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Atmospheric CO_2 Enrichment of Potato in the Subarctic: Root Distribution and Soil Biology

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The effect of increasing atmospheric CO_2 concentration on fine root distribution of potatoes and associated soil biology activity under subarctic conditions has not been studied. Potatoes (*Solanum tuberosum* L.) were grown in open top field chambers at three CO_2 concentrations [ambient (A); A＋175 μmol mol^{-1} CO_2 (A＋175); A＋350 μmol mol^{-1} CO_2 (A＋350)] and in ambient CO_2 plots with no chambers (ANC) on a Tanana silt loam (non-acid loamy, mixed Pergelic Cryaquept) at Fairbanks, AK in 1994. Soil cores to a depth of 60 cm were taken at 0, 19, and 38 cm perpendicular to row center; root variables were ascertained at four 15 cm depth increments. Soil cores to a depth of 15 cm were also collected to assess soil biology (dehydrogenase activity, nematodes, and soil microarthropods). Elevated CO_2 did not enhance root densities (i.e., both length and mass) at any depth or row position; there was no significant CO_2×depth, CO_2×position, or CO_2×depth×position interactions for measured root variables. Significant depth×position interactions were noted. In general, a higher proportion of the potato root system grew closer to the row center (root length and mass bases) most notably at the uppermost soil depths. Elevated CO_2 had no impact on the soil biology parameters evaluated in this study. Our field results suggest that increased atmospheric CO_2 concentration did not alter belowground responses in potato under subarctic conditions of Alaska.

Keywords : Alaska, rising CO_2, root length density, root mass density, *Solanum tuberosum*

INTRODUCTION

The extent of the predicted alteration in climatic conditions attributed to the increase in atmospheric greenhouse gases such as CO_2 and the subsequent impact on terrestrial ecosystems remains controversial. However, since CO_2 is a primary input for crop growth, it is important to determine if the structure and function of managed agricultural systems will be impacted by the rise in atmospheric CO_2.

Direct aboveground plant responses to enhanced atmospheric CO_2 have been documented. Research has demonstrated clear plant responses, including increased growth and yield (Kimball, 1983), increased water use efficiency (Amthor, 1995), increased photosynthetic capacity (Lawlor and Mitchell, 1991), and changes in plant structure (Pritchard et al., 1999) and tissue chemistry (Lincoln et al., 1993).

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Effects of CO_2 on belowground processes (including soil organisms) have received far less attention. Reviews indicate that CO_2 enhancement of root dry weight has been frequently observed and often the largest proportion of the extra whole plant biomass is allocated belowground (Rogers et al., 1994; 1996). Early CO_2 studies conducted under controlled environmental conditions with containerized systems have demonstrated CO_2-induced root increases (i.e., mass and/or length) in the upper soil depths (Del Castillo et al., 1989; Chaudhuri et al., 1990) or at all soil depths (Chaudhuri et al., 1986; Rogers et al., 1992). However, since the growth conditions of these system's (i.e., confined rooting volume) are not reflective of agricultural fields (Sionit et al., 1984; Thomas and Strain, 1991), more current efforts have focused on conducting in-ground CO_2 studies utilizing open top chambers (OTC) and free-air CO_2 enrichment (FACE) systems. These field studies have shown that CO_2 enrichment can increase biomass (Kimball et al., 1997), alter plant root morphology (Prior et al., 1995) and the root system's capacity to explore soil volume through shifts in fine root distribution patterns (Prior et al., 1994; Weschsung et al., 1999). Soil organisms can be beneficial or pathogenic and are responsible for the decomposition of organic matter and soil C storage. While the effects of elevated CO_2 on community composition and activity of soil organisms remain understudied, these aspects of belowground biology have begun to receive increased attention (Patterson et al., 1997; Sadowsky and Schortemeyer, 1997). However, studies to date have shown variable responses (Rice et al., 1994; Runion et al., 1994; Zak et al., 2000). These results demonstrate the importance of conducting field experiments and the need for further studies that reflect actual management practices that encompass the abiotic and biotic conditions found in field environments.

Temperature is an important factor that can influence plant response to CO_2. Leaf level photosynthesis is temperature dependent (Pearcy and Bjorkman, 1983) largely due to the temperature dependent specificity of rubisco for CO_2 (Jordan and Ogren, 1984). Although few studies have investigated the interactive effects of temperature and CO_2, there is some evidence that greater growth stimulation can occur at higher vs lower temperatures under elevated CO_2 conditions (Cure, 1985). Idso et al. (1987) reported that elevated CO_2 could decrease crop yields below 18.5°C. However, a recent review (106 experiments) indicates no clear CO_2 response pattern at low temperatures since some species responded to increased CO_2 at temperatures below 18°C while others did not (Morison and Lawlor, 1999). These findings support the contention that plants growing in disparate temperature regimes may have widely different responses to elevated CO_2 (Drake and Leadley, 1991).

