

Suppression of Fusarium Yellows of Celery with Potassium, Chloride, and Nitrate

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ABSTRACT

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Ammoniacal-N ($\text{NH}_4\text{-N}$) was more conducive to Fusarium yellows of celery, caused by *Fusarium oxysporum* f. sp. *apii*, than nitrate-N ($\text{NO}_3\text{-N}$) regardless of the accompanying ions. The inclusion of specific concentrations of KCl with NO_3 (as $\text{Ca}[\text{NO}_3]_2$) resulted in almost complete control of the disease in the greenhouse and field. The provision of both K and Cl was essential inasmuch as disease suppression was related to a specific tissue concentration ratio of K and Cl rather than absolute concentrations of either ion. Factors that affected the ratio were the predominant form of N, the availability of competing cations (Ca and NH_4) and anions (SO_4 and NO_3), and the absolute concentrations of available K and Cl in the soil. Thus, small amounts of NH_4 repressed uptake of both NO_3 and K and stimulated Cl uptake, while concentrations of K and Cl were lower in the

presence of Ca and SO_4 , respectively. In addition, excessive amounts of KCl under an NO_3 regime resulted in large accumulations of Cl but not K. Quantification of these interactions was accomplished by assessing rates of root infection (colonies per 100 cm of root). These data showed that a propagule under an NH_4 regime was about five times as likely to cause a root infection as under a NO_3 plus KCl regime. Furthermore, differences in maximum rates of root infection as a function of inoculum level indicated that either there were fewer sites of infection or these sites were more resistant under the latter regime. The process of osmoregulation, ion uptake mechanisms, and charge balance are discussed with respect to the centrality of the K:Cl ratio in the root infection process. Substantial disease control was achieved in the field with sidedress applications of $\text{Ca}(\text{NO}_3)_2$ and KCl.

Additional key words: mineral nutrition.

Fusarium yellows of celery (*Apium graveolens* L. var. *dulce* (Miller) Pers.), which is caused by *Fusarium oxysporum* f. sp. *apii* (R. Nelson & Sherb.) Snyder & Hans. (*Foa*), is a devastating disease that is spreading throughout the celery-growing districts of California and elsewhere (5,10). The disease is particularly calamitous because of its insidious nature. Symptoms may not become apparent in a field until populations of the pathogen increase to a level that causes a high incidence of vascular discoloration in the crown and severe stunting (33). In addition, there are no resistant cultivars or effective fungicides. Thus, alternative means of control must be sought.

This study was conducted to determine the influence of form of nitrogen (N), ie, nitrate (NO_3) and ammonium (NH_4), on disease development. There have been numerous reports on the influence of form of N on disease (14,29,31), including Fusarium wilts (34); however, there is a dearth of information on the influence of the accompanying ion. For example, NH_4 is commonly applied as the chloride (Cl), sulfate (SO_4), or NO_3 salt, while NO_3 can be applied as the potassium (K), calcium (Ca), or NH_4 salt. Because it is impossible to vary only the form of N without varying the associated anions and cations, the roles of K, Ca, sodium (Na), magnesium (Mg), Cl, and SO_4 also were investigated. A preliminary report was published (26).

MATERIALS AND METHODS

Soils. Two autoclaved soils were used in greenhouse experiments. A loamy sand (soil 1), collected in Tulare County, CA, was air-dried, sieved through a screen with 0.63-cm openings, and stored at room temperature. Soil 2 was a mixture of mineral soil, peat, and sand (2:1:1, v/v). Chemical characteristics (1,25) of these soils

included: exchangeable K, 4.3 and 3.1 meq/100 g; exchangeable Ca, 10.7 and 9.2 meq/100 g; exchangeable Mg, 3.3 and 2.0 meq/100 g; $\text{NO}_3\text{-N}$, 8.7 and 20.1 $\mu\text{g/g}$; $\text{PO}_4\text{-P}$, 12 and 18 $\mu\text{g/g}$; Cl, 16.4 and 2.1 meq/l in the saturation extract; and pH 6.3 and 6.0 in a saturated paste made with 0.01 M CaCl_2 (30), respectively.

Inoculum, plants, and disease assessment. Inoculum of *Foa* isolate 40-1 was prepared by inoculating sterile ground (1.0-mm sieve) barley straw moistened with 0.025 M L-asparagine with a conidial suspension and incubating it for 2 wk at room temperature (27). The barley straw culture was then dried at room temperature and refrigerated until needed. Soils were infested by incorporating 0.5 g of inoculum per kilogram of air-dry soil in a soil blender unless indicated otherwise.

Celery cultivar 52-70 Tall Utah (Ferry Morse Seed Co., Mountain View, CA) was used in all experiments. One 6-wk-old seedling was transplanted into each 20-cm-diameter pot filled with soil. Typical symptoms (10) developed 6-8 wk after transplanting. Temperature in the greenhouse ranged between 23 and 27 C. Disease severity was assessed by the following scale: 1 = symptomless; 2 = intermittent vascular discoloration in roots; 3 = continuous vascular discoloration in roots; 4 = slight vascular discoloration in crown; 5 = moderate vascular discoloration in crown or slight rot; 6 = moderate to severe rot; and 7 = wilted or dead. In some experiments, shoot and root dry weights were determined after drying at 50 C for 1 wk.

Tissue analyses. Samples were dried in a forced-air oven at 90 C and ground to pass through a 20-mesh screen (0.84-mm openings) in a Wiley mill (Arthur H. Thomas Co., Philadelphia, PA). Chloride was extracted by agitating 0.25 g of material in 50 ml of deionized water at 60 C for 30 min. The suspension was filtered and the filtrate was analyzed for Cl with a Buchler-Cotlove chloride titrator (3) (Buchler Instruments, Inc., Fort Lee, NJ). Nitrate was extracted in a solution (Orion Research, Inc., Cambridge, MA) that minimized interference from Cl during routine determinations with an NO_3 -specific electrode (model 93-07, Orion Research, Inc., Cambridge, MA). The electrode was periodically calibrated by means of the standard phenoldisulphonic

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acid method (1). K and Na were determined by flame emission spectrophotometry (model 21, Coleman Instruments Division, Oak Brook, IL), and Ca and Mg by atomic absorption (model 370, Perkin-Elmer Corp., Norwalk, CT) following standard ashing and dissolution techniques (1). Concentrations are expressed as milliequivalents per gram of dry weight.

Greenhouse nutrition studies. After incorporation of the inoculum, soils were amended with granular forms of specific nutrients in a soil blender. The following rates (microequivalents per gram of air-dry soil) were used in all experiments unless indicated otherwise: N, 16.93; and K, Ca, Mg, and Na, 17.6. Phosphate, as $\text{NaH}_2\text{PO}_4 \cdot \text{H}_2\text{O}$, was added to all treatments at 17.6 meq $\text{PO}_4\text{-P}$ per gram of air-dry soil. Care was taken in watering to avoid leaching materials from the pots. Treatments in each experiment were replicated six to eight times, and each experiment was repeated at least once.

Form of N. Soils 1 and 2 were amended with $(\text{NH}_4)_2\text{SO}_4$, NH_4NO_3 , $\text{Ca}(\text{NO}_3)_2$, and KNO_3 to give the standard concentration of N. There were eight replications (pots) per treatment, and the experiment was repeated with similar results. In addition, the experiment was repeated twice using nitrapyrin (2-chloro-6-trichloromethyl pyridine, N-Serve; Dow Chemical Co., Midland, MI) blended with the soil at $2 \mu\text{g/g}$ of soil to inhibit nitrification. Because disease severity was not influenced by nitrapyrin, it was not used in subsequent experiments. Rhizosphere soil pH was determined according to the method of Smiley and Cook (30).

Evaluation of various K and Cl salts with form of N. Soils 1 and 2 were amended with $(\text{NH}_4)_2\text{SO}_4$, NH_4Cl , $\text{NH}_4(\text{NO}_3)_2$, and $\text{Ca}(\text{NO}_3)_2$ at equivalent rates of N. Each of these treatments was subdivided and nonamended or amended with either KCl or K_2SO_4 at equivalent rates of K, so that there were three treatments for each source of N. In addition, KNO_3 was included as a separate N treatment. In other experiments, soil 2 was amended with $\text{Ca}(\text{NO}_3)_2$ at the standard N rate. The soil was then subdivided and either nonamended or amended with KCl, CaCl_2 , MgCl_2 , or NaCl at standard cation rates.

