Yield Losses to Iceberg Lettuce Due to Corky Root Caused by *Rhizomonas suberifaciens*

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ABSTRACT

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Plant growth and yield variables of closely related resistant and susceptible lettuce cultivars (440-8 and Salinas, respectively) were compared in microplots at Davis, CA, in soil infested with *Rhizomonas suberifaciens*, the causal agent of corky root of lettuce. To validate the results for large scale lettuce production, the same variables were compared for 440-8 and Salinas in fumigated soil and soil naturally infested with *R. suberifaciens* at Salinas, CA. Most plant growth variables for 440-8 in infested microplots were not significantly different from those for 440-8 or Salinas in uninfested microplots. The most important effect of corky root on Salinas lettuce was to reduce fresh weights of shoots and marketable yield. Reductions in shoot dry weight and plant area were less significant. Marketable yield losses ranged from 34 to 92%, depending on season and location, with the highest yield loss in the warmest growing season. Significant yield reductions did not occur until 20–30 days after the appearance of the first symptoms. Taproots affected by corky root were wider, had a lower moisture content, and higher dry weight. A linear regression model predicted shoot fresh weight based on the amount of disease at the nine-leaf stage in microplots. Data from the large scale field experiment did not fit to the same model, but final yield loss fell within the range of losses obtained in microplots.

Corky root of lettuce (*Lactuca sativa* L.), caused by *Rhizomonas suberifaciens* (23), is a common disease in coastal areas of California (15,22) and in other parts of North America (20). The bacterium causes greenish-brown and corky areas on taproots and main lateral roots of susceptible cultivars. Plants may wilt, become stunted, and produce small heads (22). Partial disease control may be obtained with soil fumigation (13) and cultural practices (16,19,21). Cultivars with resistance based on a single gene (2) were developed in Wisconsin (18) and Florida (6), but these cultivars are not adapted to conditions in California. Resistance to corky root is currently being incorporated into Californian lettuce cultivars (E. Ryder, *personal communication*).

R. suberifaciens has only recently been identified as the causal agent of corky root (22,23). Therefore, the epidemiology of the disease and its impact on the crop are poorly understood. However, there is evidence that corky root can significantly impair lettuce growth (22). In heavily infested soils in Florida, susceptible cultivars did poorly, whereas resistant cultivars yielded well (6). In microplot experiments in California, lettuce marketable yield, shoot weight, and root length were decreased by corky root (22). However, no quantitative estimates of crop losses have been made in field experiments with infested and uninfested plots using resistant and susceptible cultivars.

The objective of this study was to determine the effects of corky root on lettuce growth and yield by comparing closely related resistant and susceptible cultivars in the presence and absence of *R. suberifaciens*. Microplot experiments were conducted to determine the cumulative effect of disease on a variety of plant growth indices. The agronomic importance of *R. suberifaciens* was estimated in a large scale field experiment. A preliminary report has been published (11).

MATERIALS AND METHODS

Microplot experiments. In 1- × 2-m microplots (22) at Davis, CA, lettuce growth and disease incidence and severity were determined for susceptible and resistant lettuce cultivars with and without *R. suberifaciens* in fall and spring growing seasons. Approximately 10 wk before planting, the soil was treated with 500 kg/ha of methyl bromide + chloropicrin (53:47%, v/v ratio, liquid mixture under pressure) to reduce populations of *R. suberifaciens*, possibly remaining from previous experiments. Seeds of iceberg lettuce Salinas (corky root susceptible) and an F5 pedigree breeding line of Salinas and Green Lake, 440-8 (corky root resistant; E. Ryder, *personal communication*) were planted in 20 plots each. Each plot contained 14 plants in two rows on 60-cm-wide beds. Immediately after planting, 10 plots of each cultivar were sprinkled with 2 L of a four-day-old culture of *R. suberifaciens*, strain CA1 (22), grown in S broth (22) at a concentration of 5×10^8 cfu/m^2. Bacterial concentration was confirmed by dilution plating on solid S medium. The other 10 plots of each cultivar received 2 L of sterile water as a control. Standard fertilization, irrigation, and pest control methods were used (22).

Each experiment was arranged in a completely randomized design with five replications of two cultivars in infested and uninfested plots. Two adjacent microplots with the same treatment made up one experimental unit. The experiment was done four times, in the spring of 1989 and 1990 and in the fall of 1988 and 1989. Average soil temperatures, 15 cm deep under bare soil, were obtained from a weather station about 3 km away.