The potato (*Solanum tuberosum* L.) is well adapted to the cool growing season and longer day-lengths of Alaska and is the most economically important field crop grown there (Benz et al., 2002). Potatoes have a large carbohydrate sink in the form of tubers and exhibit apoplastic phloem loading of sucrose which predisposes the species to large increases in yield with elevated CO_2 (Miglietta et al., 1998; De Temmerman et al., 2002). Experiments performed in both growth chambers (Stutte et al., 1996; Wheeler et al., 1991) and in the field (Miglietta et al., 1998; Craigon et al., 2002; Conn and Cochran, 2005) have shown that potato tuber yields generally increase with elevated CO_2. However, there are no documented studies on how elevated CO_2 will impact fine root distribution or soil biology responses at higher latitudes characterized by lower temperatures and longer day-lengths.

Our objective was to investigate the effects of increasing atmospheric CO_2 concentration on fine root distribution of potatoes and associated soil biology activity under subarctic conditions of long days and cool temperatures typical of summer field conditions in Fairbanks, Alaska (latitude 64′ 49″N). This region represents the northern limit of commercial agriculture in North America.

MATERIALS AND METHODS

The experiment was conducted at the University of Alaska Agriculture and Forestry Experiment Station in Fairbanks, AK (latitude 64′49″N, longitude 147′52″W, elevation 145 m). The mean annual temperature is −3.5°C and the mean annual precipitation is 28 cm. The soil was a Tanana silt loam (non-acid loamy, mixed Pergelic Cryaquept) with a pH of 5.7 and 4.7% organic matter.

Potatoes were grown in open top field chambers (Rogers et al., 1983) at different atmospheric CO_2 concentrations and in open plots (no chambers) under ambient atmospheric conditions utilizing a randomized complete block design with four replications of four CO_2 treatments. The details of the CO_2 exposure systems and experimental setup have been previously described for this study site (Conn and Cochran, 2005). The open top field chambers were constructed of a structural aluminum frame (3-m in diameter by 2.4-m in height) equipped with frustums (2.2-m final diameter opening) and covered with a PVC film panel (8 mil). Carbon dioxide was supplied to elevated CO_2 chambers (24 h day^{-1}) from a 23.6 metric ton liquid CO_2 receiver through a high volume dispensing manifold and the atmospheric CO_2 concentration was elevated by continuous injection of CO_2 into plenum boxes. Air was introduced into each chamber through the bottom half of each chamber cover which was double-walled; the inside wall was perforated with 2.5-cm diameter holes to serve as ducts to distribute air uniformly into the chamber. Carbon dioxide concentrations were monitored using a time-shared manifold with samples drawn through solenoids to an infrared CO_2/H_2O analyzer (Model Li-6262; LI-COR, Inc., Lincoln, NE)[§]. Seasonal daytime CO_2 means ± 1 SD were: 368 ± 25 μmol mol^{-1} CO_2 (ambient plots with no chambers; ANC), 369 ± 25 μmol mol^{-1} CO_2 (ambient chamber; A), 543 ± 25 μmol mol^{-1} CO_2 (A + 175) and 707 ± 51 μmol mol^{-1} CO_2 (A + 350).

The experimental area, which had been fallow the previous year, was disked twice prior to planting 'Shepody' potatoes (May 19, 1994) using a single row potato planter that also banded fertilizer (290 kg ha^{-1} N, 63 kg ha^{-1} P, 122 kg ha^{-1} K) with the potato seed pieces. Seed pieces were planted 28 cm apart in rows that were spaced 76 cm apart. Metribuzin [4-amino-6-(1,1-dimethyl) 3-(methylethlthio)-1,2,4-triazin-5(4H)-one] was broadcast applied at 1.13 kg ha^{-1} on June 2 to control weeds. Study plots were maintained under well-watered conditions by monitoring soil moisture with tensiometers and using a drip tube irrigation system as described elsewhere (Conn and Cochran, 2005). Chamber installation occurred on June 10 as plants emerged and dispensing of CO_2 began on June 11.