Influence of form of N, K salts, and CaCl_2 on disease severity and tissue analyses. In this experiment, which was conducted in soil 2, 100 ml of the appropriate nutrient solutions were added semiweekly to the potted soils rather than incorporating dried formulations before transplanting. The solutions consisted of (meq/l): N, 13.9; P, 5.8; and K and Ca, 11.6. One stock solution containing all of the experimental materials was prepared for each treatment as follows: $(\text{NH}_4)_2\text{SO}_4$, $(\text{NH}_4)_2\text{SO}_4 + \text{KCl}$, $(\text{NH}_4)_2\text{SO}_4 + \text{K}_2\text{SO}_4$, $(\text{NH}_4)_2\text{SO}_4 + \text{KCl} + \text{CaCl}_2$, NH_4NO_3 , $\text{NH}_4\text{NO}_3 + \text{KCl}$, $\text{NH}_4\text{NO}_3 + \text{K}_2\text{SO}_4$, $\text{NH}_4\text{NO}_3 + \text{KCl} + \text{CaCl}_2$, NH_4Cl , $\text{NH}_4\text{Cl} + \text{KCl}$, $\text{NH}_4\text{Cl} + \text{K}_2\text{SO}_4$, $\text{NH}_4\text{Cl} + \text{KCl} + \text{CaCl}_2$, $\text{Ca}(\text{NO}_3)_2$, $\text{Ca}(\text{NO}_3)_2 + \text{KCl}$, $\text{Ca}(\text{NO}_3)_2 + \text{K}_2\text{SO}_4$, $\text{Ca}(\text{NO}_3)_2 + \text{KCl} + \text{CaCl}_2$, KNO_3 , $\text{KNO}_3 + \text{KCl}$, $\text{KNO}_3 + \text{K}_2\text{SO}_4$, and $\text{KNO}_3 + \text{KCl} + \text{CaCl}_2$. All treatments received the same amount of $\text{PO}_4\text{-P}$. The experiment was conducted in infested and uninfested soil. Disease severity was assessed in the inoculated treatments, and petiole samples from the healthy controls were analyzed for K, Na, Ca, Mg, and Cl as described above. Rhizosphere soil pH also was determined for two plants in each uninfested treatment.

Influence of proportion $\text{NH}_4\text{-N}$ and the K:Cl ratios on disease severity and tissue analyses. As in the previous experiment, nutrient solutions of the appropriate composition were added semiweekly to both infested and uninfested soil 2. Treatments consisted of the following proportions of $\text{NH}_4\text{-N}$, either with or without KCl: 0.0 NH_4 , 1.0 NO_3 ; 0.2 NH_4 , 0.8 NO_3 ; 0.4 NH_4 , 0.6 NO_3 ; 0.8 NH_4 , 0.2 NO_3 ; and 1.0 NH_4 , 0.0 NO_3 . Total N, K, and PO_4 in the nutrient solutions were as described above. Proportions of the two N forms were obtained with $(\text{NH}_4)_2\text{SO}_4$, NH_4NO_3 , and $\text{Ca}(\text{NO}_3)_2$ (for the 0.0 NH_4 treatment). At 6 wk after transplanting disease severity was assessed and petioles from uninoculated treatments were sampled for analyses of K, Cl, and NO_3 .

Influence of KCl concentration under an $\text{NO}_3\text{-N}$ regime. Soil 2 was amended with $\text{Ca}(\text{NO}_3)_2$ and PO_4 at the standard rates. Treatments consisted of adding 0, 17.6, 35.2, 70.4, and 140.8 $\mu\text{eq K}$ per gram as KCl to infested and uninfested soil before transplanting. Disease severity was assessed and petioles from healthy plants were

analyzed for K and Cl as described above.

Influence of inoculum density, form of N, and KCl on root infection. An orange mutant (*ora-3*) of *Foa* was used to quantify root infection as described previously (27). Barley straw inoculum of *ora-3* was prepared as described above and used to infest soil 2. At the conclusion of the experiment, roots were washed from the soil, surface sterilized by immersion in 0.21% sodium hypochlorite (4% household bleach) for 4 min, rinsed in three changes of sterile water, and plated on Komada's medium (17) which is selective for *F. oxysporum*. After incubation for 7 days at 25 C, the number of *ora-3* colonies was divided by total root length (about 60 cm) in each plate, which had been determined by the line intersect method (28). This value was multiplied by 100 to give colonies per 100 cm of root. Twelve plates were prepared for each replication for a total root length of about 700 cm per replication.

Because plant water potential (ψ_{plant}) affects root infection (*unpublished*), these experiments were conducted in soil tension plates, similar to those described by Duniway (4), so that soil water potential (ψ_{soil}) could be controlled (28). Plants were illuminated (10 hr/day) by sodium and mercury vapor lamps (Environmental Growth Chambers, Chagrin Falls, OH) and four cool-white fluorescent lamps that provided photosynthetically active radiation of $1,200 \mu\text{E m}^{-2} \text{sec}^{-1}$ at plant height. Vacuum was applied to the tension plates during the day and released at night. This resulted in ψ_{plant} of -8.4 bars at midday and -0.8 bars at midnight as determined with an isopiestic thermocouple psychrometer. Air temperature varied between 22 and 26 C.

Soil 2 was infested with barley straw inoculum of *ora-3* at 0.1, 0.5, 1.0, 2.0, or 3.0 g/kg. Each of the infested soils was divided into four equal portions and amended with $(\text{NH}_4)_2\text{SO}_4$, $(\text{NH}_4)_2\text{SO}_4 + \text{KCl}$, $\text{Ca}(\text{NO}_3)_2$, or $\text{Ca}(\text{NO}_3)_2 + \text{KCl}$ at the standard rates of N and K, for a total of 20 treatments. All soils received the standard amount of PO_4 . The soils were dispensed into the tension plates, celery seedlings transplanted therein, and root infection assessed after 4 wk. There was one tension plate per treatment, and the experiment was repeated twice. Each of the three runs was considered a replication for statistical analysis.

Influence of proportion $\text{NH}_4\text{-N}$ on the K response. Soil 2 was infested with *ora-3* at 2.0 g inoculum per kilogram of soil and divided into six portions. Each portion was then amended with the following proportion of $\text{NH}_4\text{-N}$ as $(\text{NH}_4)_2\text{SO}_4$, with the balance being $\text{NO}_3\text{-N}$ as $\text{Ca}(\text{NO}_3)_2$: 0, 0.2, 0.4, 0.6, 0.8, and 1.0. These portions were further subdivided with half receiving KCl, and the other half receiving no additional K, for a total of 12 treatments with each receiving the standard amounts of N, $\text{PO}_4\text{-P}$ and, where appropriate, K. The soils were dispensed into the tension plates and the experiment was conducted as described above. Root infection data from the two replications per treatment and the two repetitions were analyzed together for a total of four replications.

Field experiments. A 0.49-ha block at the University of California South Coast Field Station, Irvine, was used for field studies. Soil analysis was as follows ($\mu\text{g/g}$): residual NO_3 , 3; $\text{PO}_4\text{-P}$, 30; total K, Na, Mg, and Ca, 290, 75, 890, and 67, respectively; Cl, 2.5 meq/l in the saturation extract; cation exchange capacity, 10.2 meq/100 g of soil; pH, 7.4; loam to sandy loam. The site was infested with *Foa* by spreading 40 kg of dried, ground, infected celery crowns, collected from a severely affected commercial field, then rotovating twice to a depth of 30 cm. An adjacent plot of similar soil characteristics was not infested.

Replicate plots were 12 m long by 4 m wide. Eight-week-old seedlings were transplanted at 17.8-cm intervals in single-row beds 76 cm apart. Furrow irrigation was applied weekly, and weeds were removed by hand.

