Rib Discoloration in F₂ Populations of Crisphead Lettuce in Relation to Head Maturity

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ABSTRACT. Rib discoloration is a physiological disorder associated with heat stress in crisphead lettuce (*Lactuca sativa* L.). Rib discoloration resistance was studied in a 2-year field experiment using parental and F₂ plant populations from a cross of ‘Emperor’, a resistant cultivar, and ‘Eldorado’, a susceptible cultivar. Rib discoloration was evaluated in terms of incidence (percentage of plants with symptoms) and severity (on a 1–5 scale) and was correlated with maturity traits. The rib discoloration severity ratings for the two reciprocal F₂ populations were intermediate between the two parents and were not significantly different, indicating the lack of cytoplasmic inheritance for rib discoloration in ‘Emperor’ and ‘Eldorado’. In both parents and F₂ progenies, rib discoloration severity was strongly correlated with stem length, head height, head diameter, and head weight, but not with head density. In the resistant parent, more severe rib discoloration was associated with denser heads, whereas in the susceptible parent, the expression of the disorder was independent of head density. The chi-square tests rejected the hypothesis for monogenic segregation in some plantings but not in others. Resistance to rib discoloration is likely to be controlled by more than one gene with a high heritability ($h^2 = 0.57$, $P < 0.0001$).

Temperature extremes can impose major limitations on crop productivity and production in some areas. Growing lettuce above the optimal range of 7 °C to 24 °C results in a reduction in product quality associated with the development of physiological disorders such as rib discoloration, tipburn, bolting, and ribbiness (Lorenz and Maynard, 1988). The association of rib discoloration symptoms with high daytime temperature has been observed in the field (Jenkins, 1959) and has been demonstrated in a controlled environment (Jenni, 2005).

First described by Friedman in 1954, rib discoloration was observed in commercial shipments from major crisphead lettuce-producing areas of the United States (Beraha and Kwolek, 1975; Ceponis, 1985; Friedman, 1954) and Canada (Jenni, 2005). As the plants mature and the heads become firmer, small, brown streaks appear along the midribs of leaves located below the cap leaves. Lesions darken with time and are often followed in storage by soft rots caused by *Pseudomonas* Mig. species and other bacteria (Cox, 1955; Marlatt et al., 1957).

Reports on resistant breeding lines and cultivars support the idea that breeding for rib discoloration resistance has good potential (Baggett et al., 1990; Jenkins, 1962; Raleigh and Guzman, 1980). Understanding the inheritance of rib discoloration is basic to establishing an effective breeding program. To our knowledge, no information is available on the genetics controlling rib discoloration resistance or on the importance of head maturity at harvest to expression of the genes.

Inheritance studies in lettuce have investigated the following: 1) plant characters such as leaf and flower color and morphology (Lindqvist, 1960; Ryder, 1975; Ryder et al., 1999), head development (Bassett, 1975), flowering time (Ryder, 1996), and dwarfism (Waycott et al., 1995); 2) resistance to diseases such as downy mildew [*Bremia lactucae* Regel (Norwood et al., 1985)], lettuce mosaic virus (Ryder, 2002), corky root (*Sphingomonas suberifaciens*; Brown and Michelmore, 1988; van Bruggen et al.; Yabuuchi et al.), western yellows virus (Maisonneuve et al., 1991), turnip mosaic virus (Zink and Duffus, 1970), and stemphylium leaf spot (*Stemphylium botryosum* f. *lactucum* Wallr.; Netzer et al., 1985); and 3) resistance to insects such as leaf aphids (*Nasonovia ribisnigri* Mosley; Eenink and Dieleman, 1983); and *Macrosiphum euphorbiae* Thomas and *Uroleucon sonchi* L.; Reinink et al., 1995) and root aphids (*Pemphigus bursarius* L.; Ellis et al., 1994). In the present article, we are testing whether rib discoloration resistance is monogenic or multigenic, and whether the resistance is influenced by maternally inherited factors. The ratio of susceptible plants to resistant plants was compared according to various classifications of F₂ individuals derived from reciprocal crosses. An assessment key was developed for rapid quantification of rib discoloration severity in the field. The severity of rib discoloration was related to commercial maturity variables.

