Genetic and environmental considerations for evaluating crown position of wheat *

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Summary. Crown position affects winter survival of fall-sown wheat (*Triticum aestivum* L.) Direct or indirect selection for crown depth has been little practiced. Reports have suggested that short subcrown internode length was closely related to semidwarf plant height and that semidwarfism was related to poor emergence. This study determined the relationships among crown depth, plant height, and emergence rate index in three wheat populations. The efficiency of evaluating crown placement in the field was examined and additional information was obtained on its genetic control. The F_2-derived F_4 and F_5 lines from the crosses of female parents 'Daws', 'Nugaines', and 'Stephens' with male parent 'Selection 7952' were planted at Central Ferry and Pullman, Washington, respectively. Correlations from each population indicated that crown depth and subcrown internode length were not closely associated with plant height and emergence rate index. Crown depth was a more reliable indicator of crown placement than subcrown internode length. Adjustment of the data for seed depth differences was essential for evaluating subcrown internode length but less important for evaluating crown depth. After adjustment for seed depth, narrow-sense h^2 values for subcrown internode length and crown depth were 0.25–0.41. Crown depth and subcrown internode length were inherited as quantitative traits in phenotypes that expressed variable dominance. Modest gains due to selection for crown depth were achieved.

Key words: *Triticum aestivum* L. – Wheat phenology – Coldhardiness – Crown depth

Introduction

Seedling characteristics of winter wheat (*Triticum aestivum* L.) significantly affect stand establishment and adaptation. Coleoptile length has been shown to correlate with plant height, subcrown internode length, and seedling emergence. The expression of these traits has been reported to be controlled by either interrelated or pleiotropic genetic systems (Allan et al. 1961; Burleigh et al. 1965; Chowdhry and Allan 1963). However, environmental effects, minor genes, background genotypes, and recombination may be responsible for variability between the associations of these traits among different populations.

The relationship between crown depth or subcrown internode length and emergence is theorized to be the same as the relationship between coleoptile length and emergence (Allan et al. 1962, 1965; Kolp et al. 1967). Poor emergence, therefore, would result from short coleoptile, short subcrown internode length and deep crown depth. It is conceivable that intensive selection for optimal emergence may inadvertently result in winter-tender shallow-crowned cultivars for the northwestern USA. Working in that region, Webb and Stephens (1936) showed that hardier winter wheat cultivars formed crowns deeper than did less hardy cultivars.

The primary objectives of this study were to determine the relationship between subcrown internode length and crown depth with emergence rate index, and to confirm any associations between subcrown internode length and crown depth with the Rht_1 and Rht_2 semidwarf genes. The effects of location and genotype by location interactions on the expression of crown depth and subcrown internode length were examined, and additional evidence on the genetic control of crown depth was obtained.

Materials and methods

Three crosses involving four parents were studied. The three female parents, 'Daws', 'Nugaines' and 'Stephens', and the common male parent of Selection 7952 ('Luke'/WA4303/2*'Orin') exhibited deep, intermediate, shallow, and shallow crowns, respectively, based on preliminary field and greenhouse studies. Daws and Nugaines have the Rht_2 semidwarf gene, whereas 7952 and Stephens have Rht_1 (R. E. Allan, personal communication). Spikes were selected from F_2 plants with one and two gene semidwarf and standard height phenotypes in the Daws/7952 population. For the Nugaines/7952 and Stephens/7952 populations, F_2 spikes were selected from plants with one gene semidwarf phenotype.

The F_2-derived F_4 lines of each cross were planted in randomized, complete block designs with two replications at Central Ferry, Washington, on 21 October 1982. An eight-row tractor-mounted nursery planter was used to sow two-row plots for each line. Row length was 1.5 m and spacing between rows was 0.3 m. After each series of 50 progeny plots, a single plot of each parent was sown. Eight plots in each replication were sown with F_2 seed of its respective population. About 100 seeds were sown per row at an average seed depth of 53 mm. Soil type at Central Ferry was Chard sandy loam (coarse-loamy, mixed, mesic Calcic Haploxerolls).

