

ABSTRACT

MEYER, KAREN MICHELLE. Impact of nitrogen management strategies on yield, N-use efficiency, and *Rhizoctonia* diseases of Irish potato. (Under the direction of Marc A. Cubeta and H. David Shew)

An interdisciplinary approach, integrating aspects of plant pathology, soil science and horticulture, were used to study tuber initiation, plant density, N-use efficiency, *Rhizoctonia* disease development of Irish potatoes influenced by N management strategies. The impact of N rate and seed piece spacing on tuber yield and N uptake efficiency in the potato varieties Atlantic and Superior was examined in a field project conducted at the Tidewater Research Station in Plymouth, NC. A split-split field design was used with urea applied to main plots at rates of 0, 56, 112, or 168 kg N ha⁻¹, seed piece spacing varied in the sub-plot at 23 or 30 cm, and potato variety in the sub sub-plot. In 2000 and 2001, Atlantic produced a greater total yield than Superior at the 23 and 30 cm spacing, and both varieties yielded higher at a 23 cm spacing compared to a 30-cm spacing. Total and marketable yield in plots with 56, 112, or 168 kg N ha⁻¹ urea were not different, but the two highest N rates had significantly ($P=0.05$) greater yield than the 0 N treatment. Averaged across variety and spacing, total N uptake was 58 kg N ha⁻¹ with 0 N, and increased to 100 Kg N ha⁻¹ with 168 N ha⁻¹. Data suggests that growers could apply N at rates of 56-112 kg N ha⁻¹ with optimal seed piece spacing for Atlantic and Superior to produce high quality yields and reduce the potential of polluting surface and ground water reservoirs.

The form and rate of nitrogen can affect the incidence and severity of many plant disease. The effects of N rate and form on hyphal growth of *Rhizoctonia solani*

anastomosis group 3 (AG3), development of Rhizoctonia diseases, and the yield of Irish potato were determined in growth chamber, laboratory, and field studies. A significant interaction of N form and N rate on mycelial growth *in-vitro* was observed with *R. solani* grown on minimal slats culture medium with selected N sources supplying nitrate or ammonium N at rates of 0, 50, 100, and 150 ppm. High rates of ammonium sulfate and urea (ammonium N sources) produced the greatest mycelial dry weight than nitrate N sources. To evaluate the effect of N form and rate in the field, three field experiments (two in Plymouth and one in Lewiston, NC) were arranged in a split plot design to evaluate the effects of N rate (0, 84, or 168 kg N ha⁻¹) and form (nitrate vs. ammonium) supplied as NaNO₃ or urea on potato yield of Atlantic and Rhizoctonia disease incidence and severity. At the Plymouth location in 2000 and 2001, the highest total yields were similar for the 84 and 168 kg N ha⁻¹ and the 0 N treatments. A significant effect of *R. solani* was observed at Plymouth, with greater total and marketable yields in the non-infested compared to infested plots for both years. Stolon infection was significantly greater in the 168 kg N ha⁻¹ urea treatment than in the 84 kg N ha⁻¹ NaNO₃ plots at Plymouth 2001. A Phytotron experiment was conducted to determine effects of N form (supplied as NaNO₃ and urea) and rate (0, 0.25, and 0.50 g N L⁻¹) applied to either infested or non-infested pots *R. solani*. In two experiments, the highest and lowest incidence of stem and stolon canker occurred at the high rate of urea and the low rate of Sodium nitrate, respectively. The use of reduced rates of NaNO₃ in potato production may reduce the incidence of Rhizoctonia disease, give optimum yields and reduce the risk of undesirable environmental effects.

**IMPACT OF NITROGEN MANAGEMENT STRATEGIES ON YIELD, N-USE
EFFICIENCY, AND RHIZOCTONIA DISEASES OF IRISH POTATO**

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BIOGRAPHY

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DEDICATION

This thesis is dedicated with love to my mother and father, George and Lita Meyer.

The completion of my thesis is a result of the support, encouragement, and the many sacrifices they have made over the past 26 years so that I could accomplish my goals.

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INTRODUCTION

Significant changes have been observed in potato production over the past 40 years in industrialized countries, while total area planted with potatoes has decreased, higher productivity per unit area has resulted in a steady increase in annual production (Sieczka *et al*, 1993). Potatoes are important to both industrialized and developing countries as a source of income and are a staple food for the world population.

The observed increase in potato production can be attributed to modern agricultural practices that include the abundant use of inorganic fertilizers and pesticides that help ensure high quality yields. More pesticides are used in potato production than for any other crop worldwide (Sieczka and Thornton, 1993; Arsenault and Malone, 1999). The increase in productivity made possible by chemical use has been viewed as a positive outcome for economic reasons. Increased use of agricultural chemicals, however, poses a threat to the stability of the environment and our ecosystems. The development of new production and disease management technologies are increasingly more important to continue production of high quality potatoes, and at the same time maintain the quality of the environment and conserve natural resources in sustainable agriculture (Sieczka and Thornton, 1993).

Rhizoctonia Stem Rot and Canker. *Rhizoctonia solani*, anastomosis group 3 (AG3), is a common soilborne pathogen of a great genetic diversity. Rhizoctonia canker and black scurf of potato are found worldwide. The pathogen *Rhizoctonia solani* was originally described by Julius Kühn on potato in 1858 (Baker and Martinson, 1970; Banville *et al* 1996). *Rhizoctonia solani* is a basidiomycete that does not produce asexual spores (conidia), and only occasionally produces sexual spores (basidiospores). The asexual

stage (anamorph) is known as *R. solani* and the teleomorph as *Thanatephorus cucumeris*. In nature, *R. solani* primarily survives asexually and exists as vegetative mycelium and/or sclerotia (Banville *et al* 1996). Unlike many basidiomycete fungi, the basidiospores of *T. cucumeris* are not enclosed in a fleshy, fruiting body or mushroom. The sexual fruiting structures and basidiospores were first observed and described in detail by Prillieux and Delacroix in 1891 (Banville *et al* 1996).

Identification of *R. solani*. Vegetative mycelium of *R. solani* is colorless when young but becomes a tan to dark brown color with age. Young vegetative hyphae have multinucleate cells (usually more than three nuclei per hyphal cell) and branch at the point of origin at 90° angles (Banville *et al*, 1996). The formation of a septum in the branch near the origin and a prominent septal-pore apparatus also are characteristic features of *Rhizoctonia* hyphae. The doughnut shaped dolipore septa allows for movement of cytoplasm, mitochondria, and nuclei from cell to cell.

The hyphae of *Rhizoctonia* are capable of anastomosis, or hyphal fusion. In 1969, J. R. Parmeter and colleagues introduced the concept of “hyphal anastomosis” as a means of characterizing and identifying isolates of *Rhizoctonia* (Baker and Martinson, 1970; Banville *et al*, 1996). The concept implies that isolates of *Rhizoctonia* that have the ability to recognize and fuse with each other are genetically related, whereas isolates of *Rhizoctonia* that do not have this ability are genetically unrelated (Banville *et al*, 1996). Using this concept, isolates of *R. solani* are classified according to anastomosis groups or AG. Isolates of *R. solani* pathogenic to potato are predominately AG-3.

Disease Cycle. The pathogen can survive for many years as small (1–3-mm diameter) irregularly shaped, brown to black sclerotia on tubers or in soil, or as mycelium on plant

debris in the soil (Baker and Martinson, 1970, Blair, 1943). *R. solani* colonizes soil organic matter. Sclerotia and/or mycelium present in soil or on plant tissue germinate to produce hyphae of the fungus that can infect a wide range of food and fiber crops (Baker and Martinson, 1970).

Sclerotia germinate to produce hyphae that infect potato stems or emerging sprouts under favorable conditions. Chemical stimulants, released by actively growing plants or decomposing plant residues (Baker and Martinson, 1970; Banville *et al*, 1996), stimulate germination of sclerotia and new hyphal growth. After contacting plant tissue, the fungus continues to grow on the external surface of the plant. Host penetration occurs via the production of structures, appressoria or infection cushions, depending on the host and environment (Banville *et al*, 1996).

The infection process requires the production of many different extracellular enzymes that degrade components of the plant cell walls (Banville *et al*, 1996). After the fungus kills the plant cells, hyphae continue to grow and colonize dead tissue and produce sclerotia. Roots and stolons can be invaded throughout the growing season. Sclerotia formation on new tubers can be initiated at any time depending on environmental conditions, but usually occurs near the end of the growing season as plants start to senesce. Maximum development of sclerotia usually occurs as tubers remain in the soil after death of vines.

Populations of *Rhizoctonia* usually increase in soils where little or no crop rotation is practiced. Optimum environmental conditions for the pathogen are low soil temperatures and high moisture levels. The optimum soil temperature for disease development on potato is 18 C, and development decreases with increasing soil

temperatures (Blair, 1943; Baker and Martinson, 1970, Banville *et al*, 1996). High soil moisture levels in soil, especially those found in poorly drained soils, also increase sclerotia formation on tubers.

Associated yield losses with this disease are documented at approximately 5-30% in North Carolina, with 10-15% most common each season (Banville *et al*, 1996). High levels of resistance to *R. solani* have not been identified in potato. Seed treatments also are not effective in heavily infested soils. However, the use of disease-free seed combined with the seed treatments can also be used. Seed treatments with fungicides are effective in reducing inoculum present on potato tubers and the incidence and severity of Rhizoctonia disease (Meyer *et al*, 2000). However, the returns to the growers may not justify the cost associated with using fungicide treatments. Management options for *R. solani* on potato are limited.

Nitrogen Fertilization and Potato Production. The fate of N fertilizers used in potato production is an important environmental concern. Nitrogen is often excessively in potato production to avoid losses in yield and a reduction in tuber quality (Arsenault and Malone, 1999, Crozier *et al*, 2000). Recommended N applications are 112-168 kg N ha⁻¹ (Soaud *et al*, 1990; Tucker *et al*, 1996; Voss, 1997; Sanders *et al*, 1998), but typically growers apply rates of 168-224 N ha⁻¹ (Tucker, *et al*, 1996). As a result, high residual levels of N have accumulated in the soils of eastern North Carolina (Gardner & Jones, 1975). Numerous studies document yield responses to N applications (Gardner and Jones, 1975; McCollum, 1978, Vos, 1997). Nitrogen input has often been based solely on economic reasons (Nelson and Hauck, 1965). Until recently, only the effect of nitrogen rate on the quality of the potato crop was taken into account, and environmental

considerations did not play a major role in N recommendations. Excess N inputs used in potato cropping systems were eventually lost to the environment. N losses are known to cause undesirable changes as a pollutant of surface and ground water reservoirs (Nelson and Hauck, 1965).

In many countries, including the United States, legislation is being enforced or developed to limit excess N into the environment. In North Carolina, N in agricultural runoff is considered a water pollutant in the Abermarle-Pamlico drainage basin and future legislation will help to protect this valuable natural resource (Spruill *et al*, 1998).

Research is necessary to maximize nitrogen use efficiency of potato crops so that lower rates of N can be applied and pollution of the environment can be minimized. Nitrogen may also affect disease development in many host-pathogen systems. The rate and form of N can increase or decrease diseases of many crops (Huber, 1966; Huber and Watson, 1970 and 1972; Huber *et al*, 1965, Kommendahl, 1984).

Characteristics of Potato Plants. The Irish or white potato (*Solanum tuberosum* L.) is an important food crop worldwide and is grown in most countries with a temperate climate. It is believed that the Irish potato originated in the Andes Mountains of South America and gradually was introduced into new areas (Sieczka and Thornton, 1993). In North Carolina, potatoes are grown primarily in the northeastern part of the state and are used for potato chip processing (Creamer *et al*, 1999). In most fields, potatoes are planted in rotation with grain corn or soybean. Yields throughout the southeastern (18 Mg ha⁻¹) and southern (16.2 Mg ha⁻¹) states are lower than those in other U.S production regions (18.8-31.2 Mg ha⁻¹) due to diseases, soil type, climate, and production practices (Sieczka and Thornton, 1993; Crozier *et al*, 1999). There are

approximately 9000 ha of potatoes planted in North Carolina with an average yield of 22.4 T ha⁻¹ in North Carolina (Creamer *et al*, 1999).

The potato plant is an annual, herbaceous plant with potential perennial capacity because of reproduction via tubers. Potato plants may be propagated from true seed, but commercial production of most potatoes is by vegetative propagation. The vegetative propagule, or seed piece, is composed of the lateral buds formed on the tuber are commonly referred to as “eyes”. Tubers are formed at the tips of stolons as a lateral proliferation of the storage tissue, and are the result of rapid cell division and enlargement. Vascular tissue initially forms with sieve tubes, companion cells, and conducting parenchyma elements as the tuber enlarges (Hooker, 1981). Carbohydrates are stored within storage parenchyma of the pith and cortex in the form of starch granules (Hooker, 1981).

The tuber surface permits or excludes the entrance of pathogens, regulates rate of gas exchange or water loss, and protects against mechanical damage. If wounded, the surface can regenerate through biochemical reactions that affect disease incidence and severity, and seed germination and performance (Hooker, 1981). Growers cut seed tubers prior to planting, which enables the grower to maximize the number of plants obtained from a single seed tuber (Sieczka and Thornton, 1993). However, this is not a common practice among NC growers. Once cut, wound healing is allowed to occur prior to planting. Suberin forms on cut surfaces within 3-5 days. A cork cambium layer develops under the suberized cells giving rise to a wound periderm (Hooker, 1981). The rate of wound healing is dependent upon the environment and physiological age of the tuber.

Impact of Nitrogen on Plant Development. Nitrogen becomes available through biological mineralization of soil organic matter, microbial fixation of atmospheric N, or via organic and inorganic fertilizer amendments (Frederick, 1956; Allison, 1966; Parker, 1972). Mineralization and biological fixation are dynamic processes providing nitrogen initially in the ammoniacal or reduced form. The subsequent oxidation of NH_4^+ to NO_3^- results in the availability of several forms of N for plant growth (Frederick, 1959). Unlike the positively charged NH_4^+ ion, the negatively charged NO_3^- is freely mobile in the soil solution and subject to leaching and denitrification (Allison, 1966).

Ammonium is readily used for synthesis of amino acids and other compounds that contain reduced nitrogen (Allison, 1966). Absorption of ammonium therefore causes a great demand for carbon, and a depletion of carbohydrates can occur under certain conditions. Assimilation of ammonium is usually rapid and there is seldom much accumulation of free ammonium in tissue (Frederick, 1959; Parker, 1972). Nitrate nitrogen must be reduced before it can be assimilated. The immediate demand for carbohydrates is less and nitrate nitrogen can promote an accumulation of organic acids (Beevers and Gageman, 1969; Allison, 1966). The metabolic changes resulting from the absorption of ammonium and nitrate ions are affected by such factors as climate, stage of growth, plant species, and the availability of other nutrients (Robbins, 1937; Parker, 1972).

Early symptoms of nitrogen deficiency are a general yellowing of leaves, or chlorosis, due to an inhibition of chlorophyll synthesis (Webster, 1959). Reduction in photosynthesis causes a nitrogen deficient plant to lack not only essential amino acids, but also the machinery for synthesis of carbohydrates and carbon skeletons needed for

vital processes (Robbins, 1937; Webster, 1959; McKee, 1962; Allison, 1966). Before chlorosis develops, however, carbohydrates including starch may accumulate since they are not utilized for protein synthesis due to an amino acid deficiency (Webster, 1959).