The first experiment was designed to test the interactions of form of N and rates of K. Total applied N, regardless of form, was equivalent to 448 kg/ha. Because suppression of infection probably occurs at the root tip (*unpublished*), all fertilizers were spread uniformly over the soil surface in each replication, then rotovated twice to a depth of 30 cm. It was thought that this method of application, rather than periodic sidedressing, would ensure that the developing root tips would be continuously exposed to the experimental materials.

The following treatments were included (with various rates of addition of K and Cl): Ca(NO₃)₂, Ca(NO₃)₂ + three levels of KCl, Ca(NO₃)₂ + KNO₃, Ca(NO₃)₂ + K₂SO₄, KNO₃, (NH₄)₂SO₄, (NH₄)₂SO₄ + KCl, (NH₄)₂SO₄ (20% of applied N) + Ca(NO₃)₂ (80% of applied N), and the same N regime as in the latter treatment + KCl. Treble superphosphate was applied uniformly to all treatments at 280 kg of P per hectare. Incidence of vascular discoloration in the crown and plant weight were assessed at 90 days after transplanting with 40 plants in each replication.

The entire experiment was repeated simultaneously in an adjacent uninfested site and petioles from healthy plants were analyzed for K, Cl, and NO₃ at 60 days after transplanting. There were four replications per treatment.

Another experiment was conducted the following year with treatments similar to those described above except that the nutrients were sidedressed biweekly beginning 2 wk after transplanting. There were no preplant applications. Because celery requires increasing amounts of nutrients as the season progresses (36), materials were applied according to the relationship $Y = 5.08 X^{1.23}$, in which X is weeks after transplanting and Y is cumulative percent of applied material. For example, at 2 and 6 wk after transplanting, 11.9 and 46.0% of the materials had been applied, respectively. The following treatments were included: (NH₄)₂SO₄, KNO₃, KNO₃ + KCl, Ca(NO₃)₂, and Ca(NO₃)₂ + KCl. Total amounts of N and P added were 558 and 280 kg/ha, respectively. Rates of addition of K and Cl are presented in the last table.

RESULTS

Fusarium yellows was significantly more severe with NH₄- than NO₃-N (Table 1). Disease severity between the two soils was similar for (NH₄)₂SO₄, NH₄NO₃, and Ca(NO₃)₂. Severity was markedly reduced by KNO₃ compared with Ca(NO₃)₂ in soil 1; however, this effect was not observed in soil 2. Significant stunting was associated with severe symptoms of the disease.

To assess the role of K in disease suppression, the Cl and SO₄ salts of this ion also were included with each N treatment. Without exception, the use of NH₄ resulted in severe disease in both soils regardless of the inclusion of KCl or K₂SO₄ (Table 2). Again, there was significantly less disease in the Ca(NO₃)₂ treatment compared to the NH₄ treatments. The inclusion of KCl with Ca(NO₃)₂ resulted in almost complete disease control in both soils, while K₂SO₄ failed to reduce disease severity beyond that achieved with Ca(NO₃)₂ alone. Plant dry weights in the most effective NO₃ treatments were up to 6.5 times greater than in the NH₄ treatments. The reduction in disease severity by KNO₃ in soil 1 but not soil 2 was confirmed in this experiment.

Chloride salts of both Ca and Mg resulted in more severe disease when added with KNO₃ than KNO₃ alone (Table 3). Disease severity was significantly higher with CaCl₂ than MgCl₂. Dry weights of diseased plants in these two treatments were significantly lower than the control. Interestingly, disease severity in the Na and K treatments were not significantly different, but dry weight was significantly higher with KCl.

TABLE 1. Influence of form of N on severity of Fusarium yellows of celery in two soils

| Treatment ^a | Disease severity ^b | | Dry weight (g/plant) | |
|---|-------------------------------|---------------------|----------------------|--------|
| | Soil 1 ^c | Soil 2 ^c | Soil 1 | Soil 2 |
| (NH ₄) ₂ SO ₄ | 6.2 | 5.8 | 2.99 | 3.28 |
| NH ₄ NO ₃ | 4.9 | 5.0 | 3.01 | 3.47 |
| Ca(NO ₃) ₂ | 3.4 | 3.5 | 3.54 | 3.47 |
| KNO ₃ | 2.1 | 3.8 | 4.66 | 3.37 |
| LSD ^d | 1.1 | 1.2 | 0.41 | 0.37 |

^a Materials were added to the soils to give a final N concentration of 16.93 µeq/g.

^b 1 = healthy; 7 = wilted or dead.

^c Soil 1—field soil from Tulare County, CA; soil 2—greenhouse soil mix.

^d Least significant difference ($P = 0.05$).

The relationships of N forms and K sources to petiole concentrations of these nutrients and disease severity are presented in Table 4. As in previous experiments, NH₄-N, including the SO₄, NO₃, and Cl salts, always resulted in more severe disease than NO₃-N. The K ion, either as Cl or SO₄ salts, had no significant effect on disease severity when added with NH₄. Almost complete disease control was obtained with Ca(NO₃)₂ + KCl. The use of K₂SO₄ or KCl + CaCl₂ with Ca(NO₃)₂ nullified the K effect, and disease severities were not significantly different from the NH₄ treatments. KNO₃ was equivalent to Ca(NO₃)₂ in disease control; however, no additional disease reduction was observed with the addition of KCl to KNO₃. Furthermore, K₂SO₄ and KCl + CaCl₂ in combination with KNO₃ resulted in significantly more severe disease than KNO₃ alone.

Petiole analyses of the healthy controls in this experiment indicated several trends (Table 4). There were no apparent differences in K uptake among N treatments in the absence of supplemental K. However, when either KCl or K₂SO₄ was added, K uptake was reduced in the ammoniacal as compared to the NO₃ treatments regardless of the accompanying anion. The source of K, either SO₄ or Cl, had no significant effect on tissue concentrations of K in any of the N treatments. The inclusion of CaCl₂ significantly increased Ca uptake but reduced K uptake, while concentrations of Na and Mg were not generally affected. Chloride concentrations were generally higher in the presence of NH₄ with the exception of those treatments receiving K₂SO₄.

The most revealing trend in the tissue analyses concerned the ratio of concentrations of K to Cl (Table 4, Fig. 1). As expected, the smallest ratios were obtained when Cl was included as the counter ion for NH₄, K, and Ca. The largest ratios were associated with the use of K₂SO₄ in which K uptake was stimulated and Cl uptake repressed. Disease was least severe when the ratio was between 3.14 and 3.82. The coefficients of determination (R^2) for the regressions below and above 3.5 are 0.595 and 0.689, respectively, both significant at $P = 0.05$. Nutrient concentrations in the roots were generally about 50% lower than in the petioles, and the same trends were observed. Rhizosphere pH ranged between 6.0 and 6.4 with the lower values generally occurring in the NH₄ treatments. There was no statistically significant relationship between rhizosphere pH and disease severity.

The K effect was extremely sensitive to small proportions of NH₄ (Table 5). There was a significant reduction in disease severity with KCl when all of the added N was in the NO₃ form. While there was a reduction in disease with KCl when 20% of the added N was ammoniacal, the difference was not significant at $P = 0.05$. The effect was completely nullified when 40% or more of the added N was ammoniacal. Dry weights of plants were more than five-fold greater in the most effective treatments that reduced disease severity as compared to the least effective treatments.

Petiole analyses from healthy controls showed that K uptake was extremely sensitive to small concentrations of NH₄, particularly when supplemental K was added (Table 5). As in the previous experiment, disease was least severe at a K:Cl ratio of about 3.5 (Table 5, Fig. 1). There was a steep nonlinear decline in petiole NO₃ concentration as the proportion of NH₄-N increased in healthy plants (Fig. 2). Plant growth (dry weight) was not affected by form of N.

