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**GENETIC AND AGRONOMIC STUDIES OF NON-ELONGATING SUB-CROWN
INTERNODE IN SPRING BARLEY (*Hordeum vulgare* L.)**

by

Jose de Jesus Luna Ruiz

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF PLANT SCIENCES

**In Partial Fulfillment of the Requirements
For the Degree of**

**DOCTOR OF PHILOSOPHY
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In the Graduate College

THE UNIVERSITY OF ARIZONA

1995

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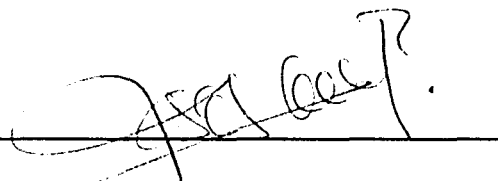
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A handwritten signature in black ink, written over a horizontal line. The signature is cursive and appears to read "James C. ...".

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To
Pepito and Frida

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ABSTRACT

This dissertation reports on studies of non-elongating subcrown internode (NE) in spring barley and its role in plant performance under reduced water use. Chapter 1 covers the inheritance study of NE. Chapter 2 reports a two year study of seeding depth and subcrown internode length (SIL) effects in performance of barley, wheat and durum genotypes. Chapter 3 reports on genetic and environmental factors that affect crown depth and crown root development under a one-irrigation cultural regime. The research was conducted between 1990 and 1993 under field and greenhouse conditions.

The NE character appears to be controlled by a major recessive gene. Selecting the NE trait is relatively easy by conventional plant breeding. SIL variation is continuous and seems regulated by several modifiers that interact strongly with the environment. Expression of genes for SIL require deep seeding.

Under field conditions and regardless of genotype, shallow seeding inhibited SIL but produced shallow crowns while deep seeding stimulated SIL but produced deeper crowns. Deep seeding increased yield, 100-seed weight, seeds/spike, and days to anthesis, but reduced tillers/m² and plant height in most genotypes. Short SIL genotypes (≤ 2.6 mm) were more favored by deep seeding than long SIL genotypes (≥ 8.2 mm). The correlations of SIL and crown depth with yield and yield components increased with deep seeding.

The time of crown root initiation varied tremendously among barley plants of CC XXXIX. Crown roots/plant could be predicted by leaves/plant ($r=0.92$; $P \leq 0.01$). Most plants in CC XXXIX had crown root initiation around the 3-leaf stage. The rate of soil

moisture decreased with soil depth. Soil moisture between day 7 and day 21 after the planting irrigation was depleted by 77 % at 0-2.5 cm and by 40 % at 12.5-15 cm depth. The construction of specific soil water tension curves based on soil moisture distribution over a dry period after the planting irrigation could be of great value in determining optimal seeding depth, choice of variety, and establishment of selection criteria for crown depth, and time of crown root initiation in a breeding program for reduced water use. Line P4 had no-SIL regardless of light and population density. Light deficiency increased SIL of Seco and the Yemen line more than high population density. The internodes below the crown in P4 are insensitive to light and population density, but internodes above the crown in the same line are as sensitive as Seco and the Yemen line. Screening for NE can be very efficient in the greenhouse at the seedling stage.

GENERAL INTRODUCTION

The development of crop varieties for areas of limited water requires a deep knowledge of the genetic and environmental factors that determine adaptation and performance under reduced water use conditions. The study of root systems represents a major part in the improvement of cultivars for dry land agriculture. Investigations of the root system of plants are limited compared to above ground parts, probably because of the difficulty to study roots. In small grains, the study of roots has been mainly focused toward the seminal root system, and little attention has been given to the crown root system. The reports on the association between crown depth and winter survival in winter cereals stimulated the study of crown roots in winter wheat and winter barley. The realization that sub-crown internode length (SIL) is a varietal character that determines crown depth increased the interest in the study of SIL and crown depth. The selection of winter genotypes with reduced SIL was suggested to improve winter survival as a result of deep crown formation. Because normal crown root development requires moisture at the crown region during crown root initiation, it was suggested that, under dryland conditions, the genotypes with short SCI could develop better crown root systems than the long SCI genotypes. This criterion has been applied in developing spring barleys for reduced water use conditions in a Male Sterile Facilitated Recurrent Selection Program. A recent study identified and isolated a spring barley plant ('line P4') without elongation of the SCI (Luna-Ruiz, 1992). The complete absence of SCI in the line P4 has a tremendous potential for basic and applied research. At this point, no information has been generated

to explain the genetic and environmental factors that determine the non-elongating SCI in this line. The inheritance of non-elongating SCI and the effect of this trait on crown depth and crown root development under reduced water use are of major importance for the breeder. Also, it is important to identify and understand other genetic and environmental factors that affect crown depth and crown root development. Factors such as seeding depth, time of crown root initiation, and rate of soil moisture depletion could influence the amount of moisture available for crown root development when irrigation water or rainfall is limited after planting. For example, the time of crown root initiation has been reported to be under genetic control in wheat, but not in barley. The availability of genetic variation for time of crown root initiation in the breeding population is very valuable. Selection for early crown root initiation could result in more use of water for crown root development. The main interest of this dissertation is to provide information to support and facilitate the selection of genotypes with non-elongating SCI and early crown root initiation under deep seedings. The goal is to generate an integrated genotype-management model to improve the performance of spring barley under a one-irrigation cultural regime.

CHAPTER 1

**INHERITANCE OF NON-ELONGATING SUBCROWN INTERNODE IN
SPRING BARLEY (*Hordeum vulgare* L.) BRED FOR A ONE-IRRIGATION
CULTURAL REGIME**

CHAPTER 1

INHERITANCE OF NON-ELONGATING SUBCROWN INTERNODE IN SPRING BARLEY (*Hordeum vulgare* L.) BRED FOR A ONE-IRRIGATION CULTURAL REGIME

INTRODUCTION

The crown of barley and other small grains is a meristematic region from which crown roots and tillers originate (Figure 1.1). Deep crown placement is a varietal character (Webb and Stephens, 1936), and has been associated with plant resistance to stress caused by freezing temperatures, root rot, wind, grazing, heaving, and soil moisture limitations (Taylor and McCall, 1936; Webb and Stephens, 1936; Sallans,

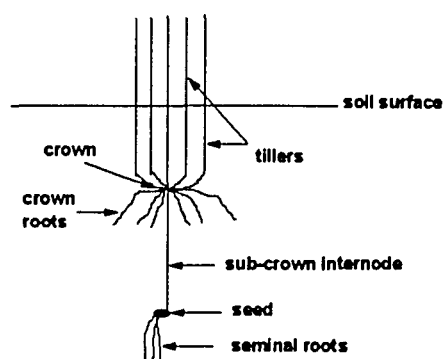


Figure 1.1 Typical root system of barley and its components

1961; Dobrenz, 1967; McKenzie, 1971; Kail et al., 1972; Martin et al., 1988). Crown depth is determined by degree of elongation of the subcrown internode (SCI), which in turn depends on temperature, light, seeding depth and genotype (Webb and Stephens, 1936; Ferguson and Boatwright, 1968; Martin et al., 1988). Shallow plantings restrict the elongation of the SCI regardless of genotype, however, deep plantings result in varying degrees of SCI elongation among different genotypes (Luna-Ruiz, 1992).

Crown depth, and soil moisture in the seed zone are critical factors for crown root

development, seedling establishment and final plant performance under reduced water conditions. Webb and Stephens (1936) concluded that wheat and barley plants grown in dry surface soils commonly yield poorly because they fail to develop crown roots. Crown root and tiller development require, among other things, adequate moisture at the crown region during the early stages of seedling establishment. Crown roots will not develop if moisture around the crown is below a critical value at the time of crown root initiation.

Hudspeth and Taylor (1961) noticed that the top half-inch of the soil on the High Plains of Texas often dries to below the permanent wilting point within 24 hours after wetting. A recent study in Marana, AZ showed a dramatic loss of moisture in the top 2.5 cm of the soil (Pima clay loam) within the first few days after the planting irrigation (Chapter 3). The drying rate depends on factors such as soil texture, temperature, wind velocity, canopy, and initial soil moisture. Regardless of the drying conditions, the degree of soil moisture retention is

expected to increase with soil depth

(Wiegand, 1962), as illustrated in

Figure 1.2. Wiegand (1962)

observed a parabolic moisture distribution in the region where seeds are normally placed, and

emphasized the importance of

proper planting depth to insure

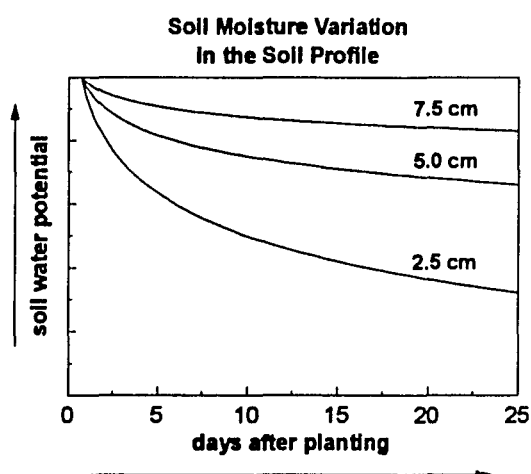


Figure 1.2 Expected variation of soil moisture content at different depths after the planting irrigation.

moisture for germination. The same author reported drying rates of 0.65% and 2.75 % per day at the 9.5 cm and 1.9 cm depths, respectively, in a sandy clay loam, 4 days after irrigation. Thus, selection of genotypes that have a non-elongated SCI or a deep crown placement under deep seedings may produce cultivars with improved crown root development, seedling establishment and final plant performance under conditions where irrigation water or rainfall is limited after planting.

Selection for short SCI and/or deep crown placement has been suggested to improve winter hardiness in winter wheat and winter barley (Ashraf and Taylor, 1974; Ferguson and Boatwright, 1968; Kail et al., 1972; Taylor and McCall, 1936), to escape damage by root rot (Sallans, 1961), and to improve performance of spring barley under semiarid conditions (Martin et al., 1988). 'Male Sterile Facilitated Recurrent Selection' (MSFRS) for short or no SCI length in the barley population 'Composite Cross XXXIX' (CC XXXIX) has been conducted under a one-irrigation cultural regime in Arizona. Two spring barleys selected from CC XXXIX (line '309-2' and selection 'P4' derived from line '8-21-B4') have shown no elongation of the SCI. Selection 309-2 initiates its crown at or near the seed, irrespective of light and temperature variation (Martin et al., 1988). Crown placement in selection P4 is usually restricted to the depth of seeding regardless of seeding depth, temperature (Luna-Ruiz, 1992) and light variation (Chapter 3). The non-elongated SCI character that is present in the lines P4 and 309-2 may be an advantageous characteristic in breeding for reduced water use conditions. However, the genetic control of the non-elongated SCI character in one-irrigation barley is unknown.

Research on the inheritance of SCI length in small grains is very limited, particularly for spring barley. Gul and Allan (1978) concluded that the inheritance of SCI length in winter wheat is not complex and Dofing and Schmidt (1984) indicated that shortness of the SCI in winter barley is primarily controlled by recessive genes with major effects, plus minor genes with small effects. McKenzie (1971) found no dominance, but heterosis for long SCI in crosses between long and short SCI spring wheat cultivars. Poulos and Allan (1987) observed dominance and overdominance for long SCI in winter wheat. McKenzie (1971) indicated that short SCI in spring wheat differs from long SCI by two genes, and that intermediate SCI differs by one gene from both short SCI and long SCI. Poulos and Allan (1987) observed a continuous variation with transgressive segregation in most segregating generations from a winter wheat cross involving short and long SCI cultivars. The same authors detected low heritabilities, small phenotypic standard deviations, and modest responses to selection with higher variation under greenhouse compared to field conditions.

The inheritance of SCI length has been studied in winter wheat, spring wheat and winter barley, but not in spring barley. Most studies report non-complex inheritance for SCI length and/or crown depth in these crops. Short SCI and/or deep crown are apparently controlled by a major recessive gene in addition to other genes with minor effects (Gul and Allan, 1978; Dofing and Schmidt, 1984). None of the studies on inheritance has included or reported wheat or barley germplasm with complete absence of SCI.

The objective of this research was to assess the genetic control of the non-elongated SCI character present in the spring barley line P4. This research is part of a series of studies on the SCI elongation in barley bred for production under a one-irrigation cultural regime.

MATERIALS AND METHODS.

Genetic Material

The barley line P4, which has no SCI, was crossed with 8 lines with SCI lengths ranging from short to long. An additional cross between two barleys with long SCI (P1 and P7) was included in the study. All lines used in this study, which were previously classified and characterized for SCI in a greenhouse (Luna-Ruiz, 1992), are described in Table 1.1.

Table 1.1 Origin and characterization of the barleys used in the study

Parent Description	Seed Source	Degree of SCI elongation	Selection Environment
P4 (Reselection of 8-21-B4) common parent	88-M-6821-B4	no-elongation	one irrigation (6-row)
P1 (7-21-13-5)	88-M-6821-I-3	intermediate	one irrigation (6-row)
P2 (7-21-18-1)	88-M-6821-J-3	long	one irrigation (2-row)
P5 (8-21-D-1)	88-M-6821-D-1	intermediate	one irrigation (6-row)
P6 (6-34-55)	88-M-6821-F-3	short	one irrigation "
P7 (7-21-13-4)	88-M-6821-I-2	intermediate	one irrigation "
P9 (8-21-M-3)	88-M-6821-M-3	short	one irrigation "
P10 (Yemen line)	86-Ma-6881-4-5	long	light showers (2-row)
Seco (PI-508552)	88-M-6821-K-5	intermediate	one irrigation (6-row)
Solum (PI-555747)	88-M-6821-K-6	intermediate	one irrigation "

The lines P2 and P10 are two-rowed and the others are six-rowed barleys. The line P10 is a land race from Yemen that is grown in low rainfall areas where rains come in infrequent, small showers. All other lines used in this study were selected from CCXXXIX populations that were grown under a one-irrigation cultural regime in Arizona.

Crosses were made in the field at Marana, AZ during the winter of 1990-91 using conventional emasculation and pollination procedures. The F1's and their parents were grown in the field at Bozeman, MT in the summer of 1991. Seven spikes from each F1 plot and three spikes from each parent plot were harvested. F2's of all crosses, along with their parents, were grown in the field at Marana in 1992. F3's of six of the crosses with P4, along with their parents, were grown in the field at Marana in 1993. Parents, F1's and F2's of three crosses (P4 x Solum, P4 x P10, and P1 x P7) were grown in a greenhouse during 1993.

Field Studies

All field evaluations were conducted under a one-irrigation cultural regime at the Marana Agricultural Center on a Pima clay loam soil (fine-sandy, mixed, thermic family of Typic Torrifuvents). Plots were grown on beds 1 m apart with two rows, 35 cm apart, on a bed. Rows were 3.2 m long. Seeding rate was 30 seeds per row. Seeding depth was about 80 mm. With the available equipment, seeding depth was difficult to control. In 1992, proper land preparation was not achieved due to late winter rains. The results were an uneven seedbed and an uneven seeding depth.

Eight rows of each F2, along with two rows of each of their parents, were planted on January 2, 1992. At maturity, 20 plants of each parent and all plants in four rows of each F2 were harvested. One spike and the crown with its SCI were harvested from each plant and taken to the laboratory. Each spike was threshed individually to be used to seed F3 rows. Subcrown internode length (seed-to-crown distance) of each plant was measured on millimetric paper.

Seed of selected F2 plants from 6 of the 9 crosses with P4 were planted in F3 rows in the field on February 3, 1993. Rows of each parent were also planted. At maturity, samples ranging from 10 to 30 plants were harvested from each row. Subcrown internode length of each plant was measured on millimetric paper.

Greenhouse Study

Greenhouse evaluations were conducted on three different dates, between October 19 and December 10, 1993, at the USDA/ARS facility (2000 E. Allen, Tucson, AZ 85719). Only three crosses were used due to seed and space limitations. The cross P4 x Solum was chosen to represent the crosses of P4 with intermediate SCI barleys, and the cross P4 x P10 to represent crosses of P4 with long SCI barleys. The cross P1 x P7 was included because both parents develop SCI's. Each experiment consisted of the evaluation of the SCI length of F1's, F2's and parents of the selected crosses.

A general procedure was previously developed to adjust for the most appropriate pot size, planting depth, seed number, sampling stage, and irrigation and fertilization

frequency (Luna-Ruiz, 1992). The final experimental procedure consisted of growing plants of parents and progenies in pots (20 cm diameter x 40 cm high) containing a mixture of equal amounts of perlite, vermiculite and peat moss. Each pot was seeded at a depth of 60 mm with 10 seeds of either a parent, an F1 or an F2 of the corresponding cross. Due to seed limitations, the number of pots used per generation varied from date to date. The number of pots used per date was replicated once or twice for parents, once for F1's, and one or three times for the F2's. Tap water, and water soluble fertilizer (20-20-20 Champion Geranium Food, 1 tsp/gallon of water) was provided to plants once a week. Artificial light was not used during the study, and temperature was monitored continuously during each experiment using a hygrothermograph. Sampling began at tillering and consisted of clipping the seminal roots and washing the soil mix out of the root system of each plant. Subcrown internode length was measured on millimetric paper.

Data Analysis

Frequency distributions were determined for parents and offspring of each cross evaluated in the field in 1992 and in the greenhouse according to 5 SCI length intervals (0, 1-12.5, 12.6-27.5, 27.6-42.5, and >42.5 mm). The quantitative classification (degree of SCI length) was converted to a phenotypic classification of elongated (E) and non-elongated (NE) SCI (qualitative classification). Because the character of interest in this study was the non-elongating SCI (NE), emphasis was given to the qualitative classification. The NE phenotype contained plants falling in the 0 mm interval, and the E

phenotype contained plants falling in the other 4 SCI length intervals. The F3's evaluated in the field in 1993 were all measured for SCI length, but classified according to the qualitative classification. Chi-square values were used to compare observed data with expected ratios.

Data from the three greenhouse experiments were combined and analyzed as a single experiment. All of the analyses were performed on SAS (Statistical Analysis System) version 6.04. Data management, figures, and tables were performed with Lotus 1-2-3 version 4.0, Freelance Graphics version 2, and WordPerfect version 6.0.

RESULTS AND DISCUSSION

The SCI length distribution for parents and F2's of the 9 crosses evaluated in the field in 1992 are presented in Table 1.2. Phenotypic classification of F3 rows of the 6 crosses evaluated in the field in 1993 are presented in Table 1.3. The number of F3 and parental plants evaluated per cross in the field in 1993, along with their means and ranges for SCI length are presented in Table 1.4. The SCI length distribution for parents, F1's and F2's of the 3 crosses evaluated in the greenhouse are presented in Table 1.5.

