Effects of Common Root Rot on Discoloration and Growth of the Spring Wheat Root System

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LRC Contribution no. 3879454.
We wish to thank A. D. Kuzyk, B. J. Nishiyama and T. M. Despins for their technical assistance in this study.
Accepted for publication 16 November 1994.

ABSTRACT

Kokko, E. G., Conner, R. L., Kozub, G. C. and Lee, B. 1995. Effects of common root rot on discoloration and growth of the spring wheat root system. Phytopathology 85:203-208.

Image analysis procedures were used to quantify the effect of common root rot on the growth and discoloration of the subcrown internode (SCI), crown roots, and seminal roots of spring wheat. Severe discoloration of the SCI was associated with diminished growth of the seminal and crown roots. The linkage of discoloration of the SCI to a reduction in root growth was most evident for the crown roots. Reduced growth of either the crown or seminal roots was not compensated for by increased growth of the other root system. The differences in root discoloration among different root rot categories were generally small. On average, the crown and seminal roots were whiter than the SCI in the healthy (nil) category. There was a weak negative relationship between discoloration of the SCI and the crown and seminal root systems. However, it was also observed that root discoloration usually increased with greater root length. Since plants with healthy SCIs usually had longer roots, they were more likely to be exposed to the pathogen and become discolored than were plants with severely diseased SCIs. The image analysis procedures developed in this study can be used to objectively and precisely measure damage caused by root diseases in other host species. This procedure validates the most commonly used field research method of rating plants for common root rot.

Additional keywords: Cochliobolus sativus, *Triticum aestivum*.

Common root rot, which is primarily caused by *Cochliobolus sativus* (Ito & Kuribayashi) Drechs. ex Dastur, is the most prevalent root disease of wheat and barley in the Great Plains region of North America. Based on the results of the most recent survey of common root rot in wheat, this disease was responsible for a 5.7% yield reduction on the Canadian prairies (17).

Wheat initially produces a primary or seminal root system that originates from nodes in the seed and is extremely important in establishing the plant (15). Crown or adventitious roots form at coleoptile nodes about the time the fourth main stem leaf appears and these roots supply nutrients and moisture to individual tillers (1).

Root rot infection can stunt plants or cause a prematurity blight, but usually aboveground symptoms of common root rot are not readily apparent (20). Common root rot damages all subterranean parts of the plant (31) and may cause considerable damage to the roots of seedlings (30). Originally, assessments of the severity of common root rot included an evaluation of plant vigor as well as measurements of the discoloration of all underground parts of the plant (13). However, the most commonly used method for evaluation of root rot severity is based on a four-category system that rates subcrown internode (SCI) discoloration (25). This method has gained wide acceptance because it allows for rapid assessment of large numbers of plants.

It has been shown that root rot ratings of the SCI of individual plants were closely related to plant biomass (37) and grain yield (17,37). Tinline et al (36) observed a negative correlation between yield and SCI discoloration, but not for external crown lesions. Studies have shown that increases in discoloration of the SCI reduced tiller formation in wheat (6,7). However, several agronomic studies with wheat (8,18,25) have not been able to establish a relationship between yield and root rot ratings of the SCI. Under optimal growing conditions, certain wheat cultivars recovered from early root rot infection and outyielded plants of the same cultivar that had not been exposed to the disease (27). A survey of wheat fields in South Australia (39) demonstrated that the relationship between root rot severity and yield in diseased and healthy plants was quite variable.

A better understanding of the effect of common root rot on the growth and discoloration of the SCI and seminal and crown roots is needed since they all affect yield. The relationship between discoloration of the SCI and damage to the root system has not been examined because of the difficulties in visually assessing root growth and discoloration. However, image analysis technology (16) now makes it possible to objectively quantify these variables with a level of precision and resolution superior to the human eye. Image analysis procedures were used in this study to examine the relationship between discoloration of the SCI and the amount of growth and discoloration of the crown and seminal roots.