Plants from one row of each plot were dug in mid-March, 1983, and transported in plastic bags to a 5°C cold room. After rinsing, ten plants from each plot were randomly selected and individually measured for seed depth and subcrown internode length. Larger samples were collected for F_2 populations. Seed depth was measured from the seed remnant to the first chlorophyll-pigmented site above the soil-blanched stem tissue. Crown depth was determined by subtracting subcrown internode length from seed depth. Plant height was determined prior to harvest by averaging three measurements, within each plot, from the soil surface to the base of the main culm spikes.

The F_2-derived F_5 lines and parental checks were sown at Spillman Farm, Pullman, Washington, on 6 September 1983, with a four-row deep-furrow drill planter. The experimental design for each population was a randomized, complete block with four replications. Genotypes were sown at 100 seeds/1.7 m in single-row plots with 0.3-m spacing between rows at an average seed depth of 73 mm. The soil type was Palouse silt loam (fine-silty, mixed, mesic pachic Ultic Haploxerolls).

Two seedling emergence counts and the final stand were recorded from 14 to 22 September 1983. Emergence rate index was determined as described by Allan et al. (1965). In mid-March, 1984, plants were dug from single-row plots of two replications of the Pullman trial, and measured as previously noted.

Data were analyzed separately for each populatin, both within and between locations. Differences among genotypes were determined from analysis of variance procedures and Fisher's protected LSD ($P=0.05$) tests. An analysis of covariance was employed to adjust treatment means for seed depth. Simple correlation coefficients were calculated among all traits. Narrow sense heritability for subcrown internode length and crown depth was determined by parent-offspring regression, using unadjusted and adjusted treatment means (Falconer 1981). Distribution of F_2 data based on environmental standard error was used to evaluate segregation patterns for crown depth.

Results and discussion

The main differences between the two locations were later planting, lighter soils, and milder winters at Central Ferry than at Pullman. Seed depth was deeper and less uniform at Pullman. Populations at Central Ferry and Pullman segregated for all characters ($P \leq 0.05$) except the Nugaines/7952 progeny, which did not segregate for subcrown internode length at Central Ferry, and for emergence rate index at Pullman. Seed depth differences were not significant ($P \geq 0.05$) at Central Ferry but they differed ($P \leq 0.05$) at Pullman.

Between the two locations, crown depth means were more similar than were the subcrown internode length means (Table 1). Shallow seed depth at Central Ferry resulted in low subcrown internode length values and suggested that subcrown internode length did not develop fully at that location. Although crown depth was less affected by the difference in seed depth than was subcrown internode length, the genotype × location interactions were significant ($P \leq 0.05$) for both traits, except for subcrown internode length of the Nugaines/7952 progeny. Since generations and locations were confounded, further testing of advanced lines would be needed to determine the efficacy of making selections in a particular field environment. Genotype × environment interactions were not significant for subcrown internode length and crown depth when a greenhouse and field experiment were compared (Poulos and Allan 1987). If field tests are to be relied upon for assessment of crown position, tests at different locations and in different seasons appear necessary.

Heritability of crown depth and subcrown internode length

Parent-offspring (F_4-F_5) regression heritabilities were lower for subcrown internode length than for crown depth, prior to adjusting for seed depth. Heritability values for crown depth of the Daws/7952, Nugaines/7952, and Stephens/7952 populations were 0.18, 0.25, 0.28, respectively; and 0.09, 0.17 and 0.03, respectively, for subcrown internode length. After correcting for seed depth, heritability ranged from 0.25 to 0.41 and averaged 0.34 for both crown depth and subcrown internode length.

Heritability for both traits was low, indicating that response to selection may be low. Limited genetic variability for crown depth could also minimize the response due to selection. Using the standard deviations of 4.2, 2.9, and 3.6 mm for the Daws/7952, Nugaines/7952, and Stephens/7952 F_4 populations, respectively, and heritability estimates from the adjusted means, the selection gains at 1% and 10% intensities were calculated (Falconer 1981). The expected response to selection per generation for both crown depth and subcrown internode length among the three populations ranged from 2.8 to 3.5 mm and 1.9 to 2.3 mm at the 1% and 10% levels of selection intensity, respectively.

