars-grin.gov/ (accessed 15 November 2001, verified 10 March 2002) ARS-GRIN.

National Water and Climate Center. 2001. [Online: current data only]. http://www.wcc.nrcs.usda.gov/scan/site.pl?sitenum=2031&state=ia (accessed 20 October 2001, verified 10 March 2002).

Nevo, E. 2001. Genetic diversity. p. 195-212. *In* S.A. Levin (ed.) Encyclopedia of Biodiversity, Vol. 3. Academic Press.

Ortiz, A. (ed.) 1979. Key to tribal territories. [Map] p. ix. *In* A. Ortiz (ed.) Handbook of North American Indians. Vol. 9. Smithsonian Institution, Washington DC.

Ortiz, A. 1994. Some cultural meanings of corn in aboriginal North America. p. 527-544. *In* S. Johannessen and C. A. Hastorf (ed.) Corn and culture in the prehistoric new world. Westview Press, Boulder, CO.

Passioura, J.B. 1986. Resistance to drought and salinity: avenues for improvement. Aust. J. Plant Physiol. 13: 91-201.

Random House. 1995. Random House Webster's college dictionary. McGraw-Hill, New York.

Ritchie, S., J. Hanway, and G. Benson 1997. How a corn plant develops. Iowa State University, Ames, IA.

Robertson, G. P., and R. R. Harwood 2001. Agriculture, sustainable. p. 99-107 *In* S.A. Levin (ed.) Encyclopedia of Biodiversity, Vol. 1. Academic Press.

Sarukhan, J. 1985. Ecological and social overviews of ethnobotanical research. Economic Botany 39(4):431-435.

Sayers, A.C. 2002. Manipulation of leaf area removal to simulate disease progression on inbred maize lines. M.S. creative component. Iowa State University, Ames, IA.

Schwartz, D.W. 1983. Havasupai. p. 13-24. *In* A. Ortiz (ed.) Handbook of North American Indians. Vol. 10. Smithsonian Institution, Washington DC.

Smith, J.S.C. 1988. Diversity of United States hybrid maize germplasm; isozymic and chromatographic evidence. Crop Sci. 28:63-69.

Soil Survey Staff. 1979. Soil survey of Boone County, Iowa. USDA. Washington D.C.

Stewart, K.M. 1983. Mohave. p. 55-85. *In* A. Ortiz (ed.) Handbook of North American Indians. Vol. 10. Smithsonian Institution, Washington DC.

Tollenaar, M., and J. Wu 1999. Yield improvement in temperate maize is attributable to greater stress tolerance. Crop Sci. 39:1597-1604.

Trimble, S. 1986. Our voices, our land. Northland Press, Flagstaff, AZ.

Troyer, A.F. 1997. The location of genes governing long first internode of corn. Genetics 145:1149-1154.

Troyer, A.F. 1999. Background of U.S. hybrid corn. Crop Sci. 39:601-626.

Tuan, Y.F., C.E. Everard, J.G. Widdison, and I. Bennett 1973. The climate of New Mexico, revised edition. State Planning Office, Santa Fe, NM.

USDA-NRCS-NSSC 1996. Soil survey laboratory methods manual. U.S. Government Printing Office, Washington DC.

Venturieri, G.A. 2001. Crop improvement and biodiversity. p. 897-912. *In* S.A. Levin (ed.) Encyclopedia of Biodiversity, Vol. 1. Academic Press.

Woodruff, D.S. 2001. Populations, species, and conservation genetics. p. 811-828. *In* S.A. Levin (ed.) Encyclopedia of Biodiversity, Vol. 4. Academic Press.

