Distinction Between Infectious and Noninfectious Corky Root of Lettuce in Relation to Nitrogen Fertilizer

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Abstract. In growth chamber experiments with five concentrations of NH_4NO_3 and inoculation of lettuce (*Lactuca sativa* L.) cv. Salinas with *Rhizomonas suberifaciens*, the causal agent of corky root (CR), symptoms of noninfectious corky root induced by high rates of N were distinct from those of infectious corky root (ICR). Nitrogen toxicity was observed at 350 $\text{kg}\cdot\text{ha}^{-1}$ and above, and was not affected by inoculation with *R. suberifaciens*. There was a curvilinear relationship between concentration of NH_4NO_3 applied and ICR severity with a maximum at 525 $\text{kg}\cdot\text{ha}^{-1}$. In a similar growth chamber experiment with NH_4NO_3 plus urea, ICR severity decreased and N toxicity increased at increasing N levels (N at 160 to 650 $\text{kg}\cdot\text{ha}^{-1}$). In microplots at Davis, Calif., sidedressing with NH_4NO_3 (N at 170 $\text{kg}\cdot\text{ha}^{-1}$) increased ICR severity on 'Salinas' lettuce over the nonfertilized control. There was a significant interaction between N fertilization and soil-infestation with *R. suberifaciens* with respect to head fresh weight: sidedressing with NH_4NO_3 increased head weight in noninfested plots, but decreased head weight in infested plots. In four field experiments at Salinas, Calif., sidedressing with N at 78 to 213 $\text{kg}\cdot\text{ha}^{-1}$, with N as $(\text{NH}_4)_2\text{SO}_4$, NH_4NO_3 , urea, or $\text{Ca}(\text{NO}_3)_2$, increased ICR over the control, but there were no significant differences between the forms of N. Head fresh and dry weights were either increased or unaffected by sidedressing with N fertilizers, depending on the residual concentrations of N in the soil. The increase in ICR was likely related to concentrations of soil NO_3 rather than NH_4 .

The name corky root was first proposed by Hoff and Newhall (1960) for a disease of lettuce with the following symptoms: "dark brown lesions and corky ridges on the taproot, rotting off of side roots, and vascular discoloration of the stele". In greenhouse experiments, they showed that these symptoms were induced by NH_3 and possibly NO_3 liberated from N fertilizers. A few years earlier, Marlatt (1955) described a similar disease, brown stele, which was induced by excessive application of steer manure. Grogan and Zink (1956) induced similar symptoms with NH_3 or NO_3 released from N fertilizers and chicken manure when applied directly onto lettuce roots. Corking of the roots was accompanied by a yellow, red, or brown discoloration of the central xylem core of the root (Grogan and Zink, 1956).

The name corky root was later used by Busch and Barron (1963) and Amin and Sequeira (1966a) to describe a root rot of lettuce that was not reproduced by high concentrations of N fertilizer. Ammonia-releasing fertilizers applied at 550 $\text{kg}\cdot\text{ha}^{-1}$ did not affect CR severity in field experiments regardless of a prior history of CR (Busch and Barron, 1963). In hydroponic culture, N concentrations at least as high as Hoagland's solution in the form of NH_4SO_4 , NH_4Cl , or urea caused discoloration and occasional fissuring of lettuce roots, but not the typical symptoms of the CR observed in muck soil in Wisconsin (Amin

and Sequeira, 1966a). Symptoms observed in the field included "yellow necrotic lesions on the taproot and lateral roots, followed by a dark brown discoloration and longitudinal ridges on the taproot and main laterals". The root pith became brown and hollow (Amin and Sequeira, 1966a). Similar symptoms of CR have been reported for California (Patterson et al., 1986), Florida (Lucas and Guzman, 1980; Guzman, 1982), Italy (D'Ercole, 1981a), New York (Hartnett and Lorbeer, 1971), and Ontario (Busch and Barron, 1963).

The etiology of this disease was controversial for many years. In Wisconsin, Ontario, Italy, and New York, the disease was attributed to toxic substances released from decomposing lettuce debris (Amin and Sequeira, 1966b; Busch and Carpenter, 1964; D'Ercole, 1981b; Hartnett and Lorbeer, 1968). However, we demonstrated that CR of lettuce is caused by a gram-negative bacterium in California (van Bruggen et al., 1988), and, thus, can be called infectious corky root (ICR). Recently, similar strains were isolated from soils of Florida, Wisconsin, and New York (van Bruggen et al., 1989). Results of taxonomic tests with strains that induced ICR did not correspond to those of any existing genus, and a new genus and species (*Rhizomonas suberifaciens*) were proposed for strains of this bacterium (van Bruggen et al., 1990).

ICR is widespread in the coastal valleys of California, and the disease occurs on various soil types (Grogan et al., 1980). A survey indicated that it was more severe in heavily irrigated fields with high concentrations of NH_4 and NO_3 (Grogan et al., 1980). However, a field experiment on a sandy loam soil in the Salinas Valley, in which sidedressing with various N fertilizers at 112, 224, and 336 $\text{kg}\cdot\text{ha}^{-1}$ was compared with a control, did not confirm these observations (Grogan et al., 1981).

Because the descriptions of symptoms of ICR and noninfectious CR are confusing, factorial experiments with N fertilization and inoculation with *R. suberifaciens* were conducted to differentiate between the two types of CR under controlled en-

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vironmental conditions. In addition, field experiments were carried out to evaluate the effect of N fertilization on ICR, and to determine whether this effect was dependent on the form of N applied.