Soil cores (38 mm diameter) measuring 60 cm in length were collected to determine root length and mass density on July 27, 1994. Soil cores were taken in-row (0 m) and at distances of 0.19 and 0.38 m perpendicular to the row; 192 soil cores were taken, representing four cores per position within each plot. Pneumatic hammers for driving steel core tubes (lined with a thin walled butyrate tube) and electric core tube extraction devices were used to collect root-soil cores (Prior and Rogers, 1992). Soil cores within the plastic tube liners (which were capped) were packed in ice and transported by air to the National Soil Dynamics Laboratory (NSDL), Auburn, AL, where they were placed in cold storage until processing. A hand-held electric band saw was used to cut each 60 cm core into four 15 cm segments. Roots were washed from each core segment with a hydropneumatic elutriation system (Gillison's Variety Fabrication, Inc., Benzonia, MI; Smucker et al., 1982) and stored in 20% ethanol (Bohm, 1979) at 4°C. After organic debris had been removed with tweezers and spring-loaded suction pipettes, root length was measured with a Comair Root

[§] Trade names and products are mentioned solely for information. No endorsement by the USDA is implied

Length Scanner (Hawker de Havilland, Victoria, Australia). Root mass determinations were made after drying samples at 55°C.

An additional set of three cores per plot were taken from directly beside randomly selected plants for soil biology assessment. The same steel core tubes (as described above with liners) were driven below a 15 cm depth with a sleeve-type post driver and manually extracted (Prior and Rogers, 1994). These samples were also packed in ice and transported by air to the NSDL.

Nematodes were extracted from root-zone soil using the methods described by Rodríguez-Kábana and Pope (1981). Root-zone soil (100 cm^3) was spread onto tissue paper on a sieve constructed from 15 cm diameter PVC pipe sections and 1-mm-mesh fiberglass screen. The sieve with the soil was placed in a 2.3 L plastic bowl containing 1.3 L sterile water so as to just cover the soil. The soil was incubated at room temperature (25°−27°C) for 72 h. The bowl contents were passed through a 250 μm stainless steel sieve (to remove debris) stacked on a 38 μm stainless steel sieve (to trap the nematodes). Nematodes retained were transferred to a counting dish and their numbers determined by direct counting with a dissecting microscope.

For the soil microarthropod assessment, soil was extracted for relative populations of Collembola and Acari by a modified version of the Tullgren system as described by Wiggins and Curl (1979). Soil samples in large funnels, with stems positioned over water in a collecting tube, were arranged in series under 40-W light bulbs. The animals, migrating in advance of the slowly drying soil (5−7 days) were collected live. Populations were expressed as numbers per kg of air-dried soil.

For the dehydrogenase assay, roots and other debris were removed from a portion (200 cm^3) of the root-zone soil. The soil was then passed through a 2 mm-mesh stainless steel sieve until 10−20 g of sieved soil was collected. Dehydrogenase activity, which is a reliable index of microbial activity in soil (Stevenson, 1959), was determined from modified procedures described by Tabatabai (1982). Sieved soil (1 g) for triplicate subsamples from each root-zone soil sample was placed in test tubes (15 × 100 mm), covered with 1 mL of 3% aqueous (w/v) 2,3,5-triphenyltetrazolium chloride and stirred with a glass rod. After 96 h incubation (27°C), 10 mL of methanol was added to each test tube and the suspension was vortexed for 30 sec. Tubes were then incubated for 1 h to allow suspended soil to settle. The resulting supernatant (5 mL) was carefully transferred to clean test tubes using Pasteur pipets. Absorbance was read spectrophotometrically at 485 nm and formazan concentration was calculated using a standard curve produced from known concentrations of triphenyl formazan. One subsample of sieved soil (1 g) from each root-zone soil sample was used for determination of soil moisture so that formazan concentrations could be expressed per gram soil dry weight.

All analyses were performed using the general linear models procedure of the Statistical Analysis System (SAS, 1985). Core position and depth increments were treated as split-plot treatments within the overall study design and an average of the replicate core samples was used for statistical analyses. Proper error terms were specified for the split-plot treatment. Contrast statements were used to determine the significance between interacting main effect variables. Differences were considered significant at the $P < 0.10$ level.