APPENDIX A. ENVIRONMENTAL CONDITIONS

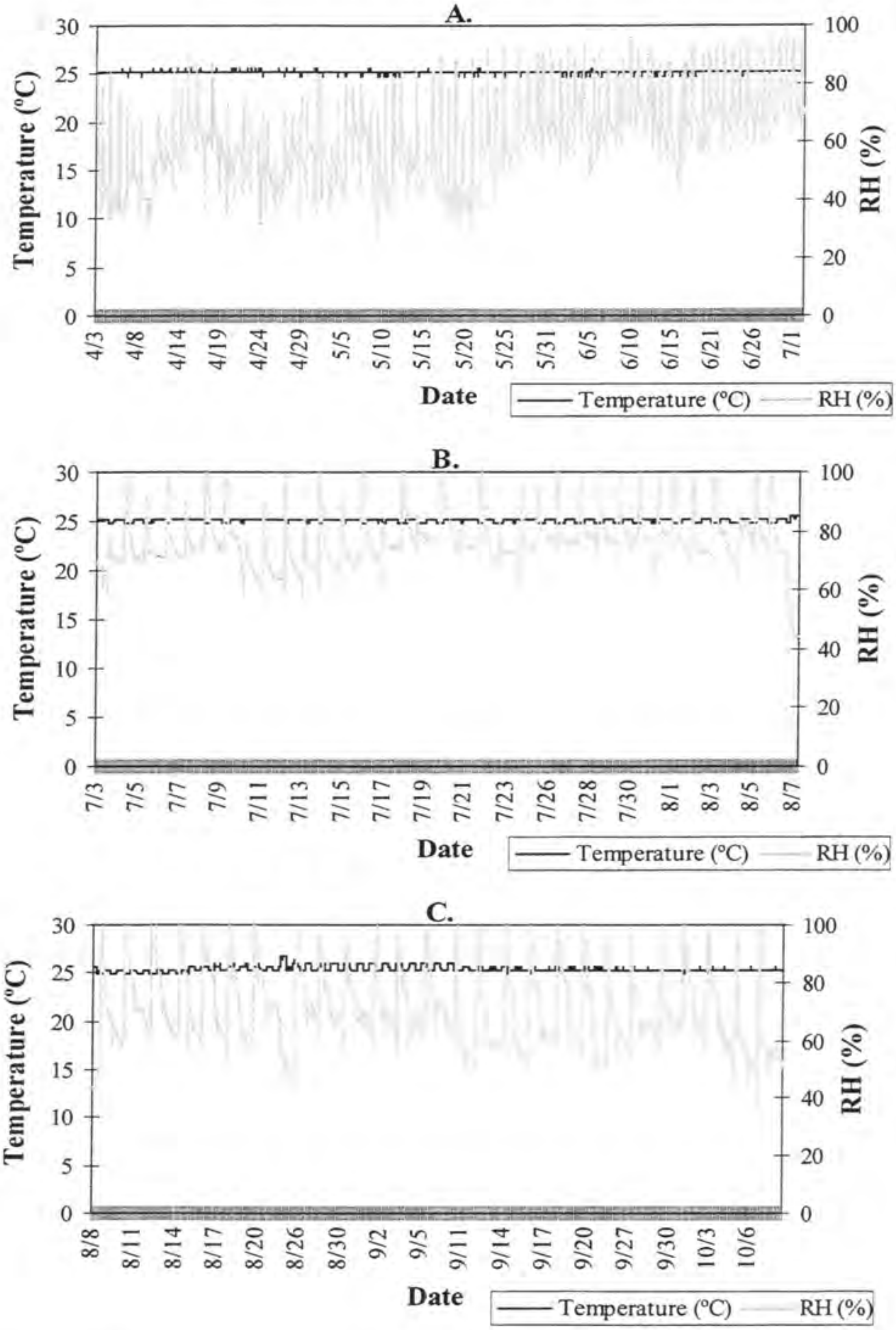

Figure 19: Temperature and relative humidity readings from the HOBO recording device located in the growth chamber. A, Experiment 1; B, Experiment 2; C, Experiment 3.