Actual selection gain was compared for crown depth among the three populations by choosing the 20 F_4 lines

Table 1. Comparisons between locations for unadjusted crown depth and subcrown internode length data from crosses between Daws, Nugaines, and Stephens, with 7952

Cross/parent/generation	Location	N[a]	Crown depth (mm)			Subcrown internode length (mm)		
			Mean	s^2	Range	Mean	s^2	Range
7952[c]	Central Ferry	8	28	2	26–31	26	16	22–33
	Pullman	8	24	18	19–29	50	29	44–59
Daws/7952								
Daws[c]	Central Ferry	8	39	1	37–41	13	1	22–33
	Pullman	8	33	12	26–37	35	44	25–45
F_2[b]	Central Ferry	578	33	28	12–50	10	49	0–45
F_4	Central Ferry	120	33	17	17–49	20	23	6–34
F_5	Pullman	120	26	8	18–34	45	42	32–61
Nugaines/7952								
Nugaines[c]	Central Ferry	8	28	2	27–30	25	6	21–29
	Pullman	8	29	10	25–34	42	20	34–48
F_2[b]	Central Ferry	564	26	31	0–50	28	47	0–50
F_4	Central Ferry	121	26	8	17–35	28	20	16–41
F_5	Pullman	121	24	12	13–32	52	49	34–71
Stephens/7952								
Stephens[c]	Central Ferry	8	32	4	29–35	21	4	18–23
	Pullman	8	21	10	17–27	51	33	40–60
F_2[b]	Central Ferry	546	28	28	10–42	25	48	0–42
F_4	Central Ferry	117	29	13	21–39	24	20	9–34
F_5	Pullman	117	23	8	16–32	49	47	37–63

[a] N = number of experimental units per replication
[b] F_2 statistics are on individual observations
[c] Parental checks grown with both F_4 lines (Central Ferry) and F_5 lines (Pullman)

within each population with the deepest crown placement. When compared to the unadjusted means of their respecitve F_4 and F_5 populations, the average percentage increases in crown depth of the 20 F_4 versus 20 F_5 lines were: 18% versus 8% (Stephens/7952), 15% versus 0% (Nugaines/7952), and 15% versus 10% (Daws/7952), respectively. Actual gains were, therefore, slightly higher than predicted gains for two of the three populations. Among the 20 lines with deep crown placement in the F_4, 6 lines of each population were also ranked among the 20 lines with the deepest crown placement in the F_5 generation.

Actual selection gain for unadjusted subcrown internode length was either nil or very low. When the 20 F_4 lines within each population with the shortest subcrown internodes were chosen, the percentage decreases in length between the 20 F_4 line means versus F_4 population mean and the corresponding 20 F_5 line means versus F_5 population mean were: 32% versus 2% (Stephens/7952), 25% versus 0% (Nugaines/7952), and 31% versus 1% (Daws/7952), respectively.