Materials and Methods

EXPERIMENTAL LAYOUT. Crosses were made for this genetic study using the method of Oliver (1910) as modified by Ryder and Johnson (1974). ‘Emperor’ was used as the resistant parent

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Fig. 1. Severity index of rib discoloration for crisphead lettuce from 4.0 (trace of spotting) to 1.0 (extreme occurrence of streaks) according to surface area with damage; 5.0 (no symptoms) is not shown, and 3.0 is the lowest limit for lettuce marketability.

and 'Eldorado' was used as the susceptible parent. 'Emperor' originated from a single plant selection of 'Empire', a cultivar developed by the U.S. Department of Agriculture for muck soil production and extensively used in early desert plantings. More tolerant to bolting and tipburn than 'Empire', 'Emperor' is adapted to the southern deserts and the San Joaquin Valley of California and has consistently shown more resistance to rib discoloration during the warmest period of the Quebec growing season. 'Eldorado' is a 'Salinas'-type crisphead lettuce that was developed from a cross between 'Kelvin' and 'Mariska' for its resistance to several downy mildew pathotypes. Adapted for the coastal areas of California and mineral soils, 'Eldorado' is susceptible to bolting and rib discoloration when grown in organic soils and in the warm, humid, and long-day conditions of the Quebec summers. 'Emperor' and 'Eldorado' were crossed in both directions, and F_2 seeds were produced by selfing F_1 plants.

Sixty transplants of parental and F_2 generations were planted at Agriculture and Agri-Food Canada's Sainte-Clotilde Research Sub-Station on 11 June and 26 June 2001 and 12 June and 25 June 2002 to get enough plants to obtain experimental 800 plants. Lettuce plants were 22 to 27 d old at transplanting. There were two planting dates per year to ensure that lettuce heads were harvested during the warmest period of the summer (i.e., between mid-July and mid-August). Each experiment was arranged in a randomized complete block design with four blocks. Temperature and rainfall data were recorded daily at a meteorological station located less than 500 m from the experimental field.

DATA COLLECTION. Lettuce heads were harvested at optimal maturity for each head between 25 and 30 July (Planting 1) and 6 and 8 Aug. (Planting 2) in 2001, and between 23 July and 1 Aug. (Planting 1) and 1 and 5 Aug. (Planting 2) in 2002. Fifty heads were evaluated for the presence and severity of rib discoloration. Severity of rib discoloration was evaluated on a scale of 1 to 5, according to a pre-established key for severity (Fig. 1). The severity index corresponded to an equivalent surface area with rib discoloration symptoms observed on one or more leaves of an individual lettuce head and measured with a planimeter LI-3100 (LI-COR Biosciences-Environments, Lincoln, NE; Table 1). Resistant and susceptible individuals were defined as follows: susceptible when severity was in the 1 to 2.9 range and resistant when severity was in the 3 to 5 range.

Because rib discoloration develops when the lettuce approaches maturity, additional agronomic data on each head were recorded to characterize the state of maturity: head weight after trimming, head height, head diameter, and stem (core) length. The head density (in $\text{g}\cdot\text{cm}^{-3}$) was calculated from head weight (in grams) and volume (in cubic centimeters), assuming the head shape was a sphere and using the average of head height and head diameter.

STATISTICAL ANALYSIS. The computer software TableCurve 2D (version 5.01; Systat Software, San Jose, CA) was used to fit regression curves between rib discoloration severity estimated by visual rating (scale of 1–5) and measured surface area of the disorder. This program was used to select the most appropriate among 8189 linear and nonlinear equations, based on adjusted R^2 , confidence intervals, and residuals. The ratio of resistant plants to susceptible plants in F_2 families was subjected to chi-square analysis to compare the observed and expected results (SAS release 6.12 for Windows; SAS Institute, Cary, NC). Other analysis procedures included analyses of variance and correlations on the individual and combined plantings, a Bartlett's test for heterogeneity of error variances between the two plantings, and a Duncan comparison of means for individual and combined plantings. Broad-sense heritability for the F_2 generations was calculated by using parental plants to estimate environmental variance, according to the methods described by Kelly and Bliss (1975).