Materials and Methods

All experiments were performed with crisphead lettuce cv. Salinas. For the growth chamber and microplot experiments, soil was infested with *R. suberifaciens* strain CA1, originally isolated from corked roots of crisphead lettuce from Salinas in 1984. The bacterium was grown in S-medium (van Bruggen et al., 1988) and stored in 15% glycerol at -80°C .

Growth chamber experiments. The effect of five N levels on ICR and N toxicity was investigated in two growth chamber experiments. In one experiment, NH_4NO_3 was used and in the other a mixture of urea and NH_4NO_3 (as often practiced by growers in Salinas). The experiments had a randomized split-plot design with CR infestation in the main plots (right or left side of a growth chamber) and N level in subplots (five pots per level). The experiments were repeated three or four times (three or four growth chambers, considered as blocks).

Light was supplied by cool fluorescent tubes for $14\text{ hr}\cdot\text{day}^{-1}$ at a light intensity of $323.7 \pm 11.8\ \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ (NH_4NO_3 experiment) or $303 \pm 21\ \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ (urea experiment), as measured with a quantum sensor (LI-190SZ, LI-COR, Lincoln, Neb.). The average minimum and maximum temperatures were $19.8 \pm 2.9^{\circ}\text{C}$ and $28.9 \pm 2.1^{\circ}\text{C}$ for the NH_4NO_3 experiment, and $18.5 \pm 0.5^{\circ}\text{C}$ and $30.5 \pm 1.2^{\circ}\text{C}$ for the urea experiment.

Chualar loam ($\approx 45\%$ clay, 35% silt, 15% sand, and 5% gravel) from the USDA experiment station at Salinas was mixed with river sand in a 2:1 ratio (v/v). The mixture was autoclave and exposed to air for 3 weeks before the start of the experiment. The initial pH of the soil mix was 7.0 ± 0.1 . Half of the soil mix was infested with a 5-day-old suspension of *R. suberifaciens* in S-broth (4×10^9 or 6×10^{10} cells/liter of soil for the NH_4NO_3 and urea plus NH_4NO_3 experiments, respectively), and half was mixed with an aliquot of S-broth. Five hundred ml of soil mix were dispensed per pot, and five lettuce seeds were planted per pot. Each pot was placed on a saucer and watered carefully to prevent splash contamination. The plants were watered daily with distilled water (75 to 125 ml/pot , depending on plant size). The seedlings were thinned to one per pot 1 week after planting. Two and 4.5 weeks after planting, N solutions were applied on the soil surface. In the NH_4NO_3 experiments, 0.5 M solutions of NH_4NO_3 were applied at levels equivalent to 0, 50, 100, 150, and 200 kg N/ha and 0, 125, 250, 375, and 500 kg N/ha , 2 and 4.5 weeks after planting, respectively. The total amounts of N applied were: 0, 175, 350, 525, and $700\text{ kg}\cdot\text{ha}^{-1}$. In the urea + NH_4NO_3 experiment, a 1.0 M solution of 30 g urea plus 40 g NH_4NO_3 /liter was applied at levels equivalent to 0, 105, 230, 325, and 430 kg N/ha and 0, 55, 110, 160, and $220\text{ kg}\cdot\text{ha}^{-1}$ 2 and 4.5 weeks after planting, respectively. The total amounts of N applied were 0, 160, 340, 485, and $650\text{ kg}\cdot\text{ha}^{-1}$.

The plants were uprooted 40 days after planting and rated for ICR severity on a 0 to 9 scale (Brown and Micheltore, 1988). Nitrogen toxicity was rated according to a similar 0 to 9 scale (0 = no symptoms; 1 = orange-red discoloration on $<5\%$ of the taproot; 2 = same on 5% to 10% of the taproot; 3 = same on 10% to 15% of the taproot; 4 = red-brown discoloration on $\approx 20\%$ of the taproot and some corky ridges; 5 = same on 25% to 30% of the taproot with pronounced corking; 6 = brown

discoloration on 30% to 40% of the taproot with pronounced corking; 7 = same on 40% to 60% of the taproot, stunted shoot, and chlorotic lower leaves; 8 = same on 60% to 80% of the taproot, shoot severely stunted; 9 = seedlings dead or nearly dead). Isolation of *R. suberifaciens* was attempted, as described previously (van Bruggen et al., 1988), from noninoculated plants that appeared to be contaminated with ICR. All isolates were tested for their reaction with polyclonal antibodies produced against strain CA1 of *R. suberifaciens* (van Bruggen et al., 1988).

Leaf tissue and soil samples of five pots per treatment were bulked per growth chamber for analysis of NH_4 and NO_3 . The tissue was dried at 80°C for 48 hr and ground in a Wiley mill with screen No. 40 (Model 475-A, Arthur H. Thomas, Philadelphia, Pa.). Subsamples of 100 mg were dispensed in 100 ml of 2% acetic acid, agitated for 10 min, and filtered through Whatman 1 filter paper. The extracts were analyzed for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ at the DANR Diagnostic Laboratory at the Univ. of California (U.C.), Davis, using Carlson's method (Carlson, 1986). Soil samples were dried overnight at 105°C and ground in a mortar. Subsamples of 5 g were placed in flasks with 25 ml of 2 N KCl and shaken for 1 hr on a mechanical shaker (150 rpm). The soil was allowed to settle, and the supernatant was filtered (Whatman 1 filter paper) and analyzed for $\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$ as described for tissue extracts. Subsamples of 10 g of soil were shaken in 50 ml of distilled water for 30 min and the electrical conductivity (EC) of the extract was measured with a conductivity meter (LaMotte Multirange Conductivity meter, LaMotte Chemical Products, Chestertown, Md.).