There was an optimum rate of addition of KCl above which disease severity was enhanced (Table 6). A concentration of 17.6 µeq K/g soil resulted in less disease than in the unamended control. Addition of 35.2 µeq K/g and above caused more severe disease although the former value was not significantly different from the optimum level. A K:Cl ratio of about 3.8 in the healthy controls was associated with the most effective treatment. Because the treatments in this experiment consisted solely of various rates of KCl, the two ions associated with disease suppression, the relationship between petiole concentrations of K and Cl can be viewed without the complications of other cations and anions or form of N (Fig. 3). Clearly, the upper limit for K absorption was reached while Cl continued to accumulate.

After the roles of K, Cl, and NO₃ in disease suppression had been established, the original experiment testing the form of N in soils 1

and 2 (Table 1) was repeated. In addition, petiole analyses for K and Cl were conducted. Results with the two soils were the same as observed in the earlier studies with the two soils (Table 7). There were large differences in petiole Cl concentrations between the two soils in all treatments even though Cl was not added. The addition of K in the KNO_3 treatment resulted in K:Cl ratios of 3.41 and 4.90 in soils 1 and 2, respectively. Disease suppression was associated with the lower ratio (Table 7, Fig. 1).

Root infection. The rate of root infection (colonies per 100 cm of root) as a function of added inoculum provided a sensitive indicator of the effects of form of N and KCl (Fig. 4). Slopes of the linear portions of the relationships (0.1 to 2.0 g of inoculum per kilogram of soil) for NH_4 , $\text{NH}_4 + \text{KCl}$, NO_3 , and $\text{NO}_3 + \text{KCl}$ were 18.4, 20.7, 10.6, and 4.3, respectively ($\text{LSD} = 4.97$ at $P = 0.05$). The apparent upper limits of root infection, beyond which no further infection occurred, for all but the second treatment were 39, 22, and 10 colonies per 100 cm of root, respectively. There was no obvious plateau in the $\text{NH}_4 + \text{KCl}$ treatment.

Root infection was particularly sensitive to the proportion of $\text{NH}_4\text{-N}$ (Fig. 5). When N was provided exclusively as NO_3 , rates of root infection with and without added KCl were significantly lower ($P = 0.05$). However, in the presence of 20% or more ammoniacal-N, the addition of KCl had no effect on root infection.

Field experiments. Results from field experiments generally confirmed the salutary effects of $\text{NO}_3\text{-N}$ and KCl observed in greenhouse studies (Table 8). The lowest incidence of disease was obtained with $\text{Ca}(\text{NO}_3)_2$ and KCl applied at 224 kg K/ha. Higher rates of KCl resulted in greater incidences of disease. Neither KNO_3 nor K_2SO_4 as sources of K were effective in reducing disease. Treatments receiving $\text{NH}_4\text{-N}$ exclusively had over 60% disease regardless of the addition of KCl. In contrast to greenhouse experiments, the inclusion of $\text{NH}_4\text{-N}$ at 20% of the total added N resulted in significantly less disease than the complete NH_4 treatments. There were indications of a reduction in disease incidence following the addition of KCl in the 20% $\text{NH}_4\text{-N}$ treatment.

Plant weight was significantly greater in the NH_4 treatments even though there was a higher incidence of disease (Table 8). The lower concentrations of NO_3 in petioles from the NO_3 compared to the NH_4 -treated plants indicated an N deficiency at 70 days after transplanting. Total petiole N concentrations (dry weight) for the two treatments were 2.9 and 4.1%, respectively. There were no significant differences in petiole concentration of K among treatments receiving $\text{Ca}(\text{NO}_3)_2$ and KCl at 224, 448, or 672 kg K/ha. Concentrations of Cl, however, increased substantially.

The ratio of K:Cl associated with the lowest incidence of disease was 0.91 (Table 8). This is considerably lower than the ratios

TABLE 2. Influence of form of N and K salts on severity of Fusarium yellows of celery

| Treatment ^a | Disease severity ^b | | Dry weight (g/plant) | |
|--|-------------------------------|---------------------|----------------------|--------|
| | Soil 1 ^c | Soil 2 ^c | Soil 1 | Soil 2 |
| $(\text{NH}_4)_2\text{SO}_4$ | 5.6 | 5.4 | 1.20 | 1.45 |
| $(\text{NH}_4)_2\text{SO}_4 + \text{KCl}$ | 5.0 | 5.4 | 1.22 | 1.70 |
| $(\text{NH}_4)_2\text{SO}_4 + \text{K}_2\text{SO}_4$ | 6.8 | 6.8 | 0.81 | 1.02 |
| NH_4NO_3 | 5.1 | 5.5 | 1.08 | 1.45 |
| $\text{NH}_4\text{NO}_3 + \text{KCl}$ | 4.6 | 5.0 | 2.34 | 2.84 |
| $\text{NH}_4\text{NO}_3 + \text{K}_2\text{SO}_4$ | 6.0 | 5.6 | 1.40 | 2.53 |
| NH_4Cl | 5.6 | 5.5 | 1.77 | 2.79 |
| $\text{NH}_4\text{Cl} + \text{KCl}$ | 5.4 | 5.1 | 2.25 | 3.02 |
| $\text{NH}_4\text{Cl} + \text{K}_2\text{SO}_4$ | 6.1 | 5.6 | 1.43 | 2.90 |
| $\text{Ca}(\text{NO}_3)_2$ | 3.6 | 3.1 | 4.11 | 4.86 |
| $\text{Ca}(\text{NO}_3)_2 + \text{KCl}$ | 2.1 | 2.0 | 4.92 | 6.71 |
| $\text{Ca}(\text{NO}_3)_2 + \text{K}_2\text{SO}_4$ | 3.8 | 3.9 | 4.36 | 4.43 |
| KNO_3 | 2.3 | 4.0 | 5.29 | 4.09 |
| LSD ^d | 1.3 | 0.8 | 0.51 | 0.31 |

^a Materials were added to the soils to give concentrations of N and K of 16.93 and 17.96 $\mu\text{eq/g}$, respectively.

^b 1 = healthy; 7 = wilted or dead.

^c Soil 1—field soil from Tulare County, CA; soil 2—greenhouse soil mix.

^d Least significant difference ($P = 0.05$).

associated with equivalent disease control in greenhouse studies. The ratio declined with increasing rates of KCl, as Cl but not K continued to accumulate.

When the experiment was repeated, $\text{Ca}(\text{NO}_3)_2$ was applied continually during the season to avoid the N deficiency associated with preplant applications of this material. Furthermore, only one rate of addition of KCl was used (224 kg K/ha) because larger amounts did not increase petiole concentrations of K. As in the previous year, the use of $(\text{NH}_4)_2\text{SO}_4$ resulted in the highest disease incidence (Table 9). There were no differences in yields among KNO_3 , $\text{KNO}_3 + \text{KCl}$, or $\text{Ca}(\text{NO}_3)_2$. The substantial degree of disease control with $\text{Ca}(\text{NO}_3)_2 + \text{KCl}$ was reflected in greater plant weight. Disease incidence and severity were generally higher in the second year, probably because of an increase in inoculum density after the first celery crop (33).

The addition of 291 kg of K/ha as KCl, either with $(\text{NH}_4)_2\text{SO}_4$ or $\text{Ca}(\text{NO}_3)_2$, did not significantly increase petiole K although Cl was nearly doubled. There were no significant differences in NO_3 concentrations among any of the treatments. Again, disease suppression was associated with a K:Cl ratio of close to 1.0 which occurred in the $\text{Ca}(\text{NO}_3)_2 + \text{KCl}$ treatment.

DISCUSSION

The use of NH_4 compared to NO_3 resulted in extremely severe symptoms of Fusarium yellows in celery. The effects of form of N

TABLE 3. Influence of various Cl salts on severity of Fusarium yellows of celery under an $\text{NO}_3\text{-N}$ regime

| Treatment ^a | Disease severity ^b | Dry weight (g/plant) |
|------------------------|-------------------------------|----------------------|
| KCl | 2.3 | 3.77 |
| CaCl_2 | 5.7 | 1.90 |
| MgCl_2 | 4.4 | 2.03 |
| NaCl | 2.9 | 1.56 |
| Control | 3.6 | 3.23 |
| LSD ^c | 0.9 | 0.53 |

^a Materials were added to give a final cation concentration of 17.96 $\mu\text{eq/g}$ soil.