Of 394 plants of P4 grown in the field in 1992 and 1993, and in the greenhouse, 393 had no SCI. The one plant with an elongated SCI (15 mm) was probably an outcross or a mixture. These results indicate that the lack of SCI is fixed in the line P4 and stable across environments.

Table 1.2 Distribution of SCI lengths of parents and F2's of 9 crosses evaluated in the field at Marana, AZ in 1992

Cross	Population	n	SCI length Intervals (mm)				
			0	1-12.5	12.6 - 27.5	27.6 - 42.5	>42.5
			No of plants				
P4 x P6	P4	20	20	0	0	0	0
	F2	110	108	1	1	0	0
	P6	21	21	0	0	0	0
P4 x P9	P4	20	20	0	0	0	0
	F2	98	96	0	1	1	0
	P9	20	16	0	3	1	0
P1 x P7	P1	20	0	2	13	4	1
	F2	93	4	4	75	10	0
	P7	20	0	2	14	4	0
P4 x P5	P4	20	20	0	0	0	0
	F2	92	63	7	20	2	0
	P5	20	0	1	19	0	0
P4 x P7	P4	20	20	0	0	0	0
	F2	106	80	8	13	5	0
	P7	20	0	8	12	0	0
P4 x Seco	P4	20	20	0	0	0	0
	F2	69	60	0	9	0	0
	Seco	20	0	2	14	4	0
P4 x Solum	P4	19	19	0	0	0	0
	F2	81	63	7	9	1	1
	Solum	20	3	1	14	2	0
P4 x P2	P4	20	20	0	0	0	0
	F2	106	48	20	30	6	2
	P2	21	0	1	15	5	0
P4 x P10	P4	20	19	0	1	0	0
	F2	102	43	10	41	8	0
	P10	20	0	0	17	3	0

Table 1.3 Phenotypic classification for SCI of F3's of six crosses evaluated in the field at Marana, AZ in 1993

Cross	F2 class	†E			NE			n
	→							
	F3 class	E	seg	N E	E	seg	NE	
	→	No of plants						
P4 x P5		3	3	0	1	35	23	65
P4 x P7		0	6	2	0	38	22	68
P4 x Seco		1	3	4	1	35	23	67
P4 x Solum		0	4	2	1	4	1	12
		0	5	1	0	4	1	11
		1	4	1	0	5	1	12
P4 x P2								
P4 x P10								

†E = elongated SCI; NE = non-elongated SCI; seg = segregating

Table 1.4 Summary SCI length for all F3's evaluated in the field in 1993.

Cross	Population	No of Plant s	SCI length (mm)	
			mean	range
P4 x P5	P4	24	0	0 - 0
	NE plants from F3's	616	0	0 - 0
	E plants from F3's	239	14.4	4 - 38
	P5	36	16.4	8 - 36
P4 x P7	P4	20	0	0 - 0
	NE plants from F3's	628	0	0 - 0
	E plants from F3's	245	15.6	6 - 38
	P7	75	16.7	6 - 28
P4 x Seco	P4	20	0	0 - 0
	NE plants from F3's	550	0	0 - 0
	E plants from F3's	250	16.8	6 - 34
	Seco	93	18.8	6 - 44
P4 x Solum	P4	20	0	0 - 0
	NE plants from F3's	80	0	0 - 0
	E plants from F3's	38	15.7	8 - 34
	Solum	86	16.3	6 - 30
P4 x P2	P4	20	0	0 - 0
	NE plants from F3's	79	0	0 - 0
	E plants from F3's	87	16.6	6 - 38
	P2	49	22.7	14 - 44
P4 x P10	P4	43	0	0 - 0
	NE plants from F3's	72	0	0 - 0
	E plants from F3's	89	18.7	6 - 36
	P10	22	25.9	18 - 50

Table 1.5 Distribution of SCI lengths of parents, F1's and F2's of 3 crosses evaluated in the greenhouse

Cross	Population	n	SCI length Intervals (mm)				
			0	1-12.5	12.6 - 27.5	27.6 - 42.5	>42.5
			No of plants				
P4 x Solum	P4	31	31	0	0	0	0
	F1	17	0	5	11	1	0
	F2	86	28	18	27	13	0
	Solum	30	0	4	15	11	0
P4 x P10	P4	36	36	0	0	0	0
	F1	29	0	1	8	19	1
	F2	56	24	8	15	8	1
	P10	56	0	0	7	24	25
P1 x P7	P1	21	0	0	0	14	7
	F1	28	0	0	1	26	1
	F2	31	0	1	5	24	1
	P7	38	0	7	15	15	1

According to field evaluations in 1992 (Table 1.2), none of the 20 plants of the line P6 had a SCI. The F2 of the cross P4 x P6 consisted of 108 plants without a SCI and two with a SCI. Of 20 plants of the line P9, 16 did not have a SCI and four had a SCI. The F2 of the cross P4 x P9 consisted of 96 plants with no SCI and two with a SCI. The lines P4, P6, and P9 have a common ancestry and probably have the same genotype for lack of SCI elongation. The four plants of line P9 that had SCI elongation were probably the result of heterogeneity within the line as it had not been selected for any character other than yield. The two plants in the F2 of P4 x P6 and the two plants in the F2 of P4 x P9 with SCI

could be the result of outcrossing in the F1 generation in Bozeman, MT in the summer of 1991. Up to 5 % outcrossing has been observed in a sister line (Solum) at Bozeman (Ramage, unpublished).

According to evaluations in the field in 1992 (Table 1.2), all plants in lines P1 and P7 had elongated SCI. The F2 of P1 x P7 consisted of 89 plants with elongated SCI and 4 plants with no SCI. According to greenhouse evaluations (Table 1.5), all plants in lines P1 and P7 had elongated SCI as did all plants in the F1 and F2 of the cross P1 x P7. The lines P1 and P7 probably have the same genotype for elongating SCI. The four NE F2 plants observed in the field were probably misclassifications due to uneven planting depth in the field in 1992, where seed placement was not precisely controlled. In the greenhouse seeding depth was precisely controlled, and SCI elongation was well expressed. Differences in the distribution of internode length classes were observed in both the field and the greenhouse for both parents and their F1 and F2. The continuous variation observed for degree of SCI length in P1, P7, and their progeny is probably due to the presence of different modifiers affecting the degree of SCI elongation, in addition to strong environmental effects. Also, the differences between field data and greenhouse data can be explained by uneven planting depth in the field in 1992. The elongation of the SCI occurs only under deep seedings (Luna-Ruiz, 1992), thus, depth of planting modifies the degree of SCI elongation, and shallow planting inhibits the expression of the E phenotype.

According to field classifications in 1992 (Table 1.2), all plants of the lines P5, P7, Solum and Seco had elongated SCI, except for 3 plants of Solum. These 3 plants in Solum

were probably misclassified due to uneven planting depth in 1992. In the greenhouse, all 30 plants of Solum had elongated SCI. These four lines (P5, P7, Solum and Seco) have a common ancestry and could have the same genotype for SCI elongation. The crosses of P4 with P5, P7, Seco and Solum produced F2's in the field in 1992 that consisted of 29 E:63 NE for P4 x P5, 26 E:80 NE for P4 x P7, 9 E:60 NE for P4 x Seco, and 18 E:63 NE for P4 x Solum. In the greenhouse, all 17 F1 plants of the cross P4 x Solum had an elongated SCI, and the F2 consisted of 58 E:28 NE plants (χ^2 fit to a 3:1 ratio is 2.620, $P=0.1$ to 0.2). The F1 and F2 ratios observed in the greenhouse with the cross P4 x Solum indicate that the NE character is due to a single recessive gene. If so, the high frequency of NE plants observed in the F2's of P4 with P5, P7, Seco and Solum in the field in 1992 could be explained by a lack of expression of the E phenotype due to uneven planting depth. This can be confirmed by F3 evaluations. Certain F2 plants were grown in the field in 1993 (Table 1.3). All NE F2 plants should produce NE progeny, and the E F2 plants should be of two types, all E or segregating E:NE. According to F3 classifications, 35 of 59 F2 NE plants of the cross P4 x P5 segregated, one was homozygous for the E phenotype, and 23 were homozygous for the NE phenotype. In the cross P4 x P7, out of 60 F2 NE plants, 38 segregated and 22 were homozygous for the NE phenotype. In the cross P4 x Seco, out of 59 F2 NE plants, 35 segregated, 1 was homozygous E, and 23 were homozygous NE. Of the 178 NE F2 plants from these 3 crosses, 38 % produced NE F3 progeny, and 62 % segregated or were homozygous for the E phenotype. The 62 % of heterozygosity and/or homozygosity for the E phenotype probably resulted from a lack of

expression of the E character in the F2 of these crosses in the field in 1992 probably due to uneven planting depth.

The average SCI lengths of P5, P7, Seco and Solum in the field in 1993 were 16.4, 16.7, 18.8, and 16.3 mm, with ranges of 8-36, 6-28, 6-44, and 6-30 mm, respectively (Table 1.4). The average SCI lengths of F3 plants that had elongated SCI in the field in 1993 were 14.4 mm for P4 x P5, 15.6 mm for P4 x P7, 16.8 mm for P4 x Seco, and 15.7 mm for P4 x Solum. The SCI length of these four crosses had ranges of 4-38, 6-38, 6-34, and 8-34 mm, respectively. The means and ranges of the SCI length of these four parents and their E plants in the F3's of crosses with P4 are very similar (Table 1.4). This is additional confirmation that P5, P7, Seco and Solum have the same genotype for elongating SCI.

All plants of the 2-row parents (P2 and P10) had elongated SCI in the field in 1992 (Table 1.2). In the greenhouse, the line P10 had all 56 plants with elongated SCI (Table 1.5). These data indicate that P2 and P10 have a different genotype for SCI elongation than P4. The lines P2 and P10 develop a very long SCI but P10 often places the crown above ground. The SCI length of P2 and P10 in the field in 1993 had means of 22.7 and 25.9 mm, and ranges of 14-44 and 18-50 mm, respectively (Table 1.4). The line P2 was selected from the CCXXXIX population and P10 is a land race from Yemen. P2 and P10 have very different genetic backgrounds.

The F2's of P4 x P2 and P4 x P10 grown in the field in 1992 contained 58 E:48 NE and 59 E: 43 NE plants (Table 1.2). In the greenhouse, the F1 of the cross P4 x P10

contained 29 E:0 E plants, and the F2 contained 32 E:24 NE plants (Table 1.5). The chi-square fit of the F2 greenhouse ratio to an expected 3 E:1 NE ratio is 9.524 ($P = 0.01 - 0.001$). One possible explanation for the excess NE plants in these crosses could be the modification of some heterozygous plants by modifying factors resulting in types with a very short SCI that were misclassified as NE. The crown of line P10 has a tendency to differentiate into several crown nodes and internodes when it is deep seeded. This characteristic is probably due to modifying factors, and is easily detected in the greenhouse, but difficult to distinguish in the field. According to greenhouse observations, the cross P4 x P10 produced F2 plants having a combination of the multicrown characteristic of line P10, and the reduced SCI of line P4. Sub-crown internode length is very difficult to determine in plants of this type, and some plants with a very short SCI were probably misclassified as NE. This could be an explanation for the high frequency of NE plants in this cross. The F3 plants that had elongated SCI in the crosses P4 x P2 and P4 x P10 had means of 16.6 and 18.7 mm, and ranges of 6-38 and 6-36 mm, respectively. These results provide additional confirmation that P2 and P10 differ from line P4 in their genotype for SCI elongation, and that the crosses of P2 and P10 with P4 produce a wide range of SCI lengths. Also, according to field evaluations of F2's in 1992 and F3's in 1993 with the crosses P4 x P2 and P4 x P10, there are no linkage relationships between long SCI and the 2-row character of P2 and P10 (data not shown).

The means and ranges of F3 plants having elongated SCI in all 6 crosses evaluated in the field in 1993 were very similar (Table 1.4). These similarities are probably due to the

effect of a major recessive gene that conditions the lack of SCI in P4. Dolfing and Schmidt (1984) reported that shortness of the SCI in winter barley is controlled by major recessive genes in addition to minor genes. The different F₂ ratios obtained with the crosses P4xP10 and P4 x Solum were probably due to the different background genotypes of P10 and Solum. These two lines may carry different modifiers that affect differently the degree of SCI length. Also, because the 2-row lines P2 and P10 and their E progenies tend to develop a very long SCI, they may be less sensitive to planting depth variation compared to barleys of shorter SCI. Thus, it may be possible that the expression of the E genotype in long SCI barleys requires shallower seedings compared to those barleys with shorter SCI. A much higher frequency of F₂ plants showing SCI (E class) was observed in the field in 1992 with crosses between P4 and 2-row barleys (51% and 55 %) compared to the crosses of P4 with 6-row barleys (13% to 28%) as shown in Table 1.2. Such difference may indicate that the classification of segregating populations from crosses involving parents with a very long SCI is more accurate because most plants carrying the E phenotype will very likely develop a long or very long SCI, compared to crosses involving parents of intermediate, short or no SCI. This may confirm that the line P10 and probably the line P2 carry different modifier factors of the SCI length.

The elongating SCI (E phenotype), when expressed, showed a continuous variation in length in the field (Tables 1.2 and 1.4) and greenhouse (Table 1.5). Such variation is probably due to the effect of several alleles (modifiers) at different loci that modify the elongation of the SCI. These modifiers are probably strongly affected by the

environment. These results agree with those obtained by Poulos and Allan (1987) with winter wheat, and by Dofing and Schmidt (1984) with winter barley. The former observed a continuous variation with transgressive segregation in most segregating generations from a winter wheat cross involving short and long SCI cultivars. According to Dofing and Schmidt (1984), shortness of the SCI in winter barley is primarily controlled by recessive genes with major effects, plus minor genes with small effects. The number of modifiers and their individual contribution to SCI length are very difficult to determine because it demands the evaluation of very large populations under strictly controlled conditions in order to separate the genetic component from the environmental component. McKenzie (1971) indicated that short SCI in spring wheat differs from long SCI by two genes, and that intermediate SCI differs by one gene from both short SCI and long SCI. The same authors detected low heritabilities, small phenotypic standard deviations, and modest responses to selection for short SCI with higher variation under greenhouse compared to field conditions. Regardless of its genetic control, the degree of SCI elongation becomes of little or no importance for the breeder when the lack of SCI (NE phenotype) is the selectable character in barley breeding for reduced water use conditions.

SUMMARY AND CONCLUSIONS

Based on phenotypic classifications (E:NE), the lack of SCI elongation (NE) in the line P4 is due to a major single recessive gene. Lines P6 and P9 have the same genotype as P4 for non-elongating SCI (NE). The lines P1 and P7 both have the same genotype for

elongating SCI (E). The lines P5, P7, Seco and Solum probably differ from the line P4 by having a dominant allele for elongation of the SCI. The 2-row lines P2 and P10 have different background genotypes, but both develop a very long SCI. Lines P2 and P10 may differ from lines P5, P7, Seco and Solum in the modifying alleles for SCI length. The continuous variation within the E phenotype may be due to the effect of several modifiers that have a strong interaction with the environment. In some cases, the NE class may be actually a combination of plants with non-elongated SCI and plants with a very short SCI that result from the effect of modifying factors on the E phenotype. There is also evidence indicating that the long SCI is independent from the 2-row character in the lines P2 and P10. Selection for the non-elongating SCI should be conducted under precisely controlled deep seedings. The seeding depth for selection will depend on factors that determine emergence from deep seedings such as coleoptile length, rate of germination, rate of emergence, and soil characteristics. Of major importance is that regardless of the number of genes, the lack of SCI can be handled as a single recessive character. Thus, transferring of the non-elongating character between barley populations should be relatively easy to accomplish by conventional plant breeding methodologies.

CHAPTER 2

**THE ROLE OF SEEDING DEPTH AND SUB-CROWN INTERNODE LENGTH
IN PERFORMANCE OF BARLEY (*Hordeum vulgare* L.) BRED FOR
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INTRODUCTION

Water is one of the major limiting factors in agriculture (Hurd, 1974). Crop production even with limited water can be increased by improving crop management practices in order to store and use water, and/or by developing high yielding cultivars for reduced water conditions (Quizenberry, 1981). Male sterile facilitated recurrent selection (MSFRS) has been used to develop barley, wheat and durum populations and cultivars under a one-irrigation cultural regime for the irrigated southwestern U.S.A. These cultivars have the genetic potential to complete a growing season with only the planting irrigation and seasonal rainfall of about 50 to 150 mm (Ramage and Ottman, 1994). Performance of these cultivars relies on, among other things, a very efficient root system.

Small grain cultivars differ in their root patterns (Hurd, 1974) and in their efficiency to utilize soil moisture (Briggs, 1978), but according to Brown et al. (1987), moisture distribution within the soil profile determines the pattern of root development. Typically, root systems of small grains have three components: the seminal roots, the crown roots, and the sub-crown internode (Briggs, 1978; Taylor and Nguyen, 1987). Seminal roots grow from the seed beginning with germination (Reid, 1985); crown roots grow from the crown as tillers develop (Briggs, 1978); the sub-crown internode (SCI) is

the main axis that separates seminal roots from crown roots (Taylor and Nguyen, 1987).

Most studies on root improvement of small grains have failed to distinguish the individual contribution of seminal roots and crown roots to final plant development. According to Boatwright and Ferguson (1967), crown roots are more physiologically active and contribute more to yield than seminal roots. The crown root biomass of spring barley has a stronger correlation with shoot biomass than seminal roots (Luna-Ruiz, 1992). The ability of the plant to extract stored moisture over the whole season from varying levels of the soil profile could be improved by selecting genotypes and cultural practices aimed to enhance the development of crown roots.

Several studies have shown that crown root development is strongly affected by crown depth, and that crown depth and crown root development are very sensitive to genetic and environmental variation (Webb and Stephens, 1936; Taylor and McCall, 1936; Ashraf and Taylor, 1974; Gregory et al., 1978). In turn, crown depth and crown root development have a strong effect on tiller performance and yield (Boatwright and Ferguson, 1967; Ferguson and Boatwright, 1968). Early studies by Taylor and McCall (1936) indicated that crown location can influence tillering, crown root development, heaving and winter injury. More recently, MacKenzie (1971) reported that deep-crowned cultivars have a greater ability to escape damage by root rot, and to establish a more extensive adventitious root system when moisture in the surface soil is limited. Boatwright and Ferguson (1967) observed a delay in tillering and a reduction of grain yield caused by restriction of adventitious roots. Black (1970) concluded that time of crown root

initiation, crown root number and crown root elongation can affect water and nutrient uptake, and that grain yield predictions based on number of adventitious roots per plant are more reliable than predictions based on tiller counts because high yield, spike development, and tiller performance depend on crown root development. Recent studies with spring barley showed significant correlations among crown depth, crown weight and shoot weight with a strong influence of temperature, seeding depth and genotype (Luna-Ruiz, 1992).