Results and Discussion

Quantification of disease severity is essential in estimating crop damage. An assessment key was developed for rapid quantification of rib discoloration severity in the field (Fig. 1). The severity of rib discoloration, evaluated on a scale of 1 to 5, corresponded to an equivalent surface area with rib discoloration symptoms observed on one or more leaves of an individual lettuce head (Table 1). Although the main objective was

Table 1. Severity index for visual estimation of rib discoloration symptoms based on surface area with lesions in crisphead lettuce.

Severity index (1–5 scale)	Surface area with symptoms [S (cm ²)]	Description
5.0	0.00	No symptoms
4.9–4.5	0.00 < S < 0.02	One small spot, light in color
4.4–4.0	0.02 ≤ S < 0.04	Two small spots or one fine streak, light in color
3.9–3.5	0.04 ≤ S < 0.05	One or two thick lesions, or two streaks
3.4–3.0	0.05 ≤ S < 0.09	Two or three small lesions or streaks, the lettuce head is still marketable
2.9–2.5	0.09 ≤ S < 0.30	Two or three larger spots or lines, the lettuce head is not marketable, brown in color
2.4–2.0	0.30 ≤ S < 1.00	Moderate levels of lesions of various sizes
1.9–1.5	1.00 ≤ S < 3.50	High occurrence of lesions and long streaks
1.4–1.1	3.50 ≤ S < 8.00	Very high occurrence of brown streaks along the ribs and veins and into interveinal tissues
1.0	8.00 ≤ S	Extreme occurrence of long streaks along main and secondary veins, secondary bacterial rots may be present

to classify diseased material into disease-intensity categories, it was possible to relate rib discoloration severity with disease surface area and estimate the actual percentage of disease (Fig. 2). The regression of rib discoloration severity made by visual rating on the measured surface area of the disorder fitted an iteratively fitted standard rational equation (adjusted $R^2 = 0.999$, $n = 9$). An index of 3 was the lowest value assigned for a marketable lettuce head, which corresponded to a surface area with symptoms of less than 0.09 cm² (Table 1).

The analysis of variance revealed significant treatment × planting interactions between and within the years for the percentage of plants showing resistance to rib discoloration, indicating wide environmental variation between and within years for this variable (Table 2).

The first plantings of 2001 and 2002 had very similar growing conditions. With almost identical average air temperatures and cumulative rainfall amounts (20.2 °C and 125 mm rainfall in 2001 and 20.7 °C and 123 mm rainfall in 2002), the lettuce heads harvested within 50 and 51 d experienced 15 d (2001) and 19 d (2002) of heat stress above 28 °C. In the first planting of 2001, the susceptible parent had 97% of plants with rib discoloration, and the resistant parent had 19% (Table 2). In the first planting of 2002, the susceptible parent had 92% of plants with rib discoloration, and the resistant parent had 17%.

Fig. 2. Regression of rib discoloration severity of crisphead lettuce estimated by visual rating (1 to 5 scale, where 1 = severe rib discoloration; 3 = moderate rib discoloration, head still marketable; and 5 = no rib discoloration) on measured surface area of the disorder as determined by a planimeter.

The second plantings of 2001 and 2002 were warmer (20.7 °C with 18 d above 28 °C and 21.8 °C with 19 d above 28 °C, respectively) and dryer (68 mm cumulative rainfall in both years) than the first plantings, and the heads matured earlier, within 42 to 44 d. In the second planting of 2001, the susceptible parent had 93% of plants with rib discoloration, and the resistant parent, 8% (Table 2). The strongest heat pressure occurred during the second planting in 2002, with the average temperature 1.1 °C warmer than in the second planting of 2001. The susceptible parent had 99% of plants with rib discoloration, and the resistant parent had 62%.

With the exception of the reciprocal F₂ in Planting 1 of 2002, the F₂ populations were distinctly intermediate between the two parents (Table 2). In all cases, there were no significant differences in rib discoloration incidences between the reciprocal cross populations, indicating no maternally inherited effect.