Nitrogen Influence on Plant Disease. Yield and tuber quality can be adversely affected by excess fertilizer applications due to direct physiological changes in the host and enhanced disease development. Although most crops can use either form of N for growth, plant composition, microbial activity in the rhizosphere, availability of minor elements, and the interactions of factors that influence disease severity are affected by the form of N utilized (McNew, 1953; Shear and Wingard, 1944; Smiley, 1974; Huber and Watson, 1972). Plant nutrition is a major component of disease management and is known to influence stages in the disease cycle of multiple host-pathogen systems (Kommendahl, 1984).

The dynamic interactions of the environment with the plant and pathogen remain areas of active research. All essential mineral elements are known to influence disease incidence or severity (Huber and Watson, 1972). Soil fertility also directly affects plant parasitic organisms (Huber and Watson, 1972). Many studies have examined the relationship of disease severity and nitrogen. Nitrogen can increase disease resistance by promoting plant health, enabling a host plant to escape infection with an arsenal of defense mechanisms like phytoalexins and enzymes (Kommendahl, 1984).

High levels of nitrogen also can delay maturity and senescence of plants, making them highly succulent for pathogens (Kommendahl, 1984). Increased disease incidence and severity have often been directly related to high rates of nitrogen applications suggesting that N concentration is an important factor in disease development (Huber and

Watson, 1972). There are many factors that affect the role of nitrogen in a specific host-pathogen interaction such as the time and rate of N application, stability, ratio of NH_4^+ to NO_3^- , and residual N in soil (Huber and Watson, 1972). Because of these factors, the effect of N on plant health or disease has to be determined for each crop and disease interaction within a given environment.

The form of nitrogen appears more important than rate (Huber *et al*, 1970; Huber and Watson, 1972, Smiley, 1974; Kommendahl, 1984). The greatest benefit for reduction in disease incidence and severity as a result of N fertilizers has been observed on moderately susceptible or partially resistant varieties (Huber and Watson, 1972). Immune plants are not usually attacked regardless of the nitrogen form available, and highly susceptible plants may not become resistant by form of nitrogen. The fact that a given form of nitrogen reduces one disease but favors another demonstrates the need for detailed understanding of the consequences of manipulating soil factors to manage disease.

The effect of nitrogen on the rhizosphere environment. Metabolic activity resulting from nitrogen absorption creates a dynamic carbon sink in the root system that may increase photosynthetic efficiency as accumulated sugars are translocated out of the leaf tissues. Modified microbial activity in the rhizosphere is often associated with the increased root metabolism, pH changes, and diversity of nutrients in root exudates following absorption of NH_4^+ (Smiley, 1974; Smiley and Cook, 1973). With take-all of wheat disease, increased availability and uptake of Fe, Mn, P, and Zn, which reduce take-all severity, have all been associated with modified rhizosphere microbial activity and a

decrease in rhizosphere pH induced by NH_4^+ uptake (Garrett, 1938 and 1941, Smiley and Cook, 1973, Huber and Watson, 1970).

Ferandino and Elmer (2000) conducted an experiment using eggplants fertilized with ammonium sulfate or calcium nitrate over three seasons with high, low, or no inoculum of *Verticillium dahliae*. They examined how tissue composition, colonization by the pathogen, rhizosphere pH, and soil densities of bacteria in the rhizosphere were affected by N rate and form. Yields increased with ammonium sulfate applications at low inoculum levels; however, the beneficial effects of fertilization with NH_4^+ disappeared with the high inoculum levels (Ferdandino and Elmer, 2000). There was no effect of nitrogen form on the densities of rhizobacteria could not be determined. Smiley and Cook (1973) had proposed that suppression of take-all of wheat was associated with NH_4^+ nutrition and interactions with fluorescent species of *Pseudomonas* associated with changes in rhizosphere pH. However, Ferandino and Elmer (2000) found no evidence that nitrogen form influenced pseudomonad densities.

Huber and Watson (1972) conducted experiments to observe the effects of organic amendments on soilborne plant pathogens. They stated that pathogen-suppression in cultivated soil is of microbial origin and is influenced more by cropping and management practices than by soil type. Evidence of “biological buffering” in older cultivated soil can be seen after sterilization. *Rhizoctonia solani* was able to kill flats of pepper seedlings in sterilized soil, but remained localized in nonsterile soil. *Vericillium albo-atrum* readily colonized sterilized soil in contrast to its limited rhizosphere activity in natural soil. In arid land, micorflora are characteristically limited (Easton, 1964). Their “biological buffering capacity” is low and newly introduced soilborne pathogens multiply

rapidly (Easton, 1964). The limited micorflora of these soils sometimes enables introduced soilborne pathogens to increase rapidly without competition. Recropping to potatoes for 3 consecutive years on newly cultivated desert soil in South Idaho increased *Streptomyces scabies* populations that the highly resistant Idaho Russet potato unmarketable (Huber, 1972).

Manganese availability has been associated with disease suppression due to its role in enzyme activation for synthesis of phenol and lignin products. Conditions that immobilize Mn and limit uptake, such as $\text{NO}_3\text{-N}$ nutrition, may compromise plant defenses and lead to greater disease severity (Huber and Watson, 1972). Higher levels of Mn and other trace metals in plant tissue have been associated with suppression of Verticillium wilt in cotton, potato, and tomato, and take-all in wheat (Walker *et al*, 1954; Smiley and Cook, 1973; Neal, 1935). The increased availability of these metals may also have resulted from rhizosphere acidification under ammonium sulfate fertilization regimes. The effect of N on take-all is interrelated with the availability of other nutrients and, in certain marginal soils, high levels of N may predispose plants to micronutrient deficiencies not apparent at lower levels of N. Copper, B, and Mn interact in N metabolism and may exert their effect on take-all through their role in N metabolism (Huber and Watson, 1972).

Fertilization of strawberry with $(\text{NH}_4)_2\text{SO}_4$ suppressed black root rot development and increased leaf area, number of runners, and berry yields compared to applications of $\text{Ca}(\text{NO}_3)_2$ (Elmer and LaMondia, 1999). Plants treated with $(\text{NH}_4)_2\text{SO}_4$ had more N and Mn in their leaves than with $\text{Ca}(\text{NO}_3)_2$ treated plants. It was hypothesized that $(\text{NH}_4)_2\text{SO}_4$ enhanced Mn uptake for disease suppression and Mn-transforming microorganisms may

be associated with black root rot as previously observed with other root diseases (Huber and Watson, 1970).

The rate of nitrification may influence the intensity of any effects observed with different sources of N. Levels of ammoniacal N may remain relatively stable in acids soils, or when chemicals that inhibit nitrification are used, but are relatively unstable in neutral to alkaline soils or following crops or manures which stimulate nitrification. Control of take-all of wheat with $\text{NH}_4\text{-N}$ is generally enhanced under conditions that restrict nitrification. Nitrapyrin [2-chloro-6-(trichloromethyl) pyridine; N-Serve, Dow Chemical, U.S.A.], which inhibits nitrification, not only ensures the availability of nitrogen for crop growth and yield later in the season, but also provides an effective means of reducing diseases such as take-all of wheat when applied with $\text{NH}_4\text{-N}$ by maintaining an optimum 3:1 $\text{NH}_4\text{:NO}_3$ ratio of total N (Goring, 1962; Swezey and Turner, 1962; Turner and Goring, 1966; Huber *et al*, 1969; Moore, 1973).

Baker and Maurer (1963) studied the effects of carbon and nitrogen compounds in soil on the severity of root rot of been caused by *F. solani*. Natural soil was infested with *F. solani phaseoli* then amended with cellulose or glucose (4,5000 ppm carbon) alone or in combination with $\text{NO}_3\text{-N}$ or $\text{NH}_4\text{-N}$ to give C:N ratios from 25:1 to 75:1. The severity of symptoms on hypocotyls was inversely related to C:N ratios. They also found that available nitrogen was readily immobilized after incorporation of these amendments.

Results of their experiments suggested that groups of fungi capable of utilizing simple carbon sources or cellulose might competitively utilize nitrogen that is necessary for germination and penetration of the host by the pathogen. Nitrification inhibitors, such as N-Serve, were effective in reducing nitrification and maintaining high levels of $\text{NH}_4\text{-}$

N. In addition, symptom expression was greater with $\text{NH}_4\text{-N}$ than with $\text{NO}_3\text{-N}$ when added with cellulose. Nitrate nitrogen consistently reduced disease severity by influencing the susceptibility of the host or because there is a lower energy requirement for assimilation of $\text{NH}_4\text{-N}$ by the pathogen (Baker and Maurer, 1963).

Interplanting red alder with conifers has been proposed for control of *Poria* and *Armillaria* root rots of conifers (Carley, 1969; Li *et al*, 1967). Soil in mixed stands of red alder and conifers contained higher levels of $\text{NO}_3\text{-N}$ than soil under an adjacent pure stand of conifers. Since *Poria* and *Armillaria* do not use $\text{NO}_3\text{-N}$, but grow well with $\text{NH}_4\text{-N}$, red alder may have potential use in the management of these soilborne pathogens by stimulating nitrification and increasing levels of $\text{NO}_3\text{-N}$.

Direct Effect of N on Pathogens and Hosts. Fungistasis is another type of microbial interaction by which root diseases are suppressed without eradicating the pathogen (Lockwood, 1964). Although the pathogen is present in the soil, it remains in a dormant or inactive state. Vankata Ram (1952) isolated two soil bacteria that stimulated chlamydospore formation (dormancy) of *F. solani* either directly or through culture filtrates. A similar mechanism was found with snowmold of winter wheat caused by *Typhula idahoensis* where associated soil bacteria prevented germination of *Typhula* sclerotia (Huber and Watson, 1972). Sclerotia readily germinated after removal of associated bacteria.

Studies on other fungi have shown that nutrients present in the infection court can influence pathogenesis. Toussoun *et al* (1960) showed that *F. solani* responded to nutrients added with spores used as inoculum. Kraft and Erwin (1967) found that a favorable source of nitrogen was necessary for infection of mung beans by *Pythium*

aphanidermatum at low inoculum densities. Boyle (1963) reported that *Sclerotium rolfsii* and *R. solani* would not function as pathogens on peanut unless the soil contained a supply of organic matter. This work demonstrated that some pathogens could take up and utilize nutrients prior to infection of a host plant.

Aphanomyces euteiches causes a severe root rot of peas under cool, moist conditions or in poorly drained and compacted soil. The disease is suppressed by $\text{NO}_3\text{-N}$ and enhanced by $\text{NH}_4\text{-N}$ in non-sterile soil (Huber and Watson, 1972). Root rot resulted when $\text{NH}_4\text{-N}$ was added to the soil but not when amounts adequate for plant growth were applied to foliage. Increased root rot following soil applications of $\text{NH}_4\text{-N}$ apparently results from a direct effect on the pathogen or effects on soil microbial interactions, rather than increased host susceptibility.

The absence of an effect on host susceptibility was further demonstrated by dividing the root system so the same plant could be grown with different N treatments. Only those roots exposed to $\text{NH}_4\text{-N}$ developed severe root rot. *Aphanomyces* root was also more severe at lower inoculum levels with $\text{NH}_4\text{-N}$ than $\text{NO}_3\text{-N}$. These results indicate that suppression by $\text{NO}_3\text{-N}$ in unsterilized soil is due to a competitive or antagonistic biological suppression of the pathogen (Carley, 1969). This may be a direct competition for nitrogen because the pathogen utilizes $\text{NO}_3\text{-N}$ poorly, or it may be the result of an increased population of antagonistic bacteria (Carley, 1969).

An altered nutritional status of the host following organic amendments may also alter disease response without affecting numbers of pathogen propagules in the soil. Studies of *Gibberella suabinctii* on wheat and corn indicate the availability of nitrogen in host tissues affects disease severity. Painter and Sympton (1969) increased the incidence

of stalk rot of corn caused by *F. moniliforme* by inhibiting nitrification of ammonium sulfate, which altered nitrate levels in the host plant tissues. Disease control was found to be a result of modified host physiology resulting from decreased infection or delayed pathogenesis after penetration.

Garrett (1938) had attributed control of take-all with nitrogen fertilization to the ability of the plant to produce new roots in place of those destroyed by *O. graminis*. Butler (1959) further stated that since root replacement would be more effective when moisture was not limiting in the soil that failure of nitrogen to reduce take-all reflects conditions of moisture stress on the host plant. However, Huber *et al* (1963) showed that take-all was most severe on dryland wheat during years of high spring precipitation. Since adequate moisture is provided, root replacement did not appear to be the primary factor involved in disease control.

Huber (1966) stated that control of take-all appeared to be a result of reduced levels of infection of plants treated with ammonium sulfate. This finding was consistent with Garrett's report that nitrogen increases the susceptibility of individual roots. The ability of nitrogen applications to limit crop loss was viewed as a result of the reduced efficiency of the plant from loss of functional root area. There were also reports that the saprophytic survival of *O. graminis* was limited by low nitrogen levels, indicating that saprophytic survival is not directly related to disease incidence (Garrett, 1938). Increased activity but reduced disease severity indicates the mechanism of suppression is probably related to host resistance or an indirect effect on the pathogen. Levels of CO₂ inhibitory to *O. graminis* in the rhizosphere resulting from increased microbial activity after residue

amendment or crop rotation were also hypothesized as a mechanism of control (Garrett, 1938).

Nitrogen Influence on Rhizoctonia Diseases. Inhibition of nitrification of $\text{NH}_4\text{-N}$ has been reported to reduce Verticillium wilt, may increase Rhizoctonia canker of cotton and beans. Cortical and root disease caused by *Fusarium*, *Rhizoctonia*, *Aphanomyces*, *Cercosperella*, *Poria*, and *Armillaria* may be reduced by $\text{NH}_4\text{-N}$ (Huber, 1960; Huber and Watson, 1970, Weinhold, 1970). Afanansiev and Carlson (1942) determined that form of N, as well as the rate, can impact the severity of black root rot caused by *Rhizoctonia solani* affecting sugar beets. Their research showed that the use of $\text{NH}_4\text{-N}$ resulted in more diseased plants than applications of $\text{NO}_3\text{-N}$.

Damping-off of lettuce increased with increasing rates of $\text{NH}_4\text{-N}$, but various rates of $\text{NO}_3\text{-N}$ had no effect on damping-off of lettuce or cauliflower seedlings by *R. solani* (Huber and Watson, 1970). As these levels of $\text{NH}_4\text{-N}$ increased, production of infection cushions, lesion enlargement, and growth of *R. solani* increased. A reported relationship of the C:N ratio to root rot severity was related to specific crop residues and C:N ratio on nitrification (Afanasiev and Carlson, 1942). Residues that stimulated the oxidation of $\text{NH}_4\text{-N}$ by biological agents to $\text{NO}_3\text{-N}$ reduced the severity of root rot while those residues and chemicals that inhibited nitrification increased root rot when applied with $\text{NH}_4\text{-N}$ (Afanasiev and Carlson, 1942).