Normal crown root development requires a minimal amount of moisture near the crown during the seedling stage (Webb and Stephens, 1936). Thus, under semiarid conditions crown depth and soil moisture depletion may have a major impact on crown root initiation and crown root elongation (McKenzie, 1971; Gregory et al., 1978; Ferguson and Boatwright, 1968). Salim et al. (1965), and Briggs (1978) reported that barley roots do not grow in dry soils at or below the permanent wilting point, and Gregory et al. (1978) pointed out that unfavorable soil physical conditions such as drying and crusting of the soil surface may cause partial development or complete failure of crown roots. Studies conducted with winter wheat by Ferguson and Boatwright (1968) showed that dry soil hindered elongation of crown roots, and that normal crown root elongation occurred when soil moisture was above 15 bars near the crown. Webb and Stephens (1936) reported that wheat and barley grown in dry surface soils commonly yield poorly because they fail to develop crown roots under these conditions, and that these plants usually break over when they reach maturity. Kail et al. (1972) suggested that plants with

deep crowns are less likely to be blown out of the ground by wind. Wiegand (1962) concluded that because soil moisture changes very rapidly with depth, increasing seeding depth may make a large difference in the amount of moisture available to the seedling. Martin et al. (1988) suggested that selection for short subcrown internode in small grains could be advantageous under semiarid conditions. Thus, it appears that deep seeding of deep-crowned genotypes could increase crown exposure to moist soil and improve crown root development when irrigation water or rainfall is limited after planting.

Selection for lack of subcrown internode in the MSFRS population 'Composite Cross XXXIX' (CC XXXIX) has been conducted in Arizona as a criterion to improve barley performance under a one-irrigation cultural regime (where the soil is wet to a depth of 152 to 183 cm at planting and no additional irrigation is provided to the crop). Additional water from seasonal rainfall may range from 2 to 6 inches (5 to 15 cm) depending on the year (Ramage and Ottman, 1994). Recent studies have confirmed that some lines derived from the original CC XXXIX population have a lack of sub-crown internode elongation. Selection '309-2' placed its crown at or near the seed, irrespective of light and temperature variation (Martin et al., 1988), while crown depth in the line '8-21-B4' ('P4') was located at the depth of seeding regardless of seeding depth and temperature variation (Luna-Ruiz, 1992). Information is not available on the effect of deep seeding on the performance of genotypes selected for one-irrigation cultural regime that differ in degree of SCI elongation.

This research was designed to evaluate the effects of seeding depth on yield and

yield components of one-irrigation genotypes, and to study the relationships of crown depth, sub-crown internode length and seeding depth with yield and yield components under a one-irrigation cultural regime. The following hypotheses were tested:

(1) deep seeding induces deeper crown formation than shallow seeding in genotypes with a very short or no SCI; (2) deep crown formation under one-irrigation conditions improves crown root development, yield components, and final yield.

MATERIALS AND METHODS

Procedure

The study was conducted under a one irrigation cultural regime during the 1992 and 1993 growing seasons on a Pima clay loam soil (fine-silty, mixed, thermic Typic Torrifluvents) The 1992 experiment consisted of six genotypes (three barleys, two bread wheats, and one durum wheat) seeded at 30 mm and 80 mm deep. In 1993, seeding depths were 25 mm and 70 mm, and the number of genotypes was increased to sixteen (barley only). Each genotype was assigned to a 2-row bed-plot. Plots were 2 rows, 0.3 m apart on beds 0.9 m wide and 3 m long. Seeding rate was 100 seeds per row. The six genotypes in 1992 were randomized within each seeding depth and replicated four times. In 1993 the experiment was seeded on plots that were distributed along four beds. The 16 genotypes were randomly arranged in pairs, the 8 pairs of genotypes were seeded shallow on two beds, and the same 8 pairs of genotypes were seeded deep, aside on the other two beds. This arrangement facilitated the planting process, reduced environmental variation, and

allowed for visual comparisons of specific genotypes in the deep and shallow plots. This arrangement was randomized and replicated five times. Sowing dates were January 2, 1992 and February 3, 1993 for the 1992 and 1993 experiments respectively.

Genotypes

All genotypes, with the exception of 'Bold', 'Signal', 'California Mariout' and the 'Yemen' line, were developed through MSFRS under a one-irrigation cultural regime in Arizona (Table 2.1). All one-irrigation barleys are advanced lines or varieties derived from CC XXXIX. 'Seco' and 'Solum' are standard one-irrigation varieties that develop an intermediate SCI. The barley P4 develops no SCI and was originally derived from one plant without SCI detected in the line 8-21-B4 during a deep seeding (12.5 cm) experiment in the greenhouse. The SCI elongation of the one-irrigation wheats and durum lines is unknown. The wheat and durum lines were checks for F4 lines in 1990-91, and originated from populations developed similar to CCXXXIX. Bold and Signal are drought tolerant barley varieties, and California Mariout is a standard salt tolerant barley. The SCI elongation of Bold and California Mariout is intermediate, and that of Signal is unknown. The Yemen line is an early 2-row barley that develops a very long SCI. The long SCI of the Yemen line is probably an adaptive characteristic for the hot and dry conditions, with scattered showers where it was originally selected. The barleys Seco, Solum and P4 were included both years.

Table 2.1 Genotypes evaluated during the 1992 and 1993 seeding depth experiments.

Genotypes Used in 1992		
Genotype	Source	Type/Description
1. Seco	91-Ma-681231-5-11	6-row Barley
2. Solum	91-Ma-C1-Increase	"
3. P4 †	"	"
4. Tall Wheat	91-Ma-681237-7-13-Check line #3	Bread Wheat
5. Short Wheat	91-Ma-681237-9-12-Check line #2	Bread Wheat
6. Durum	91-Ma-681237-1-1-Check line #1	Durum Wheat
Genotypes Used in 1993		
Genotype	Source	Type
1. Seco	91-Ma-C1-B1	6-row Barley
2. Solum	"	"
3. P4	"	"
4. Bold	"	"
5. Signal	91-Ma-681231-13-2	"
6. California Mariout	91-Ma-C1-B1	"
7. Yemen Line	"	2-row
8. 7-21-8-2	"	2-row
9. 7-21-11-2	"	6-row
10. 8-21-B4	"	"
11. 8-21-B3	"	"
12. 8-21-A3	"	"
13. 8-21-B2	"	"
14. 8-21-C2	"	"
15. 7-21-11-5	"	"
16. 8-21-M4	"	"

†P4 was derived from the line 8-21-B4

Data Collection and Statistical Analysis

The response variables were seeds per head, 100-seed weight, subcrown internode length (SIL), crown depth, and grain yield per plot for both years plus tillers per m², days to anthesis and plant height for 1993. Tillers per m² were obtained by counting tillers in 1m of one row in each plot. Days to anthesis were recorded when ~ 50 % of the tillers within a plot showed spikes with extruded anthers. Plant height was estimated on each plot by sampling the distance between soil surface and the base of the spike. Yield was obtained from two rows (2.7 m²) in 1992, and one row (1.35 m²) in 1993. Seeds per spike and 100-seed weight were estimated from ten heads collected at random from each experimental plot before harvesting for yield. Average SIL (based on seed to crown distance), and average crown depth (seeding depth minus SIL) was obtained from a sample of 20 crowns per plot collected after harvesting.

Data from the shallow and deep plantings were combined and analyzed as a split-plot experiment with seeding depth as a main plot and genotype as a sub-plot. Genotype main effects plus genotype x seeding depth interactions were tested. Because seeding depths were not randomized, t-tests were conducted to analyze the effect of depth of seeding. The relationships of seeding depth, crown depth and SIL with yield and yield components were tested by Pearson linear correlation analysis, combining data from the shallow and deep seedings for each year. All data analysis were performed on Statistical Analysis System (SAS) version 6.04, respectively.

RESULTS AND DISCUSSION

Analysis of Variance

Genotype x seeding depth interaction was non-significant for all above ground variables, but was significant for SIL and crown depth in both years (Tables 2.2 and 2.3). The main effects of seeding depth and genotype were significant for all variables in both years, with the exception of seeding depth effects on seeds/spike in 1992. The non-significant interaction for yield and yield components in this study indicated that these characteristics were similarly affected by seeding depth variation in all genotypes. On the contrary, the significant interaction detected for crown depth and SIL is clearly explained by the contrasting degree of SIL that was observed among the genotypes in the deep seeding treatment. The significant main effects for seeding depth and genotype suggested that plant performance under one-irrigation is strongly affected by these two factors.

Table 2.2 Analysis of variance for yield, seeds/spike, 100-seed weight, sub-crown internode length (SIL), and crown depth. Marana, AZ, 1992.

Source	df	MEAN SQUARES				
		Yield	Seeds /spike	100-seed weight	SIL	Crown depth
Rep	3	46.5	30.3	0.15	15.2	15.2
†Seeding Depth	1	7375.5 **	0.8	1.92 *	2184.3 **	15994.3 **
Error a	3	78.6	9.1	0.17	15.2	15.2
Genotype	5	7286.8 **	244.5 **	8.36 **	179.9 **	179.9 **
‡G x SD	5	444.9	7.8	0.06	179.9 **	179.9 **
Error b	30	1081.8	18.5	0.07	5.9	5.9

†The level of significance for seeding depth is based on T-tests

‡Genotype x Seeding Depth Interaction ** (P<0.01); * (P<0.05)

Table 2.3 Analysis of variance for yield, seeds/spike, 100-seed weight, sub-crown internode length (SIL), crown depth, flowering time, plant height, and tillers/m². Marana, AZ, 1993.

Source	df	MEAN SQUARES				
		Yield	Seeds/ spike	100-seed weight	SIL	Crown depth
Rep	4	197646.2	170.2	0.71	49.8	49.8
†Seeding Depth	1	43626.0 **	101.4 **	2.14 *	4021.0 **	48926.5 **
Error a	4	1867.2	3.3	0.21	44.3	44.3
Genotype	15	56487.0 **	1787.6 **	2.78 **	164.6 **	164.6 **
‡G x SD	15	3418.4	12.4	0.14	148.1 **	148.1**
Error b	120	6620.4	12	0.17	11.4	11.4

Table 2.3...cont.

Source	df	MEAN SQUARES		
		Flowering	Plant height	Tillers/m ²
Rep	4	8.4	206.1	8114.5
†Seeding Depth	1	4.9 *	94.6 *	7854.0 **
Error a	4	0.5	7.8	506.6
Genotype	15	75.7 **	265.3 **	16753.0 **
‡G x SD	15	0.5	6.9	687.9
Error b	120	1.0	15.3	516.0

†The level of significance for seeding depth is based on T-tests

‡Genotype x Seeding Depth Interaction

** (P<0.01); * (P<0.05)

Genotypic Responses to Deep Seeding

The response of each genotype to the shallow and deep seedings for 1992 and 1993 are presented in Tables 2.4 and 2.5 and illustrated in Figures 2.1 and 2.2. Deep seeding increased yield, seeds/spike, 100-seed weight, days to anthesis, SIL, and crown depth, but reduced tillers/m² and plant height in most genotypes. The increases in crown depth, and SIL of most genotypes in response to deep seeding were highly significant ($P < 0.01$), but the effect of deep seeding on yield and yield components had a lower significance ($P > 0.1$) for the majority of the genotypes.

I. Subcrown Internode Length and Crown Depth

Shallow seeding inhibited SCI elongation in all genotypes in 1992, and in most genotypes in 1993, but restricted crown depth to the depth of seeding (≤ 30 mm in 1992, and ≤ 25 mm in 1993) regardless of genotype. Deep seeding in both years resulted in varying degrees of SIL among the genotypes, but also in deeper crowns compared to shallow seedings. SIL under deep seedings ranged from 0 mm (line P4) to 22 mm (short wheat) in 1992, and from 0.4 mm (line 8-21-A3) to 27 mm (Yemen line) in 1993. Correspondingly, crown depth under deep seedings ranged from 58 to 80 mm in 1992, and from 43 to 70 mm in 1992-93 (Tables 2.4 and 2.5).

Deep seeding in 1993 showed three groups of barleys according to their SIL. One group had a very short SCI (≤ 2.6 mm), another group had an intermediate SCI ($\geq 8.2 \leq 17.3$ mm) and a third group (the 2-row barleys) had a very long SCI (≥ 21.5 mm).

Table 2.4 Seeding depth effects on SCI length, crown depth, yield, and 100-seed weight of barley, wheat, and durum genotypes under one-irrigation conditions. Marana, AZ 1992

Genotype	n	Seeding Depth		Seeding depth	
		Shallow	Deep	Shallow	Deep
		SIL (mm)		Crown depth (mm)	
1. Seco	4	0±0†	21.4±1.4 ***	30±0	58.6±1.4 ***
2. Solum	4	0±0	20.0±3.1 ***	30±0	60.0±3.1 ***
3. P4	4	0±0	0±0	30±0	80.0±0.0 ***
4. T. wheat	4	0±0	14.3±2.9 ***	30±0	65.7±2.9 ***
5. S. wheat	4	0±0	21.6±1.0 ***	30±0	58.4±1.0 ***
6. Durum	4	0±0	3.7±1.2 **	30±0	76.3±1.2 ***
Average	24	0.0±0.0	13.5±1.94 ***	30±0	66.5±1.9 ***
		Yield (gr/plot)		100-Seed Weight (mg)	
1. Seco	4	129±14.3	168±6.8 *	4.0±0.16	4.3±0.13
2. Solum	4	113±24.3	139±13.5	3.4±0.17	4.1±0.17 **
3. P4	4	150±17.6	168±6.7	4.3±0.11	4.7±0.05 **
4. T. wheat	4	74±11.0	119±25.8	1.7±0.07	2.0±0.27
5. S. wheat	4	94±4.7	107±21.1	2.4±0.11	2.9±0.09 ***
6. Durum	4	81±9.3	88±4.9	2.6±0.19	2.8±0.13
Average	24	106.6±7.8	131.4±8.3 ***	3.1±0.20	3.5±0.21 **

†All values correspond to the mean±standard error

*** (P≤0.01); ** (P≤0.05); * (P≤0.1) significance of the T-test for the mean difference of each genotype and across genotypes (average) in the shallow and deep seedings

Table 2.4 Cont... Seeding depth effects on seeds/spike of barley, wheat, and durum genotypes under one-irrigation conditions. Marana, AZ 1992

Genotype	n	Seeding depth	
		Shallow	Deep
		Seeds/spike	
1. Seco	4	53.8±1.4	55.8±2.0
2. Solum	4	60.8±0.6	58.8±2.2
3. P4	4	60.8±1.0	62.8±1.8
4. T. wheat	4	68.0±1.3	65.5±3.9
5. S. wheat	4	55.3±1.4	54.0±1.5
6. Durum	4	51.8±2.8	52.0±3.5
Average	24	58.4±1.27	58.1±1.37

Table 2.5 Response of 16 barley genotypes to different seeding depths under one-irrigation conditions. Marana, AZ 1993.

Genotype	n	Seeding depth		Seeding depth	
		Shallow	Deep	Shallow	Deep
		SIL (mm)		Crown depth (mm)	
1. Seco	5	0±0†	16.6±4.6 ***	25.0±0.0	53.4±4.6 ***
2. Solum	5	0±0	13.4±2.8 ***	25.0±0.0	56.6±2.8 ***
3. P4	5	0±0	2.6±1.5	25.0±0.0	67.4±1.5 ***
4. Bold	5	0±0	12.0±2.2 ***	25.0±0.0	58.0±2.2 ***
5. Signal	5	0±0	17.3±2.5 ***	25.0±0.0	52.7±2.5 ***
6. California Mariout	5	0±0	11.1±2.6 ***	25.0±0.0	58.9±2.7 ***
7. Yemen Line (2-row)	5	1.44±0.82	27.2±2.1 ***	23.6±0.8	42.8±2.1 ***
8. 7-21-8-2 (2-row)	5	0±0	21.5±2.7 ***	25.0±0.0	48.5±2.7 ***
9. 7-21-11-2	5	0±0	8.3±0.7 ***	25.0±0.0	61.7±0.7 ***
10. 8-21-B4	5	0±0	0.5±0.3	25.0±0.0	69.5±0.3 ***
11. 8-21-B3	5	0±0	0.6±0.6	25.0±0.0	69.4±0.6 ***
12. 8-21-A3	5	0±0	0.4±0.4	25.0±0.0	69.6±0.4 ***
13. 8-21-B2	5	0.16±0.16	10.4±3.6 ***	24.8±0.2	59.6±3.6 ***
14. 8-21-C2	5	0±0	2.2±0.9 **	25.0±0.0	67.8±0.9 ***
15. 7-21-11-5	5	0±0	8.2±2.5 ***	25.0±0.0	61.8±2.5 ***
16. 8-21-M4	5	0±0	9.9±2.3 ***	25.0±0.0	60.1±2.3 ***
Average	80	0.1±0.06	10.1±1.01 ***	24.9±0.06	59.9±1.01 ***

†All values correspond to the mean±standard error

*** (P≤0.01); ** (P≤0.05); * (P≤0.1) significance of the T-test for the mean difference of each genotype and across genotypes (average) in the shallow and deep seedings

Table 2.5 ...cont.

Genotype	n	Seeding depth		Seeding depth	
		Shallow	Deep	Shallow	Deep
		Yield (gr/plot)		100-Seed Weight (mg)	
1. Seco	5	666±56.2	661±40.1	4.2±0.11	4.3±0.12
2. Solum	5	564±33.5	569±35.8	3.3±0.04	3.4±0.08
3. P4	5	479±40.3	511±48.4	4.2±0.23	4.4±0.20
4. Bold	5	537±41.0	545±59.3	3.4±0.06	3.5±0.11
5. Signal	5	436±38.3	481±20.9	3.8±0.11	3.9±0.03
6. California Mariout	5	577±64.3	578±54.2	3.9±0.14	4.9±0.68
7. Yemen Line (2-row)	5	468±11.8	497±18.2	3.8±0.18	4.1±0.11
8. 7-21-8-2(2-row)	5	533±51.9	579±35.7	4.6±0.08	5.0±0.10 **
9. 7-21-11-2	5	379±32.1	404±31.2	3.8±0.08	4.1±0.11 *
10. 8-21-B4	5	462±38.5	496±61.1	4.3±0.17	4.4±0.14
11. 8-21-B3	5	548±40.3	571±41.6	4.5±0.14	4.7±0.08
12. 8-21-A3	5	508±60.7	614±60.3	4.7±0.33	4.6±0.11
13. 8-21-B2	5	430±72.5	391±62.2	3.5±0.28	3.6±0.24
14. 8-21-C2	5	574±63.7	649±92.7	4.3±0.20	4.6±0.17
15. 7-21-11-5	5	434±34.9	484±70.2	3.0±0.13	3.2±0.14
16. 8-21-M4	5	552±38.9	644±50.7	4.4±0.16	4.5±0.14
Average	80	509.1±13.3	542.1±14.7 ***	3.97±0.07	4.20±0.08 **

Table 2.5 Cont...