Five plants per replication were uprooted weekly starting 15 or 30 days after planting in the fall and spring, respectively. The microplots were sampled 10 times in each experiment. Each sampling date was combined with plant thinning to use the space efficiently while minimizing unwanted plant competition effects. The final distance between plants was 30 cm.

At each sampling date, several plant and disease variables were measured. An estimate of plant photosynthetic potential was made by determining the soil surface area occupied by leaves when viewed from above (referred to as projected plant area). Projected plant area was used instead of total leaf area because many of the leaves in lettuce heads do not contribute to photosynthetic carbon assimilation. Photographs were taken with a calibrated grid placed directly above each plant (8) and used to estimate total plant area. Phenological growth stage was recorded by comparison with a pictorial key of 14 phenological stages (14)

based on the number of true leaves per plant (stages 1–8), rosette formation (stages 9–10), and firmness of the head (stages 11–14). Plants were removed from the soil to a depth of 20 cm, and corky root severity was recorded using a 1–12 Horsfall-Barratt scale (9,12,14) based on percentage area of the taproot showing corkiness (1 = 0%, 2 = 0–3%, 3 = 3–6%, 4 = 6–12%, 5 = 12–25%, 6 = 25–50%, 7 = 50–75%, 8 = 75–87%, 9 = 87–94%, 10 = 94–97%, 11 = 97–100%, 12 = 100%). Roots were excised, washed, and blotted dry. Shoots and roots were weighed separately. Taproot diameters were measured approximately 2 cm below the soil line. Dry weights were obtained after tissue was dried for 96 h at 80 C.

At the last two sampling dates (plant maturity), the same plant measurements were made plus four additional measurements for the lettuce heads. The above ground portion of the plant was separated into trimmed head (marketable portion) and 'wrapper' (nonmarketable portion). The percentages of heads in each microplot that met commercial market standards were determined by head weight and density using an apparatus similar to that developed by Garrett et al (4). Trimmed lettuce heads, placed in plastic bags, were put in a bucket of water that rested on a scale. The head was submerged to obtain the buoyant force. Head weight was subtracted from buoyant force to give head volume. Head weight divided by volume resulted in density. Base-