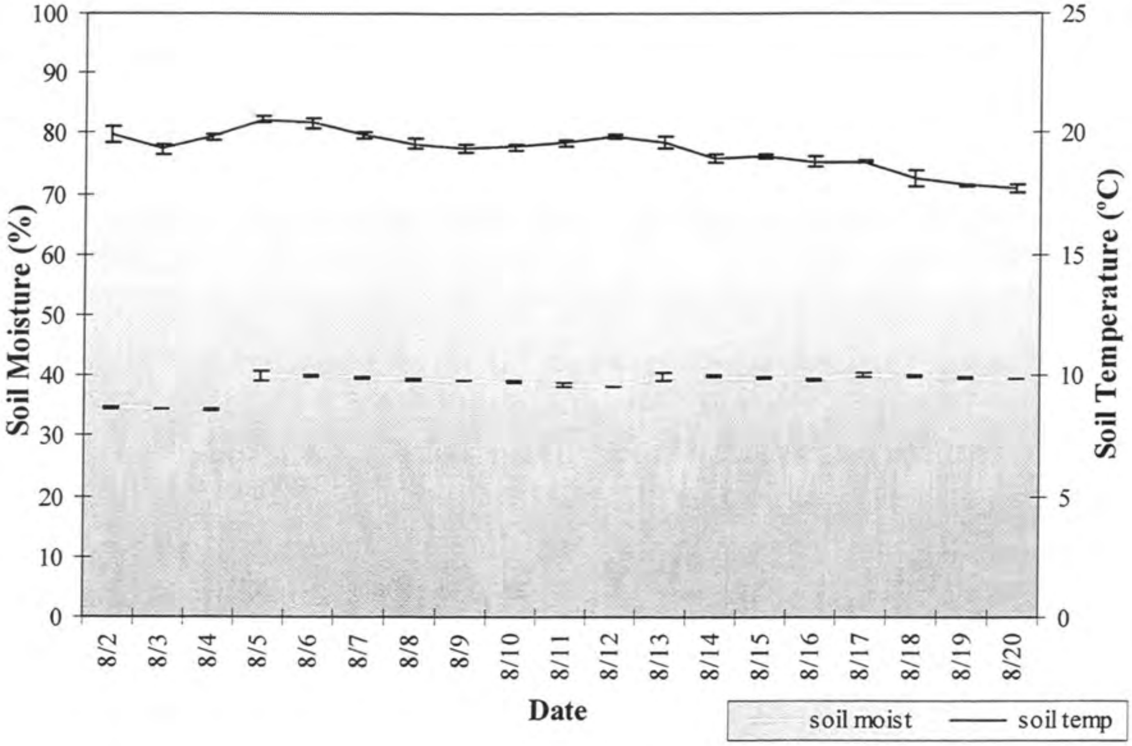

Figure 20: Soil moisture and temperature at 20 cm depth for period of Experiment 4. The experiment was planted 2 Aug 2002.