Microplot experiments at Davis. A field experiment was conducted in microplots at U.C. Davis as described by van Bruggen et al. (1988). Fertilizer (16N-20P-0K) was incorporated in all plots at a rate of 77 g/plot . Half of the plots received two additional side-dressings of $55\text{ g NH}_4\text{NO}_3/\text{plot}$, 41 and 66 days after planting. This amounted to a total of 224 kg N and 70 kg P/ha , a rate commonly used commercially in the Salinas Valley. Besides the two N treatments (with and without sidedressing), there were four inoculum levels (0 , 10^8 , 10^{11} , or 10^{12} cells/ m^2 of soil surface) in a factorial design. Inoculum preparation, inoculation, and cultural practices were as outlined by van Bruggen et al. (1988). The experiment had a randomized complete-block design with five replications. At harvest, 95 days after planting, the roots were scored for ICR severity on a 0 to 5 scale (van Bruggen et al., 1988). Fresh weights were determined for all heads (untrimmed). Dry weights of heads and roots were obtained for six plants per plot. The heads were cut in half and dried at $\approx 40^{\circ}\text{C}$ for 2 weeks, and the entire roots were dried at 80°C for 2 days.

The experiment was repeated in the same plots in Fall 1987. Between the spring and fall crops, the noninfested control plots were fumigated with 113 g methyl bromide plus chloropicrin (3:1 by weight), because they had become contaminated during the first crop. Insecticides were applied at the recommended rates. The plants were harvested 63 days after planting, and fresh and dry weights were recorded. ICR severity was assessed on the 0 to 5 scale expanded with score 6 (representing completely corked roots constricted 5 to 10 cm below the soil level). Nitrogen toxicity was not observed.

Field experiments at Salinas. Four field experiments were conducted in two growers' fields in the Salinas Valley, one designated River Road and the other Davis Road. The soil types were Pico fine sandy loam and Mocho silt loam, respectively. Lettuce had been produced continuously for many

years (two crops/year) in both fields, and ICR severity had increased over the years. Consecutive spring and fall lettuce crops were grown in each field (planting dates: 6 Feb. and 17 June 1988 in the first field, and 22 Apr. and 28 July 1988 in the second field). Fertilizer was drilled into the beds or broadcast in the field at 545 kg of 10N-50P-0K/ha and 351 kg of 5N-13P-17K/ha for the spring crop at Davis Road. No fertilizer was applied before planting of the fall crop at Davis Road. Composted steer manure (9000 kg·ha⁻¹) had been incorporated in Fall 1987 at the Davis Road site. Cultural practices were as usual in the Salinas Valley. Lettuce seedlings were grown in two rows on 1-m-wide beds, 25 mm apart, and thinned to one plant/30 cm $\approx$ 1 month after planting. Pre-emergence herbicide (Pronamide, Kerb 50-W, Rohm and Haas, Philadelphia, Pa.) was applied just before planting at 1.1 to 2.2 kg·ha⁻¹. Additional weed control was performed mechanically or manually. Sprinkler irrigation was applied during the first 3 weeks after planting and furrow irrigation afterwards. Pest and disease control was performed as usual in the Salinas Valley (three applications of a mixture of insecticides per crop, and two to three fungicide applications).

Each experiment consisted of five treatments [no additional fertilizer, and one to four sidedressings with (NH₄)₂SO₄, NH₄NO₃, urea, or Ca(NO₃)₂] with five replications in a Latin square design. The number of sidedressings and amount of N were adjusted to rates used by the grower in the surrounding field. At River Road, four sidedressings (45, 78, 45, and 45 kg N/ha) were applied to the spring crop and three sidedressings (78, 45, and 45 kg N/ha) to the fall crop. At Davis Road, one sidedressing (78 kg N/ha) was applied both to the spring and fall crops. The plot size was 4 x 8 m, with 1.5-m alleys between plots. The experimental area was surrounded by a 15-m-wide buffer area in which no additional fertilizers were applied.

Two weeks after the first sidedressing with N fertilizers, four soil samples were taken with a Dutch auger (6-cm diam, 22 cm deep) on the diagonal of each plot. The four samples were mixed, transported on ice, and frozen until they were analyzed for NH₄ and NO₃ as mentioned under growth chamber experiments. At harvest, 20 plants in the center of each plot were uprooted and scored for CR severity using a 0 to 9 scale (Brown and Michelmore, 1988). The roots were split longitudinally and the steles were rated for discoloration (three classes: healthy, dark brown streaks, and hollow, reddish-brown cores). To check if *R. suberifaciens* was associated with internal reddish discoloration, isolation of the pathogen was attempted from aseptically removed cores of five taproots per plot as described by van Bruggen et al. (1988). Twenty heads (including wrapper leaves) per plot were weighed and five heads and roots per plot were randomly selected to be dried in an oven at 80°C for 48 hr and then weighed. Dried head tissue was ground and analyzed for NH₄ and NO₃ as described for the growth chamber experiments.