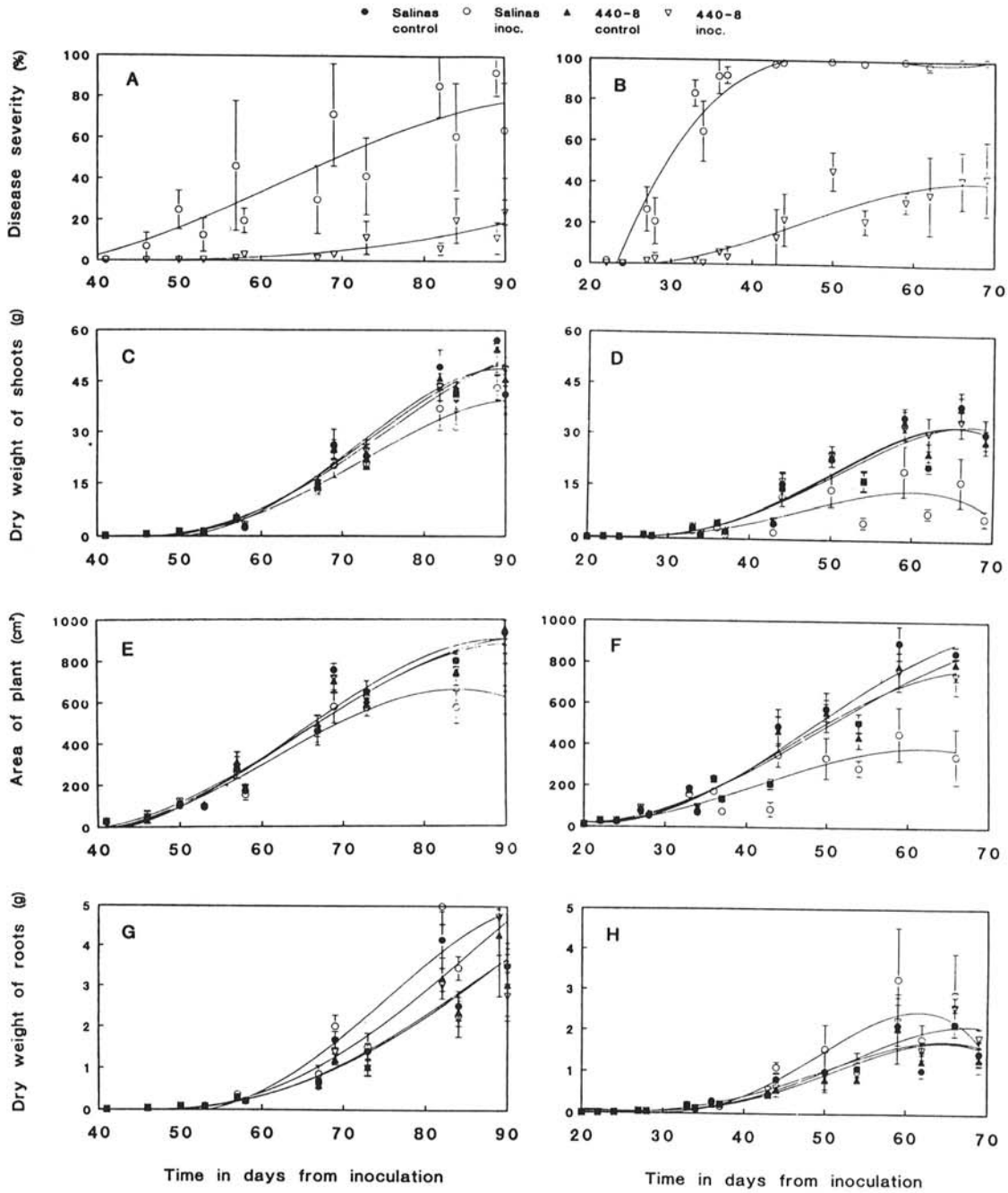

Fig. 1. Increase in corky root severity, shoot dry weight, projected plant area, and root dry weight of lettuce cultivars Salinas and 440-8 after inoculation with *Rhizomonas suberifaciens* in microplots at Davis, CA, in the spring of 1989 and 1990 and in the fall of 1988 and 1989 (data for 2 yr combined). **A** and **B,** corky root severity (percentage of taproot area diseased) in the spring and fall, respectively; **C** and **D,** shoot dry weight (g) in the spring and fall, respectively; **E** and **F,** projected plant area (cm^2) in the spring and fall, respectively; and **G** and **H,** root dry weight (g) in the spring and fall, respectively. Symbols are means of five replications, bars are standard deviations, and curves are regression lines for polynomial models with three (A,B,E,F) or four (C,D,G,H) parameter estimates.

line marketable head values were chosen after measuring 28 heads collected just before harvest from a farmer's field in the Salinas Valley of California. Eighty percent of these heads had densities greater than 0.43 g/cm^3. The smallest head in a survey at a local supermarket weighed 200 g. Thus, heads weighing greater than 200 g with densities greater than 0.43 g/cm^3 were considered marketable. These standards were similar to those reported previously (4,6).

Yield loss due to corky root was estimated by: 1 − [yield of Salinas from infested plots divided by the yield of 440-8 from infested plots]. Yield of 440-8 from infested plots was used instead of Salinas in uninfested plots, because the microplot experiments showed that corky root did not affect above ground yield in the resistant cultivar, and 440-8 and Salinas yielded the same in the absence of corky root. Losses in fresh and dry shoot weight were calculated in a similar manner.

Large scale field experiment. To observe the effects of corky root under conditions of commercial lettuce production, an experiment was conducted at the USDA experiment station in Salinas in the summer of 1989. The soil was Chualar loam naturally infested with *R. suberifaciens* (21). The field had been planted to lettuce in each of the previous 2 yr, and *R. suberifaciens* had been isolated from diseased roots (21).

The field was prepared for planting and fumigation using standard methods (13). Half of the plots were fumigated with methyl bromide + chloropicrin (57:43%, v/v, liquid mixture under pressure) to control corky root. The fumigant was injected under 0.15 mm thick clear plastic tarp and 20 cm into the soil at a rate of 400 kg/ha by a commercial applicator 22 days before the projected planting date. The tarp was removed 10 days before planting to allow the fumigant to escape. The other half of the plots were left nonfumigated. The soil in each plot was shaped into four 1- × 24-m beds. Each plot was separated from other plots by 1-m-wide paths.