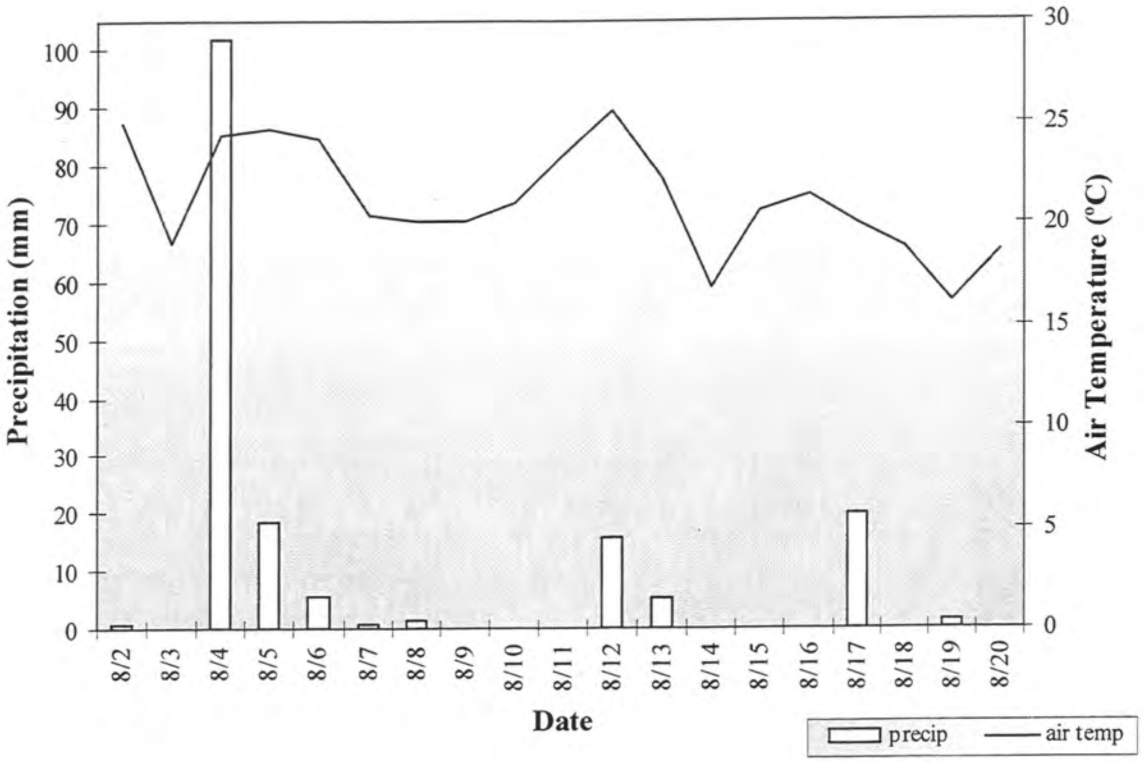

Figure 21: Precipitation and daily mean air temperature for period of Experiment 4.

APPENDIX B. ADDITIONAL TABLES

Table 16: Mean and standard deviation of mesocotyl length of each population at each planting depth for Experiment 1. Different lowercase letters indicate significant differences among populations at the 0.05 probability level by Tukey's LSD test.

	Mesocotyl Lengths			
Population	5 cm (sd)	15 cm (sd)	25 cm (sd)	Mean (sd)
	cm			
Hav	5.17 (0.86) ab	12.21 (2.31) ab	14.79 (5.57)	10.72 (2.92) ab
Hav-Hopi	4.83 (0.65) ab	13.17 (1.90) ab	15.55 (5.07)	11.18 (2.54) ab
Hopi	5.00 (0.60) ab	13.42 (1.40) a	17.32 (3.96)	11.91 (1.99) ab
Hopi-H	4.92 (0.76) ab	13.59 (1.63) ab	18.85 (4.32)	12.45 (2.24) ab
Hopi-K	5.63 (0.68) a	13.45 (1.74) ab	17.08 (5.04)	12.05 (2.49) a
Hopi-NO	5.13 (1.07) ab	13.36 (2.88) a	18.59 (5.68)	12.36 (3.21) a
Hopi-Sh	5.13 (0.96) ab	12.58 (3.32) ab	15.96 (5.57)	11.22 (3.28) ab
Mojave	4.83 (0.75) ab	12.18 (1.87) ab	15.41 (4.57)	10.81 (2.40) ab
Navajo	5.25 (0.84) ab	12.50 (2.22) ab	17.77 (4.64)	11.84 (2.57) ab
Tohono	4.83 (0.58) ab	11.27 (3.06) ab	12.75 (5.39)	9.62 (3.01) b
Zuni	5.13 (1.00) ab	13.54 (1.37) a	18.54 (4.28)	12.40 (2.22) a
Landraces Mean	5.08 (0.80)	12.84 (2.15)	16.60 (4.92)	11.51 (2.62)
BSSS	4.50 (0.60) b	10.55 (2.13) b	12.67 (3.83)	9.24 (2.19) b

Table 17: Mean and standard deviation mesocotyl length of emerged and failed seedlings from 25 cm in Experiment 1.