Chi-square fit tests for the observed ratio versus the expected 3:1 ratio were inconsistent among the four plantings (Table 3). The observed ratio fitted the expected 3:1 ratio in Planting 1 of 2001 and Planting 2 of 2002. Under the extreme hot weather conditions in Planting 2 of 2002, all plants, even the resistant parent showed a high incidence of rib discoloration (62%), making any conclusion regarding F₂ progeny unreliable. However, in Planting 2 of 2001 and Planting 1 of 2002, the resistant parent had the lowest incidence of rib discoloration (8% to 17%), making these two plantings more reliable to draw conclusions. In these two plantings, F₂ segregations deviated significantly from the 3 susceptible:1 resistant ratio ($P < 0.0001$) with any of the two scales, a finding that rejects a monogenic model.

Overall, the growing conditions experienced during 2001 and 2002 promoted the development of clear rib discoloration symptoms. The average rib discoloration ratings for all plantings were 4.3 for the resistant parent, 1.7 for the susceptible parent, and 3.0 and 3.2 for the two reciprocal F₂ populations. Values for F₂ plants were significantly different and intermediate between the two parents (Table 2).

Significant interactions for the combined-year analysis and for treatment × planting in 2001 were observed for rib discoloration ratings (Table 2). These interactions could be explained by differences in environmental conditions suitable for expression of rib discoloration in the different plantings (as described above). With the exception of Planting 1 of 2002, ‘Emperor’ had a shorter stem at maturity than ‘Eldorado’,

Table 2. Mean percentage of plants showing resistance to rib discoloration, rib discoloration severity index, and maturity parameters of crisphead lettuce for single planting, average of both plantings for 2001 and 2002.

			Plants with resistance to rib discoloration (%)	Rib discoloration index (1–5 scale) ^z	Stem length (mm)	Head wt (g)	Head density (g·cm ⁻³)
Year	Planting	Treatment					
2001	1	Eldorado	3.0 c ^y	1.6 c	—	769 a	—
		Eldorado × Emperor	23.0 b	2.5 b	—	759 a	—
		Emperor × Eldorado	25.5 b	2.7 b	—	730 a	—
		Emperor	81.4 a	4.4 a	—	587 b	—
2001	2	Eldorado	7.5 c	1.7 c	—	583 a	—
		Eldorado × Emperor	48.8 b	3.5 b	—	508 b	—
		Emperor × Eldorado	51.6 b	3.5 b	—	528 b	—
		Emperor	92.0 a	4.8 a	—	508 b	—
2002	1	Eldorado	8.1 c	—	65.8 b	—	—
		Eldorado × Emperor	55.1 b	—	83.1 a	—	—
		Emperor × Eldorado	68.5 ab	—	78.6 a	—	—
		Emperor	82.6 a	—	57.3 b	—	—
2002	2	Eldorado	1.0 c	—	133.5 a	—	—
		Eldorado × Emperor	20.6 b	—	110.2 b	—	—
		Emperor × Eldorado	17.5 b	—	121.1 ab	—	—
		Emperor	38.2 a	—	66.9 c	—	—
2001	Both	Eldorado	—	—	73.7 a	—	0.52 a
		Eldorado × Emperor	—	—	60.1 b	—	0.46 b
		Emperor × Eldorado	—	—	65.5 ab	—	0.46 b
		Emperor	—	—	41.9 c	—	0.45 b
2002	Both	Eldorado	—	1.8 c	—	758 a	0.49 a
		Eldorado × Emperor	—	3.0 b	—	748 a	0.41 b
		Emperor × Eldorado	—	3.2 b	—	737 a	0.43 b
		Emperor	—	3.9 a	—	700 a	0.49 a
Significance							
2001	1	Block (B)	NS	NS	*	*	*
		Treatment (T)	****	****	****	**	**
2001	2	B	**	*	**	****	**
		T	****	****	***	*	**
2002	1	B	NS	NS	NS	NS	NS
		T	****	****	**	NS	*
2002	2	B	NS	*	*	NS	**
		T	**	****	****	*	****
2001	Both	Planting (P)	**	**	NS	*	NS
		B(P)	**	*	***	****	***
		T	**	*	*	NS	**
		T × P	**	***	NS	**	NS
2002	Both	P	***	***	***	***	**
		B(P)	NS	*	**	NS	*
		T	NS	**	NS	NS	*
		T × P	***	NS	****	NS	NS
Both	Both	Year (Y)	NS	NS	NS	NS	NS
		P(Y)	****	****	***	**	**
		B(P × Y)	*	**	****	****	***
		T	*	*	*	NS	NS
		T × Y	NS	NS	NS	NS	*
		T × P(Y)	****	***	****	*	NS

^z1 = severe rib discoloration; 3 = moderate rib discoloration, head still marketable; 5 = no rib discoloration.