Four treatments were arranged in a randomized complete block design with three replications. Fumigated and nonfumigated soil was planted with Salinas or 440-8 lettuce. On each bed, lettuce was planted in two rows, 50 cm apart, thinned 43 days later to a spacing of 30 cm between plants, and harvested 74 days after planting. Standard methods were used for fertilization, pest control, and sprinkler irrigation (13). Average soil temperatures, 15 cm deep under bare soil, were obtained from a weather station less than 1 km away.

At harvest, 20 plants in each replicate plot were collected from one of the two center beds starting 2 m into each plot to avoid edge effects. Fresh and dry shoot weights, fresh trimmed head weights, fresh wrapper weights, fresh and dry root weights, and disease severity scores were obtained. Data on shoot and root dry weights and percentage of moisture were not obtained for 440-8. Marketable yield was determined from five heads per plot using the density and weight standards described above. Losses in yield and shoot weight due to corky root were estimated as described for the microplot experiments, namely, yield loss = 1 − [yield of Salinas in untreated plots divided by the yield of 440-8 in untreated plots].

Statistical analysis. Statistical computations were made using software from Statistical Analysis Systems (release 6.03, SAS Institute Inc., Cary, NC). The general linear models procedure was used to test polynomial models of lettuce growth and disease severity over time for the experiments at Davis. Regression equations were obtained using the regression procedure for each individual plot. Parameter estimates of these equations were used in multivariate analyses of variance to compare the treatments. Plant growth over time was tested for effects of cultivar and infestation with *R. suberifaciens*, and disease progress for cultivar effect only (because contamination of uninfested plots was negligible). At harvest, disease severities, plant growth indices, and yield loss of the different treatments were compared by analysis of variance for all experiments.

Shoot fresh weights at harvest were regressed on percentage of the taproot area with corky root at the nine-leaf stage. High correlation between yield loss and corky root severity had been observed at this stage (12,14). Linear and quadratic polynomial regressions were compared. Parameter estimates of linear equations for individual years, seasons, and cultivars were subjected to multivariate analysis of variance.

RESULTS

Seasonal effects. Shoot and root growth curves (dry weights) were best represented by four parameter models, whereas plant area growth curves and disease progress curves were adequately represented by three parameter polynomial models (Fig. 1). Multivariate analysis of variance of the parameter estimates indicated that season (spring or fall) had the largest effect on these parameter estimates and thus on the location and shape of the curves (Table

TABLE 1. Multivariate analysis of variance of parameter estimates from polynomial models with three[a] or four[b] parameters for the increase of lettuce shoot and root weight (g), projected plant area[c] (cm^2), and corky root disease severity (%) over time in microplots at Davis, CA

	Dry weight							
	Shoots		Roots		Plant area		Disease severity	
Source	Value[d]	F[e]	Value	F	Value	F	Value	F
Year	12.11	78.70***	2.18	13.98***	18.28	150.84***	0.44	3.88
Season[f]	28.19	372.08***	7.25	94.27***	43.68	731.58***	60.97	503.09***
Cultivar[g]	1.01	13.38***	0.21	2.72*	0.56	9.38***	43.01	354.83***
Infestation[h]	1.43	18.91***	0.25	3.25*	0.71	11.87***	...	...
Season × cultivar	0.74	9.81***	0.52	6.76***	0.48	8.05***	39.15	322.96***
Season × infestation	0.91	11.98***	0.15	1.93	0.59	9.92***	...	...
Cultivar × infestation	1.00	13.16***	0.14	1.86	0.85	14.29***	...	...
Season × cultivar × infestation	0.58	9.58***	0.19	2.45*	0.91	15.23***	...	...

[a] Plant area and disease severity.
[b] Shoot and root dry weight.
[c] Estimated from photographs of a calibrated grid placed directly above each plant.
[d] Hotteling-Lawley test criterion for multivariate analysis of variance.
[e] Significance level of F test. *** $P = 0.001$, * $P = 0.05$.
[f] Spring and fall.
[g] Salinas and 440-8.
[h] Soil infestation with either *Rhizomonas suberifaciens* or sterile water.

1). Growth rates of roots, shoots, and plant area were higher in the fall seasons, but the final values of these variables were smaller in the fall than in the spring (Fig. 1). Disease severity increased faster and reached higher levels for both cultivars in the fall.