Genotype	n	Seeding depth		Seeding depth	
		Shallow	Deep	Shallow	Deep
		Seeds/spike		Tillers/m ²	
1. Seco	5	58.1±0.8	58.9±1.39	136±8.9	135±7.8
2. Solum	5	62.6±1.2	64.6±1.31	149±11.0	130±9.0
3. P4	5	58.9±2.6	62.9±2.32	117±4.5	116±10.2
4. Bold	5	64.6±0.9	66.1±1.37	144±5.4	118±10.7
5. Signal	5	58.0±1.7	58.1±0.56	141±9.9	122±9.5
6. California Mariout	5	51.1±1.4	47.6±5.67	167±10.8	136±14.2
7. Yemen Line (2-row)	5	23.5±0.8	23.3±0.68	281±7.2	218±28.2 *
8. 7-21-8-2 (2-row)	5	22.5±0.5	22.6±0.77	233±30.2	224±17.9
9. 7-21-11-2	5	59.7±1.2	61.4±1.46	100±9.5	101±10.0
10. 8-21-B4	5	60.7±2.0	65.5±1.27 *	114±8.3	103±9.3
11. 8-21-B3	5	59.0±1.1	62.9±1.61 *	122±4.4	111±3.6 *
12. 8-21-A3	5	60.6±1.8	65.7±2.49	124±9.4	120±8.9
13. 8-21-B2	5	56.3±2.0	55.7±2.89	138±9.2	147±23.7
14. 8-21-C2	5	60.6±1.8	63.2±1.72	123±10.7	110±14.8
15. 7-21-11-5	5	62.4±1.7	64.3±1.30	150±2.6	129±6.1 **
16. 8-21-M4	5	61.7±1.1	62.9±0.67	123±5.1	114±5.1
Average	80	55.0± 1.4	56.6±1.6 ***	147.5± 5.6	133.5±5.0 ***

Table 2.5 Cont...

Genotype	n	Seeding depth		Seeding depth	
		Shallow	Deep	Shallow	Deep
		Plant Height (cm)		Days to Anthesis	
1. Seco	5	65.4±2.1	63.0±1.6	68.6±0.25	69.0±0.32
2. Solum	5	61.4±1.8	60.0±1.4	72.4±0.25	72.6±0.25
3. P4	5	61.4±2.2	61.4±1.7	73.6±0.68	73.6±0.51
4. Bold	5	62.6±2.4	61.0±0.6	73.4±0.40	73.2±0.49
5. Signal	5	62.8±2.5	59.4±3.4	72.0±0.55	73.4±0.40 *
6. California Mariout	5	56.2±3.0	51.8±1.1	67.6±0.25	68.0±0.0
7. Yemen Line (2-row)	5	51.6±1.9	48.6±2.1	65.8±0.20	65.8±0.20
8. 7-21-8-2 (2-row)	5	65.0±1.9	64.6±1.9	68.4±0.40	68.6±0.25
9. 7-21-11-2	5	59.8±1.7	60.6±1.4	68.0±0.32	67.8±0.20
10. 8-21-B4	5	63.8±1.0	64.0±1.2	72.2±0.80	72.6±0.93
11. 8-21-B3	5	66.6±1.8	67.8±2.1	73.2±0.20	73.6±0.25
12. 8-21-A3	5	65.6±1.5	65.6±1.7	71.8±0.73	73.0±0.77
13. 8-21-B2	5	55.6±3.2	53.2±4.0	74.8±0.49	75.0±0.55
14. 8-21-C2	5	65.0±2.6	61.8±2.1	73.0±0.32	73.6±0.51
15. 7-21-11-5	5	71.2±1.9	69.2±0.6	68.2±0.38	68.4±0.40
16. 8-21-M4	5	65.4±1.8	62.8±1.2	71.8±0.73	72.2±0.80
Average	80	62.46±0.7	60.93±0.8 **	70.9±0.3	71.3±0.3 **

1991-92

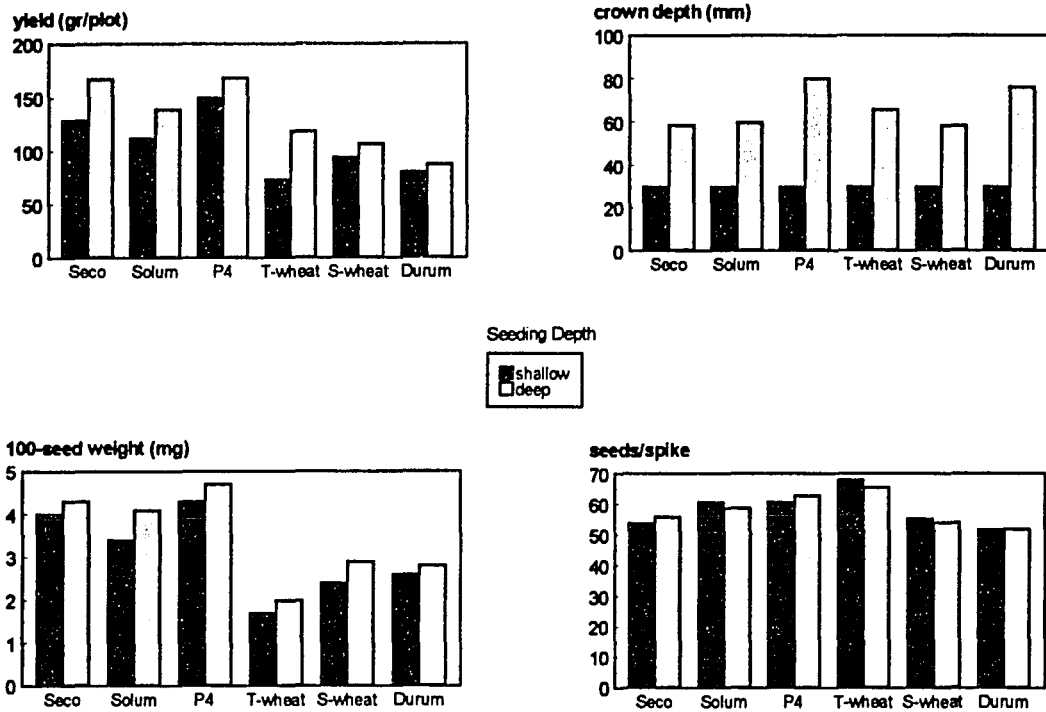


Figure 2.1 Response of six genotypes to seeding depth variation under one-irrigation conditions. Marana, AZ 1992

1992-93

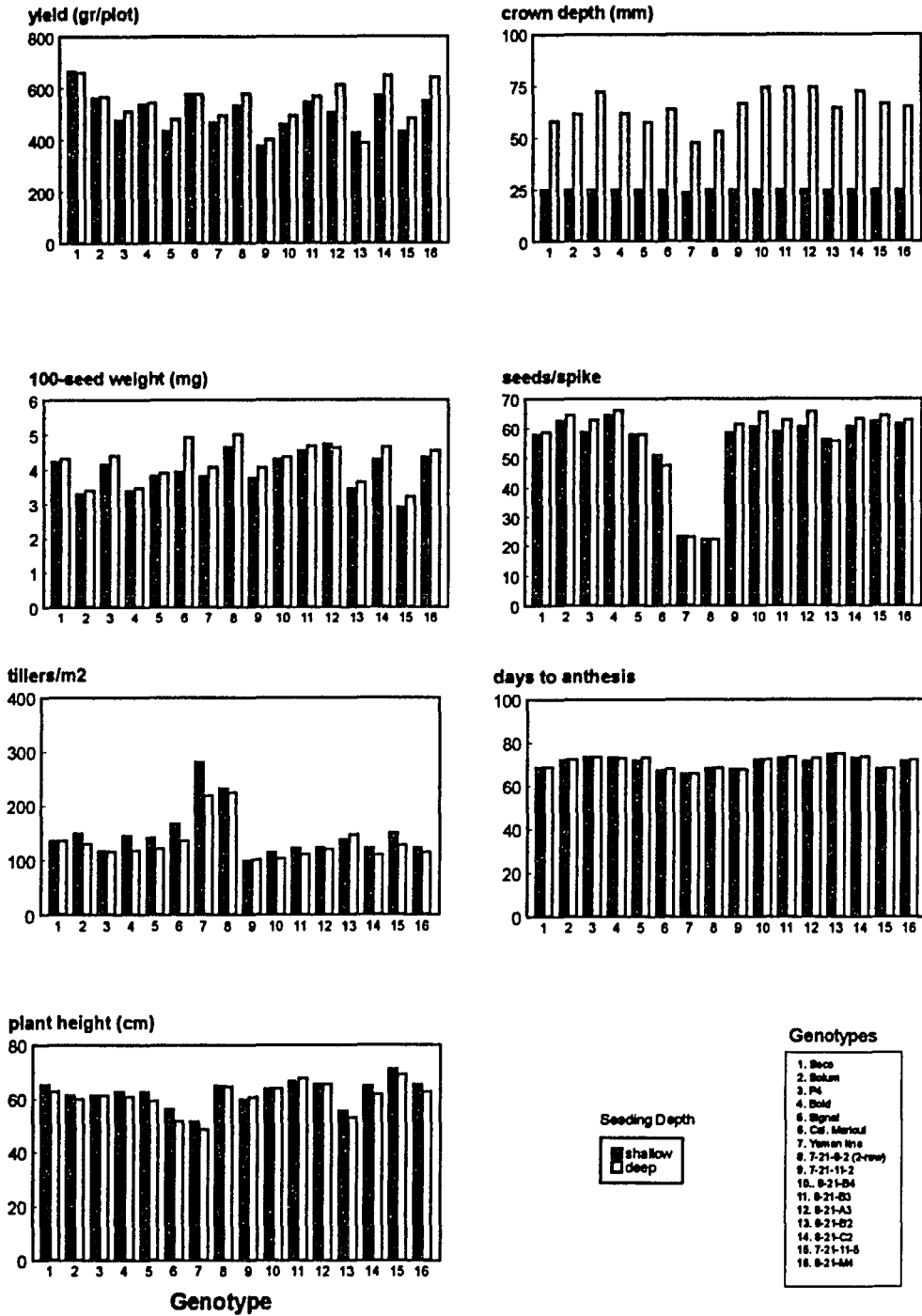


Figure 2.2 Response of 16 genotypes to seeding depth variation under one-irrigation conditions. Marana, AZ 1993

These results support the conclusions presented in Chapter I of this dissertation regarding the longer SCI of 2-row barleys (Yemen line and 7-21-8-2) compared to 6-row barleys.

The line P4 showed no SCI elongation in 1992, but had some elongation (2.6 mm) in the deep seeding of 1993. Elongation of the SCI in P4 has been observed in the greenhouse when deep seeding is accompanied by extremely high temperatures and high levels of plant density. The SCI elongation in P4 during 1993 could be due to the high temperatures prevailing during the early seedling establishment that resulted from the late planting of that year (February 3). More research is necessary to determine the degree of sensitivity of the SCI to variation in light, competition, and temperature in the barley P4 in relation to other barleys with intermediate and long SCI.

Three of the four additional barleys showing a very short SCI in 1993, had SCI lengths ≤ 0.6 mm (Table 2.5). Since these four barleys were derived from the original CC XXXIX population, they may carry the same genotype for lack of SCI elongation that is present in P4. The availability of a desirable character in different background genotypes represent an advantage for the breeder, thus, the lack of SCI character in different background genotypes may have a potential use in breeding for reduced water conditions and probably for other types of stress such as salinity and root rot. For instance, preliminary results with F1 barleys derived from the cross CC XXXIX / Solum x P4 have shown a strong sensitivity of crown root elongation to NaCl concentrations ≥ 5000 ppm. The degree of sensitivity to NaCl differed among different barleys (data not published). Since salinity in production fields is commonly restricted to the surface layer of the soil,

crown depth may influence crown exposure to salt stress. On the other hand, deep seeding is usually associated with higher incidence of root rot than shallow seedings (Duczek and Piening, 1982) because of the long SCI of the genotypes under study (Sallans, 1961).

Root rot is a major soil-borne disease of wheat and barley that infects the SCI causing the eventual separation of seminal roots from the plant, and the inhibition of crown root development and tillers. This suggests that genotypes with no SCI may be more protected against root rot compared to long SCI genotypes. Furthermore, it has been determined that in dry years with absence of root rot, deep seedings result in higher yields than shallow seedings (Duczek and Piening, 1982) probably because of a larger crown root system. Thus, although more research is needed in this area, deep seeded barleys with no SCI seem to have an advantage for crown root development in dry soils, and may provide an avoidance mechanism against salinity, and possibly a protection against root rot in dryland conditions.

II. Yield and Yield Components

In 1992 deep seeding had significant increases in yield and 100-seed weight in certain genotypes (Table 2.4). Deep seeding resulted in a 30% yield increase for Seco, and up to 21% increase in 100-seed weight for Solum and Short Wheat. Seeds/head were not affected by deep seeding in 1992.

In 1993 deep seeding increased 100-seed weight and seeds/head in two genotypes, reduced tillers/m² in three genotypes, and delayed days to anthesis in one genotype.

None of the genotypes differed in yield and plant height in response to deep seeding. The genotypes showing significance had up to 8% increases in 100-seed weight and seeds/head, up to 22 % reduction in tillers/m², and 2 % delay in days to anthesis in response to deep seeding.

The low significance of the t-tests for yield and yield components in most genotypes could be due to the high amount of precipitation received by the crop during 1992 (~250 mm), and to the late planting of the 1993 experiment (February 3). The 1992 crop probably had sufficient moisture stored in the soil for adequate development of seminal roots, crown roots, tillers, and kernels of most genotypes in both seeding depths. On the other hand, the late sowing (February 3) of 1993 that resulted from the continuous rainy season occurred between November, 1992 and the end of January, 1993 could result in a very small response of most genotypes to deep seeding. February plantings in the irrigated southwest are usually accompanied by early heat stress resulting in short phenology, reduced biomass accumulation, short grain filling period, and poor yields. Under these conditions the differences due to seeding depth for each genotype may become smaller compared to normal (December) or earlier planting dates.

In summary, the climatic conditions prevailing during the two experiments could reduce the effect of deep seeding on yield and yield components of most genotypes, and caused the low significance of the t-tests. Typical dry seasons in arid and semiarid environments are expected to show more significant responses of different genotypes to deep seeding under one irrigation. Yet, these results clearly showed a general tendency of

all genotypes to improve their performance under deep seeding, particularly in 1992. These results support the conclusions of Wiegand (1962) as he noticed that increasing seeding depth may make a large difference in the amount of moisture available to the seedling because soil moisture changes very rapidly with depth,

Crown Root Development in Relation to Genotype, Seeding Depth and Soil Moisture Depletion

One of the objectives of this study was to determine if genotypes with reduced SIL (e.g., P4) are favored by deep seeding more than those with longer and more typical SCI as a result of differences in crown depth. Deep seeding in 1992 favored yield and 100-seed weight of all genotypes, regardless of the SIL, and no clear pattern of response was detected for those genotypes with or without elongation of the SCI (Table 2.4). P4 outyielded all genotypes in the shallow seeding, and had the highest yield in the deep seeding together with Seco. Deep seeding increased yield of P4 by 12%, compared to 30% of Seco and 23% of Solum. Yield of the tall and short wheats was increased by 61% and 14% respectively in response to deep seeding, while the durum was increased by 9%. Similar results were observed for 100-seed weight.

In 1993 yield and seeds/spike of the five barleys with short SCI ($SCI \leq 2.6$ mm) were more favored by deep seeding than the barleys with longer SCI ($SCI \geq 8.2$ mm). Comparison of short SCI with long SCI barleys under deep seedings (Table 2.6) showed differences of 7.2% in yield, 9.8% in 100-seed weight and 20.3% in seeds/spike in favor of the short SCI barleys. Although deep seeding reduced tillers/m² in all genotypes, the

Table 2.6 Seeding depth effects on crown characteristics, yield and yield components of short and long SCI barleys under one-irrigation conditions during 1993

Barley group	No of barleys	n	Seeding depth		Seeding depth	
			Shallow	Deep	Shallow	Deep
			SIL (mm)		Crown depth (mm)	
Short SCI	5	25	†0±0	1.3±0.4 ***	25.0±0	68.7±0.4 ***
Long SCI	11	55	0.2±0.09	14.2±1.1	24.9±0.1	55.8±1.1
			Yield (gr/plot)		100-Seed Weight (mg)	
Short SCI	5	25	514±22	568±29	4.4±0.1	4.5±0.1 ***
Long SCI	11	55	507±17	530±17	3.8±0.1	4.1±0.1
			Seeds/spike		Tillers/m²	
Short SCI	5	25	60.0±0.8 ***	64.0±0.8 ***	120±3.3 ***	112±4.2 ***
Long SCI	11	55	52.8±2.0	53.2±2.1	160±7.5	143±6.6
			Plant Height (cm)		Days to Anthesis	
Short SCI	5	25	64.5±0.9 **	64.1±0.9 **	72.8±0.3 ***	73.3±0.3 ***
Long SCI	11	55	61.5±0.9	59.5±1.0	70.1±0.4	70.4±0.4

†Each value corresponds to the average ± standard error ; *** ($P \leq 0.01$), ** ($P \leq 0.05$) significance of the T-test for the mean difference between short SCI and long SCI barleys under the specified seeding depth

short SCI group was less affected by deep seeding (6.7 % tiller reduction) compared to the long SCI group (10.6 % tiller reduction). These results showed that deep seeding is generally advantageous for one irrigation genotypes, but that barleys with a very short or no SCI may be more favored by deep seedings compared to those with long SCI.

The role of seeding depth on genotypes with and without SCI elongation, and their effect on crown placement, crown root development, and plant performance under conditions where irrigation water or rainfall is limited after planting is illustrated in Figure 2.3.