Segregation patterns of crown depth and subcrown internode length

Because crown depth was a more reliable crown placement criterion than subcrown internode length, its phenotypic expression was examined more closely. The distributions of F_2 seedlings and their parents appear in Fig. 1. An environmental standard deviation was obtained for each population by pooling the standard deviations of its parents. This value was used to subdivide the F_2 progeny into several crown depth classes. The distribution patterns of the F_2 plants of the three populations typically expressed continuous variation and generally resembled normal distribution; the ranges in crown depth distribution of the F_2 progeny were mainly within the ranges of their respective parents. When the midparent mean and the F_2 population mean are compared for crown depth, they were very similar in the Daws/7952 cross. The F_2 population means were less than their midparent means in the other two crosses.
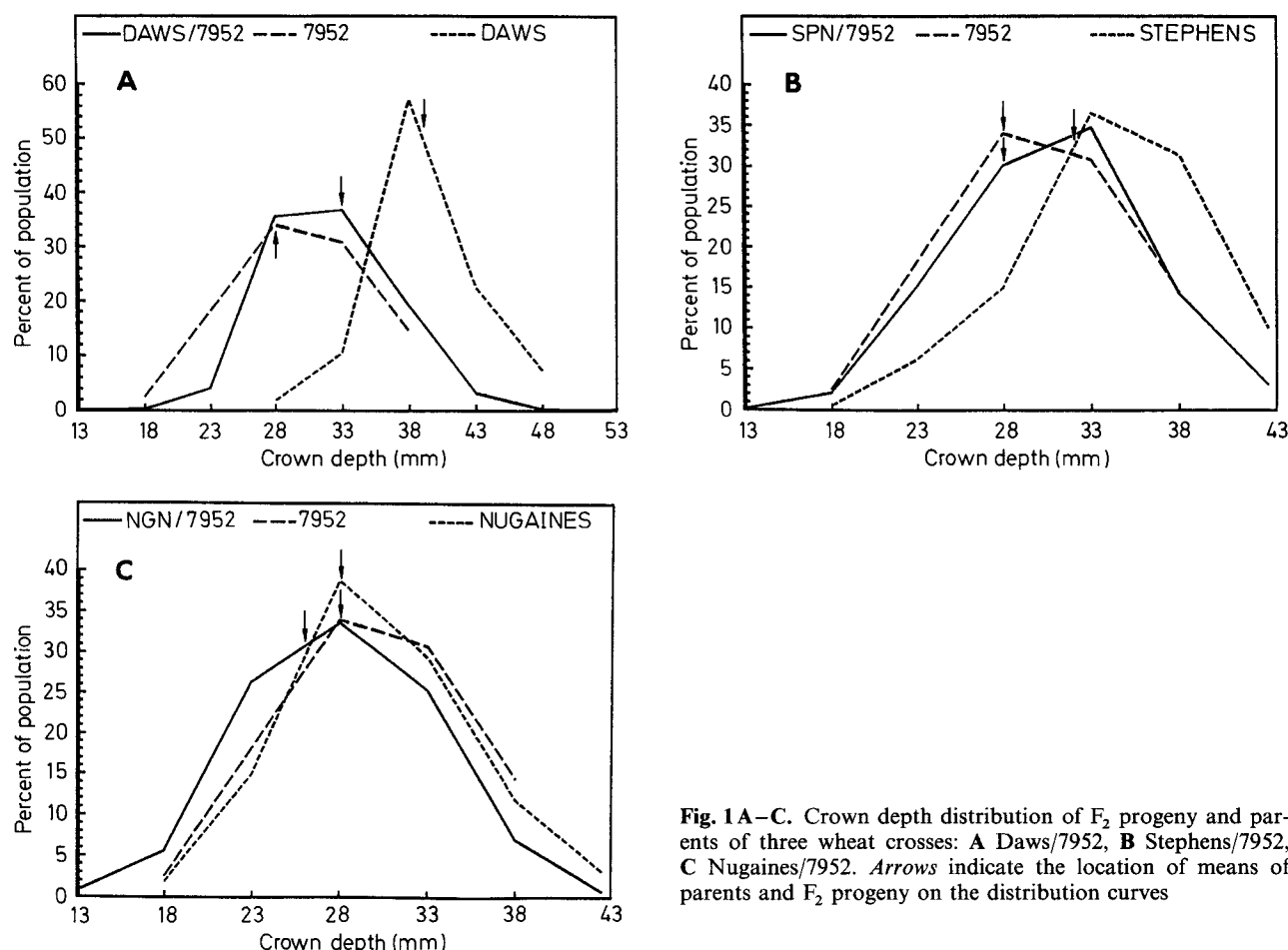
Fig. 1A–C. Crown depth distribution of F$_2$ progeny and parents of three wheat crosses: **A** Daws/7952, **B** Stephens/7952, **C** Nugaines/7952. *Arrows* indicate the location of means of parents and F$_2$ progeny on the distribution curves

Within each population, both F$_4$ and F$_5$ progeny were recovered that differed ($P \leq 0.05$) for crown depth. In fact, a few F$_4$ lines transgressed above and below their parents for crown depth for each cross ($P \leq 0.10$). Transgressive segregation did not occur in the F$_5$ generation except for shallow crown depth in the Nugaines/7952 population.