Corky root symptoms on Salinas first appeared approximately 20, 27, and 40 days after planting in fall at Davis, summer at Salinas, and spring at Davis, respectively (data not shown). Average soil temperatures were highest in the fall at Davis (23 C), moderate in the summer at Salinas (21 C), and lowest in the spring at Davis (15 C). Plants matured at approximately 90, 74, and 70 days after planting in the spring, summer, and fall, respectively.

Disease severity. In microplots infested with corky root, parameter estimates of cubic models for disease progress were significantly different for the two cultivars ($P = 0.001$), and differed also between seasons ($P = 0.001$) (Table 1 and Fig. 1). Corky root lesions appeared 5–10 days earlier on Salinas compared to 440-8, and the infected area on taproots of Salinas increased more rapidly (Fig. 1A,B) and reached a higher level at harvest (Table 2). Uninfested control plots remained almost completely free of disease (incidence <1%). At Salinas, fumigation with methyl bromide + chloropicrin resulted in lower ($P = 0.001$) disease severities for both lettuce cultivars (Table 2). Disease severity was also significantly lower on 440-8 than on Salinas ($P = 0.001$).

Shoots. The rates of increase in dry shoot weight and projected plant area of Salinas over time were significantly reduced by soil infestation with *R. suberifaciens* in microplots, whereas those of 440-8 were not affected by soil infestation (Fig. 1). Initially, dry shoot weights and plant areas were similar for all treatments, but approximately 40 and 70 days after planting in fall and spring, respectively, the values of these variables were significantly lower for Salinas in infested plots (Fig. 1C,D,E,F). Phenologically, these dates corresponded to the beginning of heading. Dry shoot weights at maturity were 59 and 22% less for Salinas in infested microplots than for the average of the other treatments in fall and spring, respectively (Table 2). Final plant areas of Salinas were approximately 55 and 29% smaller than for the other treatments in fall and spring, respectively (data not shown). Shoot fresh weight of Salinas at plant maturity were 76 and 33% less in infested microplots than the average of the other treatments in fall and spring, respectively (Table 2). Shoot moisture content of Salinas was reduced by 1–3% (data not shown). Trimmed head volume and density differed significantly ($P = 0.001$ for both volume and density) for Salinas and 440-8 in uninfested plots at the last two harvest dates (Table 2). Heads of Salinas had 18 and 19% higher volume and 18 and 20% lower density in fall and spring, respectively, than those of 440-8. No density or volume estimates were made for Salinas in infested microplots and for all of the treatments at Salinas, because most of the heads were too small (<200 g) to use the buoyant force apparatus. For the heads that were large enough, head density of diseased plants did not appear to be strongly affected by corky root (data not shown).

Regression of shoot fresh weight of mature plants on percentage of corky root severity at the nine-leaf stage was linear for each season at Davis (Fig. 2A). The intercepts and slopes were not significantly different for the spring and fall seasons ($P = 0.16$) and years ($P = 0.22$). The regression equation for cultivar Salinas in both seasons in the first year was fresh weight = 980 − 9.8 × corky root severity (R^2 = 73%) (Fig. 2A). This model was validated with data from the second year, and 80% of the data points were located within the 99% confidence limits.

In the experiment at Salinas, dry shoot weights of Salinas at

TABLE 2. Effect of lettuce cultivar and *Rhizomonas suberifaciens* on selected variables measured at harvest of mature plants in microplots at Davis, CA (2 yr combined), and at the USDA experiment station at Salinas, CA (1 yr only)[a]

Location and season	Lettuce cultivar	Infestation	Shoots: Disease Severity[b] (%)	Shoots: Fresh wt (g)	Shoots: Dry wt (g)	Marketable yield[c] (%)	Head wt (g)	Wrapper wt[d] (g)	Volume[e] (cm^3)	Density (g/cm^3)	Roots: wt (g)	Roots: Fresh wt (g)	Roots: Dry Diameter[f] (mm)
Davis, fall	Salinas	+[g]	99.5[h]	173	12.5	8	94	79	...[i]	...	14.6	2.26	25.3
	Salinas	−	0.4	744	30.5	90	431	249	797	0.70	18.9	1.70	21.2
	440-8	+	37.9	710	32.7	97	434	230	655	0.85	18.9	2.04	18.8
	440-8	−	0.8	721	28.8	96	437	243	656	0.85	17.9	1.70	16.8
	$LSD_{0.05}$		10.1	86	3.9	10	63	42	117	0.13	3.5	0.52	2.8
Davis, spring	Salinas	+	75.6	643	37.3	65	324	319	...	...	32.9	4.54	23.5
	Salinas	−	2.1	983	48.2	94	558	426	892	0.66	33.5	4.03	21.1
	440-8	+	17.2	936	47.7	98	567	368	756	0.86	28.4	3.18	20.6
	440-8	−	0.0	976	47.8	96	578	399	726	0.82	28.2	3.22	18.8
	$LSD_{0.05}$		14.3	129	5.4	13	105	64	135	0.12	4.5	0.74	2.8
Salinas, summer	Salinas	+	91.4	396	28.9	13	153	223	...	...	23.8	3.83	...
	Salinas	−	40.1	842	50.5	67	378	440	...	...	29.1	5.11	...
	440-8	+	17.4	504	...	60	296	280	...	...	16.8	...	...
	440-8	−	4.7	789	...	67	464	375	...	...	23.1	...	...
	$LSD_{0.05}$		12.3	263	15.1	31	93	56	...	...	2.8	1.15	...