MATERIALS AND METHODS

Root rot resistant and susceptible near-isogenic lines of the hard red spring wheat cultivar Neepawa (3) were seeded in root rot beds in the greenhouse, according to the procedure described by Conner et al (4). The study was repeated at four different times (experiments A, B, C, and D). Seven weeks after seeding, plants were carefully removed from the soil, and the soil adhering to the root systems was thoroughly washed off. Plants were sampled in March 1992, August 1992, December 1992, and January 1993, for experiments A, B, C, and D respectively. Root rot severity on the SCIs was visually determined using the rating system described by Ledingham et al (17) and plants were grouped into one of the four root rot severity categories. In each experiment, approximately 100 plants from each of the four root rot severity categories were randomly selected. The aboveground portions of each wheat plant were removed at the crown and discarded. The remaining portion of each plant (i.e., the root system) was then placed in a plant press and allowed to dry. After the material had dried for at least 1 mo, the SCI, seminal roots, and crown roots were removed from the plant press, separated, and cut into approximately 3-cm lengths. The crown and seminal roots from each plant were individually packaged and labeled according to their root rot severity category and plant number. Plants from each of the four experiments were examined as separate replications.

Image analysis. The image analysis protocol used in this study was based on the procedure described by Kokko et al (16). The SCIs, crown roots, and seminal roots, all from the same plant, were examined separately inside a square template on a trans-illuminator (Aristo DA-17 photographic light box, Aristo Grid Lamp Products Inc., Port Washington, Long Island, NY). Additional shadow-free lighting was provided by a fluorescent ring lamp (Luxo, Quebec) around the camera lens. Each root sample was carefully arranged inside the square template in order to minimize any overlap of root material within the sample. All samples were analyzed following the same sequence with crown roots first, followed by the SCI, and finally the seminal roots.

Images were acquired with a Dage 81 B/W video camera (DAGE-MTI, Inc., Michigan City, IN) mounted on a Bencher M2 photomacrographyphy stand (Bencher Inc., Chicago, IL). Images were input or digitized, with a resolution of 512 $\times$ 512 pixels, in a Tracor Northern 8502 image analyzer (Noran Inc., Middleton, WI). A short program was run before each image analysis session to automate and standardize the analysis. This program automatically set all the standardized instrument param-

TABLE 1. Mean and standard deviation of mean intensity and area for the different root rot categories in experiments A–D

				SCI[a]		Crown roots		Seminal roots	
Expt.	Category	N		Intensity[b]	Area[c] (mm^2)	Intensity	Area (mm^2)	Intensity	Area (mm^2)
A	Severe	103	Mean	103	32	179	138	209	62
			SD	12	6	13	87	8	36
	Moderate	109	Mean	126	30	174	168	205	92
			SD	15	6	12	95	7	61
	Slight	105	Mean	148	30	177	210	208	109
			SD	12	5	13	102	9	55
	Nil	106	Mean	157	26	169	200	194	96
			SD	11	5	11	91	13	51
B	Severe	125	Mean	89	32	149	271	187	44
			SD	10	7	13	179	14	20
	Moderate	126	Mean	105	29	139	405	180	62
			SD	12	5	10	180	14	29
	Slight	131	Mean	118	26	137	423	180	65
			SD	12	5	9	152	13	31
	Nil	118	Mean	132	26	135	447	177	70
			SD	9	6	9	164	12	29
C	Severe	111	Mean	110	25	171	101	206	30
			SD	14	4	13	54	8	15
	Moderate	110	Mean	125	24	171	142	204	30
			SD	16	6	12	79	7	17
	Slight	110	Mean	155	19	168	186	201	42
			SD	11	3	10	92	8	19
	Nil	100	Mean	166	17	167	181	197	40
			SD	9	4	9	90	11	20
D	Severe	110	Mean	117	26	187	99	207	48
			SD	12	5	12	62	9	31
	Moderate	110	Mean	127	25	182	129	202	54
			SD	17	5	12	80	8	28
	Slight	109	Mean	150	22	170	238	195	86
			SD	13	4	15	125	9	47
	Nil	109	Mean	164	21	175	235	198	92
			SD	8	4	12	94	9	43

[a] Subcrown internode.
[b] Mean gray-scale intensity of object pixels (black = 0, white = 255).
[c] Within each experiment, significant differences ($P < 0.001$, except for mean intensity of the crown in Expt. C, where $P < 0.05$) were found between all root rot severity categories for both intensity and area variables and for each of the root components.

eters, including image allocation and digital setting of the Dage 81 camera for image acquisition. In addition, all mechanical settings, magnification calibrations, optical settings, and analog camera parameters were standardized. These included camera position, focal plane, lens aperture, gain, gamma, and black-level controls.