^b 1 = healthy; 7 = wilted or dead.

^c Least significant difference ($P = 0.05$).

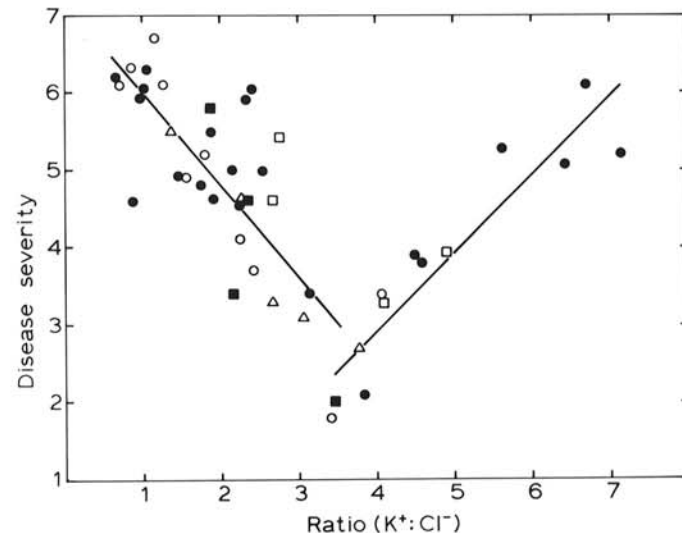


Fig. 1. Relationship between severity of Fusarium yellows of celery and ratio of concentrations of K to Cl in petioles from healthy plants. Concentrations of the two ions were affected by varying form of N in combination with different K salts and CaCl_2 (●); proportion ammoniacal-N, either with or without KCl (○); concentrations of added KCl under an $\text{NO}_3\text{-N}$ regime (Δ); and form of N in two soils with different Cl concentrations (□, ■). The coefficients of determination for the regressions below and above the ratio 3.5 are 0.595 and 0.869, respectively, both significant at $P = 0.05$. Disease severity: 1 = healthy; 7 = wilted or dead.

on disease have been well documented, particularly with *Fusarium* (34) and other vascular wilts (14). There have, however, been few published accounts of the influence of the accompanying anion or cation on root infection and disease development. The conflicting results obtained in the present study with KNO_3 in the two soils illustrate the complex interactions involved with a seemingly simple nutritional experiment. Furthermore, analysis of the roles of the common counterions requires that each of these ions be investigated for possible interactions and that all ineffective combinations be eliminated. Similarly, there is a vast literature on the effects of K (22) with virtually no studies on the role of the accompanying anion, interactions with other cations, or form of N. The complex interactions and physiological effects involving competitive uptake among anions (including NO_3^-) and cations (including NH_4^+) are well known (2,12,21) and must be addressed in

view of the potential for suppressing disease with specific nutrient regimes. Taylor et al (31) recently showed that take-all of wheat was more severe under an NO_3^- than an $\text{NH}_4\text{-N}$ regime and that yields of plants affected by take-all were greater with NH_4Cl than $(\text{NH}_4)_2\text{SO}_4$.

In the present study, the use of NH_4 clearly resulted in more severe disease than did NO_3 regardless of the accompanying ion or soil in which the tests were conducted. Moreover, the addition of KCl , but not K_2SO_4 , in conjunction with $\text{Ca}(\text{NO}_3)_2$ suppressed disease development even further. KNO_3 was significantly more effective than $\text{Ca}(\text{NO}_3)_2$ in soil 1, but significantly less effective in soil 2. Interestingly, the Cl salts of K and Na were equally effective

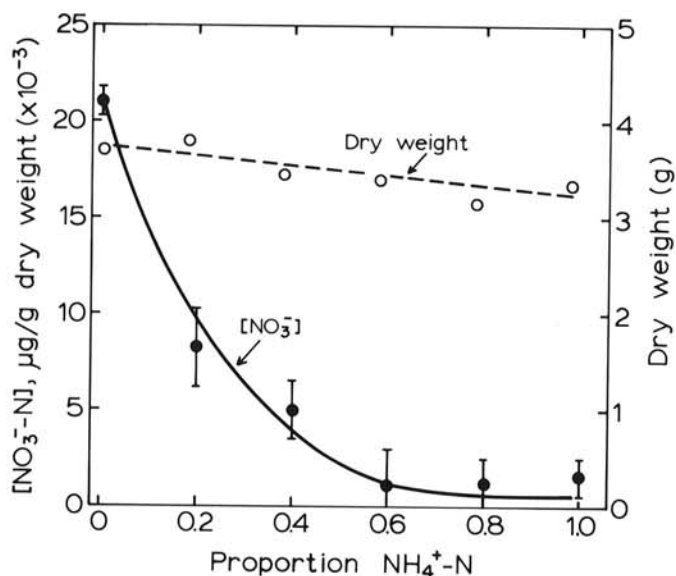


Fig. 2. Influence of the NH_4 to NO_3 ratio on petiole concentrations of NO_3 and growth of healthy celery plants.

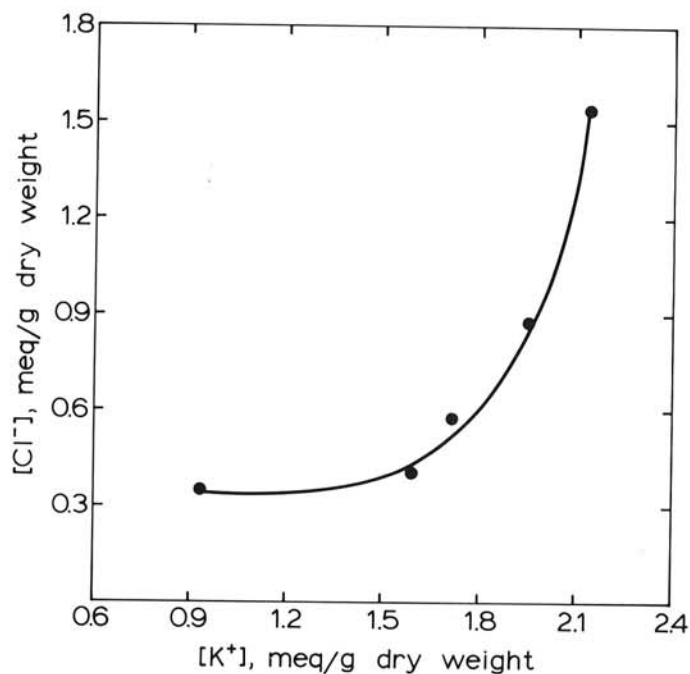


Fig. 3. Relationship between petiole concentrations of K and Cl in healthy celery plants.

TABLE 4. Influence of form on N and K, Ca, Cl, and SO_4 on severity of *Fusarium* yellows and tissue concentrations of K, Na, Mg, Ca, and Cl in celery