Weinke (1962) conducted experiments studying the impact of nitrogen form on root exudates. He was unable to detect differences in hypocotyl exudates with different nitrogen sources despite the fact that root rot increased with $\text{NH}_4\text{-N}$ compared to $\text{NO}_3\text{-N}$. In his experiment, nitrogen was applied at various depths in the soil in relation to the

plant and *Fusarium* inoculum. Root rot increased only when nitrogen was placed in the hypocotyl region. Weinke also observed a more rapid development of a larger hyphal thallus, increased pathogenicity, and more rapid lesion coalescence with $\text{NH}_4\text{-N}$ than $\text{NO}_3\text{-N}$. A change in pH was not observed in either the sand or soil conditions used, and nitrogen was the only nutrient tested that influenced bean root rot.

An increase or decrease obtained with different forms of nitrogen also could not be correlated with the inoculum potential because neither $\text{NH}_4\text{-N}$ nor $\text{NO}_3\text{-N}$ influenced chlamydospore germination or affected soil inoculum potential. Nitrate nitrogen reduces *Rhizoctonia* root rot compared with $\text{NH}_4\text{-N}$ fertilizers, however $\text{NO}_3\text{-N}$ provides a better environment for saprophytic activity and survival of the pathogen. This observation indicated that the pathogen was persisting in the soil but not causing disease (Gilpatrick, 1969; Kurtz and Fergus, 1967; Smiley *et al*, 1972). Investigations with *Rhizoctonia* have showed that after a short period of time in the soil, the pathogen becomes less capable of attacking cotton stems. This decrease in aggressiveness may result from a loss of nutrients required to support pathogenic activity (Weinhold, 1969). A direct relationship was found between the concentration of carbon or nitrogen source in a growth medium and aggressiveness as determined by the area of macerated tissue.

R. solani survives in field soil for extended periods of time, and attacks seedlings when conditions are favorable for infection to occur. Propagules of the fungus must germinate and grow towards the host, form infection structures, penetrate the epidermis, and become established themselves within the host. These processes require energy and the synthesis of new structural materials. Weinhold *et al* (1969) stated that there are only three potential sources of these nutrients: propagules of the fungus, soil solution and

organic matter in soil, and exudates from the host. If the quantity or quality of available nutrients are inadequate, fungal activity and infection is limited (Weinhold *et al*, 1969).

Weinhold *et al* (1972) studied the influence of exogenous nutrition on aggressiveness of *R. solani*. The importance of nutrition in promoting maximum aggressiveness has been demonstrated for several plant-pathogenic fungi, including *Rhizoctonia*. The relative importance of exogenous versus endogenous nutrition has important ecological implications. If the pathogen relies to a large extent on exogenous nutrients, then disease control through reduction of available energy sources might be possible.

When the mycelium of *Rhizoctonia* is deficient in either carbon or nitrogen, it can grow vegetatively, but its ability to attack plant tissues is reduced. Weinhold *et al* (1972) showed that nutritionally deficient mycelium could grow rapidly to utilize nutrients present in the external environment, which increased virulence. The increased disease resulting from inoculation with nutritionally deficient mycelium in the presence of field soil suggests that the soil contained sufficient nutrients to enhance activities of the pathogen (Weinhold *et al*, 1972). Because this response was eliminated by autoclaving, the response may have been due to the activities of the soil microflora. Disease severity was increased by the addition of nitrogen and seed exudates to the soil.

Distance of inoculum from seeds must be considered in the evaluation of the influence of pathogen nutrition on disease severity. Growth of the pathogen through soil requires energy. Therefore, as the distance between the seed and inoculum increases, the requirement for larger nutrient reserves in the inoculum increases. The extent to which *R. solani* causes disease is dependent upon the interactions of numerous factors. Nutrients

are required for growth of the pathogen from the propagules to the host, formation of infection cushions, and production of sufficient metabolites (toxins and enzymes) to destroy plant tissue. The nutrients available for these activities are a combination of those present in the propagule, organic matter, the soil solution, and host exudates. A reduction of nutrients from any of these sources would reduce the aggressiveness of *R. solani* (Weinhold *et al*, 1972).

Impact of In-Row Spacing on Potato Yield and Quality. Seed piece spacing studies have been conducted on many potato varieties with mixed results. Schotzko *et al* (1984) found that plant stands could significantly affect yield and economic return and were influenced mainly by in-row spacing of seedpieces. They determined that seed pieces should not be spaced less than 15-cm apart for optimal yields. Generally, it has been reported that total yields increase for potato plants as seed piece spacing is decreased, but varieties differ in their ability to compensate for wide gaps. Yield of Russet Burbank potatoes is not affected by changing in-row spacing from 15 to 30.5 cm. (Haldersen *et al*, 1992). However, Rupp and Thornton (1992) showed differences in responses to in-row spacing by several potato varieties. DeBuchanee and Lawson (1991) reported that Atlantic produced greater total yield when produced at 15 cm compared to a wider spacing.

Maxwell and Rhybost (1993) reported that 17-cm was the optimal seed piece spacing for Atlantic. In-row spacing greater than 23-cm resulted in reduced total and marketable yields for different varieties (Creamer *et al*, 1999). Superior was able to compensate for wider spacings and produced greater yield than Atlantic at all spacing

treatments. It was also found that a 15 cm in-row spacing produced the greatest yield for Atlantic and Superior than with any other spacing treatment (Creamer *et al*, 1999).

Seed piece spacing affects yield, but also has been implicated in affecting the internal quality of tubers. As in-row spacing increased, larger tubers are produced that are more prone to developing internal defects such as heat necrosis and hollow heart (Sterrett and Henniger, 1997). Hollow heart is a defect that results from environmental stresses such as sudden changes in temperature early in the growing season (Sterrett and Henniger, 1997). Nitrogen applications during the growth period and bulking rate may also affect the development of hollow heart (Yli-Halla *et al*, 1987).

Other studies confirmed this finding that wider in-row spacing produced large tubers and increased internal heat necrosis incidence and severity (DeBuchananne and Lawson, 1991). Narrow in-row seed-piece spacing reduces tuber size and in turn has been found to reduce the incidence and severity of internal heat necrosis and hollow heart. Creamer *et al* (1999) reported that differences of in-row spacing affecting internal defects of Atlantic. Internal heat necrosis was greater with wider in-row spacing and was reduced 15 cm spacing, and greater at a 66 cm spacing.

Present Research. Researchers also have examined the impact that nitrogen has on disease incidence and severity for many different production systems. Studies have been conducted on the impact of nitrogen rate and form on *Rhizoctonia solani* in the field and laboratory. However, no studies have looked at the impact of nitrogen rate and form on isolates of *R. solani* AG-3 that infect potato. Field and controlled-environmental growth chamber studies were conducted to examine the impact of nitrogen on *Rhizoctonia* disease incidence and severity. A nitrification inhibitor, nitrapyrin (N-Serve®), was used

in the field experiments to observe the direct effects of ammonium and nitrate nitrogen on Rhizoctonia disease development.

A series of *in-vitro* experiments were conducted using a Soil Solution Medium (SSM) to simulate levels of macro and micronutrients that *R. solani* might encounter in the soil solution (Angle *et al*, 1991). This broth was buffered to determine if nitrogen form has a direct effect on the mycelial growth of the pathogen. Several mechanisms have been proposed by researchers by which N applications could influence disease development; an effect of N on the rhizosphere environment such as pH, nutrient availability, and other microorganisms; an impact on plant development and disease resistance; a direct affect on the aggressiveness of pathogens. Mechanisms of disease suppression need to be determined for specific host-pathogen interactions given the complexity of the soil environment and environmental influences affecting disease development. A better understanding of nitrogen influence on disease development would provide a foundation for future research and the development of better management strategies for Rhizoctonia disease of potato.

Multiple researchers have looked at ways to influence yield of potato crops by varying in-row spacing. In several studies it was found that spacing increased yield and economic returns for growers. However, no study to date has examined the impact of in-row spacing on the N-uptake efficiency for Atlantic and Superior varieties of potato. An understanding of the quantity of N that is removed at harvest and the residual levels of N that remain in the soil after harvest would allow for better fertilizer rate recommendations for future crops. Maximizing the efficiency of these varieties would not only provide an

economic benefit to growers by reducing N input in their production systems, but may also help to reduce N pollution in the environment.

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Impact of seed piece spacing and nitrogen rate on N-uptake efficiency of Irish potato in North Carolina.

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ABSTRACT

High rates of nitrogen are often applied to potato in North Carolina to reduce the risk of yield loss. Maximizing the efficiency of N uptake by potato plants could provide an economic benefit to growers, and optimizing application rates could reduce surface and ground water contamination. This study examined the impact of N rate and seed piece spacing on tuber yield and N uptake efficiency in the potato varieties Atlantic and Superior. Urea was applied at rates of 0, 56, 112, or 168 kg N ha⁻¹ with seed piece spacing of 23 or 30 cm arranged in a split-split plot design. In 2000 and 2001, Atlantic produced a greater total yield than Superior at the 23 and 30 cm spacing; both varieties yielded higher at a 23-cm spacing compared to a 30-cm spacing. Total and marketable yield in plots with 56, 112, or 168 kg N ha⁻¹ urea were not different, but the two highest

N rates had significantly ($P=0.05$) greater yield than the 0 N treatment. Averaged across variety and spacing, total N uptake was 58 kg N ha^{-1} with 0 N, and increased to 100 Kg N ha^{-1} with 168 N ha^{-1} . Harvest removal of N increased from 33 kg N ha^{-1} with the 0 N treatment to 58 N ha^{-1} with 168 kg N ha^{-1} treatment. Data suggests that growers could apply N at rates of $56\text{-}112 \text{ kg N ha}^{-1}$ with optimal seed piece spacing to produce high quality yield and reduce the potential of polluting surface and ground water reservoirs.

INTRODUCTION

Average yields of Irish potato produced in northeastern North Carolina are 22 Mg ha^{-1} each season. Growers utilize approximately 10,000 hectares to produce potatoes in the state. Nitrogen is an essential nutrient for potato development and growth, but is often excessively applied in potato production to prevent yield loss. Recommended N applications are $112\text{-}168 \text{ kg N ha}^{-1}$ (Voss, 1997), but typically growers apply rates of $168\text{-}224 \text{ N ha}^{-1}$. As a result, high residual levels of N have accumulated in the soils of eastern North Carolina (Gardner and Jones, 1975).

Numerous studies have documented the positive growth response of potatoes to increasing levels of N (Gardner and Jones, 1975; Vos, 1997), as well as the possibility for reduction in N applications (Westermann *et al*, 1994). Nitrogen in agricultural runoff is a major concern for growers and consumers and is considered to be a major source of surface and groundwater pollution. In North Carolina, N is a threat to the water quality of the Abermale-Pamlico drainage basin (Spruill, 1995). Maximizing N uptake efficiency of potato is important for producing high quality yields, providing an

economic benefit to growers by possibly reducing N input in their production system, and reducing pollution in water reservoirs.

Several N management issues were examined in this study. The influence of in-row spacing on potato yields has been investigated for several varieties. In several studies, narrow in-row spacing increased yield and economic return for growers (Bishop and Wright, 1959; Nelson, 1970; Entz and LaCroix, 1984; Halderson, 1992; Arsenault *et al*, 1999; Arsenault *et al*, 2001). Different potato varieties, however, differ in their ability to compensate for varied in-row spacing. A common potato variety grown in North Carolina, 'Atlantic', is sensitive to wide spacing and is not able to compensate in yield or quality for a reduced stand density (DeBuchanne and Lawson, 1991; Creamer *et al*, 1999). Another common variety, 'Superior', is less sensitive to increased in-row spacing and reduced stand density (Creamer *et al*, 1999).

High summer temperatures of late June and early July usually signal the end of the potato-growing season in North Carolina. Excessive N applications delay tuber initiation and maturation (Marschner, 1986). The developing tuber may be exposed to high soil temperatures that can make them more prone to internal defects (Sterrett and Henniger, 1997). Early-season stress, such as N applications that affect the rate of tuber-bulking, also have been implicated in the development of internal heat necrosis and hollow heart (Yli-Halla *et al*, 1987). As a result, the production of fewer Grade 'A' and 'B' potatoes can affect total and marketable yield.

Nitrogen demand is dependent upon the efficiency of utilization by the potato plant (Soaud *et al*, 1988)). This study examined the influence of N rate on the yield and quality of Atlantic and Superior at different in-row spacing treatments, and determined

the N-uptake efficiency of the two cultivars. Nitrogen uptake efficiency was determined by examining concentrations of N present in the plant during the growing season inferred by leaf and petiole assay (N-uptake) and the amount of nitrogen present in the plant biomass and tubers (harvest removal).

Finally, the residual N levels were calculated for future potato and rotational crops so that appropriate fertilizer recommendations could be made. Maximizing N-uptake efficiency and determining residual N levels available to future crops will increase profits for growers and reduce surface and ground water pollution. The objectives of this study were to 1) determine the impact of N rate on tuber yield, leaf tissue nitrogen, N-uptake, and harvest removal for Atlantic and Superior in the field 2) determine if interactions occur with seed piece spacing, potato variety, and N rate, and 3) determine an optimal N application rate for potato in eastern North Carolina.

MATERIALS AND METHODS

Field experiments were conducted in 2000 and 2001 with the potato cultivars cv. Atlantic and Superior. Field plots consisted of a Portsmouth fine sandy loam located at the Tidewater Research Station in Plymouth, North Carolina. A split-split plot design was used, with fertilizer treatment as the main plot, planting density as the subplot, and variety as the sub-sub plot effect. Main plots were arranged in a randomized complete block design with four replications. Urea was applied at rates of 0, 56, 112, or 168 kg N ha⁻¹ and broadcast prior to bed formation and planting. Main plots were 116.8 m long and contained six rows at 97 cm spacing. Each main plot was also divided into two

subplots (7.5 m long x 6 rows) that were hand planted with a seedpiece spaced at either 23 or 30 cm (45,000 or 34,000 plants ha⁻¹), respectively.

Seed potatoes were cut and wound-healed for 3-5 days prior to planting. Plots were planted on 15 and 21 March and harvested on 8 and 3 July in 2000 and 2001, respectively. Plant stands were determined by counting the number of emerged stems after an estimated 90% of stems had emerged (14 and 19 April 2000, 16 and 21 April 2001). Soil samples were collected to a depth of 20-cm from each main plot at flowering and from each subplot prior to tuber harvest. Five leaf and petiole samples were collected from the sub-plots at flowering to determine NH₄⁺ and NO₃⁻ concentrations and petiole nitrate. The first 1.5 m of each middle treatment row was dug at maturity to determine stover yield (i.e., aboveground biomass). Tubers were harvested from 6.1 m of the middle treatment row and sorted into size classes and fresh weights were determined for each class¹. Ten tubers of approximately equal size were selected from each treatment and cut to determine the incidence and severity of hollow heart and heat necrosis. Stovers and tubers were oven dried to determine nitrogen removal, and N-uptake efficiency.