Digital gray-scale images of the SCIs and roots were acquired (I1), such that all images had a background (nonspecimen area) that was evenly white with a gray-scale intensity of 255 (black = 0, white = 255). An image math expression, $B1 = I1 < 254$, created a binary image (B1) from the original gray-scale image (I1). This binary template (B1) defined the specimen image area to be analyzed to give the densitometric variable, mean pixel intensity. In addition, dimensional variables for area and length were measured. A separate data set was created for each experiment.

Statistical methods. For each experiment and each root rot severity category, various descriptive statistics (33) were determined for the area and mean pixel intensity variables for the SCI and crown and seminal roots. For the area and intensity variables, one-way analyses of variance were conducted to determine if there were differences among the categories within each experiment. Correlations between the intensity and area variables for each of the SCI and root components were determined using the data pooled over categories within each experiment. To examine relationships between the growth and discoloration of the SCI and crown and seminal roots in each experiment, polynomial models of various orders, using a single dependent and two independent variables, were fit to the data, pooled over categories (5). Regressions of the area or mean pixel intensity of the crown and seminal roots on the corresponding variables for the SCI were obtained. The regression of these variables for the crown root on those for the seminal roots was similarly examined. For each regression, residuals from the regression models were plotted against the fitted values of the dependent variable and independent variables to judge the adequacy of the models. The regression equations obtained for the experiments were tested for homogeneity using the approximate procedure in Mead and Curnow (21). Estimated values of the dependent variables in the region of observed values of the independent variables were represented graphically on contour maps (24). Statistical analyses were carried out using SAS (28).

RESULTS

Image analysis of the SCIs revealed large significant ($P < 0.001$) differences in the average of the mean pixel intensity values among the different disease severity categories in each experiment (Table 1). However, mean intensity values for the crown and seminal roots showed only a narrow range of variation and considerable overlap among categories within experiments. Generally, root rot caused very little discoloration of the crown or seminal roots, compared with SCIs. However, with the exception of the crown roots in experiment C, differences between disease categories for crown and seminal roots were highly significant ($P < 0.001$) in each experiment. The crown and seminal roots of plants from all categories had average mean pixel intensity values that were consistently higher than those of the SCIs in the nil category, indicating they were less discolored than the healthiest SCIs.

Image analysis of the SCI and seminal and crown roots revealed that the extent of root growth was inversely correlated with the amount of discoloration of the SCI (Table 1). In each experiment, differences in the amount of growth of the crown and seminal roots were significant ($P < 0.001$). A large amount of variation was also observed for differences in root area among plants within the same category.

Simple correlation analyses of these results revealed significant ($P < 0.001$) associations between root area and discoloration of the SCI (Table 2), with the SCI becoming darker (i.e., lower mean pixel intensity) as area of the SCI increased. Depending on the experiment, correlation values for this relationship varied from −0.42 to −0.65. Differences in area of the SCI accounted for less than half of the total variation in discoloration of the SCI.

There was a significant ($P < 0.001$) negative correlation between the growth and discoloration for the crown roots in three of four experiments and the seminal roots in all four experiments (Table 2). Plants with larger roots systems generally were more discolored (i.e., had lower mean pixel intensity) compared with plants with smaller root systems. However, this relationship between root growth and discoloration accounted for only a small amount of the total variation associated with total root area.

Of the various polynomial response surface models that were fitted to the data, third-order models provided a good representation of the relationships among the area and pixel intensity variables for the SCI and root components. Plots of the residuals against the predicted values and independent variables for the models in each experiment indicated that these models fit the data well. Tests for homogeneity of the regression models indicated that models obtained using data pooled over the experiments were not appropriate, although the response patterns were generally similar among the experiments.

The amount of crown root growth was affected by the time of the year when the experiment was conducted. Experiment B, which was conducted between July and August of 1992, produced almost twice as much crown root growth as the other experiments that were conducted between the fall and spring (Table 1).

Regardless of the timing of the experiment, root growth was reduced as SCI discoloration increased. This relationship was evident for both the crown and seminal root systems, but was more apparent for the crown roots. The decrease in root areas with increased discoloration of the SCI did not follow a linear relationship. In experiments A, C, and D, a reduction in root growth was evident in both the moderate and severe categories (Table 1). In experiment B, in which environmental conditions were most favorable for plant growth, a decline in root growth was only observed in plants from the severe category.