^yMeans followed by same letter are not significantly different at $P = 0.05$ using Duncan's multiple range test.

NS, *, **, ***, **** Nonsignificant, or significant at $P < 0.05$, 0.01, 0.001, or 0.0001, respectively.

which tended to bolt rapidly under our warm and long-day conditions. Under intense heat stress (Planting 2 of 2002), the stem length of 'Eldorado' was more than twice that of 'Emperor' (Table 2). The head shape of 'Emperor', typical of the 'Empire' type, was narrower than 'Eldorado' and the F_2

progenies, which had the typical round shape of the 'Salinas' type.

Commercial maturity in crisphead lettuce is a function of head size and density, and, in long photoperiods, stem length. Lettuce is a quantitative long-day plant that tends to bolt with

Table 3. Goodness-of-fit test for single locus segregation of rib discoloration resistance in two reciprocal crisphead lettuce F₂ populations.

Treatment	Susceptible (1–2.9 scale) ^y	Resistant (3–5 scale) ^y	Chi-square <i>P</i> value ^z 3:1
2001 Planting 1			
Eldorado × Emperor	77.0	23.0	0.644
Emperor × Eldorado	74.5	25.5	0.908
Combined	75.8	24.3	0.862
2001 Planting 2			
Eldorado × Emperor	51.2	48.8	<0.0001
Emperor × Eldorado	48.4	51.6	<0.0001
Combined	49.8	50.2	<0.0001
2002 Planting 1			
Eldorado × Emperor	44.9	55.1	<0.0001
Emperor × Eldorado	31.5	68.5	<0.0001
Combined	38.0	62.0	<0.0001
2002 Planting 2			
Eldorado × Emperor	79.4	20.6	0.312
Emperor × Eldorado	82.5	17.5	0.083
Combined	81.2	18.8	0.154

^z*P* > 0.05; observed ratios are not significantly different from expected ratios (cells with borders).

^yPercentage of susceptible or resistant plants according to the following scale: 1 = severe rib discoloration; 3 = moderate rib discoloration, head still marketable; 5 = no rib discoloration.

photoperiods longer than 13 h (Wien, 1997). In this experiment, the photoperiod, ranging from 16.5 h (10 June) to 15.3 h (8 Aug.), was conducive to the induction of flowering. In the parents and F₂ progenies, head density increased with smaller

head height (*P* < 0.0001) and diameter (*P* < 0.0001) (Table 4). In bolting-resistant ‘Emperor’, head density increased with greater stem length (*P* < 0.01), whereas in bolting-susceptible ‘Eldorado’ and F₂ progenies, head density decreased with greater stem length (*P* < 0.0001), producing large and commercially undesirable fluffy heads.

In both parents and F₂ progenies, the rib discoloration index was negatively correlated (*P* < 0.0001) with head diameter, head height, head weight, and stem length (Table 4). Therefore, rib discoloration severity was strongly associated with traits characterizing an advanced maturity.

More severe rib discoloration symptoms were associated with denser heads in the resistant parent. In contrast, rib discoloration severity was unaffected by head density in the susceptible parent, as the high expression of the disorder was independent of head density. Therefore, head density does not necessarily influence the expression of rib discoloration.

Broad-sense heritability was significant for rib discoloration severity, stem length, head height, head diameter, and head weight, but not for head density (Table 5). The highly significant (*P* < 0.0001) combined-year broad-sense heritability of 0.57 for rib discoloration severity suggests that single-plant selection is an appropriate method for developing new resistant cultivars.