Data Analysis. All statistical comparisons were performed using the GLM procedure available in SAS® (SAS Institute, 2000). Mean yield and N removal comparisons were made by Fisher's protected LSD test. Nitrogen uptake efficiency was determined using the Gauss-Newton linear plateau NLIN procedure available in SAS®. Data from the N rate and spacing study was fitted to two statistical models to determine optimum fertilizer

¹ Tubers sorted at harvest using a 1 (small) – 4 (large) scale and converted to the United States Department of Agriculture size classes (>47.6 mm, Grade A; 47.6-38.1 mm, Grade B; <38.1 mm and culls; Dean, 1994). Tubers classified as size 2, 3, and 4 or >38.1 mm (Grade A and B tubers) were used to determine marketable yields. All size classes were used to determine total yield.

rates. Optimum fertilizer rates for the linear and quadratic models were determined for grade 'A' tubers, marketable, and total yield. Using these statistical models, Y was the tuber yield in Mg ha^{-1} , and a , b , and c were parameter estimates using the NLIN procedure.

RESULTS & DISCUSSION

In 2000, variety, spacing, and N rate affected total tuber yield (Tables 1 and 3). Atlantic produced more stems, and greater marketable and total yield (17.7 Mg ha^{-1} , 26.4 Mg ha^{-1}) than Superior (16.3 Mg ha^{-1} , 22.0 Mg ha^{-1}). A seed-piece spacing of 23 cm resulted in more stems, and greater marketable and total yield than the 30 cm for both varieties (Table 1). Nitrogen rate had no effect on the mean number of stems produced on marketable yield. The greatest total yield was produced with 56 kg N ha^{-1} (17.7 Mg ha^{-1}), but it was not statistically different from 112 kg N ha^{-1} (16.9 Mg ha^{-1}), or 168 kg N ha^{-1} (17.1 Mg ha^{-1}). Total yield was lowest with 0 kg N ha^{-1} (6.5 Mg ha^{-1}).

Significant effects of variety, spacing, and N rate on potato yields were observed in 2001. The mean number of stems per plant stem emergence yield was greater for Atlantic than Superior (Tables 2 & 4). Higher seed piece density produced a greater number of stems, and marketable and total yields for both varieties. A significant effect of N rate on total yield was observed, with the greatest yield produced at 168 kg N ha^{-1} (21.9 Mg ha^{-1}). There were no statistical differences in total yield between 56 , 112 , or 168 kg N ha^{-1} . Nitrogen rate had no impact on marketable yield. None of the treatments affected the occurrence of hollow heart or internal heat necrosis in either year of the (Table 1 & 2). In 2000, N rate ($P < 0.05$) and variety ($P < 0.05$) affected yield of grade A

tubers and marketable yield. Grade B yield was affected only by spacing and variety ($P < 0.05$) (Table 2). In 2001, grade A tuber yield was affected by N rate, spacing, and variety (Table 4); grade B tuber yield was affected only by spacing ($P < 0.05$). The ratio of grade A tubers to small tubers (tuber < 38 mm diameter) was calculated for yields in 2000 and 2001. In 2000, the ratio produced at 168 kg N ha^{-1} was greater than 0 and 56 kg N ha^{-1} (Fig. 1). In 2001, ratios were comparable for N rates (Fig. 1).

A nitrogen response curve was developed to identify optimum N rates that produce the greatest marketable yield and are economical to growers. Two statistical models, linear and quadratic plateau, were used to generate the response curves for total plant N, grade A tubers, and tuber N. The data were best fit by the linear plateau model. As a result, the linear model was used to generate and N responses curves for the data. In 2000, the optimum N level to produce the greatest marketable yield was determined to be 52 kg N ha^{-1} (Fig. 2). In 2001, nitrogen applications of 168 kg N ha^{-1} were determined by the model to produce the greatest marketable yield (Fig 2). These optimal N fertilizer rates were determined to be the most economical levels due to the cost of fertilizer and the quantities need for applications to a comparable area of land.

Leaf and petiole samples collected at flowering were used to determine nitrate-N (%) for potato plants and the N rate treatments. In 2000, leaf N was within the sufficiency range for 0 kg N ha^{-1} ; nitrogen levels were found to be higher and similar for 50 , 112 , and 168 kg N ha^{-1} (Figure 3 and 4). In 2000, petiole N concentrations were below published sufficiency ranges (1.4-2.7%). The lowest petiole N concentration was observed with 0 kg N ha^{-1} ; higher levels of petiole N were found with 112 and 168 kg N ha^{-1} .

Nitrogen uptake by the potato plant was calculated for total N and tuber biomass removed at harvest. Data showed that the potato plants removed the greatest amount of N at 168 kg N ha⁻¹ for total N uptake (2000 and 2001), and was significantly different from 0 and 56 kg N ha⁻¹ (Fig. 5). Tuber N levels were greatest at 168 kg N ha⁻¹ and were different from 0, 56, 112 kg N ha⁻¹ (2000). In 2001, no significant effect of N rate was observed on tuber N levels. The N-use efficiency by the potato plants exposed to the N-rate fertilization regimes was calculated from N uptake and harvest removal yields. Nitrogen uptake efficiency was calculated at 22% with 12% harvest removal efficiency at 168 kg N ha⁻¹. The nitrogen uptake efficiency of 56 kg N ha⁻¹ was calculated to be 21% with 11% harvest removal efficiency.

DISCUSSION

The cultivar Atlantic produced greater yields than Superior in both years of the study. Both varieties had reduced mean number of stems per plant, marketable, and total yields at the 30-cm spacing. Total yield was similar, however, at the N rates of 56, 112, and 168 kg N ha⁻¹. Our data suggests that low rates of N could be applied without significantly reducing potato yield. The lowest rate of N (56 kg N ha⁻¹) used in this study is significantly less than recommended for potato production in North Carolina. In this study, potato plants grown in soil amended with 56 kg N ha⁻¹ produced marketable and total yields comparable to higher N rates. High N rates have been reported to delay tuber initiation and can influence the development of internal defects (Sterrett and Henniger, 1997). However, no significant effect of N rate on hollow heart and heat necrosis was observed in this study.

In 2000 and 2001, leaf N concentration was found to be within sufficiency ranges for all N treatments, but petiole N was below normal ranges at 0 and 56 kg N ha⁻¹ (Plant Analysis Handbook for Georgia, 1996). Optimum N rates were calculated as 52 kg N ha⁻¹ in 2000 and 119 kg N ha⁻¹ in 2001. However, the 56 and 168 kg N ha⁻¹ had comparable N uptake (22 % and 21%) and harvest removal efficiencies (12% and 11%). Thus, this study provides evidence that low N rates result in high yields with increased profitability for growers by reducing production costs.

Nitrogen fertilization recommendations must optimize crop yield and quality, and at the same time maximize profitability, to reduce the risk of environmental pollution. For this study, data were fitted to several statistical models to determine the optimal fertilizer rate. The selection of an appropriate model is usually not obvious for a particular cropping situation (Bock and Sikora, 1990). The model selection can also have an effect on estimating optimal fertilizer rates. Different models can give comparable coefficients of determination (r^2), but result in different optimal fertilizer rates (Cerrato and Blackmer, 1990). The quadratic model has been used to describe crop response to fertilizers, but can overestimate the response if the maximum point on the curve is taken as the best fertilizer rate (Neeteson and Wadman, 1987; Cerrato and Blackmer, 1990; Colwell, 1994). The linear model has been used commonly to describe the crop response to fertilizers with agronomic and vegetable crops (Neeteson and Wadman, 1987). For this study, it was determined that the quadratic model overestimated the yield response of the potato crop in determining the optimal fertilizer rate.

Previous studies have determined that several varieties of Irish potato are sensitive to reduced stand densities. Atlantic has been reported to be sensitive to wide in-

row spacing, whereas Superior is able to compensate for the reduced stand density (Creamer *et al*, 1999). In this study, marketable yields in 2000 and 2001 were influenced by spacing and variety, but there was no significant interaction of these effects. The data for this study suggests that the interaction of seedpiece spacing and N rate does not enhance the ability of potato plants in the field to take up N from the soil necessary for growth and tuber development. However, this study has provided valuable information on N uptake and removal in the form of plant biomass. This information will allow growers to accurately assess the N demand of their potato crop with optimal seed-piece spacing, residual N levels in the soil available to future crops, and apply N fertilizers at levels appropriate for optimal plant growth and tuber development.

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TABLE 1. Effect of N rate applied as urea on mean number of stems and yield for potato cultivars Atlantic and Superior at 23 or 30 cm seedpiece spacing in 2000.

Variety	Stems1 ^a	Stems2	Marketable ^b	Yield Total	HH ^c	HNI ^c	HNS ^c
	(Mean No./Plant) 14 Apr.	(Mean No./Plant) 19 Apr.	(Mg/ha)	(Mg/ha)	(%)	(%)	(%)
Atlantic	41.5a	51.1a	17.7a	26.4a	5.5	62.2	72.5
Superior	27.8b	40.4b	16.3 b	22.0b	-----	-----	-----
LSD (P=0.05)	2.5	4.1	4.3	3.6	-----	-----	-----
Spacing (cm)							
23	39.8a	51.9a	18.7a	25.4a	5.2	70.3	70.5
30	29.4b	39.3b	15.4b	23.0b	6.2	69.5	73.8
LSD (P=0.05)	3.5	4.6	4.1	4.6	n.s.	n.s.	n.s.
N Rate (kg ha ⁻¹)							
168	34.4	44.3	12.1a	17.1a	3.0	62.5	72.0
112	35.5	44.6	11.1a	16.9a	5.2	65.0	69.9
56	33.8	47.4	11.9a	17.7a	3.5	63.8	73.4
0	34.9	47.3	6.5b	10.2b	3.0	58.5	69.0
LSD (P=0.05)	n.s.	n.s.	5.5	6.6	n.s.	n.s.	n.s.

^a Values represent the mean of four replicates. Values followed by the same letter are not statistically different (P=0.05) according to Fischer's protected LSD, n.s.=not significant.

^b Marketable yield includes all tubers > 38.1 mm in diameter.

^c HH= Hollow Heart Incidence; HNI=Heat Necrosis Incidence; HNS=Heat Necrosis Severity; Hollow heart incidence determined by the number of tubers with the defect; Heat necrosis incidence determine by number of tubers with the defect; Heat necrosis severity rated with a scale 9 (no heat necrosis) to 1 (severe heat necrosis) based on the percentage of the pith affected (Sterrett and Henniger, 1997). Values calculated only for the variety, Atlantic.

TABLE 2. Effect of N rate applied as urea on mean number of stems and yield for potato cultivars Atlantic and Superior at 23 or 30 cm seed piece spacing 2001.

Variety	Stems1 ^a	Stems2	Yield		HH ^c	HNI ^c	HNS ^c
	(Mean No./Plant) 14 Apr.	(Mean No./Plant) 19 Apr.	Marketable ^b Mg/ha	Total (Mg/ha)	(%)	(%)	(%)
Atlantic	35.5a	40.4a	8.0a	21.6a	4.5	59.9	74.2
Superior	34.3b	38.2b	7.4b	18.9b	-----	-----	-----
LSD (P=0.05)	3.5	2.7	3.6	3.9	-----	-----	-----
Spacing (cm)							
23	38.6a	42.6a	8.2a	21.6a	4.5	64.3	72.1
30	31.0b	36.0b	7.1b	18.9b	5.1	63.5	71.9
LSD (P=0.05)	2.7	3.7	3.4	5.2	n.s.	n.s.	n.s.
N Rate (kg ha ⁻¹)							
168	34.4	44.3	16.3a	21.9a	1.2	65.5	76.0
112	35.5	44.6	16.0a	21.7a	2.5	65.0	71.9
56	33.8	47.4	16.0a	19.9a	7.5	63.0	71.4
0	34.4	47.4	12.1b	13.1b	3.8	73.8	70.6
LSD (P=0.05)	n.s.	n.s.	4.7	5.8	n.s.	n.s.	n.s.

^a Values represent the mean of four replicates. Values followed by the same letter are not statistically different (P=0.05) according to Fischer's protected LSD, n.s.=not significant.

^b Marketable yield includes all tubers > 38 mm in diameter.

^c HH= Hollow Heart Incidence; HNI=Heat Necrosis Incidence; HNS=Heat Necrosis Severity; Hollow heart incidence determined by the number of tubers with the defect; Heat necrosis incidence determine by number of tubers with the defect; Heat necrosis severity rated with a scale 9 (no heat necrosis) to 1 (severe heat necrosis) based on the percentage of the pith affected (Sterrett and Henniger, 1997). Values calculated only for the variety, Atlantic.

TABLE 3. Analysis of variance significance levels for Grade A, Grade B, marketable, and total yields in 2000.

Source of Variation	Yield			
	Total	Marketable	Grade A	Grade B
N rate	0.1 ^x	0.05	0.05	NS
Spacing	0.01	0.05	NS	0.001
Variety	0.001	0.001	0.001	0.01
N X Spacing	NS	NS	NS	0.1
N X Variety	NS	NS	NS	NS
Spacing X Variety	NS	NS	NS	NS
N X Sp. X Var.	NS	NS	NS	NS

^x Significant differences at $P < 0.05$, based on a Fisher's protected LSD test. NS=not significant.

TABLE 4. Analysis of variance significance levels for Grade A, Grade B, marketable, and total yields, 2001.

Yield				
Effect	Total Yield	Marketable Yield	Grade A Yield	Grade B Yield
N rate ^x	0.05	0.05	0.001	NS
Spacing	0.0	0.01	0.05	0.05
Variety	0.01	0.01	0.05	NS
N X Spacing	NS	NS	NS	NS
N X Variety	0.1	NS	NS	NS
Spacing X Variety	NS	NS	NS	NS
N X Sp. X Var.	0.1	0.1	0.01	NS

^x Significant differences at $P < 0.05$, based on a Fisher's protected LSD test. NS=not significant.

FIGURE LEGENDS

Figure 1. Ratio of mean Grade A yield and small tubers (< 38 mm tuber diameter) averaged between varieties at 23 or 30 cm in 2000 and 2001. Letters denote mean separation by LSD at $P=0.05$.

Figure 2. Optimal fertilizer N rates determined for Atlantic and Superior in 2000 and 2001. Letters denote mean separation by LSD at $P=0.05$.

Figure 3. Fertilizer N impact on leaf or petiole nitrate-N averaged between variety at 23 or 30 cm spacing in 2000. Letters denote mean separation by LSD at $P=0.05$.

Figure 4. Fertilizer N impact on leaf or petiole nitrate-N averaged between variety at 23 or 30 cm spacing in 2000. Letters denote mean separation by LSD at $P=0.05$.

Figure 5. Total N uptake and tuber N for Atlantic and Superior at 23 and 30 cm spacing in 2000 and 2001. Letters denote mean separation by LSD at $P=0.05$.

FIGURE 1.