[a] Experiments at Davis were performed in 1- × 2-m microplots. Means are from five replicates of two pooled harvests of five plants per harvest per treatment. Experiments at Salinas were performed in 4- × 24-m plots. Means are from three replicates of a single harvest of 20 plants per treatment.

[b] Expressed as percentage of the taproot surface area showing corkiness.

[c] Marketable yield was the percentage of heads > 200 g with a density > 0.43 g/cm^3 in each plot.

[d] The wrapper consisted of the outside leaves and stem normally removed during harvest.

[e] Volume and density were calculated from head weight and buoyant force.

[f] Diameter of taproot, 2 cm below the soil line.

[g] Infestation at Davis was obtained by sprinkling the surface of the microplots with 5×10^8 cfu/m^2 of *Rhizomonas suberifaciens* (+) or sterile water (−). At Salinas, naturally occuring populations provided infestation (+), or bacteria were partially controlled by soil fumigation with methyl bromide + chloropicrin (−).

[h] All cultivar × infestation interactions were significant at $P = 0.01$ except for shoot fresh weight and root dry weight at Salinas. Cultivar effects were significant at $P = 0.01$ for head volumes and densities, root fresh and dry weights (spring only) and root diameter at Davis, and head weight and root fresh weight at Salinas. Infestation effects were significant for all growth parameters ($P = 0.01$) except for root dry weight at Davis in the spring.

[i] Heads were too small (< 200 g) for the buoyant force apparatus to measure head density and volume.

maturity were 43% less in nonfumigated plots than in fumigated plots ($P = 0.001$; Table 2). Fresh shoot weights of both cultivars were lower in nonfumigated plots than in fumigated plots ($P = 0.001$). The difference between fumigated and nonfumigated plots was larger for Salinas than 440-8, but there was no significant interaction ($P = 0.15$).

Regression of fresh shoot weights of mature plants on corky root severity at the nine-leaf stage at Salinas resulted again in a significant ($P = 0.001$) linear relationship (Fig. 2B). Disease severity was relatively low at the nine-leaf stage, similar to that in the spring at Davis. The intercept for the regression equation for the experiment at Salinas was not significantly different from that at Davis, but the slope was significantly more negative, so that a different model was required for Salinas. The model was fresh weight = 889 − 35.8 × corky root severity ($R^2 = 80\%$). This model could not be validated because the experiment was conducted in 1 yr only.

Roots. There was a significant interaction between cultivar, soil infestation, and season with respect to their effect on dry root weights measured over time when fitted to a four-parameter model (Table 1). In the spring, dry root weights continued to increase throughout the season, whereas in the fall, dry root weights reached a maximum value approximately 65 days after inoculation and either declined (Salinas in infested plots) or remained the same (the other three treatments) (Fig. 1G,H). In both seasons, root weights of Salinas in infested soil seemed to increase more rapidly than those of the other treatments (Fig. 1G,H), but there was no significant interaction between cultivar and infestation (Table 1).