| Treatment ^a | Disease severity ^b | Petiole analyses (meq/g dry weight) ^c | | | | | Ratio K:Cl |
|---|-------------------------------|---|------|------|------|------|---------------|
| | | K | Na | Mg | Ca | Cl | |
| $(\text{NH}_4)_2\text{SO}_4$ | 5.9 | 0.98 | 0.13 | 0.08 | 0.12 | 0.49 | 2.00 |
| $(\text{NH}_4)_2\text{SO}_4 + \text{KCl}$ | 5.5 | 1.48 | 0.14 | 0.07 | 0.09 | 0.79 | 1.87 |
| $(\text{NH}_4)_2\text{SO}_4 + \text{K}_2\text{SO}_4$ | 6.1 | 1.41 | 0.16 | 0.10 | 0.10 | 0.21 | 6.71 |
| $(\text{NH}_4)_2 + \text{KCl} + \text{CaCl}_2$ | 6.1 | 1.14 | 0.11 | 0.10 | 0.19 | 1.12 | 1.02 |
| NH_4NO_3 | 5.0 | 0.95 | 0.15 | 0.07 | 0.13 | 0.37 | 2.57 |
| $\text{NH}_4\text{NO}_3 + \text{KCl}$ | 4.8 | 1.38 | 0.18 | 0.06 | 0.08 | 0.79 | 1.75 |
| $\text{NH}_4\text{NO}_3 + \text{K}_2\text{SO}_4$ | 5.3 | 1.29 | 0.15 | 0.11 | 0.11 | 0.23 | 5.61 |
| $\text{NH}_4\text{NO}_3 + \text{KCl} + \text{CaCl}_2$ | 4.6 | 0.72 | 0.10 | 0.07 | 0.20 | 0.88 | 0.82 |
| NH_4Cl | 6.3 | 0.89 | 0.15 | 0.09 | 0.11 | 0.83 | 1.07 |
| $\text{NH}_4\text{Cl} + \text{KCl}$ | 5.9 | 1.34 | 0.12 | 0.12 | 0.08 | 1.37 | 0.98 |
| $\text{NH}_4\text{Cl} + \text{K}_2\text{SO}_4$ | 6.0 | 1.32 | 0.16 | 0.09 | 0.10 | 0.55 | 2.40 |
| $\text{NH}_4\text{Cl} + \text{KCl} + \text{CaCl}_2$ | 6.2 | 0.98 | 0.13 | 0.10 | 0.21 | 1.50 | 0.65 |
| $\text{Ca}(\text{NO}_3)_2$ | 3.4 | 1.07 | 0.14 | 0.10 | 0.22 | 0.34 | 3.14 |
| $\text{Ca}(\text{NO}_3)_2 + \text{KCl}$ | 2.1 | 1.72 | 0.13 | 0.11 | 0.14 | 0.45 | 3.82 |
| $\text{Ca}(\text{NO}_3)_2 + \text{K}_2\text{SO}_4$ | 5.2 | 1.64 | 0.11 | 0.07 | 0.11 | 0.23 | 7.13 |
| $\text{Ca}(\text{NO}_3)_2 + \text{KCl} + \text{CaCl}_2$ | 4.6 | 1.40 | 0.11 | 0.06 | 0.24 | 0.71 | 1.97 |
| KNO_3 | 3.8 | 1.38 | 0.15 | 0.13 | 0.07 | 0.30 | 4.60 |
| $\text{KNO}_3 + \text{KCl}$ | 3.9 | 2.21 | 0.14 | 0.09 | 0.07 | 0.49 | 4.51 |
| $\text{KNO}_3 + \text{K}_2\text{SO}_4$ | 5.1 | 1.94 | 0.14 | 0.10 | 0.10 | 0.30 | 6.47 |
| $\text{KNO}_3 + \text{KCl} + \text{CaCl}_2$ | 5.0 | 1.63 | 0.09 | 0.08 | 0.20 | 0.76 | 2.14 |
| LSD ^d | 1.0 | 0.23 | 0.06 | 0.05 | 0.08 | 0.13 | 0.38 |

^a Materials were added to give N and cation concentrations of 16.93 and 17.96 $\mu\text{eq/g}$ soil, respectively.

^b 1 = healthy; 7 = wilted or dead.

^c Healthy controls were used for tissue analyses.

^d Least significant difference, $P = 0.05$.

in suppressing disease, but Na retarded plant growth. These two ions are generally considered to be interchangeable in physiological functions, although there is a wide divergence among plant species in tolerance to Na and Cl (2,18). Celery is highly tolerant of Cl, accumulating this ion in preference to SO₄ (9,35). Interestingly, the application of NaCl in commercial practice has resulted in increased yields of celery and other vegetables (9).

The ameliorating influence of K and Cl was well documented in this study. However, there were no simple relationships between petiole concentrations of either ion and disease severity. Rather, disease suppression occurred at the specific K:Cl ratio of ~3.5 (in greenhouse studies) with more severe disease occurring at ratios above and below this value. This conclusion is particularly obvious in comparing the effects of KCl and K₂SO₄ when added with Ca(NO₃)₂. Petiole concentrations of K were equivalent for both salts, but Cl concentrations differed by about two-fold resulting in K:Cl ratios of 3.8 and 7.1, respectively. The disease was almost completely controlled with KCl and extremely severe with K₂SO₄.

Factors affecting the K:Cl ratio included the form of N, availability of Ca, the predominant anion (either Cl or SO₄), and rate of addition of KCl under an NO₃ regime. Petiole concentrations of K and Cl were lower and higher, respectively, when plants were fed ammoniacal-N, either (NH₄)₂SO₄ or NH₄NO₃, as compared to Ca(NO₃)₂. The inclusion of KCl and CaCl₂ with the NH₄ treatments resulted in extremely high concentrations of Cl and correspondingly low K:Cl ratios. Competition for uptake among NH₄, Ca, and K, and between Cl and SO₄ has been demonstrated for other plants (2,12,13,35).

TABLE 5. Influence of the proportion of NH₄-N and KCl on the severity of Fusarium yellows of celery and petiole concentrations of K and Cl

| Proportion NH ₄ -N ^a | KCl | Disease severity ^b | Dry weight (g/plant) | Tissue analyses (meq/g dry weight) ^c | | Ratio K:Cl |
|--|-----|-------------------------------|----------------------|---|------|------------|
| | | | | K | Cl | |
| 0 | + | 1.8 | 5.23 | 1.67 | 0.49 | 3.41 |
| 0 | - | 3.4 | 4.07 | 1.14 | 0.28 | 4.07 |
| 0.20 | + | 3.9 | 4.10 | 1.37 | 0.57 | 2.40 |
| 0.20 | - | 4.5 | 3.70 | 0.95 | 0.42 | 2.26 |
| 0.40 | + | 4.9 | 3.25 | 1.08 | 0.70 | 1.54 |
| 0.40 | - | 5.2 | 1.93 | 0.83 | 0.46 | 1.80 |
| 0.80 | + | 6.3 | 1.05 | 0.99 | 1.17 | 0.85 |
| 0.80 | - | 6.1 | 1.14 | 0.65 | 0.51 | 1.27 |
| 1.0 | + | 6.1 | 0.98 | 0.92 | 1.34 | 0.69 |
| 1.0 | - | 6.7 | 0.89 | 0.67 | 0.58 | 1.15 |
| LSD ^d | | 1.2 | 0.73 | 0.23 | 0.16 | 0.23 |

^aThe treatment receiving no NH₄-N was prepared with Ca(NO₃)₂. All others received various amounts of (NH₄)₂SO₄ and NH₄NO₃. Total N and K were equivalent to 16.93 and 17.96 μeq/g soil, respectively.

^b1 = healthy; 7 = wilted or dead.

^cHealthy controls were used for tissue analyses.

^dLeast significant difference, P = 0.05.

TABLE 6. Influence of concentration of KCl on severity of Fusarium yellows of celery and ratio of tissue concentrations of K to Cl under an NO₃-N regime

| Concentration of added K as KCl (μeq/g soil) | Disease severity ^a | Petiole concentration (meq/g) ^b | | Ratio K:Cl |
|--|-------------------------------|--|------|------------|
| | | K | Cl | |
| 0 | 3.4 | 0.93 | 0.35 | 2.66 |
| 17.6 | 2.3 | 1.59 | 0.42 | 3.79 |
| 35.2 | 3.1 | 1.70 | 0.56 | 3.04 |
| 70.4 | 4.6 | 1.96 | 0.88 | 2.22 |
| 140.8 | 5.5 | 2.13 | 1.54 | 1.38 |
| LSD ^c | 0.9 | 0.20 | 0.23 | 0.64 |

^a1 = healthy; 7 = wilted or dead.

^bHealthy controls were used for tissue analyses.

^cLeast significant difference, P = 0.05.