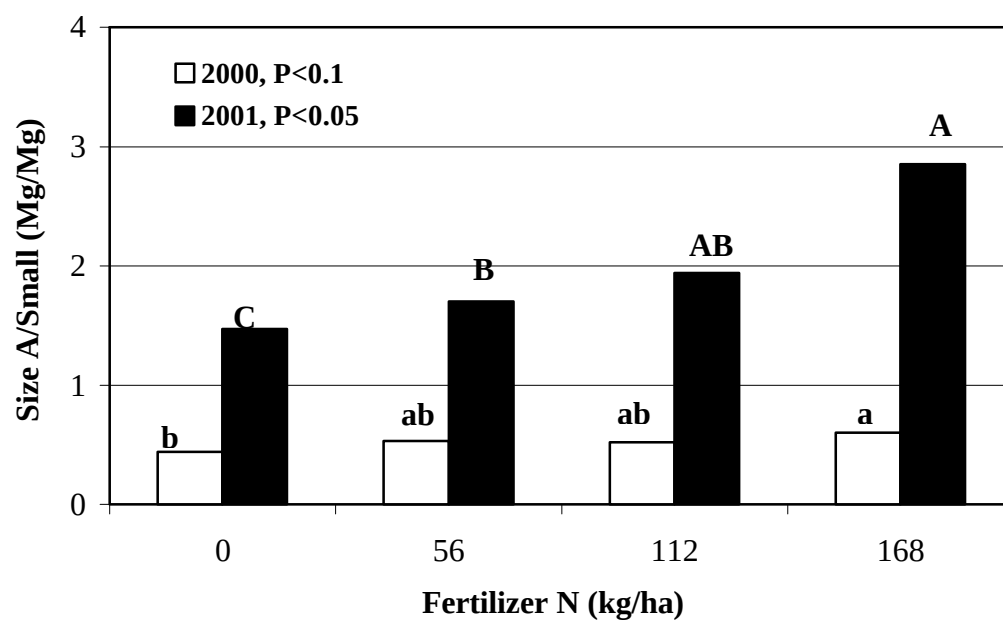


FIGURE 2.

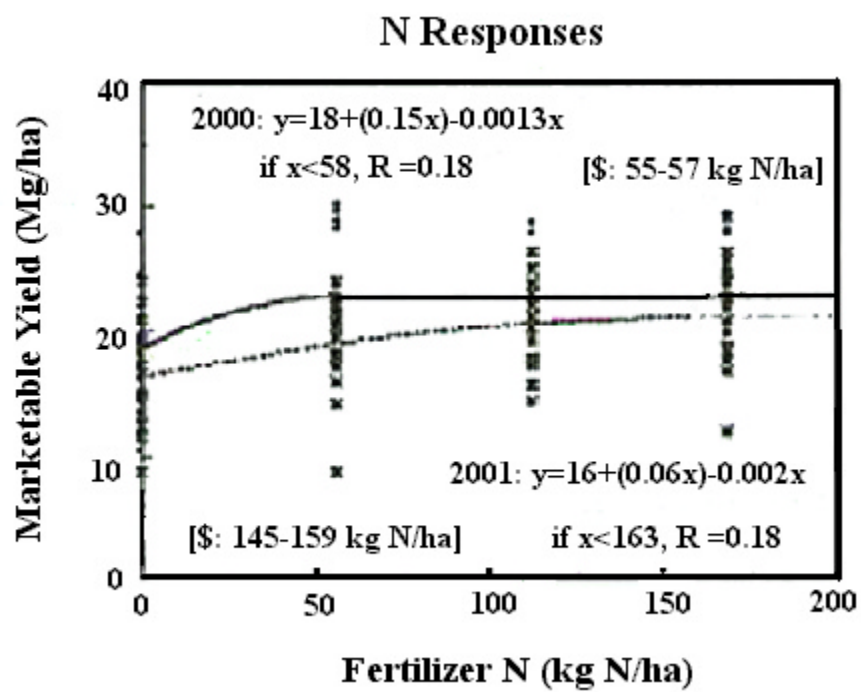


FIGURE 3.

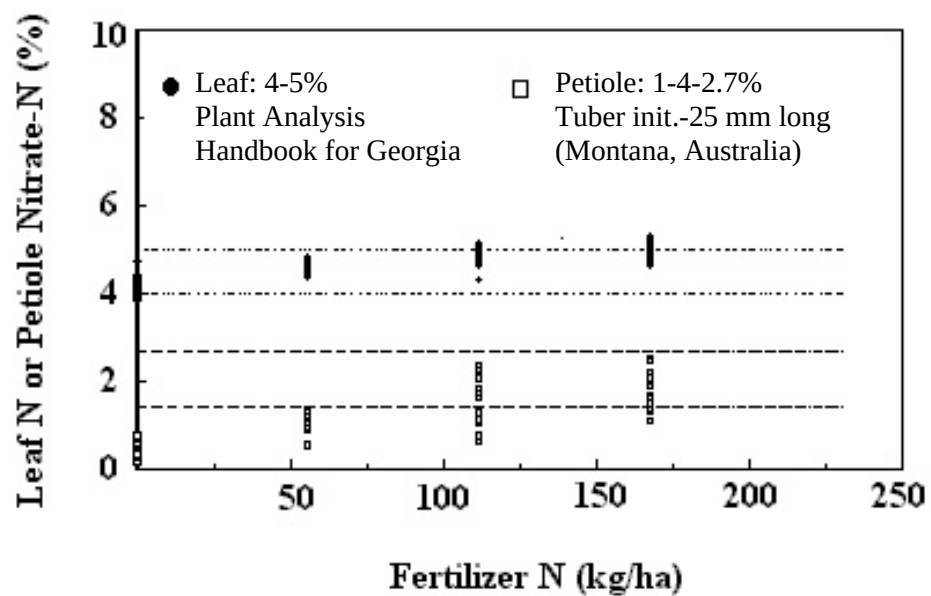


FIGURE 4.

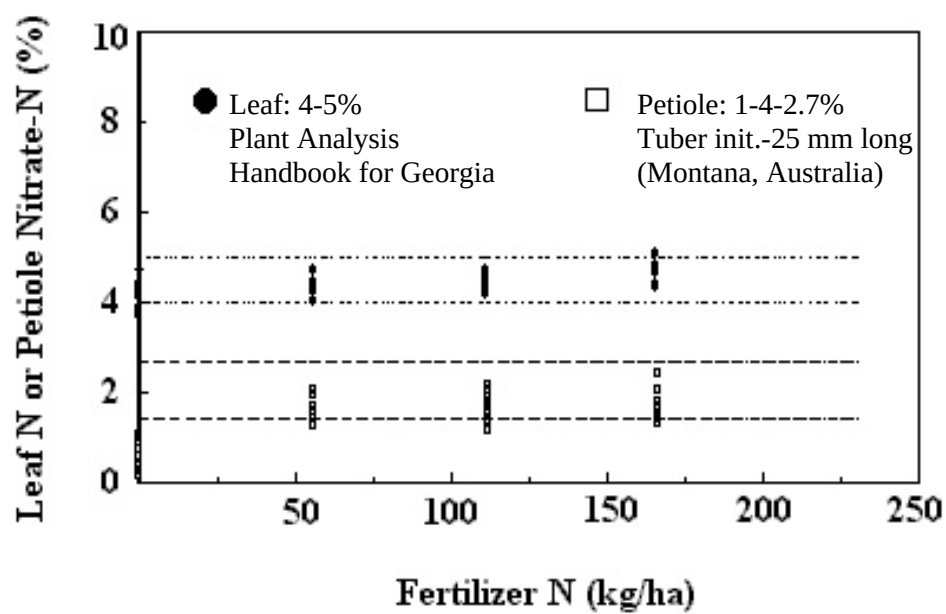
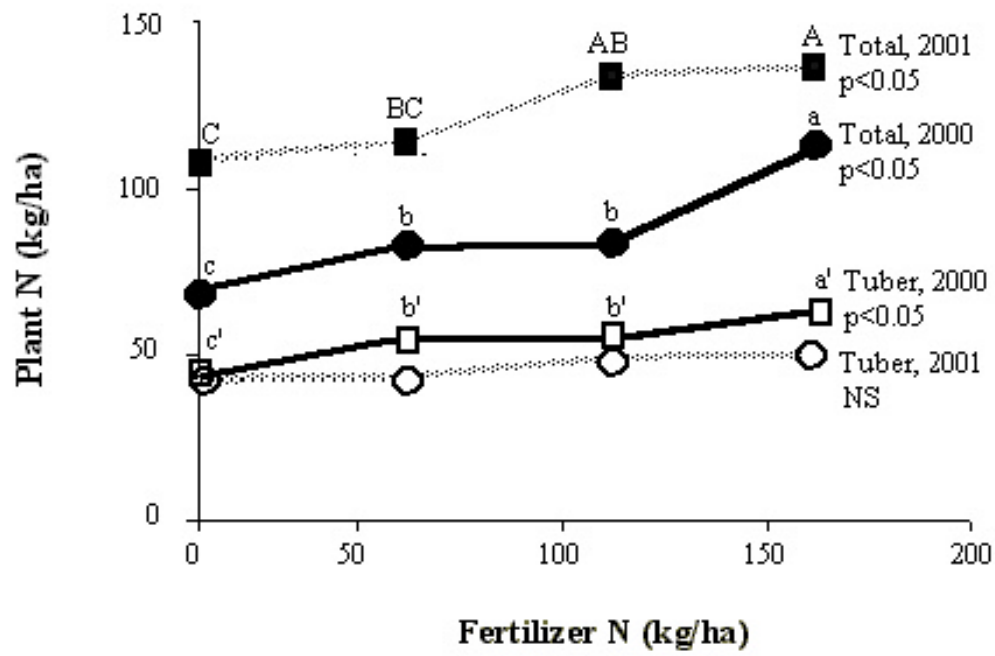


FIGURE 5.



Influence of N form and rate on yield of Irish potato and Rhizoctonia diseases

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ADDITIONAL KEYWORDS: *Solanum tuberosum*, nitrapyrin

ABSTRACT

The form and rate of nitrogen can affect the incidence and severity of many plant diseases. Excess applications of nitrogen (N) also can have undesirable off-site environmental effects. The effects of N rate and form on hyphal growth of *R. solani* anastomosis group 3 (AG3) development of Rhizoctonia diseases, and the yield of Irish potato were determined in growth chamber, laboratory, and field studies. There was a significant interaction between N form and rate on the average dry weight of hyphae produced by *R. solani* grown in minimal salts culture medium at 25 C. Mycelial dry weights were greatest with high rates of (NH₄)₂SO₄ and urea. Mean hyphal dry weights were similar with NaNO₃ at 10 and 50 ppm, NH₄NO₃ at 10 ppm, and 0 N control treatment. Three field experiments (two in Plymouth and one in Lewiston, NC) were conducted to evaluate the effects of nitrogen form and rate on potato yield and the incidence and severity of disease caused by *R. solani* on the potato variety Atlantic. There were five N treatments, 84 kg N ha⁻¹ or 168 kg N ha⁻¹ applied as NaNO₃ or urea

plus a nitrification inhibitor, and a 0 N control treatment. The main plots were divided into subplots that were either infested or not infested with *Rhizoctonia solani* AG-3. Disease incidence and severity were assessed on stems 6 wks after planting, and yield determined at the end of the growing season. At the Plymouth location in 2000 and 2001, the highest total yield was produced in plots that received 84 kg N ha⁻¹ NaNO₃. Marketable yields were similar for the 84 and 168 kg N ha⁻¹ urea and the 0 N treatments. A significant effect of *R. solani* was observed at Plymouth, with greater total and marketable yields in the non-infested compared to infested plots for both years. Stolon infection was significantly greater in the 168 kg N ha⁻¹ urea treatment than in the 84 kg N ha⁻¹ NaNO₃ plots at Plymouth in 2001. A Phytotron experiment was conducted to determine effects of N form and rate on development of stem and stolon canker of potato. Three nitrogen treatments, 0, 0.25, and 0.50 were added to a liter of potting medium in the form of NaNO₃ or urea. The predominate form of N was mixed in a 3:1 ratio at the appropriate concentrations with the other form of N used in the project. In two experiments, the highest and lowest incidence of stem and stolon canker occurred at the high rate of urea and the low rate of NaNO₃, respectively. The use of reduced rates of NaNO₃ in potato production may reduce the incidence of Rhizoctonia disease, give optimum yields and reduce the risk of undesirable environmental effects.

INTRODUCTION

Potatoes are grown in several northeastern North Carolina counties for production of potato chips. The soilborne pathogen *Rhizoctonia solani* is an annual threat to the quality and yield of potato, with estimated yield losses of 10-15% in North Carolina

(Meyer *et al*, 2000). Symptoms of the disease are cankers that form on the stems and stolons of plants. Soilborne inoculum, either sclerotia of mycelium, and sclerotia present on seed tubers imported from seed production regions serve as initial sources of inoculum for the disease. Potato sprouts are infected and killed by *R. solani* in cool (18 C), moist followed by dry soil conditions (Baker and Martinson, 1970, Banville *et al*, 1996, Cubeta and Vigalys, 1997). A delay in emergence and plant maturity can affect tuber yield and quality. The characteristic symptoms of the disease are cankers that form on the stems and stolons of the potato plant. Sclerotia develop late in the growing season on the tubers, black scurf stage, as plants begin to senesce.

High levels of resistance to *R. solani* AG-3 have not been identified in commercial Irish potato cultivars. Seed treatments with fungicides are only partially effective in reducing seed piece inoculum and disease incidence in the field (Meyer *et al*, 2000). It is recommended that a three-year rotation be used to reduce levels of soilborne inoculum, but this is only partially effective because in general *R. solani* is a highly competitive saprophyte that thrives in the soil environment in the absence of a suitable host. However, the saprophytic ability of *R. solani* AG-3 is not well documented. Integrated approaches and new, more effective management strategies are necessary to reduce losses to Rhizoctonia diseases on Irish potato.

Nitrogen is often excessively applied in potato production to prevent yield loss and can delay tuber initiation and reduce yields (Arsenault & Malone, 1999). Recommended N applications are 112-168 kg N ha⁻¹ (Voss, 1997), but typically growers apply rates of 168-224 N ha⁻¹. As a result, high residual levels of N have accumulated in the soils of eastern North Carolina (Gardner and Jones, 1975). Increases in disease

incidence and severity of soft rot affecting potato have been directly correlated with increasing the rate of N on potato (Somani and Shekhawt, 1990). Excessive nitrogen can increase brown patch disease of turf (Hearn, 1943) and the damping-off of broad-leaf tree seedling by *R. solani* (Wright, 1941). Nitrogen influences disease development by affecting plant physiology or the aggressiveness of plant pathogens (Weinhold, 1970). Disease potential can also be influenced by the immobilization of essential nutrients that result in deficiencies within the host plant (Alexander, 1961; Huber and Watson, 1970). Phytotoxic compounds can be produced during nutrient decomposition (Cochrane, 1948) and plant metabolism can be altered, that affect exudates used by *R. solani* (Toussoun and Patrick, 1963, Huber and Watson, 1974). An adequate food base is required to initiate the growth of *R. solani*, however, energy must also be acquired from the soil to continue growth and development (Blair, 1943). Plant exudates have been found to be important for the formation of infection structures (Flentje, *et al.*, 1963) and for penetration of the fungus into host tissue. Host exudates stimulate growth of *R. solani* in the soil (Martinson and Baker, 1962), and provide energy to *R. solani* for growth prior to penetration (Schroth and Cook, 1964). Plant exudates ultimately affect the production of infection cushions (Flentje, *et al.*, 1963) and the amount of disease. (Toussoun and Patrick, 1963, Schroth and Cook, 1964). Compounds found in the exudates of host tissues help to increase the inoculum potential of *R solani*.