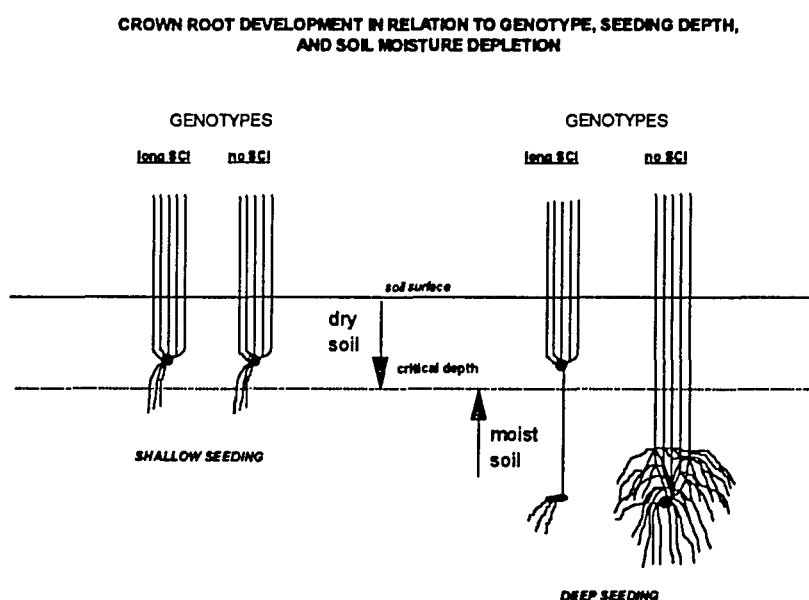


Figure 2.3 Crown root development in relation to genotype, seeding depth, and soil moisture depletion

It is well known that soil moisture around the crown during crown root initiation is required for a well developed crown root system (Webb and Stephens, 1936; Salim et al., 1965; Briggs, 1978; Gregory et al., 1978; Ferguson and Boatwright, 1968). The pattern of soil moisture depletion during crown root initiation, the degree of elongation of the SCI, and the depth of seeding are factors that determine crown depth and crown root development. It is hypothesized that shallow seeding inhibits SCI length regardless of genotype and restricts crown exposure of any genotype to the dry surface layer of the soil. Deep seeding, on the other hand, stimulates SCI elongation in the sensitive genotype (long SCI), but has no effect in the other genotype (no SCI), resulting in shallow and deep crowns, respectively. The shallow crown of the sensitive genotype becomes exposed to a dry soil which inhibits crown root development, while the deep crown of the insensitive genotype becomes exposed to a moist soil resulting in a well developed crown root system (Figure 2.3). Sallans (1961) reported cultivar differences for crown depth in wheat and barley, and suggested that selection of plants under field conditions would be best at planting depths of 6.4 to 7.6 cm. Webb and Stephens (1936) reported that crown depth was influenced by cultivar, seeding depth and temperature, but also detected cultivar differences in the time and ability to form crown roots under certain cultural and environmental conditions. This information suggests that there are other factors that need to be investigated such as: (1) the time of crown root initiation in one irrigation barley, and (2) the minimum moisture required (soil water potential) for crown root development, (3) the genetic variation for these characteristics (crown root initiation and moisture

requirements for crown root development), and (4) the interaction among these factors under one irrigation and deep seeding in the field.

General Effects of Deep Seeding

The average of each seeding depth and the significance of the t-test for seeding depth comparisons across genotypes are shown at the bottom of Tables 2.4 and 2.5. Deep seeding differed from shallow seeding in all but one variable (seeds/head in 1992). The effect of deep seeding across genotypes in relation to shallow seedings is illustrated in Figure 2.4 for each year.

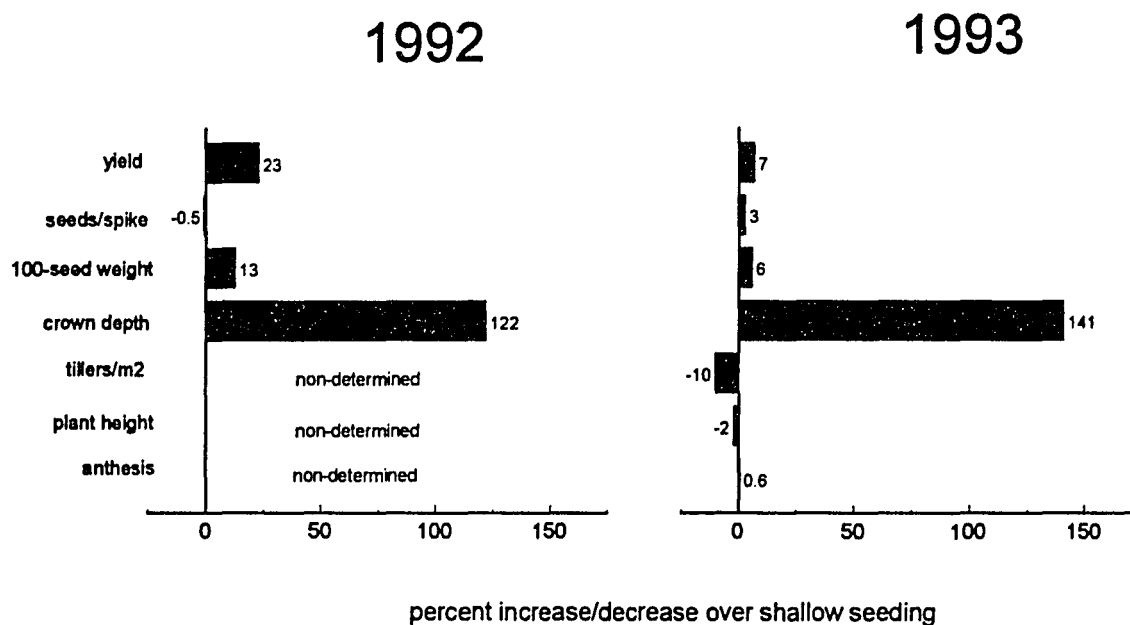


Figure 2.4 General response of barley and wheat genotypes to deep seeding under one-irrigation conditions

Deep seeding in 1992 increased yield by 23 %, 100-seed weight by 13 %, and crown depth by 122 %, but no effect was detected on seeds/spike. Deep seeding in 1993 showed increases of 7 % in yield, 3 % in seeds/spike, 6 % in 100-seed weight, 141 % in crown depth, 0.6 % in days to anthesis, and reductions of 10 % in tillers/m² and 2 % in plant height. Crown depth and crown root development have a strong effect on yield, spike development and tiller performance (Boatwright and Ferguson, 1967; Ferguson and Boatwright, 1968; Black, 1970). The consistent increase in crown depth, 100-seed weight and yield with deep seeding in both years (Figure 2.4) suggested that selection based on these characteristics under deep seeding could improve barley performance under one irrigation. The small effect of deep seeding on seeds/spike, plant height, and days to anthesis may be larger in different years. These results suggested that a relationship may exist among seeding depth, crown depth, SIL, yield, and yield components.

Correlation Analysis

The relationships among seeding depth, crown depth, SCI length, yield, and yield components was analyzed by linear correlation analysis. The data were analyzed separately for each year, using genotypic means. Two types of associations were studied: one considering the associations of seeding depth with crown characteristics and yield components, and the other considering the influence of seeding depth on the relationships between crown characteristics and yield components.

Associations of Seeding Depth with Crown Characteristics and Yield Components

Correlations of crown characteristics, yield and yield components with seeding depth were determined by combining data from each year over the two seeding depths (Table 2.7). Seeding depth showed small and no significant correlations with yield and yield components, but the correlation of seeding depth with SCI length and crown depth was much larger, highly significant ($P \leq 0.01$), and positive in both years.

Table 2.7 Linear correlation coefficients of seeding depth with yield, yield components, and crown characteristics for two years.

Characteristic	Seeding depth	
	1992†	1993‡
Yield Components		
yield	0.39844	0.21518
100-seed weight	0.20845	0.21499
seeds/spike	-0.02603	0.061
tillers/m ²	-----	-0.17072
days to anthesis	-----	0.06537
plant height	-----	-0.15045
Crown Characteristics		
SIL	0.74093 ***	0.68021 ***
crown depth	0.94814 ***	0.96527 ***

*** ($P \leq 0.01$); † (n = 12); ‡ (n = 32)

The positive correlation between seeding depth and crown depth confirmed that deep seeding increases crown depth, particularly in genotypes with reduced SCI length. On the other hand, the positive association between seeding depth and SIL resulted because SCI was inhibited by shallow seedings, and elongation of the SCI occurred only under deep seedings.

Crown depth in both years showed a stronger correlation with seeding depth compared to SIL. This occurred because SIL had no effect on crown depth in the shallow seedings, and, although deep seedings stimulated SCI elongation, it was negatively associated with crown depth. These results suggest that care must be taken with control of seeding depth when considering crown depth and/or SCI length determinations. Taylor and McCall (1936) indicated that the morphological study of SCI elongation should always consider the effect of seeding depth. Poulos and Allan (1987) claimed that in order to select for crown depth it is important to determine if SIL determines crown depth, or if crown depth determines SIL. According to the same authors, crown depth is a better selection criteria than SIL due to the higher variation that occurs with SIL under deep seedings.

The low significance and small correlation coefficients of yield and yield components with seeding depth could be due to the small differences that occurred between shallow and deep seedings within each genotype. As previously discussed, typical dry years may reflect larger and more significant differences in yield and yield components between shallow and deep seedings and between shallow crowned and deep crowned

genotypes. More research is necessary to determine if the correlation of seeding deep with yield and yield components increases in degree and significance in dry years.

Influence of Seeding Depth on the Associations between Crown Characteristics and Yield Components

A separate correlation analysis for the shallow and deep seedings was conducted with each year's data to determine if seeding depth modifies the association between above ground and below ground variables. The analysis using data from the shallow treatment of 1992 was omitted because of the lack of variation in SIL and crown depth in that treatment. Results of 1992 using data from the deep seeding showed non-significant correlations of SIL and crown depth with yield and yield components (Table 2.8).

Table 2.8 Linear correlation analysis for 1992 using data from the deep seeding treatment (n = 6).

Characteristic	1992		
	SIL	Crown depth	Yield
	DEEP SEEDING		
yield	0.04005	-0.04005	-----
100-seed weight	-0.1039	0.1039	0.82033 **
seeds/spike	-0.17994	0.17994	0.42748
SIL	-----	-1.0000 ***	0.04005
crown depth	-1.0000 ***	-----	-0.04005

*** (P<0.01); ** (P<0.05)

In 1993, SCI length and crown depth were significantly correlated with seeds/spike, tillers/m², days to anthesis, and plant height in both seeding depths (Table 2.9).

Table 2.9 Linear correlation analysis for 1993 using separate data from the shallow and deep seedings (n = 16)

Characteristic	1993		
	SIL	Crown depth	Yield
SHALLOW SEEDING			
yield	-0.18287	0.19167	-----
100-seed weight	-0.10785	0.11607	0.35028
seeds/spike	-0.65125 ***	0.64916 ***	0.02616
tillers/m ²	0.75974 ***	-0.75663 ***	0.04159
days to anthesis	-0.46422 *	0.45119 *	0.01108
plant height	-0.64346 ***	0.65426 ***	0.2105
SIL	-----	-0.99950 ***	-0.18287
crown depth	-0.99950 ***	-----	0.19167
DEEP SEEDING			
yield	-0.07738	0.07738	-----
100-seed weight	-0.16499	0.16499	0.51117 **
seeds/spike	-0.75964 ***	0.75964 ***	0.05671
tillers/m ²	0.78889 ***	-0.78889 ***	-0.02320
days to anthesis	-0.58045 **	0.58045 **	0.04691
plant height	-0.52491 **	0.52491 **	0.30468
SIL	-----	-1.0000 ***	-0.07738
crown depth	-1.0000 ***	-----	0.07738

*** (P<0.01); ** (P<0.05); * (P<0.1)

In almost all cases, the correlations of crown characteristics with yield and yield components were larger and of higher significance under deep seedings compared to those of shallow seedings. The associations of crown characteristics with yield and yield components under deep seedings are expected to increase in typical years and with deep crowned genotypes. Also, although the correlations of SIL and crown depth with yield and 100-seed weight were of low significance ($P > 0.1$), all correlations with crown depth, except tillers/m², were positive, while those with SIL were negative. The opposite associations of crown depth and SIL with yield and yield components are clearly illustrated by the negative, highly significant ($P \leq 0.01$), and perfect correlation ($r = -1.0$) detected between crown depth and SIL, which in turn is explained by the general equation for crown depth (crown depth = seeding depth - SIL).

These results show that deep crowns, induced by deep seeding, reduced tillers/m², but increased seeds/spike. The reduction of tillers/m² under deep plantings may be due to hard crust formation, and by the pressure exerted by the soil on the crown, and on tiller primordia, which could inhibit tiller emergence. The increase in seeds/spike could be a compensation effect in response to tiller reduction and accompanied by some delay to anthesis. Although the correlation between crown depth and 100-seed weight was not significant, it was positive in both years. Thus, the increase of yield under deep seeding may be explained by increases in 100-seed weight, and seeds/spike due, at least partially, to the reduction of tillers/m², to a deeper crown, and probably to a better development of the crown root system. A small delay in days to physiological maturity caused by deep

seeding could also explain, at least in part, a longer grain filling period, as reflected by 100-seed weight. A delay in physiological maturity caused by deep seeding in typical years following a one-irrigation cultural regime may or may not be disadvantageous, depending on the phenology of the genotype. A deep seeded genotype with fast emergence, deep crown, and earliness, may delay its phenology and avoid water stress by maintaining adequate rates of water absorption. However, the use of late genotypes with slow emergence and shallow crowns under deep seedings may result in premature death of tillers, seedless spikes and poor grain filling, all caused by a delayed phenology under water stress.

These results also indicated that emergence is affected by deep seeding (data not shown). Time of emergence was estimated from observations of the first appearing coleoptile tips on each plot, and percent emergence was based on seedling countings made on each plot during the first 14 days after planting. Although the data on time and percent of emergence were collected only from one replication, it indicated that percent of emergence was not affected by seeding depth, but that deep seeding delayed the time of emergence in all genotypes by about one day. It was noticed also, that some genotypes (e.g. Yemen line) emerge faster than others. Fast emergence may be a desirable characteristic under deep seeding and to escape stress caused by surface crusting. Long coleoptile and rapid emergence have been considered as major genotypic characteristics for performance under deep seedings (Sunderman, 1964; Kaufman, 1968; Bacaltchuk and Ullrich, 1983). Genetic variation for rate of emergence has been observed in these barleys

under greenhouse conditions (Luna-Ruiz, 1992), however, it is unclear if rapid germination is associated with rapid emergence, or earliness. Control of germination is independent from the control of growth and development after germination (Ramage, personal communication), however, observations with the Yemen line suggests some linkage or pleiotropism among rapid germination, rapid emergence and earliness. More research is necessary in this area to understand the association among rapid germination, fast emergence and earliness in small grains, and to identify possible sources of variation for these characteristics.

SUMMARY AND CONCLUSIONS

- **SIL and crown depth of all genotypes were more affected by deep seeding than yield and yield components in both years.**
- **Shallow seeding inhibited the elongation of the SCI in all genotypes, but restricted the crown to a shallow placement regardless of genotype.**
- **Deep seeding stimulated SCI elongation in most genotypes, but resulted in deeper crown formation in all genotypes. Deep seeding in 1993 showed three groups of barleys according to their SIL: five barleys with $SIL \leq 2.6$ mm; nine barleys with $SIL \geq 8.2 < 21.5$ mm; and two barleys (2-row) with $SIL \geq 21.5$ mm.**
- **Deep seeding increased yield, 100-seed weight, seeds/spike, and days to anthesis, but reduced tillers/m² and plant height in most genotypes. The differences in yield and yield components detected between deep and shallow seedings were of low significance ($P > 0.1$) in most genotypes, but of larger significance ($P < 0.05$) across genotypes.**
- **The group of barleys with short SIL ($SIL \leq 2.6$ mm) had more average increases in crown depth, yield, and seeds/spike, and less reduction in tillers/m² than the long SCI barleys ($SCI \geq 8.2$ mm) in response to deep seeding. Except for tillers/m², all yield components, yield, and crown depth of the short SIL barleys averaged more than the long SIL barleys in both seeding depths.**
- **Seeding depth showed large and highly significant correlations with SIL and crown depth, but small and low significant correlations with yield and yield components in both years.**

- The correlations of crown characteristics (SIL and crown depth) with yield and yield components increased in degree and significance with deep seeding in 1993.
- The environmental conditions at Marana, AZ in 1992 and 1993 may not represent the typical one-irrigation conditions for the evaluation of deep seeding and SIL on yield and yield components. Larger responses to deep seeding, and stronger differences between genotypes with and without SCI are expected to occur in more typical years.

CHAPTER 3

**GENETIC AND ENVIRONMENTAL FACTORS THAT AFFECT
CROWN DEPTH AND CROWN ROOT DEVELOPMENT OF
SPRING BARLEY (*Hordeum vulgare* L.) GROWN UNDER A
ONE-IRRIGATION CULTURAL REGIME**

CHAPTER 3

GENETIC AND ENVIRONMENTAL FACTORS THAT AFFECT CROWN DEPTH AND CROWN ROOT DEVELOPMENT OF SPRING BARLEY (*Hordeum vulgare* L.) GROWN UNDER A ONE-IRRIGATION CULTURAL REGIME

INTRODUCTION

Breeding for reduced water use is becoming a priority of national and international programs related to agriculture. Barley bred for performance under a one-irrigation cultural regime has been very successful in many barley producing regions of the world where irrigation water or rainfall after planting is limited. One-irrigation barley is currently being used by national programs in North Africa, and in the Southwest USA as a winter crop in rotation with cotton, and as a cover crop for soil conservation purposes.

Two of the most critical limitations for developing successful cultivars are (1) the ability to generate sufficient genetic variation and (2) to identify the most favorable genetic combinations in breeding populations. The phenotype of a plant results from all genes in the plant interacting with each other and with the specific environment in which it is being grown (Ramage, 1990). Thus, breeding for reduced water-use conditions demands familiarity with both the genetic component involved in the response and the specific environmental conditions.

Performance of barley under a one-irrigation cultural regime has large genetic and environmental components. Plant selection has been based on several characteristics such as turgidity at anthesis and large, dense seed (Ramage and Ottman, 1994). The ability of

the plant to produce plump and dense seed under limited water conditions relies on, among other things, a very efficient root system. Crown depth, sub-crown internode length (SIL), and the time of crown root initiation are varietal characters of great importance for crown root development and crop performance under semiarid conditions (Webb and Stephens, 1936; Black, 1970; Martin et al., 1988). Microscopic observations of the cross sectional anatomy of the sub-crown internode and lower internodes in one-irrigation barleys grown in the greenhouse have revealed that such internodes are semi-solid in young plants, but that they become hollow in a few minutes in the absence of water (unpublished). These observations suggested that one-irrigation barleys may accumulate carbohydrates and probably water in the lower internodes early in development to be retranslocated later during maturation. These findings encouraged the search for semi-solid lower internodes in one-irrigation barleys under field conditions. Before anthesis, the lower culm internodes appear to be semi-solid, but they are hollow at harvest (Ramage and Ottman, 1994).

Breeding for one-irrigation conditions has included SIL and/or crown depth as part of the selection criteria, but effective selection for time of crown root initiation may be difficult to accomplish under field conditions. In order to select effectively for time of crown root initiation, it is necessary to determine the degree of variation available for this characteristic in the breeding population, and to establish selection criteria for this trait based on a phenological stage.