Population	Mesocotyl Lengths	
	Emerged (sd)	Failed (sd)
	---cm---	
Hav	18.43 (1.72)	9.70 (5.04)
Hav-Hopi	18.83 (2.93)	11.60 (4.22)
Hopi	19.07 (3.49)	14.25 (2.87)
Hopi-H	20.67 (1.63)	16.13 (5.92)
Hopi-K	19.71 (4.39)	13.40 (3.45)
Hopi-NO	20.28 (4.66)	11.00 (2.83)
Hopi-Sh	20.14 (1.65)	10.10 (2.75)
Mojave	16.28 (4.45)	11.50 (3.54)
Navajo	19.58 (4.03)	15.60 (4.77)
Tohono	16.42 (2.73)	7.25 (2.75)
Zuni	20.33 (2.69)	13.17 (3.75)
Landraces Mean	19.07 (3.12)	12.15 (3.81)
BSSS	15.20 (3.83)	10.86 (2.81)

Table 18: Mean and standard deviation of radicle length of each population at each planting depth in Experiment 1. Different lowercase letters indicate significant differences among populations at the 0.05 probability level by Tukey's LSD test.

Population	Radicle Lengths			
	5 cm (sd)	15 cm (sd)	25 cm (sd)	Mean (sd)
	---cm---			
Hav	37.67 (12.42) bc	29.58 (8.20) b	25.63 (6.29) ab	30.96 (8.97) c
Hav-Hopi	48.50 (12.26) abc	37.79 (10.49) ab	33.00 (5.51) ab	39.76 (9.42) ab
Hopi	47.17 (8.35) abc	37.79 (9.42) ab	33.13 (8.44) ab	39.36 (8.74) ab
Hopi-H	42.54 (9.01) abc	40.27 (14.97) ab	24.04 (8.72) b	35.62 (10.90) bc
Hopi-K	45.33 (9.62) abc	40.17 (6.46) ab	32.25 (6.74) ab	39.25 (7.61) ab
Hopi-NO	52.50 (16.10) a	34.17 (16.02) ab	28.46 (6.95) ab	38.38 (13.02) ab
Hopi-Sh	51.88 (10.71) ab	44.04 (6.76) a	35.17 (5.89) a	43.69 (7.79) a
Mojave	43.63 (9.47) abc	41.45 (7.62) ab	29.83 (8.54) ab	38.30 (8.54) abc
Navajo	49.83 (13.65) abc	40.00 (10.27) ab	29.92 (10.39) ab	39.92 (11.44) ab
Tohono	45.33 (8.54) abc	40.71 (8.03) ab	26.92 (10.52) ab	37.65 (9.03) abc
Zuni	48.25 (9.03) abc	40.08 (5.70) ab	32.42 (5.96) ab	40.25 (6.89) ab
Landraces Mean	46.60 (10.83)	38.73 (9.45)	30.07 (7.63)	38.47 (9.30)
BSSS	36.58 (7.00) c	28.75 (7.15) b	25.83 (7.18) ab	30.39 (7.11) c

Table 19: Mean and standard deviation of initial seed weight and total seedling dry weight in Experiment 1 for each depth.