The third-order polynomial regression analyses provided a more detailed picture of the relationship between root growth and SCI discoloration and area over the four qualitative rating categories that were given by the summary in Table 1. The analyses accounted for the association between the SCI discoloration and area variables. The regressions were highly significant ($P < 0.001$, Table 3),

TABLE 2. Correlations between mean pixel intensity, an indication of discoloration, and total area of different plant components

	Experiment			
Plant component	A	B	C	D
Subcrown internode	−0.42[a]	−0.51	−0.65	−0.49
Crown roots	0.05	−0.48	−0.26	−0.37
Seminal roots	−0.34	−0.47	−0.30	−0.19

[a]All correlations are significant ($P < 0.001$) except for the crown roots in experiment A.

TABLE 3. Percentage of the total variation (R^2) accounted for by third-order regression models relating mean pixel intensity and total area variables for different plant components

Variables			R^2 values for experiments			
Y	X1	X2	A	B	C	D
TACR[a]	TASI[b]	MISI[c]	13.3	18.5	23.7	26.1
TASR[d]	TASI	MISI	8.0	14.0	17.2	17.7
MISR[e]	TASI	MISI	10.9	3.8[f]	6.6	13.5
MICR[g]	TASI	MISI	5.0[f]	13.4	8.2	13.5
TACR	TASR	MISR	6.6	21.3	32.6	44.8
MICR	TASR	MISR	10.8	15.5	12.8	17.9

[a]Total area of the crown roots.
[b]Total area of the subcrown internode.
[c]Mean pixel intensity of the subcrown internode.
[d]Total area of the seminal roots.
[e]Mean pixel intensity of the seminal roots.
[f]All R^2 values except for these are significant ($P < 0.001$).
[g]Mean pixel intensity of the crown roots.