Early studies related the effect of various nitrogen sources on hyphal growth of *R. solani* to changes in pH of the medium during growth. Nitrogen sources that acidified an unbuffered medium resulted in poor hyphal growth by the fungus. However, these N sources were found to be adequate sources for the fungus if the pH of the medium was

buffered and maintained in a suitable range (Townsend, 1957; Rao, 1959). The effect of nitrogen fertilization has been implicated for increasing disease by altering the rhizosphere pH in field soil (Smiley and Cook, 1973; Taylor *et al.* 1983; Huber, 1990).

The role of N in disease development varies with the specific host-pathogen interaction being studied. Therefore, it has been difficult to generalize on the potential effects of N on disease development. The form of N, as well as the rate of N, may impact disease incidence and severity. For example, ammonium N increases Rhizoctonia disease incidence on cotton and bean (Weinke *et al.*, 1972; Weinhold *et al.*, 1970). To date, no studies have examined the impacts of inorganic N rate and form on Rhizoctonia diseases of Irish potato under field conditions.

High residual levels of N have accumulated in native soils and have the potential to be released into the environment; nitrogen is a major source of surface and groundwater pollution. In North Carolina, N poses a significant threat to the water quality of the Abermarle-Pamlico drainage basin (Spruill, 1995). Optimizing N application rates is important for increasing profits for growers, decreasing losses to Rhizoctonia diseases on potato, and reducing surface and ground water pollution. The effect of nitrogen on host nutrition and disease severity has been studied extensively (Gardner and Jones, 1975; Vos, 1997, Crozier *et al.*, 2000). The objectives of this study were to determine the influence of N rate and form on: 1) mycelial growth of *R. solani* (AG3) *in-vitro*; 2) sprout emergence, yield, and Rhizoctonia diseases of Atlantic; 3) incidence and severity of Rhizoctonia disease in the field and in a controlled-environmental chamber.

MATERIALS AND METHODS

Mycelial Growth. The effect of nitrogen form and rate was tested in the laboratory on *R. solani* (AG3, RS189). A completely randomized design was used to arrange three replications of each treatment. Three nitrogen sources of Sodium nitrate ammonium nitrate, and ammonium sulfate (Experiment I), and Sodium nitrate, ammonium nitrate, and urea (Experiment II) were incorporated at rates of 0, 50, 100, and 150 ppm N. Each experiment was repeated for a second run to verify results. The N treatments were added to 125 mL Erlenmeyer flasks each containing 50 mL of a liquid culture medium. The soil solution medium of Angle and McGrath (1991) was used to simulate nutrients *R. solani* might encounter in the soil solution. MES buffer (Fisher Scientific, Ltd.) was used to moderate pH changes in the broth at a concentration of 1.95 g L⁻¹.

Measurements of pH were recorded with a pH meter when the N treatments were added to the background solution and after autoclaving for 20 min. Plugs of *R. solani* AG-3 were taken from the advancing edge of 3-day-old cultures grown on 2% water agar (Bacto Agar, Difco, Detroit, MI). A 5 mm diameter plug was placed into each flask and incubated for 72 h in the dark at 25 C. After 72 h, pH was recorded for the medium in each treatment flask. Mycelium was removed from the flask and placed in a weigh tin, dried at 60 C for 24 h, and weighed.

Preparation of Inoculum for Field and Growth Chamber Experiments. Four hundred grams of crimped oats and 400 mL of dH₂O were added to 1-gallon milk jugs. The milk jugs were sealed with foam plugs and parafilm and sterilized on three consecutive days for 60 min. One plate of *R. solani* anastomosis group 3 (AG3) were

prepared on potato dextrose agar (PDA, Difco, Detroit, MI) and grown in the dark for 72 h *in-vitro*. Colonized agar was sliced into approximately 15 square pieces of unequal size and added to the cooled oat grains. Inoculum was grown on the oat grains for 6 wks at 25 C.

Seed Piece Preparation. Potato tubers were washed in water and surface disinfested in a 1.85% formaldehyde solution. The seed tubers were allowed to dry and were cut into 56-g (± 5 g) seed pieces containing at least 1 eye. After cutting, seed pieces were placed into paper bags in a well-ventilated room and allowed to heal for 7 d at 11 C at 90% relative humidity.

Field Experiments. Three field experiments were conducted at the Tidewater Research Station² in Plymouth, North Carolina (2000 and 2001) and the Peanut Belt Research Station in Lewiston³, North Carolina (2001). Sencor DF herbicide (2.8 kg ha⁻¹) was applied prior to planting for weed management and Kryocide DF (13.4 kg ha⁻¹), Asana XL (0.6 kg ha⁻¹), and Bravo Weather Stick (1.1 L ha⁻¹) were applied as needed for management of Colorado potato beetle and late blight.

A split-plot design was used, with fertilizer treatment as the main plot, and inoculum as the subplot. Main plots were arranged in a randomized complete block design with four replications and a 5 X 2 fertilizer treatment. Main plots were 116.8 m long and contained three rows at 0.97 m (Tidewater) and 0.90 m (Peanut Belt) spacing. Urea and NaNO₃ N were applied at rates of 0, 84, or 168 kg N ha⁻¹ and broadcast prior to bed formation and planting. The nitrification inhibitor, N-Serve® (Nitrapyrin [2-chloro-6-trichloromethyl] pyridine; Dow Chemical, U.S.A), was applied to plots with urea to

² Portsmouth fine sandy loam

³ Norfolk sandy clay

reduce the conversion of ammonium to nitrate (Swezey and Turner, 1962). The plots were tilled to a depth of 6-cm to incorporate the fertilizers. Twenty-four hours after applying the fertilizers, seed pieces were placed 23 cm apart (45,000 plant ha⁻¹) in a 7.5 open furrow on 14 Mar. (Tidewater, 2000), 12 Mar. (Tidewater, 2001), 22 Mar. (Peanut Belt, 2001). Oat grains colonized with *R. solani* AG-3 were applied to each furrow at 15 g m⁻¹ of row immediately after planting.

Plant stand was determined by counting the number of emerged stems after an estimated 90% of the stems had emerged on 14 Apr. (Tidewater, 2000), 19 Apr. (Tidewater, 2000), 16 Apr. (Tidewater and Peanut Belt, 2001), 21 Apr. (Tidewater and Peanut Belt, 2001), 21 Apr. (Tidewater and Peanut Belt, 2001). After assessing emergence, a 3.6 m section at the beginning of each plot was hand-dug and stems and stolons were evaluated of Rhizoctonia disease incidence on 18 May (Tidewater, 2000), 21 May (Peanut Belt, 2001), 25 May (Tidewater, 2001). Canker incidence and severity was assessed at Tidewater in 2000. Stem and Stolon incidence were rated at Tidewater and Peanut Belt in 2001. Total number of stolons produced per plant in the 3.6 m section was also recorded in 2001 at both locations. The remaining section of the plot was harvested mechanically on 7 July (Tidewater, 2000), 25 June (Peanut Belt, 2001), 3 July (Tidewater, 2001). Tubers were harvested from 6.1 m of the treatment row and fresh weights were determined for each class.⁴ Ten tubers of approximately equal size (>38.1 mm tuber diameter) were selected from each treatment and cut to determine the incidence and severity of hollow heart and heat necrosis (Sterrett and Henniger).

⁴ Tubers sorted at harvest using a 1 (small) – 4 (large) scale and converted to the United States Department of Agriculture size classes (>47.6 mm, Grade A; 47.6-38.1 mm, Grade B; <38.1 mm and culls; Dean, 1994). Tubers classified as size 2, 3, and 4 or >38.1 mm (Grade A and B tubers) were used to determine marketable yields. All size classes were used to determine total yield.

Controlled-Environmental Growth Chamber Experiments. Formaldehyde

disinfested potato seedpieces (40 g) were planted in the controlled-environment room at the Southeast Plant Environmental Laboratory (NCSU Phytotron).⁵ A combination of T-12, 1500ma, cool-white fluorescent and 100 W incandescent lamps were used to light the chamber, giving a fluorescence of 600 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ and a photoperiod of 16 h.

Relative humidity levels were maintained above 70% at 22 C (a vapor pressure of 1.82 kPa) using a misting system. Controlled injection of commercial grade gas maintained CO₂ levels between 300-400 ppm. Daytime temperatures were maintained at 16 C and nighttime temperatures lowered to 12 C using a long day light regime. The nitrogen sources were added to a ½ strength modified Hoagland #1 solution to supply other essential macro and micronutrients.

A randomized complete block design was used, with four replications of a 5 X 2 fertilizer treatment. Three nitrogen treatments, 0, 0.25, and 0.5 g N L⁻¹ of either NaNO₃ or urea were added to a modified Hoagland solution and 200 mL of the solution was applied to the potato plants.⁶ The soil in each pot was moistened with the solutions once a week. Pots were watered as needed throughout the week with dH₂O when approximately 2.5 cm of the top layer of soil was dry. Selected pots were infested with *R. solani* anastomosis group 3 (AG3) colonized on oat grains. Potato plants were grown in the chamber for 8 wk. Plants were rated for incidence and severity of Rhizoctonia stem and stolon canker with a severity scale ranging from 0 (no infection) to 4 (severe infection with > 80% area covered by canker). After the plants were rated for infection,

⁵ Seed pieces were planted into 15 cm pots containing Biocomp® potting soil.

⁶ Nitrogen was supplied in a 3:1 ratio using NaNO₃ and urea N because plants require both NH₄⁺ and NO₃⁻ for growth and development.

the aboveground biomass and roots were collected, oven dried at 60 C for 72 h, and weighed.

Data Analysis. Statistical comparisons made with Waller Duncan k-ratio t test for *in-vitro* experiments. All statistical comparisons were performed for the field and Phytotron experiments using the GLM procedure available in SAS® (SAS Institute, 2001). Mean comparisons were made with Fisher's protested LSD test. Weather parameters were monitored in the field plots.

RESULTS

Mycelial Growth. Data were combined for three runs of each experiment. The greatest mean mycelial dry weight was observed in experiment I with 100 ppm N of $(\text{NH}_4)_2\text{SO}_3$ (19.9 mg) and was significantly different from all other N sources and concentrations (Table 1). Mycelial growth was reduced for N treatments of 0 (5.0 mg) and 150 NaNO_3 (4.2 mg). Growth of *R. solani* with 50 ppm N applied as NaNO_3 (7.6 mg), NH_4NO_3 (7.6 mg), or $(\text{NH}_4)_2\text{SO}_3$ (7.2) resulted in comparable mycelial growth that was significantly greater than no nitrogen. The highest rate (150 ppm) of NH_4NO_3 and $(\text{NH}_4)_2\text{SO}_3$ produced a greater mean than 150 ppm NaNO_3 (Table 1). Similar results were observed in experiment II with the greatest mean mycelial growth produced with 100 ppm N (13.2 mg) added to the experimental flasks as urea. Mycelial growth was significantly reduced for no added N and the low rate (50 ppm) of NaNO_3 (Table 2). High rates of N (150 ppm) produced comparable amounts of mycelium for NaNO_3 (7.4), NH_4NO_3 (6.8 mg) and $(\text{NH}_4)_2\text{SO}_3$ (6.9 mg). No significant differences in pH

measurements recorded before placing the plugs in the flasks or after 3 d growth *in-vitro* were observed.

Field experiments. The weather in 2001 at the Tidewater Research Station was cooler and wetter during tuber bulking than the 2000 growing season. Mean soil temperatures in March and April 2000 were 13 and 16 C, respectively and 10 and 14 C in 2001 at Tidewater. Mean soil temperatures at the Peanut Belt Research Station were higher at 13 and 16 C than the temperatures observed at Tidewater in 2001. Precipitation totals were 46.3 cm during the growing season, with monthly totals of 11.0 cm, March; 7.9 cm, April; 10.5 cm, May; 16.9 cm, June at Tidewater, 2000. Precipitation at Tidewater in 2001 were 43.5 cm during the potato growing season with monthly totals of 9.3 cm, March; 7.9 cm, April; 11.3 cm, May; 15.0 cm, June. Rainfall at the Peanut Belt site was reduced compared to Tidewater in 2001 with precipitation totals of 34.5 cm during the growing season. Monthly rainfall totals were 10.9 cm, March; 9.5 cm, April; 7.5 cm, May; 6.6 cm, June.

In 2000 at the Tidewater Research Station, no significant effect of N treatment or inoculum was observed for stem emergence on 14 Apr or 19 Apr. Total and marketable tuber yields were impacted by N treatment and inoculum. The greatest total yield was observed in non-infested plots with 84 kg N ha⁻¹ (32.1 Mg ha⁻¹), and the lowest total yield in infested plots with 168 kg N ha⁻¹ urea (17.5 Mg ha⁻¹) (Fig. 1a). Total yield was comparable in non-infested plots for all treatments (P<0.05). The infested plots of 168 kg N ha⁻¹ urea produced significantly lower total yields than treatments of 84 kg N ha⁻¹ NaNO₃, 84 kg N ha⁻¹, and 168 kg N ha⁻¹ within infested plots. Marketable yield showed a similar trend at the Tidewater site in 2000. The greatest marketable yield was produced

in non-infested plots with 84 kg N ha⁻¹ NaNO₃ (17.6 Mg ha⁻¹), and the lowest marketable yield produced in infested plots with no nitrogen (10.2 Mg ha⁻¹) (Fig. 1b). Plots infested with *R. solani* AG-3 with no nitrogen and 168 kg N ha⁻¹ urea produced comparable marketable yields, but were significantly lower than all other treatments either infested or non-infested plots ($P < 0.05$). In 2000, the incidence of infection on the stems of the potato plants was negligible (<10%). Stolon infection was not rated.

At the Tidewater Research Station in 2001, similar results were observed. There was no significant effect of N treatment or inoculum on stem emergence on 19 Apr or 24 Apr. Total and marketable yield were influenced by N treatments and inoculum infested in the plots. The greatest total yield was produced in non-infested plots at 84 kg N ha⁻¹ NaNO₃ (31.7 Mg ha⁻¹) and the lowest yield was produced in infested plots with 168 kg N ha⁻¹ urea (20.2 Mg ha⁻¹) (Fig. 2a). For the non-infested plots, there were no differences for total yield with no nitrogen, 84 kg N ha⁻¹ NaNO₃, 84 kg N ha⁻¹ urea, and 168 kg N ha⁻¹ NaNO₃. For the infested plots, total yields were comparable for low and high rates of NaNO₃ and the low rate of urea. Total yield for the low and high rates of NaNO₃ were also significantly greater than 168 kg N ha⁻¹ urea. The greatest marketable yield was produced in non-infested plots with 84 kg N ha⁻¹ (21.3 Mg ha⁻¹), and the lowest marketable yield produced in infested plots no nitrogen (11.5 Mg ha⁻¹) (Fig. 2b). In infested plots, there was no difference in marketable yield with no nitrogen and 168 kg N ha⁻¹ NaNO₃. Low and high rates of NaNO₃, and 84 kg N ha⁻¹ urea produced comparable marketable yield within infested plots.