There is sufficient evidence in the literature supporting the selection of deep-

crowned genotypes to improve winter survival in winter cereals (Taylor and McCall, 1936; Ferguson and Boatwright, 1968; Kail et al., 1972; Ashraf and Taylor, 1974), but the role of crown placement under semiarid conditions has been little investigated, particularly for spring barley. SIL is negatively associated with crown depth, but highly modified by genotype and seeding depth (Luna-Ruiz, 1992). Selection for short SCI and/or deep crown was suggested by Martin et al. (1988) to improve crown root development of spring barley under semiarid conditions. Black (1970) pointed out that the time of crown root initiation, the number of crown roots, and the degree of crown root elongation can affect water and nutrient uptake. Boatwright and Ferguson (1967) noticed that restriction of adventitious roots caused late tillering and reduction of grain yield. Since normal development of crown roots requires moisture at the crown region (Webb and Stephens, 1936), unfavorable soil physical conditions such as drying and crusting of the soil surface during seedling establishment may cause partial or complete failure of crown root development (Gregory et al., 1978). Hudspeth and Taylor (1961) noticed that the top half-inch (1.27 cm) of the soil on the High Plains of Texas often dries to below the permanent wilting point within 24 hours after wetting. Wiegand (1962) emphasized the importance of proper sowing depth as moisture at the seed zone (1.9 cm deep) was depleted within four days after irrigation.

Some of the frequent questions arising during the study of crown root development are related to the time and moisture requirements for crown root initiation, and the degree of genetic variation available in a breeding population for these

characteristics. Hurd (1974) suggested that breeding for limited water use conditions requires, among other things, the selection of early and fast growing parents to build up a reserve of assimilates to be used by the plant during later stages when stress occurs. Ferguson and Boatwright (1968) showed that crown roots of winter wheat grew normally when soil moisture at the crown region was above 15 bars, but that lower tensions inhibited crown root elongation. Since the rate of soil moisture depletion is much higher in shallow layers compared to deeper layers of the soil (Stanhill, 1955; Hudspeth and Taylor, 1961; Wiegand, 1962), the deep seeding of barleys with deep crown placement and early crown root initiation could be an advantageous genotype-management combination for proper crown root development and crop performance under semiarid conditions.

In this chapter I analyze, integrate and discuss genetic and environmental factors involved in crown root development under one-irrigation conditions. Crown depth, SIL, time of crown root initiation, and moisture required for crown root elongation are analyzed in relation to seeding depth and rate of soil moisture depletion at the crown region. Emphasis is given to the study of soil moisture depletion at different soil depths during seedling establishment, to the study of genetic variation for crown root initiation in the barley population CC XXXIX, and to the association between number of crown roots and leaves in the population. Additional information is presented on the effects of light deficiency and high population density on internode elongation of three genotypes (P4, Seco and the Yemen line) that have contrasting SIL.

The objectives were: (1) to estimate the degree of variation for time of crown root initiation in the barley population CC XXXIX; (2) to determine the degree of association between number of crown roots/plant and leaves/plant; (3) to determine the rate of soil moisture depletion at different soil depths during the period of seedling establishment in a once-irrigated field; and (4) to integrate and discuss the genotypic and environmental factors affecting crown root development under one-irrigation conditions; (5) to determine light deficiency and high population density effects on the degree of internode elongation in the line P4 (no SCI) compared to genotypes that have intermediate (Seco) and long (Yemen line) SCI.

MATERIALS AND METHODS

Study of Crown Root Initiation

The study of crown root initiation was conducted between September 17 and October 15 of 1993 in a greenhouse at the ARS/USDA facility (2000 E. Allen, Tucson, AZ 85719).

Genetic Material

The barley CC XXXIX was selected for this study because of its degree of genetic variation, and because it represents the base population for developing one-irrigation barleys. Composite cross XXXIX is a population that was developed through 'Male Sterile

Facilitated Recurrent Selection' (MSFRS) (Ramage and Thompson, 1981). This program was established in 1974 to select for performance under a one-irrigation cultural regime. The original population included a male sterile source and barleys from different arid regions of the world. Selection in early generations was based on turgidity of plants at anthesis. After several cycles of intercrossing selected F2 plants, bulking the crosses, and growing F1's in an off-season nursery, later generations have been selected mainly for large, dense seed. The F2 generation has been combine-harvested and screened for large and dense seed using sieves and a gravity table. New introductions and selected F2, F3 and F4 plants have been crossed with selected F2 male sterile plants of the next cycle to maintain a large genetic variation and to simultaneously increase the frequency of desirable genes in the population. Selection for large, dense seed has resulted in plants with the ability to produce a large plump kernel under water and heat stress during maturity (Ramage and Ottman, 1994).

Procedure

Each of seven pots (20 cm diameter x 40 cm height) containing a mixture of equal amounts of perlite, vermiculite, and peat moss received a random sample of 30 seeds of the barley population CC XXXIX (seed source 92-Ma-CC XXXIX x Solum/CC XXXIX). Each pot was seeded at 60 mm and irrigated once a week alternating tap water and tap water plus water soluble fertilizer (20-20-20 Champion Geranium Food, 1 tsp/gallon of water). No artificial light was supplied, and temperature was monitored continuously

during the experiment using a hygrothermograph (Figure 3.1).

Samples were taken every three days starting on the 10th day after planting (pot 1) and ending on the 28th day (pot 7) after planting. The pots were sampled according to the calendar presented in Table 3.1.

Table 3.1 Sampling calendar for the study of crown root initiation in the barley population CC XXXIX

Pot No.	days after planting	date of sampling
pot 1	10	Sep 27
pot 2	13	" 30
pot 3	16	Oct 3
pot 4	19	" 7
pot 5	22	" 9
pot 6	25	" 12
pot 7	28	" 15

Seedlings were recovered by clipping the seminal roots ~3 cm from the seed (~9 cm from the soil surface) and washing the soil mix out of the remaining roots. Crown depth, crown node number, crown root number and leaf number were recorded for each seedling on each sampling day. Frequency distributions for crown root number/plant and leaf number/plant were determined for each day. Crown root initiation was recorded when a seedling showed at least one visible crown root. The percent of plants showing crown root initiation on each sampling day was used to determine the degree of variation for this characteristic. The relationship between number of crown roots/plant and number of leaves/plant was studied by regression analysis using data from all seedlings.

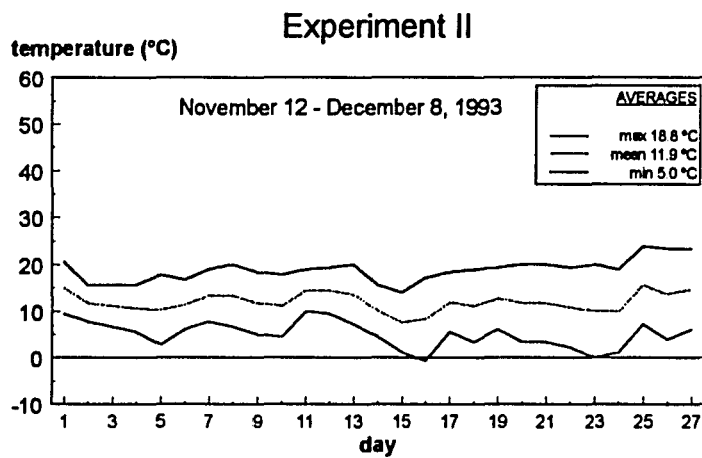
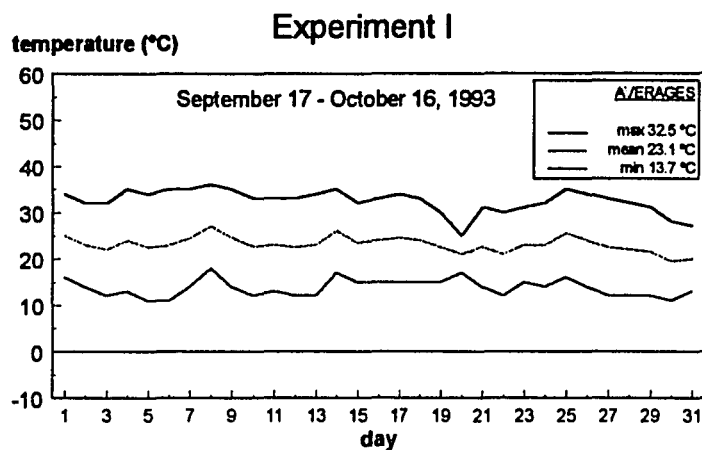


Figure 3.1 Average daily temperatures in the greenhouse during the conduction of experiments I and II

Study of Soil Moisture Depletion

This study was conducted at the Marana Agricultural Experiment Station, Marana, AZ between November 27 and December 11 of 1990.

Soil Description

According to Post et al. (1978), the soil of the experimental site is a Pima clay loam (fine-silty, mixed, thermic family of Typic Torrifuvents), which has 41 % sand, 25 % silt, 34 % clay, 1.2 % organic matter, pH 7.8, and electrical conductivity of the extract 1.27 mmhos/cm.

Procedure

One irrigation barley was sown on November 18, and the land was irrigated on November 20, 1990 to wet the soil to a depth of 5 to 6 feet (152 to 183 cm). Soil columns 15 cm deep were taken from five different sites (ranges) with a core sampler on days 7, 8, 10, 12, 14, 17, 19, and 21 after irrigation (Figure 3.2). Each column was divided in six 2.5 cm segments. After obtaining a soil column, each segment was immediately transferred and stored in an hermetic

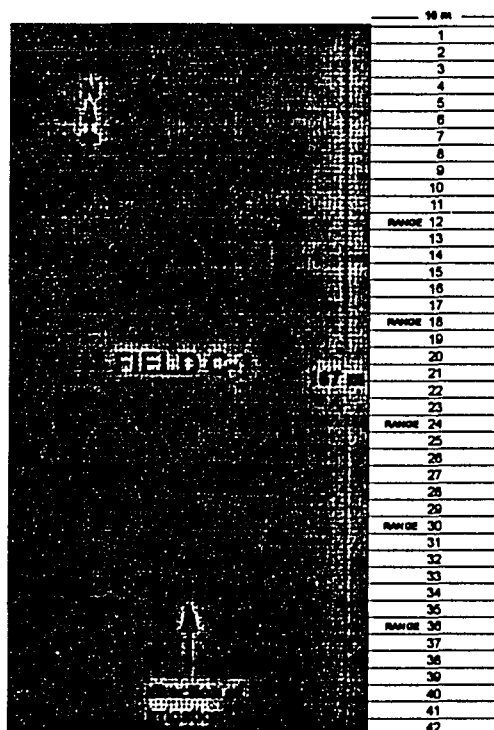


Figure 3.2 Description of the experimental site at Marana, AZ and specific location of sampling sites

aluminum container that was previously labeled to identify depth, range, and day. All samples on the same day were weighed on an electronic balance and oven dried for ~ 48 hours at 70 °C. Dry samples were weighed and soil moisture content of each segment was calculated by weight difference and expressed in percentage according to the following equation:

$$\text{RWC} = \frac{\text{moist soil} - \text{dry soil}}{\text{dry soil}} \times 100$$

where

**RWC = relative water content of the soil segment
or % soil moisture on the day of sampling**

moist soil = weight of soil segment before drying

dry soil = weight of soil segment after drying

Data on soil RWC was analyzed as a split-plot experiment with day as a main plot, sampling depth as a subplot and range as replication (Table 3.2).

Table 3.2 Sampling protocol for estimating the drying pattern at different soil depths during the period of seedling establishment in a Pima clay loam. Marana, AZ 1990

Soil Segment (cm)	Sampling days after the planting irrigation (Nov 27 to Dec 11)	Ranges	samples per day
0.0 - 2.5	7, 8, 10, 12, 14, 17, 19, 21	12, 18, 24, 30, 36	5
2.5 - 5.0	"	"	"
5.0 - 7.5	"	"	"
7.5 - 10.0	"	"	"
10.0 - 12.5	"	"	"
12.5 - 15.0	"	"	"
6 segments	8 sampling days	5 ranges	240 samples

Linear regression analysis between RWC of the soil and sampling day were conducted for each sampling depth. All the regression equations were linearized by *ln* transformation of the independent variable (days of sampling). The effect of sampling depth on rate of soil moisture depletion after the planting irrigation was studied by (1) visual comparison of the slope of the logarithmic curves generated with original data, and (2) by exploring the b-values, and R² values of the linearized regression equations for each sampling depth. The analysis of variance was performed on a PC using SAS (Statistical Analysis System) version 6.04. The scatterplots, logarithmic curves, and determination of linear regression equations were performed on Freelance Graphics version 2 for windows.

Study of Internode Elongation under Light Deficiency and Population Density

This study was conducted in the greenhouse at the USDA/ARS facility between November 12 and December 8, 1993. The study evaluated the effects of plant competition and light deficiency on the elongation of the SCI, coleoptile, and other internodes in the barley genotypes 'P4', 'Seco' and the 'Yemen line'. These barleys have shown contrasting degrees of SCI elongation under field and greenhouse conditions. The line P4 develops no SCI and was originally derived from a plant without SCI detected in the line 8-21-B4. Seco (PI 508552) has intermediate SCI, and the Yemen line is an early 2-row barley that develops a very long SCI. Seco and the parental line of P4 (8-21-B4) were developed through MSFRS under a one-irrigation cultural regime in Arizona, and the Yemen line was selected in a dry and warm environment.

Procedure

Pots (10 cm diameter x 10 cm height) were seeded at 60 mm with 4 or 20 seeds of each genotype. At emergence, two of the four coleoptile tips in the pot receiving 4 seeds, were covered with PVC tubes (2.5 cm diameter x 12.7 cm long) and remained covered until sampling. The other two coleoptiles in the same pot grew uncovered. The non-covered seedlings were controls, the covered seedlings grew with limited light, and the seedlings that grew in the pot receiving 20 seeds were considered to be under plant competition. There were three replications. Pots were randomized within genotypes, and genotypes within replications. No artificial light was supplied during the experiment. Watering and fertilization of pots, and monitoring of temperature in the greenhouse were as previously described.

On day 27 after sowing (December 8, 1993), seedlings were recovered as previously described, and the lengths of the SCI, coleoptile, seed to the tip of the longest leaf (seedling length), and seed-to-first leaf node, plus crown depth (seeding depth - SIL) were recorded for each seedling. For the competition treatment, a sub-sample of 10 seedlings growing under full competition were measured and their average was used as an experimental unit. For both, the control and the covered treatment, one experimental unit was represented by the average of two seedlings. The data were analyzed as a split plot factorial experiment with genotype as a main plot, and treatment as a sub-plot. The data were analyzed following the Analysis of Variance (ANOVA) procedure using the Statistical Analysis System software (SAS Institute Inc., 1988) version 6.04. The effects

of plant competition and light deficiency on each genotype were studied by mean comparisons against the control using the Least Significant Difference (LSD). Main plots were compared using Duncan's Multiple Range Test.

RESULTS AND DISCUSSION

Study of Crown Root Initiation

Table 3.3 shows the number of seedlings with and without apparent crown root initiation on different days after planting. Evidence of crown root initiation in the population was not apparent until day 13 as none of the seedlings observed on day 10 showed crown roots. The maximum number of seedlings with crown roots (88.5 %) was observed on day 28. The percent of seedlings having crown roots on days 10, 13, 16, 19, 22, 25 and 28 was 0.0 %, 7.1 %, 70.0 %, 76.7 %, 81.5 %, 84.6 %, and 88.5 %, respectively.

Table 3.3 Degree of variation for crown root initiation in the barley population CC XXXIX at different days after planting

Day of sampling	n	No of plants		% of plants with crown roots
		With crown roots	Without crown roots	
10	30	0	30	0
13	28	2	26	7.1
16	30	21	9	70
19	30	23	7	76.7
22	27	22	5	81.5
25	26	22	4	84.6
28	26	23	3	88.5

The results showed a dramatic shift in percent crown root initiation between day 13 (7.1%) and day 16 (70%). The degree of variation in CC XXXIX for crown root initiation is illustrated in Figure 3.3. According to these results, the time required for crown root initiation varies tremendously among different barley plants of CC XXXIX.

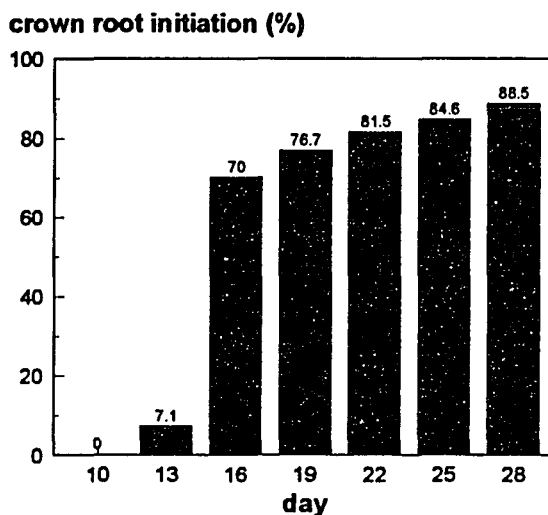


Figure 3.3 Variation in time of crown root initiation within the barley population CC XXXIX

The availability of genetic variation for time of crown root initiation can be of major importance to breeding one-irrigation barleys. Genotypic selection for early crown root initiation in the barley population CC XXXIX could improve crown root development and plant performance under conditions where irrigation water or rainfall is limited after planting. Black (1970) indicated that time of crown root initiation, crown root number and crown root elongation can affect water and nutrient uptake. Breeding wheat for drought resistance, according to Hurd (1974), requires, among other things, the selection of parental material that grows fast at early stages to build up a reserve of assimilates to be used by the plant at later stages when stress occurs. One-irrigation barleys may accumulate carbohydrates and probably water in the lower internodes early in

development to be retranslocated later during dry periods. Under field conditions, the lower culm internodes appear to be semi-solid before anthesis, but at harvest they are hollow (Ramage and Ottman, 1994).

Genotypes with early crown root initiation may be more desirable than genotypes with late crown root initiation, particularly in fast drying soils, and/or when no additional water can be supplied after planting. Normal crown root development demands a minimum amount of moisture at the crown region during early seedling establishment (Webb and Stephens, 1936). Some workers have shown that crown roots do not grow in dry soils at or below the permanent wilting point (Ferguson and Boatwright, 1968), while others have indicated that unfavorable soil physical conditions such as drying and crusting of the soil surface may cause partial development or complete failure of crown roots (Gregory et al., 1978). Black (1970) emphasized the importance of rapid crown root development under dryland conditions because of the limited time when sufficient water exists in the soil surface for crown root initiation. These findings support the selection of genotypes with early crown root initiation under semiarid conditions.