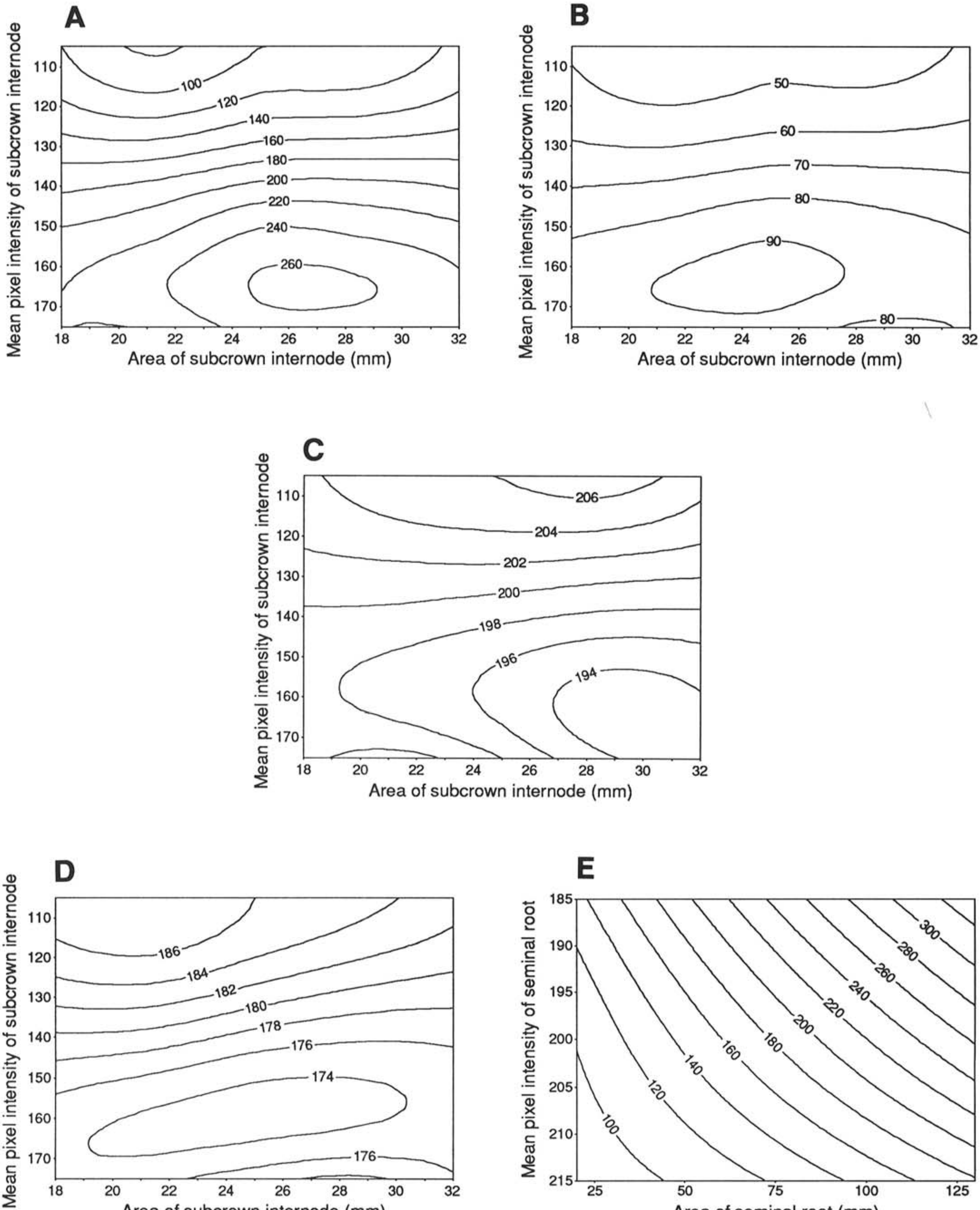

Fig. 1. Contour figures illustrating relations among mean pixel intensity and total area of six root system parameters in experiment D. Note that a lower numerical value for mean pixel intensity represents an increase in discoloration of subcrown internode (SCI). **A,** Effect of mean pixel intensity and total area of SCI on total area of crown roots. **B,** Effect of mean pixel intensity and total area of SCI on total area of seminal roots. **C,** Effect of mean pixel intensity and total area of SCI on mean pixel intensity of seminal roots. **D,** Effect of mean pixel intensity and total area of SCI on mean pixel intensity of crown roots. **E,** Effect of mean pixel intensity and total area of seminal roots on total area of crown roots.

but the proportions of variation in the root areas accounted for by regression were only 13–26% for the crown roots and 8–18% for the seminal roots. The decrease in crown root areas with increased discoloration of the SCI was evident across the range in area of the SCI and is illustrated for experiment D (Fig. 1A). The largest crown roots were observed when SCIs were larger and less discolored. Similarly, notwithstanding the area of the SCI, the area of the seminal roots generally decreased with increasing discoloration of the SCI (Fig. 1B).

Analysis of the relationship of mean pixel intensity of the seminal roots to the area and mean pixel intensity of the SCI showed that, across the range of mean pixel intensity values of SCI, increases in the area of the SCI had little effect on the discoloration of the seminal roots (Table 1, Fig. 1C). There was a slight negative relationship between discoloration of the SCI and the seminal roots. It appeared that mean pixel intensity of the seminal roots increased as mean pixel intensity of the SCI decreased. The regressions, although generally significant, were not pronounced, as the percentage of variation accounted for ranged from 4 to 14% (Table 3).

There was a weak negative relation between mean pixel intensity of the crown roots and discoloration and area of the SCI (Tables 1 and 3, Fig. 1D). The percentage of variation accounted for by the regression was not large (5–14%) (Table 3). Increases in discoloration of the crown roots, as the area of the SCI became larger, were most apparent when mean pixel intensity levels of the SCI were in the smaller range. The mean pixel intensity of the crown roots generally increased as discoloration of the SCI decreased (Fig. 1D). This relationship was more evident when the area of the SCI was smaller. It was observed that within and across disease categories, plants with larger root systems usually had more root discoloration (Table 2). Part of the reason for this relationship appeared to be that plants with healthier SCIs usually had longer roots, which were more likely to become discolored.

There was a positive relationship between the extent of growth of the crown and seminal roots (Table 3, Fig. 1E). The independent variables area and mean intensity of the seminal roots accounted for 7–45% of the variation in the area of the crown roots in the experiments. This relationship was most pronounced in experiments B, C, and D. Area of the crown roots appeared to rise with increased discoloration of the seminal roots, particularly when the area of the seminal roots was large. There was only a weak relationship between the mean intensity of the crown and seminal roots (Table 3).