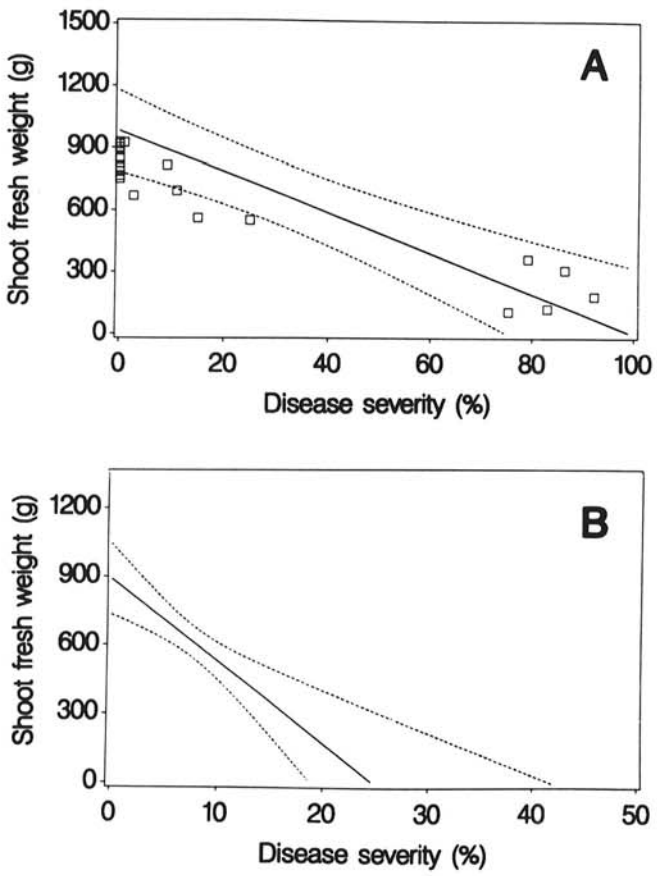

Fig. 2. Critical point models and 99% confidence limits for the linear regression of head fresh weight (g) on corky root severity (percentage of taproot area diseased) at the nine-leaf stage of Salinas lettuce at **A,** Davis and **B,** Salinas, CA. Solid lines represent regression lines and dashed lines 99% confidence limits for data obtained in the first year. Symbols stand for the mean fresh weights per plot in the second year. The regression equations are: A, fresh weight = 980 − 9.8 × corky root severity, $R^2 = 73\%$; B, fresh weight = 889 − 35.8 × corky root severity, $R^2 = 80\%$.

At final harvest, soil infestation with *R. suberifaciens* resulted in higher root dry weights for both cultivars in the fall at Davis but not in the spring (Table 2). Root fresh weight and percentage of moisture in the fall, and percentage of moisture in the spring were significantly lower ($P = 0.01$) for Salinas in infested microplots than for the other treatments. Taproot diameters 2 cm below the soil line were larger for Salinas than for 440-8. In addition, taproots from infested plots were wider than those from uninfested plots.

At Salinas, root dry weights were slightly higher for Salinas in fumigated soil than in nonfumigated soil ($P = 0.07$). Root fresh weights were higher for Salinas than for 440-8 and higher in fumigated than in nonfumigated plots ($P = 0.05$).

Yield loss. For most plant variables measured at harvest, the resistant lettuce cultivar 440-8 grown in infested microplots was not significantly different from the susceptible cultivar Salinas grown in uninfested microplots (Table 2). Thus, yield loss was expressed as a percentage of the yield of 440-8 in infested plots. Reductions in plant growth and yield varied with the variable measured. Marketable yield was reduced most (34–92%), followed by shoot fresh weight (21–76%), and shoot dry weight (21–60%). Marketable yield losses were highest in the fall at Davis, intermediate at Salinas, and lowest in the spring at Davis ($P = 0.001$, effect of season).

DISCUSSION

The most important effect of corky root on lettuce was to reduce fresh weights of shoots and marketable yield. Reductions in shoot dry weight and projected plant area were less important. Significant growth responses to corky root did not occur until 20–30 days after the appearance of the first symptoms, which is relatively late in the development of a lettuce crop. In both spring and fall seasons, reductions in growth began at phenological stage 11, which corresponds to the beginning of head formation. At this stage, water uptake may be crucial for proper growth.

Roots affected by corky root were quite different from healthy roots. In general, infected taproots were wider and had lower moisture contents and higher dry weights. These results confirm earlier observations of denser, heavier taproots associated with corky root infection (22). Although the physiology of the disease process is not yet known, corky root infection may be associated with a hormonal imbalance, possibly resulting in hypertrophy, hyperplasia, and impaired water uptake.