In the Daws/7952 cross, 62 F$_4$ and 27 F$_5$ progeny had crown depth means equal ($P \geq 0.10$) to Daws; 20 lines equaled Daws for crown depth at both sites. Several F$_4$ and F$_5$ lines of Stephens/7952 also had crown depths equal ($P \geq 0.10$) to Daws in their respective trials; two lines were similar ($P \geq 0.10$) to Daws in both trials.

Crown depth behaved as a quantitative trait and phenotypes varied in the degree of dominance for its expression. The results generally agreed with a previous study that demonstrated quantitative inheritance and dominance for shallow crown depth in the progenies of the cross 'Daws'/'Cappelle Desprez' (Poulos and Allan 1987). Even though Nugaines and Stephens had crown depth means that were phenotypically similar to 7952 at Central Ferry and at Pullman, respectively, their genetic mechanisms controlling the trait must differ. Segregation

for crown depth was apparent in both the F$_4$ and F$_5$ generations of the Stephens/7952 and Nugaines/7952 crosses.

Association among traits

Several significant associations ($P \leq 0.05$) among seed depth, subcrown internode length, crown depth, plant height, and emergence rate index (ERI) within and among the two locations occurred (Table 2). The decision to adjust data for seed depth at Central Ferry was based on these moderately high correlations, even though variation in seed depth was statistically nonsignificant. In the F$_5$ generation at Pullman, seed depth had a high positive association ($P \leq 0.01$) to subcrown internode length (avg. $r = 0.91$), but was only moderately associated with crown depth (avg. $r = 0.37$) (Table 2).

At Pullman, variation in seed depth apparently caused changes in subcrown internode length not directly associated with changes in crown depth. The average r between subcrown internode length and crown depth was -0.05 for unadjusted data. A biological interpretation would suggest that crown depth has higher heritability

Table 2. Simple correlations between several criteria among progeny of three wheat crosses

Traits, location and generation[a]	Crosses (r values[d])		
	Daws/ Sel. 7952	Nugaines/ Sel. 7952	Stephens/ Sel. 7952
Seed depth (CF, F_4) vs. crown depth (CF, F_4)	0.01	0.00	0.11
Seed depth (P, F_5) vs. crown depth (P, F_5)	0.31[c]	0.49[c]	0.31[c]
Seed depth (CF, F_4) vs. subcrown internode (CF, F_4)	0.53[c]	0.77[c]	0.60[c]
Seed depth (P, F_5) vs. subcrown internode (P, F_5)	0.91[c]	0.90[c]	0.92[c]
Seed depth (P, F_5) vs. ERI (P, F_5)	−0.67[c]	−0.64[c]	−0.72[c]
Plant height (CF, F_4) vs. crown depth (CF, F_4)	0.19[b]	−0.17	−0.29[c]
Plant height (CF, F_5) vs. crown depth (P, F_5)	−0.13	−0.14	−0.16
Plant height (CF, F_4) vs. subcrown internode (CF, F_4)	−0.15	−0.03	0.24[c]
Plant height (CF, F_4) vs. subcrown internode (P, F_5)	0.10	0.21[b]	0.13
Plant height (CF, F_4) vs. ERI (P, F_5)	0.38[c]	0.23[c]	0.08
Subcrown internode (CF, F_4) vs. crown depth (CF, F_4)	−0.84[c]	−0.63[c]	−0.72[c]
Subcrown internode (P, F_5) vs. crown depth (P, F_5)	−0.12	0.07	−0.09
Subcrown internode (CF, F_4) vs. ERI (P, F_5)	0.02	0.12	0.11
Subcrown internode (P, F_5) vs. ERI (P, F_5)	−0.62[c]	−0.59[c]	−0.67[c]
Crown depth (CF, F_4) vs. ERI (P, F_5)	0.16	0.06	0.16
Grown depth (P, F_5) vs. ERI (P, F_5)	−0.18[b]	−0.28[c]	−0.20[b]