The degree of variation for time of crown root initiation that was detected in CC XXXIX (Table 3.3, Figure 3.3) during this study is only a first estimation, and therefore, the results of this study should be taken with caution. However, these results provide important information that justifies additional research in this area. It is suggested that a larger population size, and varying conditions of temperature, soil texture, soil moisture, seeding depth, and plant competition be used in future experiments.

Number of Leaves and Crown Roots

Past experience with one-irrigation barleys indicates that seedling emergence in the field occurs around day 12 after planting in December at Marana, AZ. In greenhouse experiments, emergence occurred between day 5 and 6 (data not shown), which is more than twice as fast as emergence in the field. The faster emergence observed in the greenhouse compared to field emergence may be explained by temperature differences prevailing during the conduction of each experiment. The differences detected in the rate of emergence suggested that the time of crown root initiation may also be influenced by environmental factors. Thus, the time required for crown root initiation of the earliest barleys in the field may be longer than the time required by the same barleys in the greenhouse. Black (1970) observed that low temperature, low moisture, and low phosphorus availability restricted adventitious root development and tillering in spring wheat. Recent studies showed that temperature has a strong effect on rate of emergence, crown root weight and shoot weight of spring barley (Luna-Ruiz, 1992). The duration of different developmental periods of barley plants according to Briggs (1978) is widely variable and depends on area of cultivation, sowing date, and cultivar. This part of the study was conducted to determine a phenological stage to predict the occurrence of crown root initiation.

Table 3.4 shows the range, mean, mode and standard deviation (sd) of crown roots and leaves per plant for each sampling day. Both crown roots and leaves per plant

Table 3.4 Number of leaves and crown roots per plant in the barley population CC XXXIX on different days after planting

Day	n	No of leaves/plant				No of crown roots/plant			
		Range	Mean	Mode	sd†	Range	Mean	Mode	sd
10	30	2-2	2	2	0	0-0	0	0	0
13	28	3-3	3	3	0	0-3	0.1	0	0.6
16	30	2-5	4	4, 5	1	0-5	1.7	2, 0	1.4
19	30	3-9	5.7	4, 8	2	0-7	2.5	0, 2	2
22	27	3-12	6	4	3	0-9	3.4	0, 1	3.1
25	26	3-18	8.7	4, 5	5	0-20	6.5	2, 0	6.5
28	26	4-17	9.8	17, 0	4	0-24	9.8	14, 6	7.1

†standard deviation

increased with sampling day. The number of crown nodes/plant and SIL/plant showed no apparent response to sampling day (data not shown). The average number of crown roots per plant in the population ranged from 0 on day 10 to 9.8 on day 28. Average leaf number per plant ranged from 2 on day 10 to 9.8 on day 28. Crown roots/plant had a close linear and positive relationship ($R^2 = 0.84$; $n = 197$) with number of leaves/plant (Figure 3.4A). When the average number of leaves/plant and crown roots/plant were plotted against days of sampling, the two corresponding regression lines were almost parallel (Figure 3.4B). The R^2 values were 0.97 for leaves/plant and 0.90 for crown roots/plant. The close and direct association between crown roots/plant and leaves/plant ($r = 0.92$; $P < 0.01$), in addition to the similar response of both characteristics to sampling day suggests that leaf number may be a good indicator of degree of crown root development. According to the regression equations, by day 14.7 (when 50 % of the

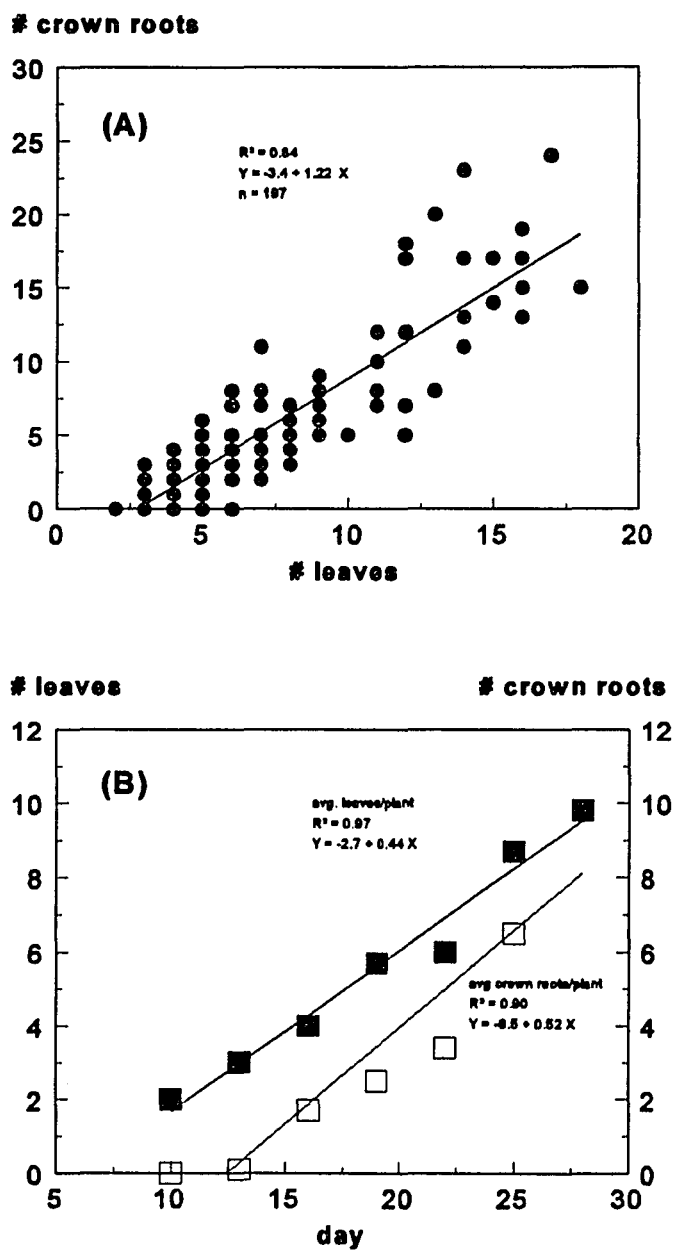


Figure 3.4 Relationships among crown roots/plant, leaves/plant, and days after planting

leaves/plant was 3.8, which corresponded to an average number of crown roots/plant of 1.1. Klepper et al. (1984) reported that number of roots per culm in winter wheat can be calculated from number of leaves, and that crown roots begin to appear at the time of tillering when the third leaf is expanding. Mac Key (1973; 1980; 1987) has studied shoot:root relationships in cereals, and has shown significant correlations between several root and shoot characteristics. He reported r values of 0.73 and 0.67 for the relationship between number of adventitious roots and tillers in wheat and barley, respectively. Black (1970) showed correlations of adventitious roots/plant with tillers/plant ($R^2 = 0.96$) and spikes/ha ($R^2 = 0.94$). According to Mac Key (1980) the highest interdependence between shoot and roots occurs before anthesis when supply and demand regulate such interaction. He pointed out that shoot and roots benefit from each other when the lower green surfaces of the shoot supply the roots with assimilates, while seminal and adventitious roots benefit the main culm and tillers correspondingly. The results of the present study agree with most reports on shoot:crown roots relationships (Black, 1970; Mac Key, 1973, 1980, 1987).

Soil Depth and Rate of Soil Moisture Depletion

The analysis of variance (Table 3.5) showed significant effects ($P < 0.01$) of day, sampling depth, and day x sampling depth interaction. These results denoted that moisture in the soil profile varies with sampling day, but that the degree of variation depends on soil depth. The rate of soil moisture depletion decreased with soil depth as shown in Table 3.6.

Table 3.5 Analysis of Variance for relative soil moisture content in a barley field during early seedling establishment. Marana, AZ 1990

Source of variation	Degrees of freedom	Mean squares
Range	4	8.61 *
Day	7	116.47 **
Error a	28	2.35
Sampling Depth	5	46.09 **
Sampling Depth x Day	35	3.82 **
Error b	160	1.40
Total	139	-----

** $P \leq 0.01$; * $P \leq 0.05$

Table 3.6 Average soil moisture content (%) at different sampling depths and days during early seedling establishment of one-irrigation barley. Marana, AZ 1990

Sampling Depth (cm)	Sampling Day								Average LSD = 0.81
	7	8	10	12	14	17	19	21	
----- percent soil moisture content -----									
0-2.5	10.8	8.4	6.7	5.6	5.0	3.6	3.5	2.5	5.8 c†
2.5-5.0	10.3	9.1	6.6	4.3	5.5	3.3	4.1	3.7	5.9 bc
5.0-7.5	10.5	8.3	6.2	4.7	5.2	4.3	4.2	4.4	6.0 bc
7.5-10	9.9	7.7	5.5	6.8	5.0	4.8	5.1	4.8	6.2 bc
10-12.5	9.5	7.3	6.1	5.5	6.1	5.8	5.4	5.2	6.4 b
12.5-15	11.3	8.3	9.8	8.6	8.5	7.4	8.1	6.8	8.6 a
Average LSD = 0.52	10.4 a†	8.2 b	6.8 c	5.9 d	5.9 d	5.1 e	4.9 de	4.6 e	

†Means within a group followed by the same letter are not significantly different ($P \leq 0.05$) according to the Duncan's Multiple Range Test

Average soil moisture content between day 7 and day 21 decreased by 77 %, 64 %, 58 %, 52 %, 45 %, and 40 % in the 0 to 2.5, 2.5 to 5, 5 to 7.5, 7.5 to 10, 10 to 12.5, and 12.5 to 15 cm depths, respectively. The effect of sampling depth on the rate of soil moisture depletion is illustrated in Figure 3.5. The rate of soil moisture depletion at each sampling depth is reflected by the slope of the regression line (b-value), and by the R² value. High b and R² values indicate a stronger relationship between soil moisture content (Y) and days after the planting irrigation (X). All b-values were negative indicating that soil RWC decreased with days after the planting irrigation. The b values and R² values decreased in proportion to sampling depth (Table 3.7) indicating that the rate of soil moisture depletion decreases with soil depth.

Table 3.7 Linearized regression equations, regression coefficients (b values) and coefficients of determination (R² values) for the relationship between soil moisture content (Y) and days after the planting irrigation (X) at different sampling depths. Marana, AZ Nov. 20-Dec. 11, 1990.

Sampling Depth	Linearized regression equation	b value	R ² value
0.0 - 2.5 cm	Y = 22.9 - 6.8 ln X	- 6.8	0.96
2.5 - 5.0 cm	Y = 21.0 - 6.0 ln X	- 6.0	0.85
5.0 - 7.5 cm	Y = 18.9 - 5.1 ln X	- 5.1	0.81
7.5 - 10.0 cm	Y = 16.1 - 3.9 ln X	- 3.9	0.74
10.0 - 12.5 cm	Y = 13.8 - 3.0 ln X	- 3.0	0.70
12.5 - 15.0 cm	Y = 15.8 - 2.8 ln X	- 2.8	0.66

A reduction of 143 % in the b value and 46 % in R² occurred with a change from the shallowest sampling depth (0 - 2.5 cm) to the deepest sampling (12.5 - 15 cm).

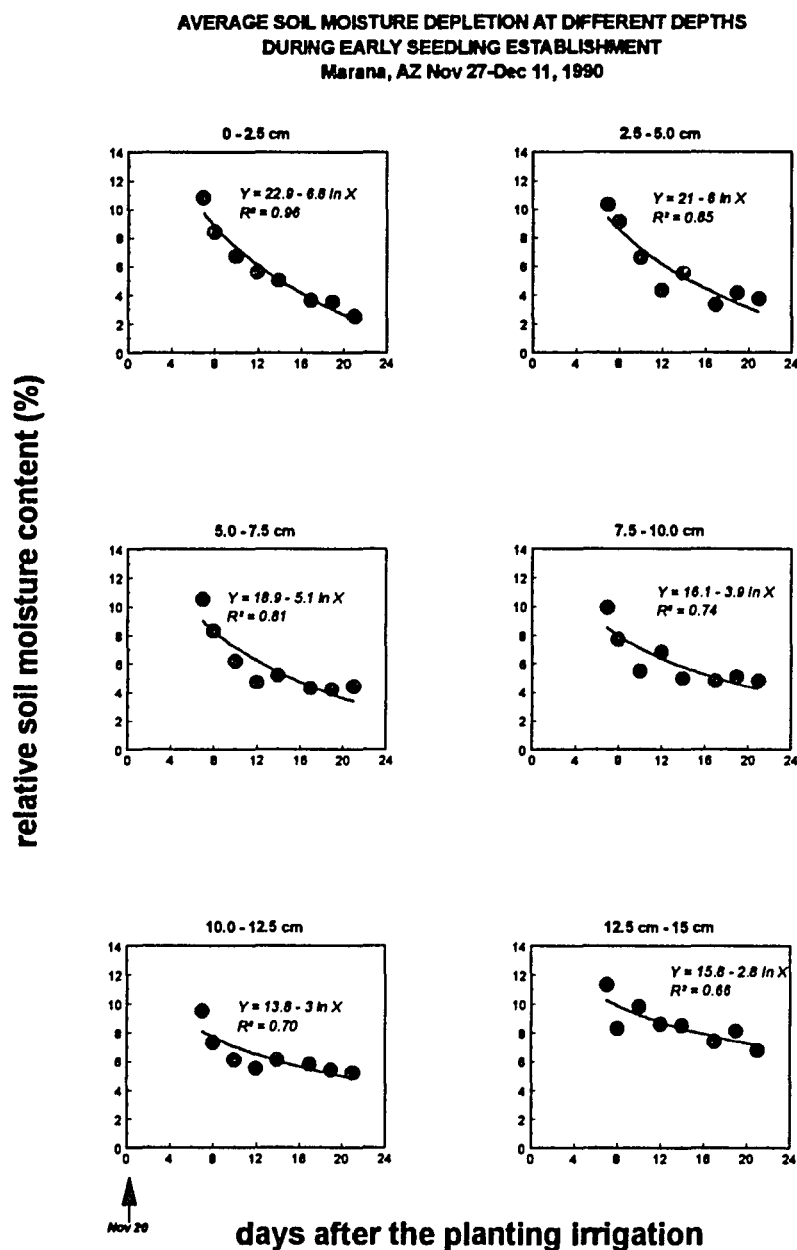


Figure 3.5 Average rate of soil moisture depletion at different sampling depths in a Pima clay loam soil during the period of seedling establishment. The scatterplots and curves were generated using actual data. The equation of each curve was linearized by logarithmic (\ln) transformation of the independent variable (X). The original scatterplots (curves) can be converted to regression lines by \ln transformation of the X values.

The higher rate of soil moisture depletion observed at shallow depths compared to deeper layers of the soil may be explained by higher soil desiccation rates in the top 2.5 cm caused by evapotranspiration, wind, and radiation effects. These results suggest that the period of adequate soil moisture available to the plant increases with soil depth. These findings have important implications for seeding depth, crown placement, crown root development, and crop performance under conditions where irrigation water or rainfall after planting is limited. The lower rates of soil moisture depletion detected in deeper layers of the soil suggest that increasing depth of seeding may increase the period that soil moisture is available for germination and crown root development. Similar but more dramatic results were obtained by Stanhill (1955), Hudspeth and Taylor (1961) and Wiegand (1962). Stanhill (1955) reported moisture reductions of 55 %, 29 % and 16 % in the surface inch, second inch, and third inch 21 days after field capacity; Hudspeth and Taylor (1961) reported that the top half-inch (1.27 cm) of the soil in the High Plains of Texas often dries to below the permanent wilting point within 24 hours after wetting.

Wiegand (1962) reported daily drying rates of 0.65 % and 2.75 % at 9.5 cm and 1.9 cm respectively in a sandy clay loam four days after irrigation. The results of the present study were obtained with a Pima clay loam, which has more potential for water retention compared to sandy soils, and the sandy clay loam used by Wiegand (1962). It is evident that the effect of soil depth on rate of soil moisture depletion in sandy soils is more dramatic.

Crown Root Development in Relation to Genotype, Seeding Depth and Rate of Soil Moisture Depletion

Factors Affecting Crown Differentiation

Crown root development is a complex process that depends on several genetic and environmental factors as listed in Table 3.8 (Luna-Ruiz and Ramage, 1992).

Table 3.8 Classification of factors affecting the development and differentiation of the crown system of barley

ENVIRONMENTAL	GENETIC
<p><i>Abiotic</i></p> <ol style="list-style-type: none"> 1. Seeding Depth 2. Temperature 3. Light 4. Soil <ul style="list-style-type: none"> moisture minerals texture compaction depth <p><i>Biotic</i></p> <ol style="list-style-type: none"> 5. Competition 6. Pests <ul style="list-style-type: none"> diseases insects weeds 	<ol style="list-style-type: none"> 1. Number of nodes and internodes 2. Degree of internode elongation 3. Number of crown roots and tillers arising at each node 4. Time of crown root initiation 5. Rate of crown root elongation

Crown root development depends on crown differentiation which is determined by the amount and degree of elongation of the various internodes comprising the crown, and by the number and elongation of crown roots at each node. The degree of crown differentiation is difficult to study, and can be detected only under deep seedings. The degree of internode elongation in most barleys is mainly controlled by seeding depth, light,

and temperature, although soil texture and compaction become more important as seeding depth increases. Biotic factors such as degree of plant competition within the population (determined by seeding rate), and competition against other living organisms such as weeds, insects and pathogens, can directly affect the degree of crown differentiation.

Genotype, Seeding Depth, and Rate of Soil Moisture Depletion

Results of this study showed that the time of crown root initiation can differ by several days from one barley genotype to another, and that soil moisture in the top 2.5 cm is depleted dramatically during the first few days after planting. Deeper seedings and early crown root initiation could prolong the period of adequate moisture for crown root development, but, as discussed in Chapters I and II of this dissertation, deep seeding can result in shallow or deep crown placement depending on the degree of SIL of the genotype. Thus, the results obtained in these studies strongly suggest that deep seeding of deep-crowned genotypes with early crown root initiation could be advantageous for crown root development and crop performance under one-irrigation conditions. Most commercial plantings in irrigated fields are shallow (~2.5 cm) as deep sowings usually reduce the rate and percent of emergence and final stand establishment of most cultivars. However, there is enough evidence showing that the rate of emergence, and the ability to emerge from deep seedings can differ among cultivars (Sunderman, 1964; Kaufman, 1968; Bacaltuchuk and Ullrich, 1983; Luna-Ruiz, 1992). After two years of field research, deep seeding of deep-crowned genotypes appears a promising combination for one-irrigation

conditions (Chapter II). Deep seeding (~8 cm) was shown to increase 100-seed weight and final grain yield in one-irrigation barleys compared to shallow seeding (~2.5 cm).

Although none of the two years presented the typical dry conditions usually experienced with one-irrigation, deep seeding of the barleys with short SCI (deep crowns) resulted in more yield and heavier seed compared to barleys with long SCI (shallow crowns).