	Initial Seed Weights			Seedling Dry Weights		
Population	5 cm (sd)	15 cm (sd)	25 cm (sd)	5 cm (sd)	15 cm (sd)	25 cm (sd)
	g					
Hav	0.25 (0.02)	0.27 (0.02)	0.25 (0.05)	0.33 (0.21)	0.29 (0.18)	0.20 (0.10)
Hav-Hopi	0.27 (0.04)	0.27 (0.03)	0.29 (0.03)	0.29 (0.15)	0.25 (0.20)	0.25 (0.10)
Hopi	0.27 (0.03)	0.27 (0.03)	0.26 (0.04)	0.30 (0.06)	0.25 (0.09)	0.21 (0.15)
Hopi-H	0.22 (0.03)	0.22 (0.03)	0.24 (0.03)	0.22 (0.09)	0.20 (0.06)	0.18 (0.07)
Hopi-K	0.22 (0.03)	0.22 (0.02)	0.22 (0.03)	0.26 (0.07)	0.22 (0.10)	0.20 (0.08)
Hopi-NO	0.23 (0.01)	0.23 (0.01)	0.23 (0.02)	0.22 (0.12)	0.24 (0.08)	0.20 (0.07)
Hopi-Sh	0.23 (0.02)	0.25 (0.02)	0.23 (0.01)	0.22 (0.04)	0.32 (0.14)	0.16 (0.04)
Mojave	0.27 (0.03)	0.27 (0.02)	0.27 (0.04)	0.37 (0.07)	0.32 (0.37)	0.27 (0.06)
Navajo	0.26 (0.02)	0.27 (0.04)	0.26 (0.03)	0.31 (0.18)	0.28 (0.12)	0.22 (0.11)
Tohono	0.24 (0.03)	0.24 (0.02)	0.25 (0.03)	0.38 (0.06)	0.25 (0.14)	0.23 (0.06)
Zuni	0.25 (0.02)	0.25 (0.04)	0.26 (0.02)	0.32 (0.17)	0.25 (0.07)	0.22 (0.11)
Landraces Mean	0.25 (0.02)	0.25 (0.03)	0.25 (0.03)	0.29 (0.11)	0.26 (0.14)	0.21 (0.09)
BSSS	0.33 (0.04)	0.35 (0.03)	0.33 (0.03)	0.41 (0.13)	0.37 (0.11)	0.27 (0.06)

Table 20: Mean initial seed weight utilization in Experiment 1.

	Seed Weight Utilization			
Population	5 cm	15 cm	25 cm	Mean
	%			
Hav	80	76	80	79
Hav-Hopi	82	73	77	77
Hopi	81	83	72	79
Hopi-H	66	71	63	67
Hopi-K	83	81	82	82
Hopi-NO	80	71	72	74
Hopi-Sh	81	80	77	80
Mojave	81	81	82	81
Navajo	86	84	81	84
Tohono	71	82	83	79
Zuni	85	81	84	83
Landrace Mean	80	79	78	79
BSSS	74	77	80	77

Table 21: Mean seedling dry weight allocation for each depth in Experiment 1.

	Remain Seed Weight			Shoot Weight			Root Weight		
Population	5 cm	15 cm	25 cm	5 cm	15 cm	25 cm	5 cm	15 cm	25 cm
	g								
Hav	0.05	0.06	0.05	0.09	0.11	0.07	0.19	0.12	0.07
Hav-Hopi	0.05	0.07	0.07	0.10	0.09	0.09	0.14	0.09	0.10
Hopi	0.05	0.05	0.07	0.11	0.12	0.08	0.14	0.08	0.06
Hopi-H	0.08	0.06	0.09	0.08	0.07	0.04	0.07	0.06	0.05
Hopi-K	0.04	0.04	0.04	0.10	0.07	0.07	0.13	0.11	0.09
Hopi-NO	0.05	0.07	0.06	0.07	0.11	0.07	0.10	0.07	0.07
Hopi-Sh	0.04	0.05	0.05	0.10	0.09	0.06	0.07	0.19	0.05
Mojave	0.05	0.05	0.05	0.14	0.14	0.12	0.19	0.13	0.10
Navajo	0.04	0.04	0.05	0.10	0.11	0.08	0.17	0.13	0.09
Tohono	0.07	0.04	0.04	0.13	0.11	0.10	0.18	0.09	0.09
Zuni	0.04	0.05	0.04	0.11	0.11	0.10	0.17	0.09	0.08
Landraces Mean	0.05	0.05	0.06	0.10	0.10	0.08	0.14	0.10	0.08
BSSS	0.09	0.08	0.07	0.21	0.18	0.13	0.11	0.10	0.08

Table 22: Mean dry weight root-to-shoot ratios in Experiment 1. Different lowercase letters indicate significant differences at the 0.05 probability level by Tukey's LSD test.