[a] CF and P indicate Central Ferry and Pullman locations, respectively
[b,c] Significantly different from 0 at $P=0.05$ and $P=0.01$, respectively
[d] All r values determined from unadjusted means

than subcrown internode length in respect to environmental variation. Adjustment for seed depth is essential for evaluating subcrown internode length, but less necessary for evaluating crown depth. Crown depth can be more efficiently estimated by directly measuring the distance from the crown node to the soil line. Hence, the necessity to measure seed depth and subcrown internode length is eliminated.

Plant height was not highly correlated to subcrown internode length or crown depth for any of the crosses in either generation (Table 2). The ranges in subcrown internode length and crown depth among F_4 lines were rather similar among the various plant height groups of the three crosses. The Sel 7952/Daws population $(Rht_1 Rht_1 Rht_2 Rht_2, Rht_1 Rht_1 rht_2 rht_2, rht_1 rht_1 Rht_2 Rht_2, rht_1 rht_1 rht_2 rht_2)$ had the greatest variation in plant height (70–115 cm) among its progeny. Tall F_4 lines (>100 cm) of this population had subcrown internode and crown depth ranges of 11–23 mm and 27–40 mm, respectively; the short F_4 lines (100 cm) had subcrown internode and crown depth ranges of 15–35 mm and 18–40 mm, respectively. Hence, it should be possible to recover lines with either semidwarf or nonsemidwarf plant height phenotypes with deep crown placement. These results differed from those of Allan and Pritchett (1973), who did not recover F_2-derived progeny with short subcrown internodes and nonsemidwarf plant heights.

Plant height was only weakly associated with subcrown internode length and crown depth in the Stephens/

7952 population $(Rht_1 Rht_1 rht_2 rht_2)$ at Central Ferry, but the associations should not materially impede selection for either trait. Like Daws, Nugaines possesses the Rht_2 gene. A low positive $(P \leq 0.05)$ correlation was measured between plant height (Central Ferry) and subcrown internode length (Pullman) in the Nugaines/7952 population. Otherwise, the Rht_1 and Rht_2 genes appeared to have neutral effects on crown placement in the Nugaines/7952 and Daws/7952 populations. These results concurred with those of Gul and Allan (1978), who indicated that the Rht_2 gene had little influence on subcrown internode length.

At Pullman, emergence rate index had a moderately high negative association $(P \leq 0.01)$ to seed depth and subcrown internode length in all three populations. Phenologically, a negative correlation between emergence rate index and subcrown internode length was unexpected. However, since adjusted subcrown internode length had little relationship to emergence rate index $(r = −0.19–0.0)$, poor emergence and elongated subcrown internode length were probably consequences of deep sowing. Although subcrown internode length and emergence rate index were highly correlated at Pullman, seed depth differences appeared to be largely responsible for their association. Partial correlation coefficients between subcrown internode length and emergence rate index independent of seed depth were small $(r = −0.03–0.05)$ and nonsignificant for each cross. Emergence rate index was not highly correlated to crown depth or plant height (Table 2).

In conclusion, it is suggested that crown depth is more useful than subcrown internode length for evaluation of crown placement, because it is less influenced by differences in seed depth. Heritability of crown depth was low, but higher than for subcrown internode length. Crown depth can be directly measured, which saves time from measuring seed depth and subcrown internode length. Adjustment for seed depth differences was essential for subcrown internode length comparisons, but less important for crown depth comparisons. No restrictive associations were measured between crown depth and plant height or emergence rate index. Crown depth appeared to be quantitatively inherited and manifested with variable degrees of dominance. Small gains due to selection for crown depth were achieved.

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