Data analysis. Corky root severity data were analyzed by χ^2 tests with MINITAB (Statistics Dept., The Pennsylvania State Univ., University Park, Pa.). Continuous data were analyzed with the General Linear Models Procedure of SAS (SAS Institute, Cary, N.C.). The growth chamber data were analyzed as split plots with the mean values per growth chamber as the experimental unit. The microplot data were analyzed according to a randomized complete-block design, and the data from field experiments in Salinas according to a Latin square design. The residual values were tested for normality by the Shapiro-Wilk statistic (SAS, 1985).

Growth chamber experiments

Ammonium nitrate experiments. Symptoms of CR, caused by N toxicity, and of ICR were similar in some respects, but distinct in others. At intermediate N levels (350 to 525 kg N/ha), N toxicity was expressed as a reddish discoloration on the taproot and main laterals, sometimes accompanied by thin longitudinal ridges on the taproot. At high N concentrations, the stele became reddish-brown and the whole taproot was sometimes brown and rotten. In contrast, ICR was not accompanied by pink or red lesions on the root. At low N levels (0 to 175 kg N/ha), ICR was characterized by yellow, superficial discoloration of the roots with some corking. At higher N levels, the taproots were increasingly corky and brittle so that they snapped readily when bent. Corkiness induced by excessive N was different from that induced by *R. suberifaciens*: thin corky ridges for non-infectious CR and broad corky areas interspersed by longitudinal grooves for ICR. At the highest N concentration, it was difficult to distinguish between severe ICR and N toxicity, but the extent of corkiness typical for ICR and reddishness typical for N toxicity enabled us to assess the relative contributions of ICR and N toxicity to the syndrome.

Severity of ICR on inoculated plants increased curvilinearly as levels of NH₄NO₃ increased ($P < 0.01$), with a maximum severity at 525 kg N/ha (Fig. 1A). At higher N levels, N toxicity prevailed. Nitrogen toxicity increased exponentially from 350 kg N/ha ($P < 0.01$) and was not significantly affected by inoculation with *R. suberifaciens* ($P = 0.61$) (Fig. 1B). Reddish discoloration of the pith was observed at ≥ 350 kg N/ha in ICR-infected and uninfected roots.

Six of the 100 noninoculated plants developed ICR, and *R. suberifaciens* was isolated from two of those plants.

Final concentrations of NH₄ and NO₃ in soil were not affected by infestation with *R. suberifaciens*, but increased significantly ($P < 0.01$) from 6 and 7 ppm at 0 kg N/ha to 249 and 287 ppm at 700 kg N/ha. The soil pH was significantly ($P < 0.01$) reduced from 6.6 in the controls to 6.1 at 350 to 700 kg N/ha. The EC of the soil extract increased significantly ($P < 0.01$) from 0.8 to 4.2 dS·m⁻¹ at 0 to 700 kg N/ha applied. The concentrations of NH₄-N and NO₃-N in shoot tissue were not affected by inoculation with the pathogen, but increased ($P < 0.01$) with increasing N (Table 1).

Urea plus ammonium nitrate experiment. In contrast to the experiment with NH₄NO₃, severity of ICR decreased with increasing levels of N when urea was added to the NH₄NO₃ ($P = 0.02$) (Fig. 2A). Symptoms of N toxicity were similar to those in the previous experiment, but occurred at much lower concentrations (160 vs. 350 kg N/ha in the experiment with NH₄NO₃) (Fig. 2B). Again, N toxicity was not affected by infestation with *R. suberifaciens* ($P = 0.13$), but increased at increasing N levels ($P < 0.01$).

Nine of the 60 noninoculated plants had ICR symptoms, and the pathogen was isolated from three of these.

The concentration of NH₄-N in shoot tissue was not affected by inoculation with *R. suberifaciens*, but increased as N increased ($P < 0.01$) (Table 1). The concentration of NO₃-N was slightly ($P = 0.02$) higher in shoots of ICR-infected plants than in noninfected plants, and increased as N increased ($P < 0.01$). There were no significant interactions between N fertilization and inoculation with the pathogen.

Fig. 1. Effect of sidedressing with NH_4NO_3 on (A) severity of infectious corky root (0-9 scale) on lettuce plants inoculated with *R. suberifaciens*, and (B) N toxicity (0-9 scale) on lettuce roots in growth chambers. Data averaged over inoculated and noninoculated plants. Vertical bars denote SE.

Field experiments

Microplot experiments at Davis. In the spring, there was a significant increase in ICR severity as inoculum levels increased, despite some contamination of noninoculated plots in the course of the season (Table 2). No significant effect of N on ICR severity or interaction between N and inoculum level was observed. Immediately after the roots were dug, they were dull green and turned dark brown to black after exposure to the air. Internal discoloration of the pith was only observed in severely infected roots and was greyish-brown, not red. The dry

weight of the taproots was significantly increased by ICR infection, regardless of N level ($P < 0.01$) (Fig. 3A). The diameter of corky taproots appeared to be wider than that of healthy ones. On moderately corked roots, the corky ridges seemed to be hypertrophic, whereas the areas between the ridges seemed to reflect normal growth. Untrimmed head fresh weights decreased progressively at increasing ICR levels ($P < 0.01$) (Fig. 3B). There was a significant ($P = 0.04$) interaction between N level and inoculum level in their effect on head fresh weight. In noninfested plots, head weight was increased by additional N, whereas in infested plots, it was reduced by extra N (Fig. 3B). Head dry weight also progressively decreased at increasing inoculum levels ($P < 0.01$), but there was no significant interaction between CR infestation and N sidedressing in their effect on head dry weight ($P = 0.8$).