The inheritance of characters can range from control by one major gene whose expression is not influenced by the environment (qualitative character) to control by many genes whose expression is influenced by the environment (quantitative characters). The results of this study suggest that rib discoloration resistance is controlled by a few major genes with relatively high heritability. Further studies involving data beyond the F₂ generation and quantitative trait locus analysis

Table 4. Phenotypic correlations among six traits measured on 800 individual crisphead lettuce heads of the parents and reciprocal F₂ populations. Correlations are for combined data from two planting dates in 2001 and 2002.

Treatment	Trait	Density (g·cm ⁻³)	Diam (cm)	Ht (cm)	Rib discoloration ^z (1–5 scale)	Stem length (mm)
Eldorado	Diameter	–0.66 ****				
Eldorado × Emperor	Diameter	–0.45 ****				
Emperor × Eldorado	Diameter	–0.52 ****				
Emperor	Diameter	–0.27 ****				
Eldorado	Height	–0.39 ****	0.47 ****			
Eldorado × Emperor	Height	–0.48 ****	0.52 ****			
Emperor × Eldorado	Height	–0.57 ****	0.51 ****			
Emperor	Height	–0.39 ****	0.35 ****			
Eldorado	Rib discoloration	–0.06 NS	–0.23 ****	–0.16 ****		
Eldorado × Emperor	Rib discoloration	–0.09 *	–0.31 ****	–0.25 ****		
Emperor × Eldorado	Rib discoloration	0.04 NS	–0.29 ****	–0.25 ****		
Emperor	Rib discoloration	–0.15 ****	–0.33 ****	–0.09 **		
Eldorado	Stem length	–0.28 ****	0.57 ****	0.46 ****	–0.39 ****	
Eldorado × Emperor	Stem length	–0.32 ****	0.48 ****	0.55 ****	–0.26 ****	
Emperor × Eldorado	Stem length	–0.42 ****	0.50 ****	0.59 ****	–0.26 ****	
Emperor	Stem length	0.10 **	0.40 ****	0.27 ****	–0.45 ****	
Eldorado	Head weight	–0.06 NS	0.65 ****	0.73 ****	–0.33 ****	0.56 ****
Eldorado × Emperor	Head weight	0.06 NS	0.73 ****	0.64 ****	–0.44 ****	0.44 ****
Emperor × Eldorado	Head weight	–0.05 NS	0.72 ****	0.64 ****	–0.38 ****	0.44 ****
Emperor	Head weight	0.28 ****	0.69 ****	0.55 ****	–0.40 ****	0.51 ****

^z1 = severe rib discoloration; 3 = moderate rib discoloration, head still marketable; 5 = no rib discoloration.

NS, *, **, ***, ****Nonsignificant or significant at *P* < 0.05, 0.01, 0.001 or 0.0001, respectively.

Table 5. Broad-sense heritability of crisphead lettuce traits and rib discoloration ratings.

Year	Planting	Density (g·cm ⁻³)	Diam (cm)	Ht (cm)	Rib discoloration ^z (1–5 scale)	Stem length (mm)	Wt (g)
2001	1	0.04 NS	0.25 **	0.38 ****	0.59 ****	0.71 ****	0.36 ****
2001	2	0.02 NS	0.29 ***	0.44 ****	0.62 ****	0.77 ****	0.19 *
2001	Both	0.03 NS	0.27 ****	0.41 ****	0.61 ****	0.74 ****	0.31 ****
2002	1	–0.09 NS	0.41 ****	0.26 **	0.58 ****	0.81 ****	0.27 **
2002	2	0.03 NS	0.19 *	0.63 ****	0.48 ****	0.68 ****	0.24 **
2002	Both	–0.02 NS	0.26 ****	0.48 ****	0.53 ****	0.71 ****	0.26 ****
Both	Both	0.01 NS	0.26 ****	0.45 ****	0.57 ****	0.71 ****	0.28 ****

^z1 = severe rib discoloration; 3 = moderate rib discoloration, head still marketable; 5 = no rib discoloration.

NS, *, **, ***, **** Nonsignificant, or significant at $P < 0.05, 0.01, 0.001$ or 0.0001 , respectively.

will be necessary to develop a firm genetic basis. Because there were no significant differences between the reciprocal cross populations, resistance to rib discoloration is not influenced by maternally inherited factors, and one-way cross pollinations could be planned in future studies.

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