The use of closely related susceptible and resistant cultivars allows for estimation of yield loss due to a disease in naturally

TABLE 3. Yield loss to susceptible lettuce cultivar Salinas caused by corky root of lettuce in microplot and field experiments[a]

Location	Yield loss (%)[b]		
	Marketable yield[c]	Shoot weight	
		Fresh	Dry
Davis, fall 1988 and 1989	91.8[d]	75.6[d]	60.0[d]
Davis, spring 1989 and 1990	33.7	31.3	20.6
Salinas, summer 1989	78.3	21.4	...[e]

[a] Experiments at Davis, CA, were performed in 1- × 2-m microplots. Means are from five replicates of two pooled harvests of five plants per harvest per treatment. Experiments at Salinas, CA, were performed in 4- × 24-m plots. Means are from three replicates of a single harvest of 20 plants per treatment. Treatments were susceptible (Salinas) and resistant (440-8) lettuce cultivars grown in plots infested with *Rhizomonas suberifaciens*.

[b] Yield loss $= \left[1 - \frac{\text{(Salinas in infested plots)}}{\text{(440-8 in infested plots)}}\right] \times 100\%$

[c] Percentage of trimmed heads in each plot > 200 g with a density > 0.43 g/cm^2.

[d] Effect of season significant at $P = 0.001$.

[e] Dry shoot weights were not obtained for 440-8 at Salinas.

infested soil (10). Microplot experiments showed that yields of the two lettuce cultivars employed in this study were not significantly different in the absence of disease, and that the resistant cultivar yielded the same both with and without disease. Thus, for the calculation of percentage of yield loss, yield from 440-8 grown in infested soil could be substituted for yield from Salinas grown in uninfested soil. This enabled us to estimate loss in marketable yield of Salinas at 78% in naturally infested soil at Salinas, where growth-promoting effects of soil fumigation and incomplete disease control prevented computation of losses due to corky root by comparing lettuce yield in fumigated and nonfumigated plots (13). Although marketable yields of Salinas and 440-8 were equal in the absence of disease, densities of Salinas heads were slightly lower than those of 440-8, indicating that more days to harvest would be required for Salinas than for 440-8. Nevertheless, an earlier estimation of yield loss by comparison of a lettuce crop in fumigated soil with one in nonfumigated soil in the Salinas Valley was very similar to our estimate, namely 60% (5). Marketable yield loss due to corky root at Salinas was slightly higher than that in Florida (about 50%), calculated in relation to yield of a resistant cultivar (3). These estimates indicate that corky root can be an extremely serious lettuce disease. Part of the calculated yield loss in our experiment included plants that were not of marketable size or density at the time of harvest, but would have attained marketable quality if given more time to mature. However, lettuce producers in the Salinas Valley usually harvest a lettuce crop only once, and immature heads would be considered unmarketable. Thus, in addition to yield loss as measured in our experiments, the longer period from planting to harvest and the increased variability in maturity can be considered as negative consequences of corky root.

Previous work has shown that the amount of disease observed when the plants have nine true leaves corresponds closely to final yield loss (12,14). In this study, we showed that a critical point model (10) predicted shoot fresh weights based on the amount of disease at the nine-leaf stage at Davis. However, a different model was needed for Salinas, because relatively low infection levels at the nine-leaf stage resulted in steeper reductions in plant growth. One possible reason for the higher yield loss at relatively low infection levels early in the season may be the high nitrate levels in the soil and irrigation water (21), which may exacerbate the effects of corky root (19).

Corky root severity and yield loss varied with season, presumably because of differences in temperature. Higher average temperatures in the fall corresponded to greater disease severities and higher yield loss. Healthy plants grew faster but were smaller at harvest in the fall, indicating that temperatures were supraoptimal for good lettuce development (17) and more conducive to disease development. Higher corky root severity in the fall than in the spring was also observed in the Salinas Valley (19). Failure of late season plantings due to corky root has been observed in Wisconsin (1). In New York, however, corky root was reported to be more prevalent in the spring and fall than in the summer (7). Severe root rot in the spring in New York may have been partly due to excessive ammonia in soil produced in cool, wet springs (19).

Differences in lettuce development and corky root severity between seasons as observed in this and previous research (19) indicate that temperature may be an important factor affecting yield loss due to corky root. Critical point models for yield loss were the same for spring and fall seasons at Davis, indicating that temperatures early in the growing season (up to the nine-leaf stage) might be more important than those closer to lettuce maturity. However, temperatures at harvest time were within 2 C from each other in the spring and fall. Thus, we cannot conclude that late season temperatures would not be important for corky root development.

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