Moreover, the extreme sensitivity of disease reaction to small proportions of NH₄-N corresponded to alterations in the ratio. In this case, 20% NH₄-N plus KCl resulted in an 18% reduction in K and a 16% increase in Cl concentrations, while without additional

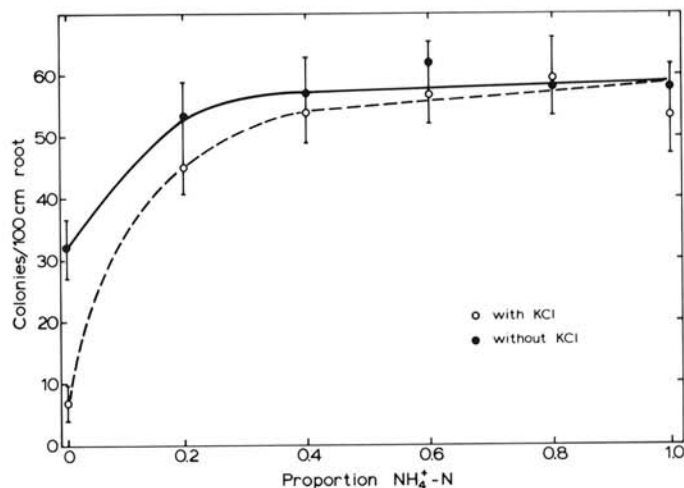


Fig. 4. Influence of the NH₄ to NO₃ ratio with or without added KCl on rate of celery root infection by *Fusarium oxysporum* f. sp. *apii*.

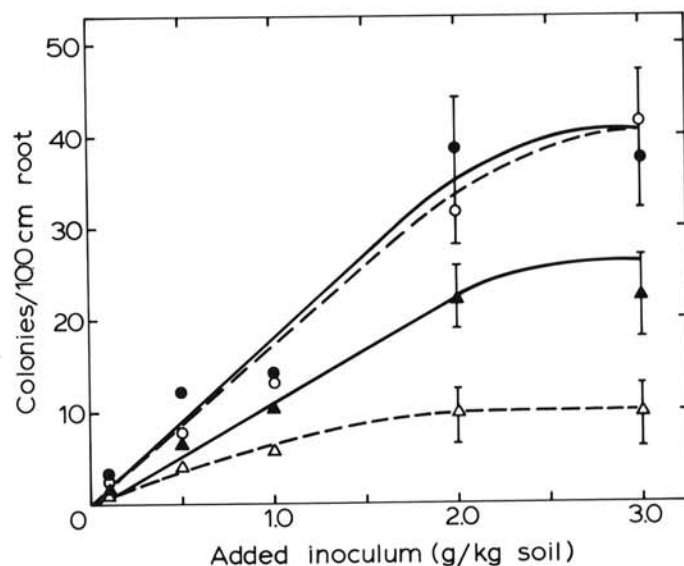


Fig. 5. Influence of inoculum density on rate of celery root infection by *Fusarium oxysporum* f. sp. *apii* as affected by NH₄ with (o) or without (•) added KCl or NO₃ with (Δ) or without (▲) added KCl.

TABLE 7. Influence of form of N on Fusarium yellows of celery and concentrations of K and Cl in petioles of plants grown in two soils

| Treatment ^a | Disease severity ^b | | Petiole concentrations (meq/g) in indicated soil ^d | | | | Ratio K:Cl | |
|---|-------------------------------|---------------------|---|------|------|------|------------|------|
| | Soil 1 ^c | Soil 2 ^e | K | | Cl | | 1 | 2 |
| (NH ₄) ₂ SO ₄ | 5.8 | 5.8 | 1.14 | 1.01 | 0.61 | 0.37 | 1.87 | 2.73 |
| NH ₄ NO ₃ | 4.6 | 4.6 | 1.03 | 0.80 | 0.45 | 0.30 | 2.29 | 2.67 |
| Ca(NO ₃) ₂ | 3.4 | 3.3 | 1.07 | 1.09 | 0.50 | 0.27 | 2.14 | 4.04 |
| KNO ₃ | 1.8 | 3.9 | 1.98 | 1.47 | 0.58 | 0.30 | 3.41 | 4.90 |
| LSD ^c | 1.2 | 0.9 | 0.31 | 0.20 | 0.13 | 0.09 | 0.28 | 0.16 |

^aMaterials were added to the soils to give a final N concentration of 16.93 μeq/g.

^b1 = healthy; 7 = wilted or dead.

^cSoil 1—field soil from Tulare County, CA; soil 2—greenhouse soil mix.

^dHealthy controls were used for chemical analyses.

^eLeast significant difference, P = 0.05.

KCl there was a 17% decrease in K and a 50% increase in Cl. It appears that celery is much more effective in absorbing Cl than K, although Cl is generally present in extremely small concentrations in nonsaline soils (1,25,35). In addition, the relationships among proportion of added $\text{NH}_4\text{-N}$, petiole concentrations of NO_3 , and dry weight indicate that celery plants preferentially absorb NH_4 and are capable of utilizing this ion as the sole source of N. Inhibition of uptake and enzymatic reduction of NO_3 by small amounts of NH_4 has been documented for several other plant species (12). Thus, it is not surprising that small proportions of $\text{NH}_4\text{-N}$ greatly enhanced Cl uptake inasmuch as this is the preferred counter-ion for the absorption of cations (2,12,13,20). Regardless of the mechanism by which it was affected, the K:Cl ratio appeared to be the primary determinant of disease severity, rather than form of N or absolute concentrations of K, Cl, or NO_3 .

This conclusion was further substantiated by the interactions of added KCl under an NO_3 regime, K:Cl ratio, and disease severity. The addition of increasing amounts of KCl resulted in a disproportionate uptake of the two ions such that the ratio and disease severity were greatly affected. Clearly, the upper limit for K absorption was surpassed in this experiment, while Cl uptake was

unimpeded. Limitations on K uptake have been demonstrated for other plants (2).

When the centrality of the K:Cl ratio was established, the reason for the contradictory results with KNO_3 in soils 1 and 2 were obvious. Soil 1, collected from a moderately saline area, provided the plant with an adequate supply of Cl, while soil 2 did not. Thus, even though KCl was not added to soil 1, a favorable K:Cl ratio was established under an $\text{NO}_3\text{-N}$ regime.

While the effects of form of N, particularly small amounts of NH_4 , K, and Cl on disease severity were striking, the severity index is nonparametric and difficult to analyze quantitatively. However, rates of root infection provided absolute numerical data which were amenable to quantitative analyses. Inoculum competence, *sensu* Grogan et al (8), as affected by form of N and KCl was assessed by comparing the slopes of the linear portions of the regressions that relate inoculum level to rate of root infection. Thus, KCl had no effect on competence under an NH_4 regime. The use of KNO_3 alone reduced competence by about 50%, and the addition of KCl resulted in a further reduction of about 30%. Moreover, the K effect was completely nullified in the presence of 20% NH_4 . By this technique it is concluded that a propagule under

TABLE 8. Influence of form of N and K on petiole concentrations of K and Cl and incidence of Fusarium yellows of celery in the field. Materials were applied by preplant broadcasting followed by incorporation with a rotovator

| Treatment ^a | Rate of amendment (kg/ha) | | Disease incidence (%) ^b | Plant weight (kg) ^c | Tissue concentrations (meq/g dry weight) ^d | | | Ratio K:Cl |
|---|---------------------------|-----|------------------------------------|--------------------------------|---|------|---------------|------------|
| | K | Cl | | | K | Cl | NO_3 | |
| $\text{Ca}(\text{NO}_3)_2$ | 0 | 0 | 16.2 | 0.815 | 0.44 | 0.12 | 0.08 | 3.67 |
| $\text{Ca}(\text{NO}_3)_2$ + KCl | 224 | 207 | 3.0 | 0.817 | 0.53 | 0.56 | 0.07 | 0.95 |
| $\text{Ca}(\text{NO}_3)_2$ + KCl | 448 | 417 | 7.5 | 0.861 | 0.55 | 0.67 | 0.07 | 0.82 |
| $\text{Ca}(\text{NO}_3)_2$ + KCl | 672 | 620 | 28.7 | 0.498 | 0.56 | 0.84 | 0.03 | 0.67 |
| $\text{Ca}(\text{NO}_3)_2$ + KNO_3 | 448 | 0 | 18.7 | 0.453 | 0.55 | 0.33 | 0.03 | 1.67 |
| $\text{Ca}(\text{NO}_3)_2$ + K_2SO_4 | 448 | 0 | 16.3 | 0.679 | 0.58 | 0.26 | 0.06 | 2.23 |
| KNO_3 | 448 | 0 | 17.4 | 0.634 | 0.54 | 0.28 | 0.05 | 1.93 |
| $(\text{NH}_4)_2\text{SO}_4$ | 0 | 0 | 61.2 | 1.223 | 0.38 | 0.64 | 0.16 | 0.59 |
| $(\text{NH}_4)_2\text{SO}_4$ + KCl | 448 | 417 | 66.9 | 1.042 | 0.47 | 1.09 | 0.14 | 0.43 |
| $(\text{NH}_4)_2\text{SO}_4$ (20% N) + $\text{Ca}(\text{NO}_3)_2$ (80% N) | 0 | 0 | 28.7 | 0.725 | 0.44 | 0.69 | 0.09 | 0.64 |
| $(\text{NH}_4)_2\text{SO}_4$ (20% N) + $\text{Ca}(\text{NO}_3)_2$ (80% N) + KCl | 448 | 417 | 19.2 | 0.544 | 0.54 | 0.87 | 0.03 | 0.63 |
| LSD ^e | | | 11.8 | 0.272 | 0.08 | 0.16 | 0.08 | 0.12 |