Additional research (Chapter I) has shown that the reduced SIL character is under genetic control and appears to be relatively easy to transfer by conventional breeding.

Selection of Genotype and Seeding Depth Using Soil Water Tension Curves

The values of soil moisture content obtained in this study can be transformed to and expressed as soil water tension (bars, atm, etc.) in order to avoid the confounding effects of soil texture on capacity for soil water retention, and also, to determine a critical depth of moisture based on soil moisture requirements for crown root development.

Although the minimum moisture required for normal crown root growth may differ with genotype and environmental conditions, some workers have reported that crown roots of barley normally do not grow below the permanent wilting point (Briggs, 1978), or when soil moisture at the crown region is below 15 bars (Ferguson and Boatwright, 1968). Data from this research showed that a given soil water tension (e.g. the one required for crown root development) in the soil profile increases in depth over a dry period after the planting irrigation (data not shown). Accordingly, the critical depth of moisture (soil water tension) for crown root development should follow a curve that results from plotting the depth of

the given soil water tension (at which crown roots theoretically grow) against time (days after the planting irrigation). Hypothetical distribution curves for different soil water tensions are shown in Figure 3.6.

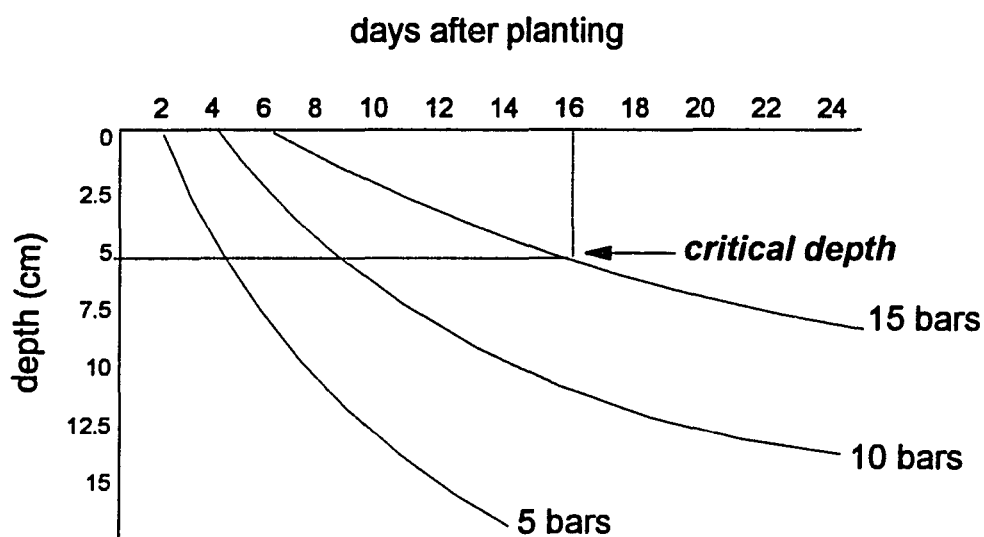


Figure 3.6 Hypothetical distribution curves for different soil water tensions. The critical depth of moisture can be determined by the number of days required for crown root initiation (X axis) and the maximum soil water tension for crown root development (soil water tension curve). In the example, crown roots initiate 16 days after planting and require a maximum soil water tension of 15 bars. The critical depth of moisture (Y axis) for these values is 5 cm.

The curves can be used as a decision support model to determine optimal depth of seeding, choice of variety, and to establish a selection criteria for crown depth and time of crown root initiation in a conventional breeding program for one-irrigation barley. For instance, if the time of crown root initiation of a given genotype is 16 days, and moisture requirements for normal crown root development is 15 bars, the crown has to be placed at or below the depth of the intersection between day 16 (X axis) and the 15 bar-curve.

In this example, the intersection occurs at the 5 cm depth, which would be the critical depth of moisture. To determine the depth of seeding, it is necessary to know the SIL of the genotype. To insure proper placement of the crown, the seed should be at least 5 cm deep for genotypes without SIL, and deeper than 5 cm for genotypes with long SCI. Although this model works for the specific soil type and conditions of Marana, AZ, it is possible and relatively easy to determine soil water tension curves for other regions. The results presented in this study need to be confirmed with additional research.

Study of Internode Elongation under Light Deficiency and Population Density

The analysis of variance is presented in Table 3.9.

Table 3.9 Analysis of variance for the study of light and competition effects on three genotypes

Source	df	MEAN SQUARES			
		SIL	Coleoptile length	Seedling length	Seed to first leaf node
Replication	2	26.7	45.5	2443	34.5
Genotype (G)	2	5094 **	307.8 *	5978 *	2010 **
Error a	4	24.4	23.3	1144	56.4
Treatment (T)	2	1045 **	91.6 **	38262 **	5476 **
G x T	4	274 **	41.3 *	796	86 *
Error b	12	9.8	11.5	468	26.2

** ($P \leq 0.01$); * ($P \leq 0.05$)

There were significant main effects in all the observed variables, and significant interactions between genotype and treatment for all but one variable (seedling length).

These results indicated that the elongation of internodes below and above ground in response to plant competition and light deficiency differs among the genotypes under study. The significant interaction detected for SIL and crown depth was due to a complete absence of SIL in P4 in all treatments. The significant interaction detected for seed-to-first leaf node was due to the higher response of the Yemen line to the treatments in relation to P4 and Seco.

Response of the Genotypes to Light Deficiency and Population Density

Table 3.10 and Figure 3.7 show the average response of each genotype to the treatments. P4 had no elongation of the SCI regardless of light and population density, and therefore placed the crown at the depth of seeding (60 mm) in all treatments.

The SCI of Seco and the Yemen line was 63 % and 81 % longer when the seedling was covered compared to SIL in the control. The competition treatment in relation to the control had a 25 % reduction of SIL in Seco but had no significant effect on SIL in the Yemen line.

The effect of light and competition on seedling length, and distance of seed-to-first leaf node was very similar in the three genotypes. For these two variables, all genotypes showed the highest elongation with the covered treatment, and, except for seedling length in the Yemen line, there was no significant difference between the control and the competition treatment. Seedling length increased by 38 % in P4, 70 % in Seco, and 37 % in the Yemen line with the covered treatment compared to the control.

Table 3.10 Average response of three genotypes to light and competition effects in the greenhouse. All values correspond to the mean \pm standard error

Treatment	n	P4	Seco	Yemen line	Average (LSD 3.2)
		SIL (mm)			
control	3	0 \pm 0	32 \pm 0.8	36 \pm 2.6	23 \pm 5.8 b †
competition	3	0 \pm 0	24 \pm 1.2 **	33 \pm 1.2	19 \pm 5 c
covered	3	0 \pm 0	52 \pm 2.6 **	65 \pm 5.2 **	39 \pm 10.1 a
Average (LSD 6.5)	9	0 \pm 0 c †	35.8 \pm 4.4 b	45 \pm 5.4 a	
Treatment	n	crown depth (mm)			Average (LSD 3.2)
control	3	60 \pm 0	28 \pm 0.9	24 \pm 2.6	37 \pm 5.8 b
competition	3	60 \pm 0	36 \pm 1.2 **	27 \pm 1.2	41.1 \pm 5 a
covered	3	60 \pm 0	7.7 \pm 2.6 **	-5.3 \pm 5.2 *	21 \pm 10.1 c
Average (LSD 6.5)	9	60 \pm 0 a	24 \pm 4.4 b	15 \pm 5.4 c	
Treatment	n	coleoptile length (mm)			Average (LSD 3.5)
control	3	43 \pm 3.5	49 \pm 3.5	61 \pm 1.3	51 \pm 3.1 b
competition	3	50 \pm 0.9 *	56 \pm 1.8 *	59 \pm 1.2	55 \pm 1.4 a
covered	3	52 \pm 4.6 **	60 \pm 0.3 **	60 \pm 0.9	57 \pm 1.9 a
Average (LSD 6.3)	9	48 \pm 2.2 b	55 \pm 2 a	60 \pm 0.7 a	
Treatment	n	seedling length (mm)			Average (LSD 22.2)
control	3	202 \pm 22.9	182 \pm 7.2	249 \pm 9.4	211 \pm 12.4 b
competition	3	186 \pm 6.3	169 \pm 8.4	207 \pm 9.7 *	187 \pm 6.8 c
covered	3	279 \pm 36.4 **	310 \pm 3.3 **	342 \pm 17.6 **	310 \pm 14.8 a
Average (LSD 44.3)	9	222 \pm 19.1 b	220 \pm 22.6 ab	266 \pm 21 a	
Treatment	n	seed to first leaf node			Average (LSD 5.3)
control	3	62 \pm 1.8	69 \pm 3.5	90 \pm 2	74 \pm 4.4 b
competition	3	67 \pm 0.3	66 \pm 2.9	87 \pm 1	73 \pm 3.6 b
covered	3	97 \pm 1.2 **	115 \pm 4.6 **	136 \pm 7.1 **	116 \pm 6.1 a
Average (LSD 9.8)	9	75 \pm 5.6 b	83 \pm 8.2 b	104 \pm 8.2 a	

† Genotype and Treatment means followed by the same letter are not significantly different ($P < 0.05$) according to the Duncan's Multiple Range Test; LSD = least significant difference ($P < 0.05$) for main effects

** ($P < 0.01$) and * ($P < 0.05$) indicate the level of significance for the LSD comparison between a treatment and the control within the same genotype

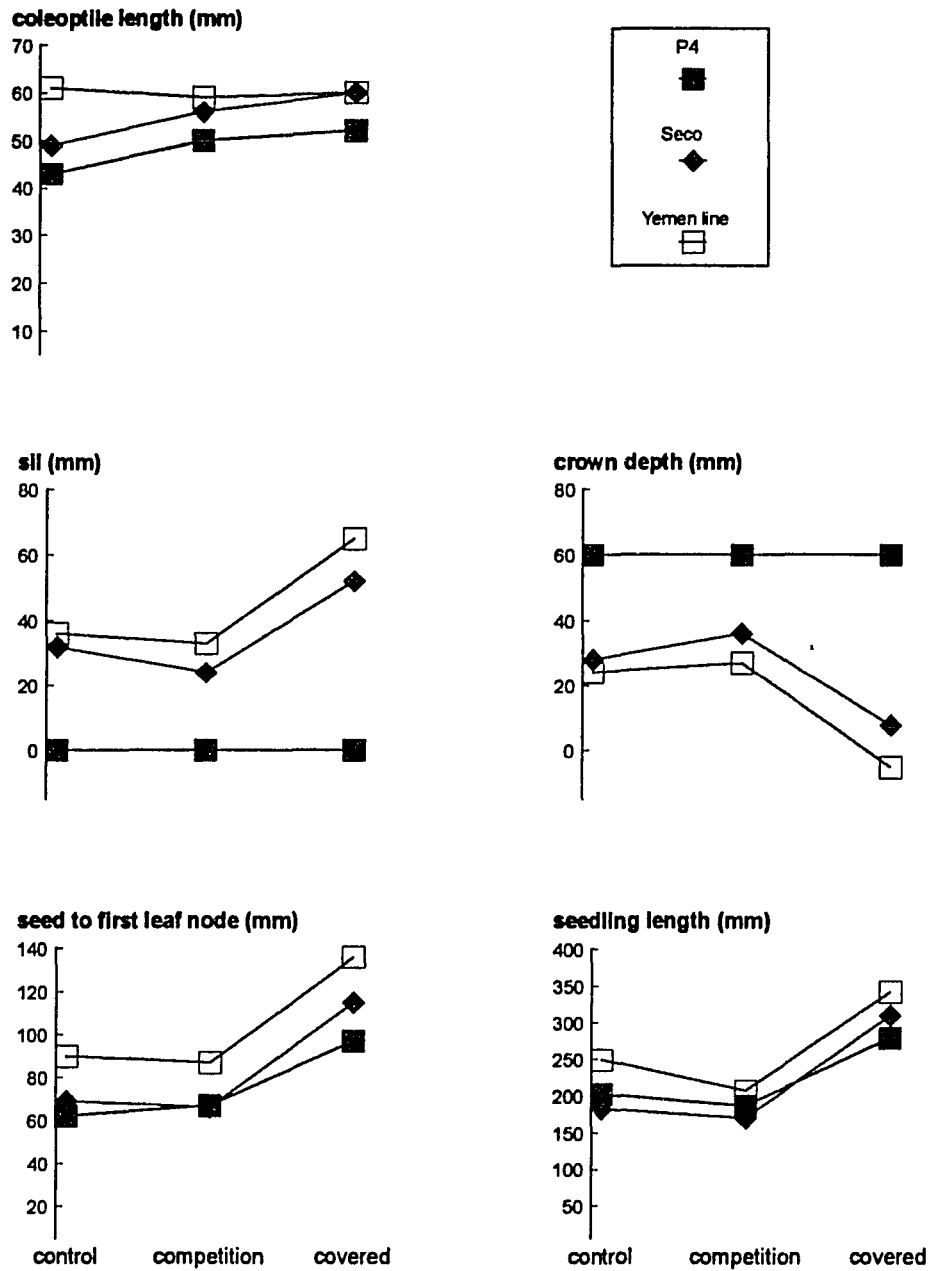


Figure 3.7 Response of three genotypes to light and plant competition effects during the seedling stage

With competition, the Yemen line had a 17 % reduction in seedling length in relation to the control.

The distance from seed to first leaf node had a significant increase of 56 % in P4, 67 % in Seco, and 51 % in the Yemen line with the covered treatment compared to the control, but regardless of genotype, the same variable was not significantly affected by competition.

Coleoptile length was significantly affected by light and competition in P4 and Seco, but not in the Yemen line. As with the other variables, coleoptile length was affected more by the covered treatment than it was by population density. Coleoptile length is determined by genotype and environmental conditions (temperature, light, seeding depth) during emergence. The elongation of the coleoptile is stimulated in the dark, and inhibited in light. Coleoptile elongation in the control ceased when the tip reached the light (soil surface), but when the tip was covered, the coleoptile had some additional elongation. On the other hand, the small but significant response of the coleoptile to plant density in P4 and Seco could be due to competition during emergence. Coleoptile length in the Yemen line was the same in all treatments, and appears to be less sensitive to the effects of light and population density compared to P4 and Seco.

The results of this study indicated that light deficiency after emergence has strong effects on the elongation of the SCI, and other internodes in Seco and the Yemen line. Unexpectedly, the population density used in this experiment reduced internode elongation during the period of seedling establishment. The reduction of internode elongation may be

the result of less cell division and cell elongation in response to competition.

This study clearly showed that compared to Seco and the Yemen line, the SCI of P4 is relatively insensitive to the effects of light deficiency and population density. The absence of SCI in P4 contrasted with the strong effect that the covered treatment had on the SIL of Seco and the Yemen line. The study also revealed that seedling length and distance of seed-to-first-leaf node in P4 is affected in a similar manner to Seco and the Yemen line. It appears that internodes above the crown in P4 are as sensitive as Seco and the Yemen line to the effects of light and population density, but that contrary to the other genotypes, internodes below the crown in P4 are insensitive. The lack of sensitivity of internodes below the crown in P4 seems to be what determines the absence of SCI and the deep crown placement in this line. The treatments and conditions used in this study did not stimulate SCI elongation in P4. The elongation of SCI in this line may require higher temperatures and larger plant population densities. Average temperatures in the greenhouse during the experiment ranged from 7.5 to 15.6 °C, with a mean of 11.9 °C (Figure 3.1).

This study shows that selection for lack of SCI could be very efficient at the seedling stage. Line P4 has been crossed with male sterile plants of a sub-population that was derived from the original CC XXXIX population. Selection in the sub-population has been for lack of SCI at maturity. Observations of an F1 bulked sample of the crosses between P4 and male sterile plants showed that 12 (30 %) out of 40 seedlings had no SCI. Seedlings of this population can be efficiently screened for lack of SCI in the greenhouse.

It is intended that line P4 be included in the world collection of barley for its unique SCI characteristics. A germplasm release note is being prepared for publication.

SUMMARY AND CONCLUSIONS

- The time required for crown root initiation varied tremendously among barley plants in CC XXXIX. Some plants (7.1 %) initiated crown roots very early (13 days after planting), most plants (70 %) had initiated crown roots by day 16, but others (11.5 %) had no crown roots by day 28.
- Leaf number/plant showed a strong correlation ($r = 0.92$; $P \leq 0.01$) with crown roots/plant, suggesting that crown roots/plant could be predicted by the number of leaves.
- The selection of barleys with early crown root initiation could improve crown root development and plant performance under one-irrigation conditions. As efficient selection for time of crown root initiation may be strongly influenced by the environmental conditions (e.g. temperature, light and soil moisture), the prediction and selection of barleys with early crown root initiation has to rely on a phenological stage associated with the desirable character. In this experiment, most plants in the population had crown root initiation around the 3-leaf stage
- The rate of soil moisture depletion was strongly influenced by sampling depth. Soil moisture in the top 2.5 cm was reduced by 77 % between day 7 and day 21 after the planting irrigation, but at a depth of 12.5-15 cm soil moisture decreased only by 40 %.
- The rate of soil moisture depletion at different sampling depths is reflected by the slope of the regression line, by the regression coefficient (b value), and by the coefficient of determination (R^2) that result from plotting soil moisture content (Y) against time (ln X). Large values of b indicate high rates of soil moisture depletion.

- The construction of specific soil water tension curves based on soil moisture distribution in the soil profile over a dry period, could be of great value in determining optimal seeding depth, choice of variety, and establishment of selection criteria for crown depth, and time of crown root initiation in a conventional breeding program for one-irrigation conditions.
- Light deficiency after emergence increased SIL by 63 % in Seco and by 81 % in the Yemen line, but SCI in P4 had no elongation regardless of light and population density. Light deficiency also produced a tremendous increase in the length of above ground seedling parts in the three genotypes, and in the coleoptile of P4 and Seco.
- High population density in general had smaller and less significant effects than light deficiency on internode elongation and coleoptile length of the genotypes. In most cases, high population density reduced internode elongation, but increased coleoptile length.
- The study suggested that the internodes below the crown in P4 were insensitive to the effects of light and population density, but that the internodes above the crown in the same line were as sensitive as Seco and Yemen line.
- The treatments and conditions used in this study did not stimulate SCI elongation in P4. The elongation of the SCI in this line may require higher temperatures and larger plant population densities.
- Screening for lack of SCI can be very efficient in the greenhouse at the seedling stage.

Future Work

- These results need to be confirmed by additional research. It is suggested to determine the degree of genetic variation for time of crown root initiation with a larger population size, and varying conditions of temperature, soil texture, soil moisture, seeding depth, and plant competition.
- Additional research is suggested to detect varietal differences for carbohydrate accumulation in the lower internodes, to determine their role in grain filling and plant performance under one-irrigation conditions, and to study their associations with early crown root initiation.

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