DISCUSSION

This is the first study to show the adverse effect of severe root rot on the development of the spring wheat root system. The reduction in root growth with increasing SCI discoloration was more apparent on the crown roots than on the seminal roots. Reductions in growth of either the seminal or crown roots were not compensated for by enhanced growth of the other root system. Root amputation studies (26,30,32) have demonstrated that seminal roots play a vital role in the establishment of the young wheat plant. Seminal roots are extremely important under dry conditions, when crown root development can be inhibited (2). Seminal roots have been shown to be much more important than the more shallow crown root system in accessing water deep in the soil (1). However, crown roots provide nutrients and water to specific tillers of the wheat plant (15). Crown roots are also important for anchoring the plant and providing resistance to lodging (9). Wang and Below (38) demonstrated that growth of the crown roots is strongly influenced by late applications of nitrogen fertilizers, which suggests that severe root rot impairs the plant's ability to efficiently utilize nitrogen fertilizers. A reduction in crown root growth would result in the production of fewer tillers, a symptom observed in wheat with severe root rot symptoms (6,7). A reduction in root growth would explain the association of lower yield and biomass production of individual plants with severe root rot ratings on the SCI (37).

Our results show that the four-category system developed by Ledingham et al (17) for rating root rot severity, which is based on the extent of lesions on the SCI, relates directly to the extent of root growth of individual plants. However, in our study there was very little difference in root growth between the nil and slight categories. Only plants in the severe category consistently had smaller root systems than plants in the other categories. This indicates that ratings based solely on the extent of lesion formation on the SCI do provide a rapid means of disease assessment that relates directly to growth of the root system.

The effect of common root rot on root discoloration has not been previously reported. Based on the results of this study, significant differences in root discoloration occur between root rot categories. While these differences were significant, they were not large. It appears that common root rot does not cause extensive discoloration of the root system, but it is not clear if this limited amount of root discoloration is sufficient to impair the movement of water and nutrients within the plant.

The low level of root discoloration observed in this study might have been due to the prevalence of *C. sativus*, which is seldom a root colonizer, as the major causal agent of common root rot in western Canada. It has been demonstrated in Australia that infection of wheat by *C. sativus* was largely confined to the plant crown and SCI, with only a low incidence of infection on the crown and seminal roots (10). The same distribution of infection with other root rot fungi, such as *Fusarium acuminatum* Ellis & Everh. and *F. oxysporum* Schlechtend. emend. Snyd. & Hans, was also observed. However, *F. equiseti* (Corda) Sacc. infection was confined primarily to the wheat root system.

It was observed in this study that, regardless of the disease category, plants with larger root systems were usually the most discolored. For this reason, plants with healthier SCIs, based on discoloration, usually had more root discoloration because they usually produced the most root mass. This suggests that plants with longer roots are more likely to be discolored simply because the increase in root surface area provides the pathogen with more potential infection sites.

In this study, root rot severity on the SCI increased with area and length of the SCI. This confirms earlier observations made by Kokko et al (16) using image analysis, and agrees with the results of field studies (12,34) that demonstrated that factors favoring the development of long SCIs, such as deep seeding, also increase lesion formation on the SCI.

A number of studies (14,23,27,35) have demonstrated that increased root rot severity on the SCI has little impact on the yields of certain tolerant cultivars of barley. Examination of the SCI and the root systems during the course of the growing season could be useful in providing a better understanding of how certain cultivars can sustain high levels of disease on the subcrown internode, yet with little impact on yield.

The image analysis protocol described in this study would be useful for studies on the development of root diseases in other host crops. Lindow (19) observed that visual estimation of disease is prone to a number of different sources of error, such as subjectivity and the difficulty in accurate assessment of intermediate levels of disease. Sherwood et al (29) reported that experienced scorers tended to overestimate disease severity, especially when disease levels were low. O'Brien and Van Bruggen (22) compared several methods of measuring corky root of lettuce and found that all were subject to human bias. Factors such as shape, orientation, shading, and scorer's personality can all influence perceptions of disease severity (11,29). Forbes and Jeger (11) reported estimations of disease intensity of plant roots were more prone to inaccuracy than similar measurements of other plant parts. Image analysis avoids these problems and provides an unbiased and highly precise measurement of root growth and discoloration that could be used to study root diseases of other crops.

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