In 2001, stolons were rated for infection by *R. solani*. Data showed a significant effect of N treatment, inoculum, and an interaction effect between the experimental

variables (Nitrogen X Inoculum). Percent stolon infection was calculated based on the total number of stolons infected per plant rated for middle row in each treatment plot. The greatest percent stolon infection was observed with 168 kg N ha⁻¹ urea (37.2%) and was different from 84 kg N ha⁻¹ NaNO₃ with the lowest percent infection (16.4 %) (Fig. 3a). The total number of stolons produced per plant rated was also recorded. The greatest total number of stolons was produced with non-infested plots of 84 kg N ha⁻¹ NaNO₃ (mean of 32.5 stolons/plot) and was significantly greater than the other experimental treatments. The lowest number of stolons was produced with infested plots of 168 kg ha⁻¹ urea (mean of 20.0 stolons/plot) (Fig. 3b).

At the Peanut Belt site in 2001, no significant effect of N treatment or inoculum was apparent on stem emergence on 15 Apr and 27 Apr. The experimental treatments also had no impact on total yield, but N treatment did affect marketable yield (Fig. 4). Marketable yield was greatest for 84 kg N ha⁻¹ NaNO₃ in non-infested plots, and were significantly different from no nitrogen and 168 kg N ha⁻¹ urea in both infested and non-infested plots. There was no difference among experimental treatments in the percentage of stolon infection for the experimental treatment (Fig. 3a). No difference for the total number of stolons produced with the non-infested and infested plots was observed with low rates of NaNO₃ (mean of 33.2 stolons/plot), urea (mean of 32.5 stolons/plot), and the high rate of NaNO₃ (mean of 31.7 stolons/plot) (Fig. 3b). These treatments, however, were significantly different from infested plots of 168 kg N ha⁻¹ (mean of 19.9 stolons/plot).

Controlled-Environmental Growth Chamber. The data collected showed a significant effect of N treatment and inoculum on stem and stolon canker, and shoot and

root biomass. Stem canker and stolon infection was negligible for all treatments that were not infested with *R. solani* (Run I & II). In Run I, pots infested with *R. solani* at 0.25 g N L⁻¹ NaNO₃ had the lowest incidence stem canker (10.3%), and 0.50 g N L⁻¹ NaNO₃ had the lowest incidence of stolon infection (14.7%) (Table 3). Nitrogen treatments that were applied to infested pots with low and high rates of NaNO₃, the low rate of urea, and 0 N showed no differences for stem infection. Infested plots with 0.50 g N L⁻¹ urea produced the highest percent stem and stolon infection (39.5 % and 46.5%, respectively). Incidence of stolon infection for low and high rates of NaNO₃ was significantly lower than 0.50 g N L⁻¹ urea. The greatest shoot biomass among all treatments was produced in non-infested pots of 0.25 g N L⁻¹ NaNO₃ (2.68 g/plant). The lowest shoot biomass was produced in control pots (1.67 g/plant) infested with *R. solani* AG-3, but were not statistically different infested pots with 0.50 g N L⁻¹ urea (1.82 g/plant), or non-infested pots of 0 N (1.97 g/plant). Applications to infested pots with 0.25 g N L⁻¹ NaNO₃ resulted in the greatest root biomass (2.11 g/plant), and were statistically different from 0 N applied to infested pots (1.20 g/plant).

In Run II, pots infested with *R. solani* AG-3 fertilized with 0.50 g N L⁻¹ NaNO₃ (11.3%) had the lowest incidence of stolon infection, but were not different from the low rate of NaNO₃ (11.5%) (Table 4). A significantly greater percentage of stolon infection was observed with 0.50 g N L⁻¹ urea (43.2%) compared to all other N treatments. The greatest percentage of stolon infection was also observed with 0.50 g N L⁻¹ urea (37.6%), and was significantly greater than the other N treatments. Infested pots treated with 0.50 g N L⁻¹ urea and 0 N produced less shoot biomass compared to other experimental treatments except 0 N applied to non-infested pots. A similar trend was observed with

root biomass. Infested pots treated with 0.50 g N L⁻¹ urea and 0 N produced significantly less root biomass compared the other N treatments.

DISCUSSION

The apparent sensitivity of *R. solani* to nitrate forms of nitrogen was observed with *in-vitro* experiments where the fungus was allowed to grow with different sources of N added to a buffered soil solution medium of defined nutrient composition to appropriate soil solution concentrations of micro and macronutrients. Previous studies had shown that in an unbuffered medium, the pH rises as the fungus uses nitrate and falls to levels that inhibit growth with ammonium nitrogen unless the medium is well buffered (Deshpande, 1959).

The incorporation of the MES buffer into the SSM liquid broth stabilized the pH of the solution used for this study. The reduction in hyphal mass of *R. solani* AG-3 by ammonium N compared to nitrate N suggests a direct effect on the physiological processes of the fungus important for growth, development, and is not related to pH changes in the growth medium. These results also suggest that high concentrations of N may decrease mycelial growth. Disease reduction was greatest when high rates of nitrogen were added and correlated with a lower competitive saprophytic activity of *R. solani* (Davey and Papavizas, 1960). Mineral nutrients, such as nitrogen, are known to be important for the process leading up to host penetration and ultimately affect inoculum potential of the fungus (Dodman and Kerr, 1963; Martinson, 1965). However, it is not known whether N rate and form has an impact the ability of *R. solani* to penetrate host tissue. The nutrients available to destroy plant tissue are a combination of those present in

host exudates, the soil solution, and the propagule (Weinhold *et al* 1971). A reduction or nutrients from any of these sources would affect the ability of *R. solani* to penetrate host tissue.

Results of the field and controlled-environmental chamber experiments suggest that ammonium N at higher rates can promote disease development compared to nitrate forms. Experiment conducted under field condition suggest that lower rates of N could be applied to produce high quality yields. However, the form of nitrogen did not appear to affect potato development in the non-infested pots. Differences in soil type and environment between the Tidewater and Peanut Belt Research Stations may have been important factors influencing disease development.

The Tidewater Research Station is located in northeastern North Carolina where potatoes are abundantly produced in organic soils with lower soil temperatures recorded in 2000 and 2001 than the Peanut Belt Research Station. The Peanut Belt Station is located in Northern North Carolina where sandy soils predominate and potato production is not common. Lower temperature and wetter soils are important components for disease development and may account for a higher incidence of stolon infection observed at Tidewater than Peanut Belt in 2001. Some studies have also suggested that the use of nitrification inhibitors can be detrimental to plant growth (Sweezy and Turner, 1962). Ammonium, a positive cation, can be absorbed in considerable amounts by negatively charged cation exchange sites of clay or organic particles that attain toxic levels in plants and could increase susceptibility to disease. Nitrification is slowed by conditions unfavorable to the activity of soil bacteria such as dryness or cold and can further enhance the activity of nitrification inhibitors like Nitrapyrin. The effective life of

nitrification inhibitors are shortened by warmer temperatures and use on sandy soils.

Nitrapyrin inhibits the actions of the *Nitrobacter* organisms to slow the conversion of ammonium ions to the nitrate form. The environmental and soil conditions present at the Peanut Belt Research Station may have hindered the activity of Nitrapyrin applied with urea N, allowing more nitrate to be produced or lost by leaching or denitrification.

Cropping history is also important for background inoculum levels that could contribute to differences in disease incidence and severity. Tidewater showed low levels of background inoculum in the control plots, and is consistent with the fact that potatoes were not planted in the experimental plots in previous seasons. Rhizoctonia disease of potato is common and inoculum can persist for many seasons after the production of potatoes in a particular field. Since potatoes are not commonly grown at Peanut Belt, it is unlikely that inoculum was present in the field before planting. Studies have shown that the saprophytic ability of *R. solani* and growth rate are positively correlated, and also have prolonged survival in colonized substrates (Garrett, 1959; Papavizas, 1964 and 1965). These studies, however, have a limited application to a field situation based on how the experiments were conducted. The field experiments conducted for this research study suggest that low levels *R. solani* were successfully established at Tidewater. A higher inoculum potential is required for infection than for colonization. The depletion or absence of certain nutrients in soil food bases would result in a decline parasitic activity more rapidly than saprophytic activity.

The sandy soils at Peanut Belt have a lower biological buffering capacity that would allow introduced inoculum to thrive under ideal conditions without competition. However, the availability of essential nutrients, adequate moisture, and temperature

levels may not have been optimal for *R. solani* at the Peanut Belt Research Station. Rhizoctonia may have more biological competition in the organic soil, but the fungus is highly adapted to the environmental conditions as a soil inhabitant and thrives as a competitive saprophyte at Tidewater. High applications of quickly available nitrogen were found to be detrimental to soil microorganisms competitive with *R. solani* (Ayers and Papavizas, 1963). Field plots with applied urea may have negatively influenced the activity of soil antagonists in the rhizosphere to *R. solani*.

Nutrient deficiencies, such as Ca that is an important component of cell walls, have also been implicated for disease control. The role of calcium in disease resistance is to form insoluble pectates in the plant cell wall, which are resistant to hydrolysis by Rhizoctonia polygalacturonases (Bateman, 1964). Limiting Ca in the soil would affect cell wall integrity that increase susceptibility of potato plants to infection, and affect tuber bulking. The soil at Tidewater would have a higher cation exchange capacity than at the Peanut Belt Research Station because of the higher organic and clay levels. However, most soils can resist pH changes when large amounts of fertilizers, either acidic or basic are added. This buffering capacity would then be effective in controlling soluble concentrations of such nutrients as calcium. For this reason, it does not appear that nutrient deficiencies are a critical component for facilitating infection by *R. solani*.

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Table 1. Mycelial growth of *Rhizoctonia solani* AG-3 in a minimal salts medium amended with different forms and concentrations of nitrogen.

Nitrogen Source	Mean mycelial dry weight (mg) [*]			
	Concentration (ppm) of N added to SSM broth			
	0	50	100	150
NaNO ₃ ^x	-	7.6 c ^y	8.4 c	4.2 d
NH ₄ NO ₃	-	7.6 c	16.1 b	7.7 c
(NH ₄) ₂ SO ₃	-	7.2 c	19.9a	7.6 c
Control	5.0 d	-	-	-

^x Letters within columns indicate significant differences at P<0.05, based on a Fisher's protected LSD test.

^y Nitrogen sources were added to broth before sterilization and water agar plugs colonized by *R. solani* AG-3 were added to each flask. Cultures were incubated for 72 hr at room temperature (25 C), then mycelial mats were removed and dried at 60 C for 24 hr prior to determining dry weights. Data were combined for three runs of the experiment and each value is the mean dry weight produced with nine replications of each N treatment.

Table 2. Mycelial growth of *Rhizoctonia solani* AG-3 in a minimal salts medium amended with different forms and concentrations of nitrogen.

Nitrogen Source	Mean mycelial dry weight (mg)			
	Concentration of N added to SSM broth (ppm)			
	0	50	100	150
NaNO ₃ ^x	-	4.0d ^y	7.8c	7.4c
NH ₄ NO ₃	-	6.1c	9.8b	6.8c
Urea	-	6.6c	13.2a	6.9c
Control	4.6d			

^x Letters within columns indicate significant differences at P<0.05, based on a Fisher's protected LSD test.

^y Nitrogen sources were added to broth before sterilization and water agar plugs colonized by *R. solani* AG-3 were added to each flask. Cultures were incubated for 72 hr at room temperature (25 C), then mycelial mats were removed and dried at 60 C for 24 hr prior to determining dry weights. Data were combined for three runs of the experiment and each value is the mean dry weight produced with nine replications of each N treatment.

Table 3. The effect of N form and rate on disease incidence and shoot and root biomass on potatoes grown in a controlled environment chamber.^x

N Source	Concentration (g N L ⁻¹)	Disease Incidence (%)		Shoot Biomass (g/plant)	Root Biomass (g/plant)
		Stems	Stolons		
<i>non-infested</i>					
Control	0	0 a ^y	0 a	1.97 b	1.59 ab
NaNO3	0.25	0 a	0 a	2.68 a	1.95 a
Urea	0.25	0 a	0 a	2.63 a	2.01 a
NaNO3	0.50	0 a	0 a	2.60 a	1.82 a
Urea	0.50	0 a	0 a	2.67 a	1.87 a
<i>infested</i>					
Control	0	25.9 bc	21.0 bc	1.67 b	1.20 b
NaNO3	0.25	10.3 b	15.1 b	2.67 a	2.11 a
Urea	0.25	18.5 bc	23.8 c	2.58 a	1.93 a
NaNO3	0.50	13.3 b	14.7 b	2.56 a	1.83 a
Urea	0.50	39.5 c	46.5 d	1.82 a	1.94 a

^x Run 1 of a phytotron experiment conducted for 8 wk. Plants were grown at a daytime temperature of 16 C and a nighttime temperature of 12 C. A photoperiod of 16 hr. Plants were fertilized with urea or Sodium nitrate.

^y Letters indicate significant differences within a column, P<0.05, based on a Fisher's protected LSD test. Four replications were used per treatment with three plants per pot.

Table 4. The effects of N form and rate on disease incidence and shoot and root biomass of potatoes grown in a controlled environment chamber. ^x

N Source	Concentration (g N L ⁻¹)	Disease Incidence (%)		Shoot Biomass (g/plant)	Root Biomass (g/plant)
		Stems	Stolons		
<i>non-infested</i>					
Control		0 a ^y	0 a	2.21 ab	1.11 b
NaNO3	0.25	0 a	0 a	2.56 a	1.92 a
Urea	0.25	0 a	0 a	2.52 a	1.93 a
NaNO3	0.50	0 a	0 a	2.54 a	1.98 a
Urea	0.50	0 a	0 a	2.52 a	1.72 ab
<i>infested</i>					
Control		18.1 c	11.0 b	1.73 b	0.89 c
NaNO3	0.25	11.5 b	8.3 b	2.59 a	1.99 a
Urea	0.25	15.5 c	9.1 b	2.52 a	1.58 b
NaNO3	0.50	11.3 b	7.9 b	2.60 a	2.00 a
Urea	0.50	43.2 d	37.6 c	1.70 b	1.01 c

^x Run 2 of a phytotron experiment conducted for 8 wk. Plants were grown at a daytime temperature of 16 C and a nighttime temperature of 12 C. A photoperiod of 16 hr. Plants were fertilized with urea or Sodium nitrate.

^y Letters indicate significant differences within a column, P<0.05, based on a Fisher's protected LSD test. Four replications were used per treatment with three plants per pot.

Figure legends:

Figure 1a. Total yield of potato (cv. 'Atlantic') grown in soil amended with 0, 84, and 168 kg N ha⁻¹ NaNO₃ or urea, either infested or not infested with *R. solani*, at the Tidewater Research Station in Plymouth, North Carolina (2000). Letters denote mean separation by LSD at P=0.05.

Figure 1b. Marketable yield of potato (cv. 'Atlantic') grown in soil amended with 0, 84, and 168 kg N ha⁻¹ NaNO₃ or urea, either infested or not infested with *R. solani*, at the Tidewater Research Station in Plymouth, North Carolina (2000). Letters denote mean separation by LSD at P=0.05.