In the fall, ICR was so severe that there were no differences in disease severity between inoculum levels in infested plots. Noninfested plots became more contaminated than in the spring, but ICR severity was still significantly lower in noninfested than in infested plots (Table 3). Thus, only the data for the noninfested plots and those infested with the lowest inoculum level are presented. In infested plots, most taproots were constricted 5 to 10 cm below soil level, resulting in shorter and thicker taproots. There was a significant interaction between sidedressing with NH_4NO_3 and inoculation with the ICR bacterium on ICR severity (Table 3). Nitrogen increased ICR more in infested than in noninfested plots. There was also a significant interaction between N application and ICR infestation in their effects on head fresh weight (Table 4). Head fresh weights were increased by N sidedressing in control plots, whereas they were not affected by N in infested plots. Head dry weights were reduced by ICR infestation only (Table 4). Root dry weights were unaffected by the treatments, probably due to shorter but thicker taproots of infected plants (Table 4).

Field experiments at Salinas. Results for the spring and fall crops were similar at both experimental sites. The only difference was that ICR severities of the fall crops were consistently higher than those of the spring crops for all treatments. Thus, only the data for the fall crops are presented. Sidedressing with $(\text{NH}_4)_2\text{SO}_4$, NH_4NO_3 , urea, or $\text{Ca}(\text{NO}_3)_2$ increased ICR severity over the unfertilized control at both experimental sites (Table 5), but the difference was more pronounced at River Road. There were no significant differences in ICR severity between the forms of N.

At River Road, head fresh and dry weights and root dry weights were significantly lower in control plots than in fertilized plots (Table 6). Control plants were visibly N deficient and had significantly lower NO_3 in their tissues (Table 7). There were no significant differences in NH_4 concentrations in lettuce

Table 1. NH_4 - and NO_3 -N concentrations in lettuce leaf tissue' at the end of a growth chamber experiment with five levels of N applied as NH_4NO_3 or urea plus NH_4NO_3 (3:4 by weight) to the soil.

Experiment with NH_4NO_3			Experiment with urea plus NH_4NO_3		
N applied ($\text{kg}\cdot\text{ha}^{-1}$)	NH_4 -N (ppm)	NO_3 -N (ppm)	N applied ($\text{kg}\cdot\text{ha}^{-1}$)	NH_4 -N (ppm)	NO_3 -N (ppm)
0	92 $\pm$ 86	398 $\pm$ 132	0	313 $\pm$ 161	805 $\pm$ 169
175	227 $\pm$ 94	5,330 $\pm$ 2,210	160	430 $\pm$ 94	6,480 $\pm$ 1,960
350	447 $\pm$ 98	7,130 $\pm$ 2,360	340	535 $\pm$ 249	10,300 $\pm$ 2,270
525	755 $\pm$ 141	9,740 $\pm$ 4,320	485	573 $\pm$ 269	12,500 $\pm$ 3,010
700	2,250 $\pm$ 1,110	13,600 $\pm$ 2,730	650	602 $\pm$ 227	12,500 $\pm$ 3,120

'Tissue infected with *R. suberifaciens* and healthy tissue combined.

Fig. 2. Effect of sidedressing with urea plus NH_4NO_3 (1:1 based on N content) on (A) severity of infectious corky root (0-9 scale) on lettuce plants inoculated with *R. suberifaciens*, and (B) N toxicity (0-9 scale) on lettuce roots in growth chambers. Data averaged over inoculated and noninoculated plants. Vertical bars denote SE.

tissue. Symptoms typical of N toxicity were not observed in fertilized plots. At Davis Road, plants in nonfertilized plots did not exhibit N deficiency symptoms, and there were no signifi-

cant differences in head or root weights (Table 6). Tissue NO_3 concentrations were again significantly lower in nonfertilized plants than in fertilized plants (Table 7), but they were about twice as high in nonfertilized plants at Davis Road than at River Road. At Davis Road, plants fertilized with urea showed typical symptoms of N toxicity on the root surface, but there were no significant differences in NH_4 concentration in the tissues (Table 7). Many roots showed internal discoloration. Chi-square tests on the number of roots in three classes of core discoloration (healthy, brown steaks, or a hollow and reddish-brown core) failed to detect differences between treatments. On the average, 27% of the plants had brown steaks and 58% had hollow, reddish-brown cores. Attempts to isolate *R. suberifaciens* from discolored cores were mostly negative; only one colony of the pathogen was detected.

Ammonium concentrations in soil samples collected 2 weeks after sidedressing were significantly higher in the urea treatment than in all other fertilizer treatments at both locations (Table 7). The NH_4 concentration in nonfertilized control plots did not differ significantly from that in fertilized plots, but the NO_3 concentration was significantly lower in control plots (Table 7). Soil in plots sidedressed with $(\text{NH}_4)_2\text{SO}_4$ had intermediate levels of NO_3 that were significantly lower than those in plots sidedressed with other fertilizers.