	Root to Shoot Ratios			
Population	5cm	15cm	25cm	Mean
Hav	2.24 a	1.20	1.30	1.58 a
Hav-Hopi	1.41 abc	1.13	1.01	1.18 ab
Hopi	1.29 abc	0.80	0.99	1.03 ab
Hopi-H	1.10 bc	0.71	1.71	1.18 ab
Hopi-K	1.75 ab	2.15	1.48	1.79 a
Hopi-NO	1.40 abc	1.07	0.99	1.15 ab
Hopi-Sh	0.76 bc	1.97	0.91	1.21 ab
Mojave	1.29 abc	0.91	0.91	1.04 ab
Navajo	1.64 abc	1.50	1.38	1.51 a
Tohono	1.37 abc	0.91	0.87	1.05 ab
Zuni	1.76 ab	0.82	0.82	1.13 ab
Landraces Mean	1.46	1.20	1.12	1.26
BSSS	0.60 c	0.65	0.75	0.67 b

Table 23: Mean and standard deviation of emergence success from 25 cm in Experiment 3.

Population	Emergence (sd)
	%
Hav	45 (0.13)
Hopi	40 (0.08)
Hopi-K	55 (0.17)
Hopi-NO	43 (0.05)
Hopi-Sh	68 (0.17)
Mojave	50 (0.26)
Zuni	73 (0.17)
Landraces Mean	53 (0.13)
BSSS	10 (0.08)

Table 24: Mean and standard deviation of emergence success of all populations and depths in Experiment 4.

	Emergence			
Population	5 cm (sd)	15 cm (sd)	25 cm (sd)	Mean (sd)
	---------------------%	---------------------		
Hopi-NO	97 (0.06)	70 (0.30)	30 (0.17)	66 (0.18)
Mojave	97 (0.06)	90 (0.10)	20 (0.17)	69 (0.11)
Zuni	97 (0.06)	67 (0.06)	67 (0.15)	77 (0.09)
Landraces Mean	97 (0.06)	76 (0.15)	39 (0.16)	71 (0.13)
BSSS	100 (0.00)	90 (0.17)	20 (0.00)	70 (0.06)

ACKNOWLEDGEMENTS

Seed stocks used in this study were provided by the USDA-ARS North Central Regional Plant Introduction Station, Ames IA; Native Seeds/SEARCH, Tucson, AZ; Silas Ghate, Zuni, NM; and Dr. Arnel Hallauer, Agronomy Department, Iowa State University. Dr. Dan Nettleton, Iowa State University Statistical Laboratory, provided guidance on data analyses. Thanks to Julie McGlaughlin of the Soils Laboratory for help with soils data. Preliminary protocols were developed by Jeremy Johnson.

This project would not have been possible without the help of several people; the general assistance of Lindsay Werth and Ryan Peterson are gratefully acknowledged. Also, thanks to Dr. Allen Knapp's group, Dr. Joan Peterson, Allen Vogl, the Gem's Project, Dr. Lance Gibson's group, Maria Hartt-Eckerman, Jon Bahrenfus and Dr. Mark Millard (NCRPIS) for all their help.

I would like to thank my Program of Study committee, Dr. Lorna Michael Butler, Dr. Allen Knapp and above all my major professor Dr. Deborah Muenchrath. The guidance and direction Deb provided was beyond measure; I cannot thank her enough. I would also like to thank my friends and family for their support during this journey, especially my twin sister Joni McGuire and my wonderful husband Aaron Bousselot.