^aTotal applied N was 448 kg/ha.

^bPercent of plants with vascular discoloration in crown at 90 days after transplanting.

^cFresh weight determined at 90 days after transplanting.

^dHealthy controls were used for tissue analysis at 60 days after transplanting.

^eLeast significant difference, $P = 0.05$.

TABLE 9. Influence of form of N and K on incidence of Fusarium yellows and petiole analyses of K, Cl, and NO_3 in field-grown celery. Materials were provided by biweekly sidedress applications

| Treatment ^a | Total added nutrients (kg/ha) | | Disease incidence (%) ^b | Plant weight (kg) ^c | Petiole analyses (meq/g dry weight) | | | Ratio K:Cl |
|----------------------------------|-------------------------------|-----|------------------------------------|--------------------------------|-------------------------------------|------|---------------|------------|
| | K | Cl | | | K | Cl | NO_3 | |
| $(\text{NH}_4)_2\text{SO}_4$ | 0 | 0 | 80.0 | 3.6 | 0.52 | 0.30 | 0.16 | 1.73 |
| KNO_3 | 1,628 | 0 | 42.5 | 4.5 | 0.63 | 0.21 | 0.14 | 3.00 |
| KNO_3 + KCl | 1,920 | 269 | 56.2 | 3.9 | 0.74 | 0.50 | 0.12 | 1.48 |
| $\text{Ca}(\text{NO}_3)_2$ | 0 | 0 | 52.5 | 5.2 | 0.49 | 0.26 | 0.12 | 1.88 |
| $\text{Ca}(\text{NO}_3)_2$ + KCl | 291 | 269 | 16.2 | 5.8 | 0.54 | 0.58 | 0.13 | 0.93 |
| LSD ^d | | | 19.3 | 0.9 | 0.08 | 0.11 | 0.05 | 0.09 |

^aTotal N added was 558 kg/ha.

^bPercent of plants with vascular discoloration in crown at 90 days after transplanting.

^cFresh weight of 10 plants determined at 60 days after transplanting.

^dLeast significant difference ($P = 0.05$).

an ammoniacal regime was 4.6 times as likely to cause a root infection as under an NO₃ plus KCl regime. Furthermore, the differences in plateaus in root infection with increasing inoculum density indicate that either there were about four times as many susceptible sites under the former regime as compared to the latter, or these sites were more susceptible to fungal invasion. There was no obvious plateau in the NH₄ + KCl treatment; however, this graphical deduction may have been obscured by the relatively large standard error. Root tips are known to be the sites of infection for several vascular pathogens (15), including *Foa* in celery (11,27). In observing patterns of colony development during the root infection assays, particularly on long unbranched segments, it was obvious that colonies were smaller and spaced farther apart in the NO₃ treatments. Thus, theory suggests (15) that the root tip was less susceptible to infection as it advanced through the soil.

The specific K:Cl ratio associated with disease suppression, and the similarly shaped curves for rate of root infection and petiole concentrations of NO₃ as functions of proportion of NH₄-N, suggest that certain physiological processes are involved in the K effect. Certainly, the mechanisms of uptake of K and Cl, their interactions with NH₄ in the absorption process, and their function in the root must be considered. In addition, differences in amino acid metabolism between NO₃- and NH₄-fed plants (12) may play a role. Changes in rhizosphere pH, as suggested by Smiley and Cook (29,30), did not seem to be a factor in these studies.

The disease-suppressive effect of the specific K:Cl ratio, rather than absolute petiole concentrations of these ions, suggests that the maintenance of charge balance is a primary determinant in the response. It is well known, for example, that in the absence of a compatible inorganic anion such as Cl, uptake of K and other cations stimulates carboxylate synthesis, primarily malate, such that a charge balance is maintained within narrow limits (13,20,23). One of the primary functions of K and Cl is osmoregulation (2,23). When K is unavailable, simple sugars and carboxylates fulfill this role (20). Thus, it is to be expected that during diurnal cycling of plant water potential in the absence of Cl, enhanced K uptake would be associated with accelerated rates of malate synthesis and exudation. Such was the case for celery (*unpublished*). Inasmuch as *Fusarium* spp. (7), including *Foa* (33), can utilize various sugars and carboxylates as energy sources, it is tempting to speculate that the process of osmoregulation and the fundamental mechanism of K uptake, namely charge balance by organic anion synthesis, provide the pathogen with soluble substrates before the initiation of pathogenesis.

Results obtained in the field were encouraging and generally confirmed greenhouse findings. Specifically, there was an optimum rate of addition of K (as KCl) above which disease incidence was increased. Furthermore, K₂SO₄ was ineffective and a small proportion of NH₄-N reduced the K effect, though not as drastically as in the greenhouse. The latter effect was probably caused by nitrification in the field as compared to the inhibition of nitrification in sterilized soils in the greenhouse. This is clearly seen in the higher tissue concentrations of NO₃ in the NH₄ treatments in the field.

Perhaps the most significant finding in the field was the relationship between added KCl and petiole concentrations of K and Cl. The addition of 224 kg of K/ha under an NO₃ regime resulted in a 17% increase in tissue concentration of this ion without affecting plant growth as compared to the unamended control. However, additions of up to 672 kg/ha did not increase K uptake further. Thus, the soil apparently provided most of the plant's K requirement without supplemental additions. On the other hand, petiole concentrations of Cl were directly related to rates of addition of KCl and were higher with NH₄. As in greenhouse studies, Cl uptake was uninhibited in comparison to K.

The K:Cl ratio at which disease suppression occurred was approximately 1.0. The apparent discrepancy in ratios between greenhouse- and field-grown plants probably resulted from the continuous accumulation of Cl as compared to K, the later stage of sampling, and higher rates of transpiration in the field. However, disease suppression was related to the ratio rather than absolute concentrations of either ion.

Preplant application of Ca(NO₃)₂ resulted in smaller plants and lower petiole concentrations of NO₃ as compared to those that had received the NH₄ treatments. This was probably caused by a portion of the NO₃ being denitrified or leached beneath the effective rooting depth. Because the soil contained adequate amounts of K, and Cl is extremely mobile in the soil solution (19), the task of simultaneously manipulating the K:Cl ratio and providing the plant with NO₃ was greatly simplified. Thus, the following year excellent disease control (again associated with a K:Cl ratio of about 1.0) was achieved by intermittent sidedress applications of KCl and Ca(NO₃)₂ such that petiole concentrations of NO₃ and K were sufficient for maximum plant growth (6).

Results from this study will be useful in making specific fertility recommendations for controlling *Fusarium* yellows on the basis of soil analyses. Water-soluble Cl in the soil is a good indicator of Cl availability (16), and there are several tests for available K (6,24,25,32). Thus, depending on soil analyses, applications of KNO₃, Ca(NO₃)₂, KCl, or other Cl salts should result in appreciable disease control.

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