Discussion

Symptoms of infectious and noninfectious corky root. In two growth chamber experiments, we showed that the symptoms of CR caused by N toxicity are different from those of ICR. A pink or red discoloration of the root surface was typical of N toxicity, but not of ICR. Corkiness induced by excessive N was also different from that of ICR: thin corky ridges for N toxicity and broad corky areas interspersed with longitudinal grooves for ICR. Besides corkiness, we observed red and hollow xylem cores of roots at high rates of NH_4NO_3 or medium and high rates of urea plus NH_4NO_3 . *R. suberifaciens* was not isolated from noninoculated plants with these symptoms. Red internal discoloration and hollow xylem cores were not observed in roots inoculated with the pathogen at low or medium N rates. Thus, these symptoms seemed to be characteristic for N toxicity. Sim-

Table 2. Number of lettuce plants in each of six classes of ICR at two N levels (with and without NH_4NO_3 sidedressing) and four inoculum levels of *R. suberifaciens* in a microplot experiment at Univ. of California, Davis, in Spring

Treatment (tmt)	N side dressing	Inoculum level (cells/ml)	ICR rating					
			0	1	2	3	4	5
1	—	0	56	12	2	0	0	0
2	—	3×10^6	0	0	0	8	56	6
3	—	3×10^7	0	0	0	0	53	17
4	—	3×10^8	0	0	0	0	40	30
5	+	0	62	6	0	2	0	0
6	+	3×10^6	0	0	2	3	57	8
7	+	3×10^7	0	0	0	0	55	15
8	+	3×10^8	0	0	0	0	41	29

χ^2 tests

Inoculum effect

χ^2 (tmt 1 + 5 vs. others) = 516, df = 3 $\alpha < 0.01$

χ^2 (tmt 2 + 6 vs. 3 + 7) = 20, df = 2 $\alpha < 0.01$

χ^2 (tmt 3 + 7 vs. 4 + 8) = 12, df = 1 $\alpha < 0.01$

N effect and interaction

χ^2 (tmt 1 + 6 + 7 + 8 vs. tmt 2 + 3 + 4 + 5) = 1,

df = 3, $\alpha > 0.05$ (interaction not significant)

χ^2 (tmt 1-4 vs. 5-8) = 3, df = 5, $\alpha > 0.05$ (no significant N effect)

Fig. 3. Dry weight (g) of lettuce taproots (A) and fresh weight (kg) of lettuce heads (B) at four inoculum levels of *R. suberifaciens* in microplots (0, 3×10^6 , 3×10^7 , and 3×10^8 bacteria/ml), with and without NH_4NO_3 sidedressing. Vertical bars denote SD.

ilar symptoms were attributed to free ammonia by Grogan and Zink (1956).

At increasing N levels; the EC of the soil solution also increased, and the high EC per se could have contributed to the red discoloration and breakdown of the central cores. However, in experiments with NaCl in irrigation water at EC levels ranging from 0 to 5 dS·m⁻¹, Grogan et al. (1982) observed symptoms on lettuce roots that differed from those typical of N toxicity or ICR. Corkiness typical of ICR and N toxicity were observed on the same roots in the fall crop in one field at Salinas, where

urea had been applied as sidedressing. Nitrogen toxicity symptoms were probably brought about by NH_3 liberated from urea by microbial or chemical degradation (Grogan and Zink, 1956). In the same field, the stele of most roots was reddish-brown and hollow, regardless of the type of fertilizer applied. This symptom was probably not caused by *R. suberifaciens*, because only one colony was isolated from the central core. In addition to N fertilizers, steer manure had been applied to this field at the end of the previous season, and the red discoloration of the central core could have been caused by NH_3 released by microbial degradation of the manure (Grogan and Zink, 1956). Marlatt (1955) attributed a disorder he called 'brown stele' to excessive cow manure, and Grogan and Zink (1956) induced red or brown discoloration of the central core by chicken manure.

In microplots infested with *R. suberifaciens*, symptoms characteristic of N toxicity were not observed. ICR was accompanied initially by yellow bands and later by dull green in the corked regions of the root. Severely infected roots became brittle and snapped off easily. Green discoloration of the roots became brittle and snapped off easily. Green discoloration of the roots was also mentioned or shown for CR in Ontario (Busch and Barron, 1963) and Italy (D'Ercole, 1981 b). Brittleness of the roots has not been reported for other areas, but was observed by us in New York and Florida (unpublished data). Corked areas of moderately infected roots seemed to be hypertrophic compared to healthy areas on the same roots, and dry weights of infected taproots were higher than those of uninfected roots. Swollen areas on taproots and main laterals were also characteristic for CR in Ontario (Busch and Barron, 1963) and Florida (Lucas and Guzman, 1980).

Nitrogen in relation to noninfectious corky root. Nitrogen toxicity is generally thought to be caused by NH_3 or NO_2^- , rather than by NO_3^- (Goyal and Huffaker, 1984). In nutrient solution culture, Arnin and Sequeira (1966a) induced root discoloration and fissuring by NH_4SO_4 , NH_4Cl , or urea at N concentrations similar to or higher than those of Hoagland's solution, but not by the same amount of N applied as NO_3^- . Internal discoloration of the roots was not reported. Grogan and Zink (1956) and Hoff and Newhall (1960) induced N toxicity in the greenhouse by applying NH_3 - or NO_2^- -releasing fertilizers directly onto lettuce roots.

In our growth chamber studies, external reddish discoloration and corkiness of the roots were induced at 160 kg N/ha (the lowest level included) when both urea and NH_4NO_3 were applied, and at ≥ 350 kg N/ha when only NH_4NO_3 was used. These application levels corresponded to similar concentrations

Table 3. Number of lettuce plants in seven classes of ICR ratings with or without NH_4NO_3 sidedressing and inoculation with *R. suberifaciens* in microplots at Univ. of California, Davis, in Fall 1987.