Figure 2a. Total yield of potato (cv. 'Atlantic') grown in soil amended with 0, 84, and 168 kg N ha⁻¹ NaNO₃ or urea, either infested or not infested with *R. solani*, at the Tidewater Research Station in Plymouth, North Carolina (2001). Letters denote mean separation by LSD at P=0.05.

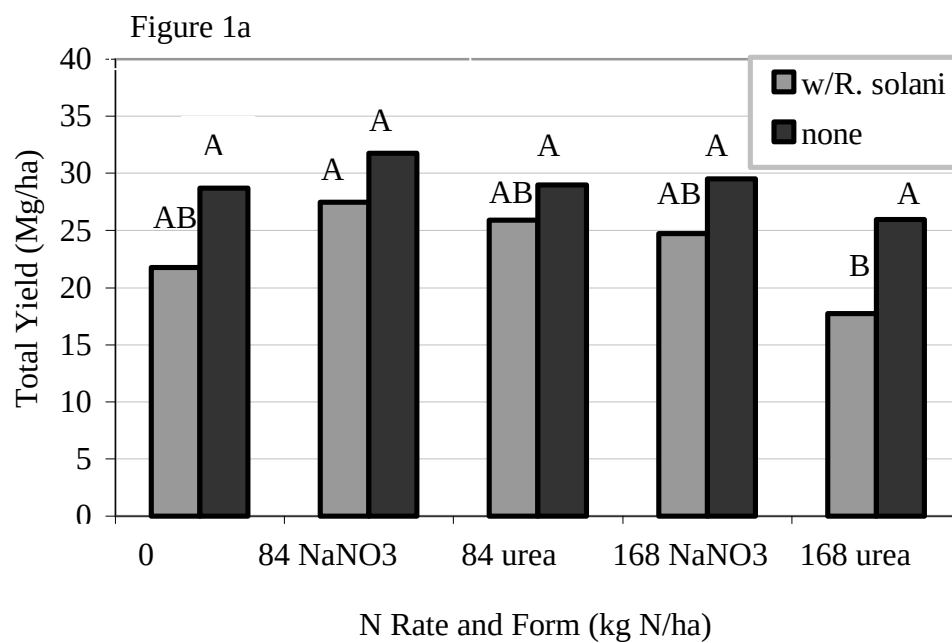
Figure 2b. Marketable yield of potato (cv. 'Atlantic') grown in soil amended with 0, 84, and 168 kg N ha⁻¹ NaNO₃ or urea, either infested or not infested with *R. solani*, at the Tidewater Research Station in Plymouth, North Carolina (2001). Letters denote mean separation by LSD at P=0.05.

Figure 3a. Percentage of stolon with canker symptom on potato (cv. 'Atlantic') assessed 6 wk after planting stolon in the first 3.6 m of the middle treatment row grown at the Tidewater and Peanut Belt Research Stations in Plymouth and Lewiston, North Carolina (2001). Letters denote mean separation by LSD at $P=0.05$.

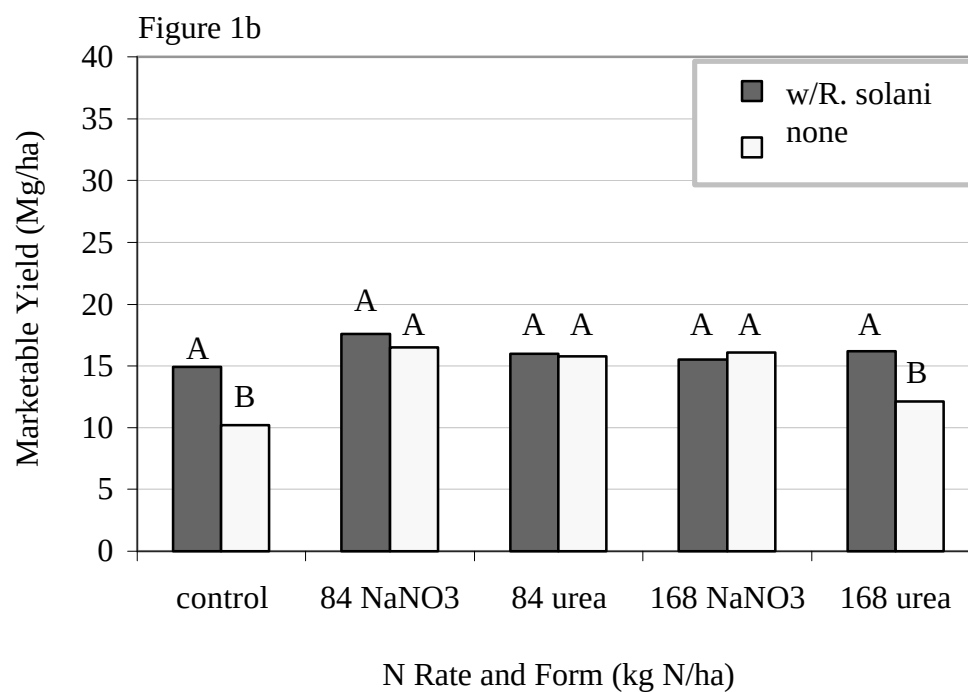
Figure 3b. Total number of stolons produced on potato (cv. Atlantic) assessed 6 wk after planting in the first 3.6 m of the middle treatment row at the Tidewater and Peanut Belt Research Stations in Plymouth and Lewiston, North Carolina (2001). Letters denote mean separation by LSD at $P=0.05$.

Figure 4. Marketable yield of potato (cv. 'Atlantic') grown in soil amended with 0, 84, and 168 kg N ha⁻¹ NaNO₃ or urea, either infested or not infested with *R. solani*, at the Peanut Belt Research Station in Lewiston, NC (2001). Letters denote mean separation by LSD at $P=0.05$.

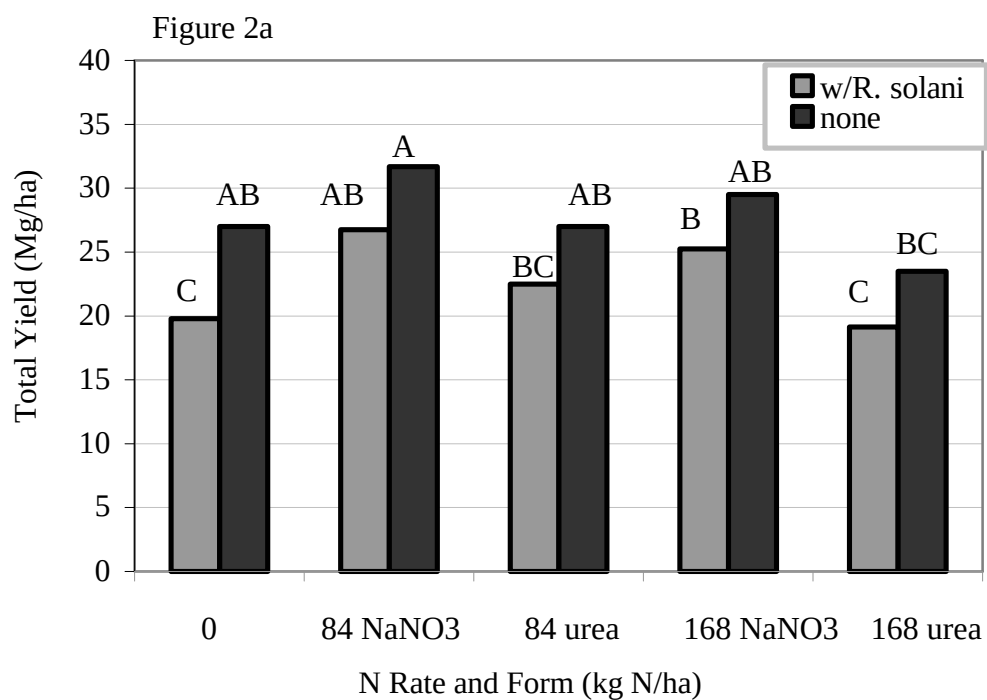
Tidewater, 2000



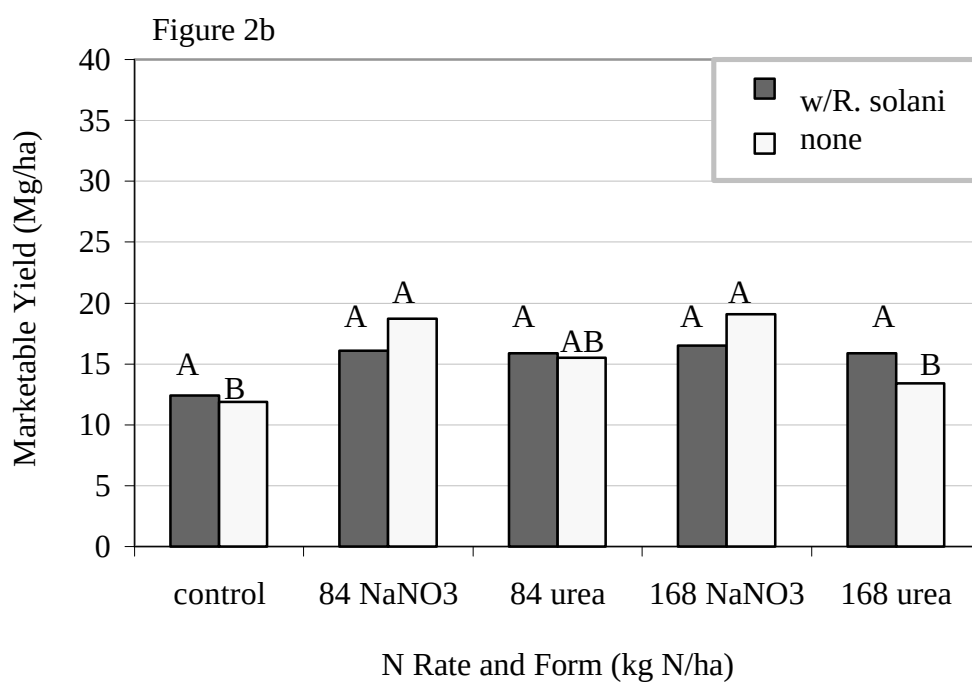
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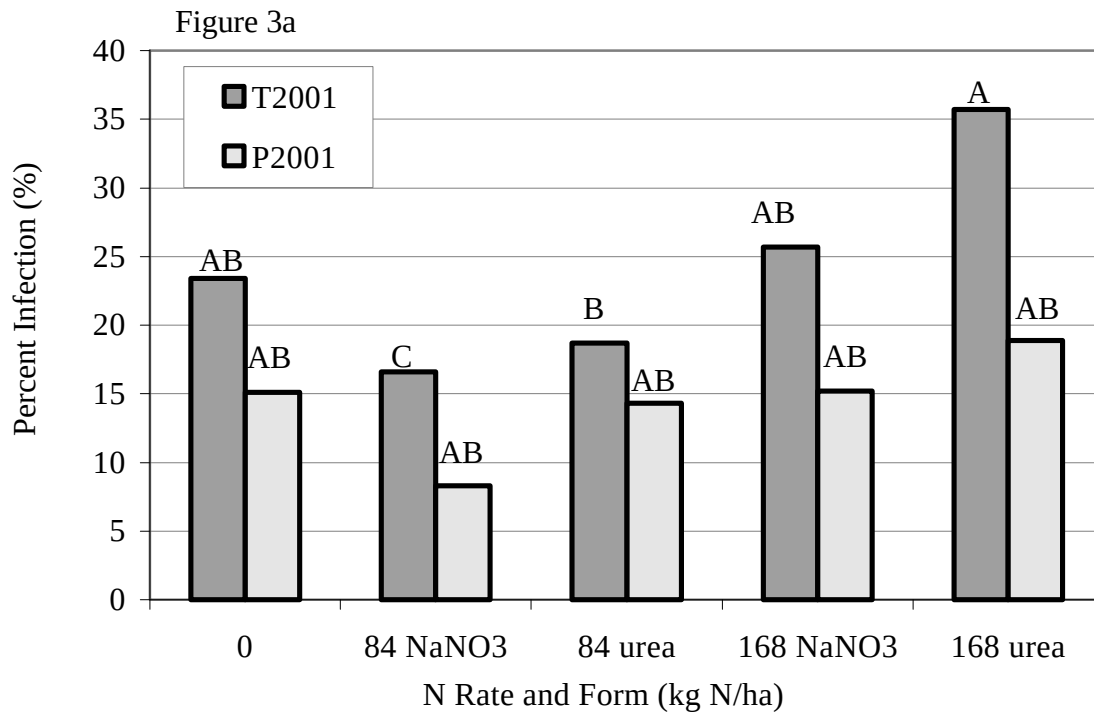
Tidewater, 2001



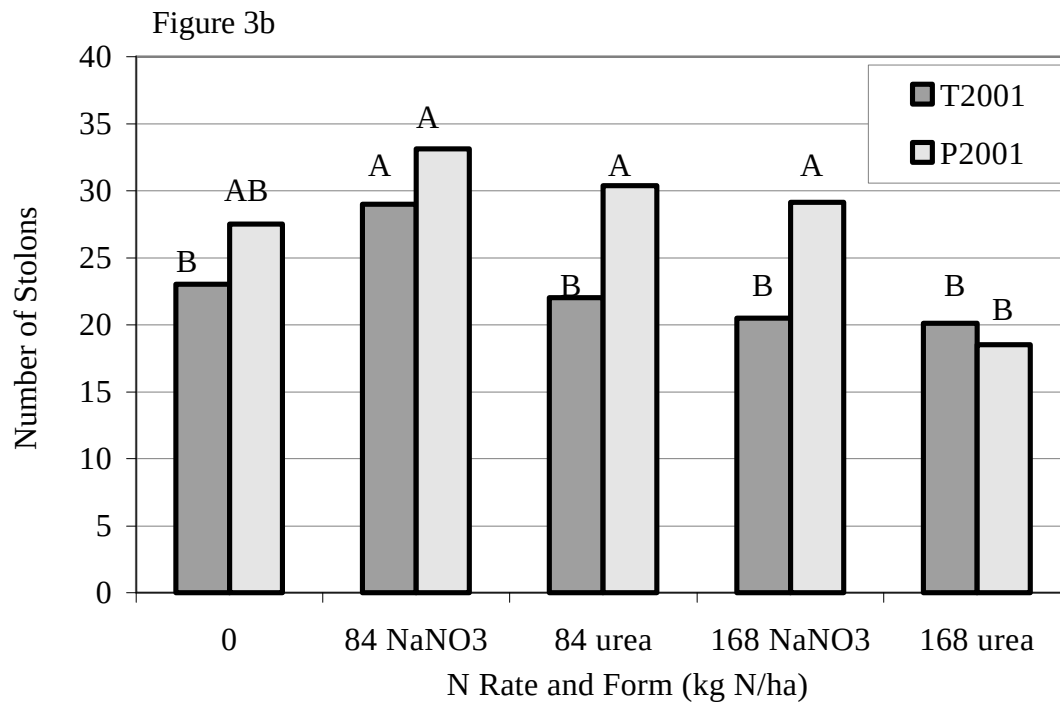
Tidewater, 2001



Percent Stolon Infection in Infested Rows



Total Number of Stems vs. N Rate and Form



Peanut Belt, 2001