Treatment (tmt)	NH_4NO_3	Inoculation	ICR rating						
			0	1	2	3	4	5	6
1	-	-	11	22	8	2	4	5	0
2	+	-	7	10	6	9	13	6	2
3	-	+	0	0	0	7	29	15	11
4	+	+	0	0	0	0	1	19	46

χ^2 tests

$$\chi^2 (\text{total}) = 226, \text{df} = 18, \alpha < 0.01$$

$$\chi^2 (\text{tmt 1 + 4 vs. 2 + 3}) = 64, \text{df} = 6, \alpha < 0.01 (\text{significant interaction})$$

$$\chi^2 (\text{tmt 1 vs. 2}) = 17, \text{df} = 6, \alpha < 0.05$$

$$\chi^2 (\text{tmt 3 vs. 4}) = 55, \text{df} = 3, \alpha < 0.01$$

Table 4. Effects of NH_4NO_3 sidedressing and inoculation with *R. suberifaciens* on head fresh weight, head dry weight, and root dry weight of 'Salinas' lettuce in a microplot experiment at Univ. of California, Davis, Fall 1987.

Treatment (tmt)	NH_4NO_3	Inoculation	Head fresh wt (g)	Head dry wt (g)	Root dry wt (g)
1	—	—	322 ± 18	13 ± 2	1.0 ± 0.2
2	+	—	397 ± 43	15 ± 2	1.4 ± 0.3
3	—	+	165 ± 49	9 ± 2	1.3 ± 0.2
4	+	+	156 ± 49	10 ± 2	1.3 ± 0.3
Contrast estimates					
Tmt (1 + 4) vs. (2 + 3)			42**	0.5 ^{NS}	2.1 ^{NS}
Tmt 1 vs. tmt 2			75**		
Tmt 3 vs. tmt 4			9 ^{NS}		
Main ICR effect				4.5**	0.1 ^{NS}
Main N effect				1.5 ^{NS}	0.2 ^{NS}

^{NS},**Nonsignificant or $\alpha = 0.01$, respectively.

Table 5. The effect of N sidedressing on severity of ICR of 'Salinas' lettuce at harvest time at two sites in the Salinas Valley in Fall 1988.

Fertilizer	Site							
	River Road				Davis Road			
	ICR rating				ICR rating			
	3	4	5	6-7	3	4	5	6-7
No. of plants								
None	7	37	52	4	7	43	48	2
$(\text{NH}_4)_2\text{SO}_4$	0	3	50	47	0	19	72	9
NH_4NO_3	0	4	53	43	0	14	73	13
Urea	0	6	59	35	1	11	73	15
$\text{Ca}(\text{NO}_3)_2$	0	3	57	40	0	13	76	11
χ^2	146.9**				75.8**			
None	7	37	52	4	7	43	48	2
All fertilizers	0	16	219	165	1	57	294	48
χ^2	143.1**				71.4**			

** $\alpha = 0.01$.

of NH_4^+ -N in the tissue (430 and 450 ppm in the respective experiments). The tissue NO_3 level was 0.55% at 160 kg N/ha in the urea + NH_4NO_3 experiment (resulting in N toxicity), and 0.53% at 175 kg N/ha in the NH_4NO_3 experiment (without

N toxicity). This result indicates that N toxicity was related to the NH_4 rather than NO_3 concentrations in the tissue, which is in agreement with previous findings that NH_3 - and NO_2 -releasing fertilizers are toxic to lettuce roots, whereas NO_3 fertilizers are not (Amin and Sequeira, 1966a; Grogan and Zink, 1956; Hoff and Newhall, 1960).

Nitrogen in relation to infectious corky root. ICR severity was increased by various N fertilizers (78 to 213 kg N/ha) in the field and by NH_4NO_3 up to a concentration of 525 kg N/ha in growth chambers. Increases in disease severity due to N fertilization have been reported for many other bacterial plant diseases (Bartz et al., 1979; Kelman, 1950; McGovern et al., 1985; Naidu et al., 1979) and relatively few are unaffected (Logan et al., 1987). When bacterial plant diseases were reduced by N fertilization, the N levels were probably supra-optimal for plant growth or bacterial infection (Haygood et al., 1982; Kelman, 1950). The N concentration optimal for disease development or plant growth may depend on the form in which it is applied (Huber and Watson, 1974; McGovern et al., 1985). *Erwinia* rot of chrysanthemum was more severe at high levels of NH_4SO_4 than at the same levels of $\text{Ca}(\text{NO}_3)_2$ and NH_4NO_3 (McGovern et al., 1985). In another study, NH_4NO_3 increased susceptibility to bacterial wilt more than $\text{Ca}(\text{NO}_3)_2$ (Kelman, 1950). Similarly, bacterial leaf blight of rice was more severe after application of NH_4SO_4 or urea than with $\text{Ca}(\text{NO}_3)_2$ or NH_4NO_3 (Naidu et al., 1979). This relationship indicates that NH_4 may enhance severity of these bacterial plant diseases more than NO_3 .

In this paper we showed that increased susceptibility to ICR was due to NO_3 rather than NH_4 , because there were significant differences in NO_3 but not in NH_4 concentrations in the soil between fertilized and control plots. There were no differences among the fertilizer types in soil NO_3 concentration or ICR severity. However, the NH_4 concentration in soil was significantly higher in plots fertilized with urea, and ICR severity was not higher than in plots that received other N fertilizers. In the growth chamber, ICR was decreased by a mixture of urea and NH_4NO_3 (160 to 650 kg N/ha), possibly due to excess NH_3 .

In a field study, Grogan et al. (1981) did not observe significant effects of sidedressing with various N fertilizers (112, 224, and 336 kg N/ha) on ICR severity in a sandy loam soil in the Salinas Valley. However, all plots received 560 kg of a 13N-13 P-13K fertilizer/ha before planting (Grogan et al., 1981), and

Table 6. Effects of N sidedressing on head fresh and dry weight and root dry weight of 'Salinas' lettuce at two sites in the Salinas Valley in Fall 1988.

Fertilizer	Site					
	River Road			Davis Road		
	Head fresh wt (g)	Head dry wt (g)	Root dry wt (g)	Head fresh wt (g)	Head dry wt (g)	Root dry wt (g)
None	677 ± 314	35 ± 15	2.6 ± 0.3	751 ± 72	41 ± 4	4.0 ± 0.2
$(\text{NH}_4)_2\text{SO}_4$	1009 ± 107	50 ± 9	3.9 ± 1.0	731 ± 58	36 ± 4	4.3 ± 0.3
NH_4NO_3	1011 ± 27	45 ± 10	3.5 ± 0.7	763 ± 101	42 ± 7	3.9 ± 0.3
Urea	986 ± 55	45 ± 5	3.1 ± 0.4	742 ± 54	41 ± 4	4.3 ± 0.4
$\text{Ca}(\text{NO}_3)_2$	1009 ± 107	48 ± 6	3.3 ± 0.9	714 ± 80	39 ± 5	4.3 ± 0.1
Contrast estimates						
None vs. fertilizers		327**	12**	0.9*	13 ^{NS}	2 ^{NS}
Urea vs. other fertilizers		23 ^{NS}	3 ^{NS}	0.5 ^{NS}	6 ^{NS}	0.1 ^{NS}

Table 7. Effects of N sidedressing on concentrations of NH_4 and NO_3 in soil and leaf tissue of 'Salinas' lettuce at two sites in the Salinas Valley in Fall 1988.

Fertilizer	Site							
	River Road				Davis Road			
	Soil		Tissue		Soil		Tissue	
	$\text{NH}_4\text{-N}$ (ppm)	$\text{NO}_3\text{-N}$ (ppm)	$\text{NH}_4\text{-N}$ (ppm)	$\text{NO}_3\text{-N}$ (%)	$\text{NH}_4\text{-N}$ (ppm)	$\text{NO}_3\text{-N}$ (ppm)	$\text{NH}_4\text{-N}$ (ppm)	$\text{NO}_3\text{-N}$ (%)
None	7.6 ± 0.4	69 ± 8	182 ± 69	0.16 ± 0.10	4.6 ± 0.2	22 ± 7	200 ± 24	0.31 ± 0.09
$(\text{NH}_4)_2\text{SO}_4$	7.8 ± 0.5	82 ± 11	318 ± 199	0.52 ± 0.10	4.6 ± 0.3	28 ± 4	236 ± 70	0.51 ± 0.08
$(\text{NH}_4)\text{NO}_3$	7.3 ± 0.3	144 ± 35	328 ± 247	0.51 ± 0.14	4.6 ± 0.6	110 ± 25	214 ± 53	0.49 ± 0.11
Urea	8.7 ± 0.9	118 ± 14	160 ± 57	0.49 ± 0.16	13.9 ± 10.8	110 ± 21	206 ± 34	0.51 ± 0.11
$\text{Ca}(\text{NO}_3)_2$	7.5 ± 0.7	159 ± 54	194 ± 128	0.49 ± 0.13	4.4 ± 0.1	134 ± 27	226 ± 33	0.53 ± 0.10
Contrast estimates								
None vs. fertilizers	0.2 ^{NS}	57 ^{**}	68 ^{NS}	0.40 ^{**}	2.9 ^{NS}	74 ^{**}	21 ^{NS}	0.20 ^{**}
Urea vs. other fertilizers	1.2 [*]	10 ^{NS}	120 ^{NS}	0.02 ^{NS}	9.4 [*]	19 ^{NS}	19 ^{NS}	0.01 ^{NS}
$(\text{NH}_4)_2\text{SO}_4$ vs. other fertilizers	0.03 ^{NS}	59 ^{**}	91 ^{NS}	0.03 ^{NS}	3.6 ^{NS}	90 ^{**}	21 ^{NS}	0.02 ^{NS}

NS,*,**Nonsignificant or $\alpha = 0.05$ or 0.01, respectively.

the base N level in the soil might have been too high to detect any differences among the treatments. Similarly, we observed only a slight increase in ICR severity after sidedressing with N in one experimental field at Salinas where the residual N concentration was relatively high.

Implications for lettuce production in the coastal valleys of California. Under field conditions, ICR and noninfectious corky root may occur simultaneously. A reduction in NH_4 and NO_3 concentrations in soil and tissue could contribute to controlling both types of CR. However, residual N levels are high in some areas in the coastal valleys of California, as shown for one of the fields in this study. In previous N fertilization experiments in this area of California, residual N concentrations were so high that it took several lettuce crops to deplete the reserves (Welch et al., 1987). High NO_3 concentrations (>45 mg NO_3 /liter) have also been found in $\approx 10\%$ of the small wells tested in that region (Friedrich and Zicarelli, 1987). High N levels in soil and irrigation water could be one of the reasons why ICR has become such a severe problem in the central coastal valleys of California in recent years. Thus, the soundness of current fertilization practices in the Salinas Valley needs to be reassessed, based upon levels of N in soil and irrigation water, and their impact on ICR and noninfectious corky root of lettuce.

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