RESULTS AND DISCUSSION

Previous research has demonstrated that root growth usually increases under elevated atmospheric CO_2 conditions (Prior et al., 1994; Rogers et al., 1994; Weschsung et al., 1999); this encompasses findings from both growth chamber and field studies. However, in the present study no significant effect of CO_2 concentration was found for either root length or root mass density regardless of position or depth increment (Figs. 1 and 2). In this same study, Conn and Cochran (2005) reported a reduction in aboveground biomass allocation, with a concomitant increase in allocation

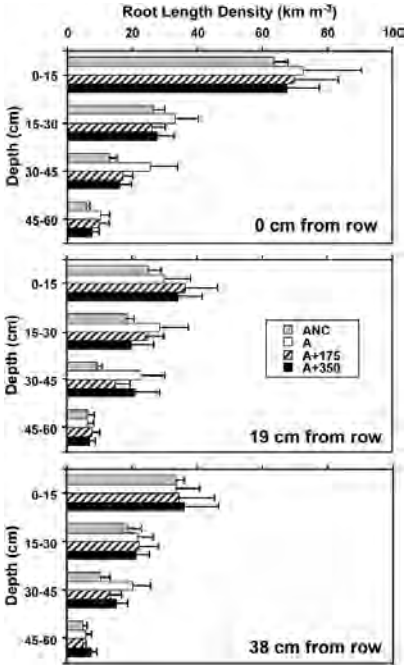

Fig. 1 The effect of CO_2 level (ANC = ambient with no chamber; A = ambient with chamber; A + 175 = A + 175 μmol mol^{-1} CO_2; A + 350 = A + 350 μmol mol^{-1} CO_2) on potato root length density at three positions (0, 19, and 38 cm away from the crop row center) under subarctic conditions in Fairbanks, Alaska. Means and standard errors are shown (n = 4).

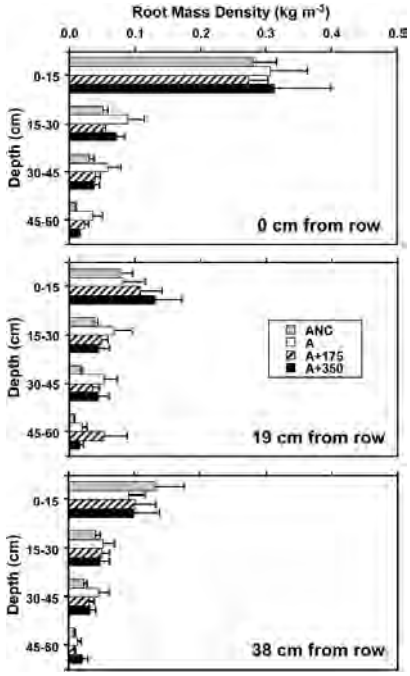

Fig. 2 The effect of CO_2 level (ANC = ambient with no chamber; A = ambient with chamber; A + 175 = A + 175 μmol mol^{-1} CO_2; A + 350 = A + 350 μmol mol^{-1} CO_2) on potato root mass density at three positions (0, 19, and 38 cm away from the crop row center) under subarctic conditions in Fairbanks, Alaska. Means and standard errors are shown (n = 4).

to tubers, under elevated CO_2 resulting in a 55–90% increase in root: shoot (RS) ratio for the elevated CO_2 treatments. Idso et al. (1988), reported an approximate 36% increase in RS ratio for tuber crops exposed to elevated CO_2, while RS ratio of non-tuber crops showed no response to CO_2. In a review of 264 determinations of RS ratio in crop species, Rogers et al. (1996) found that the highest and most consistent RS ratio response to elevated CO_2 occurred in tuber crops. Conn and Cochran (2005) attributed the reduction in aboveground biomass allocation in part to the fact that tubers represent a stronger sink for carbon. They also speculated that the low average growing season temperature (18.3°C) may have limited potato response to CO_2. It is likely that the lack of a fine root response observed in this study was also due to these factors.

Although there were no root responses to CO_2, we did find that, generally, more of the potato root system grew closer to the row center (root length and mass bases) particularly at the uppermost soil depths. While this root distribution pattern is common for major row crops (Prior et al., 1994; Weschsung et al., 1999), the low soil temperature at the lowest depth increment (14.6°C) may have contributed to lower root growth.

Populations and activity of soil organisms are known to be highly variable on both temporal and spatial scales (Wollum, 1994); the same holds true in elevated CO_2 studies (Rice et al., 1994;

Table 1 Effects of CO_2 level (ANC＝ambient with no chamber; A＝ambient with chamber; A＋175＝A＋175 μmol mol^{-1} CO_2; A＋350＝A＋350 μmol mol^{-1} CO_2) on soil biology activity (dehydrogenase activity, nematodes, and soil microarthropods) under subarctic conditions in Fairbanks, Alaska. Dehydrogenase activity and soil microarthropods (Collembola and Acari) are expressed on oven dry soil basis. Nematodes are expressed per 100 cm^3 air dried soil. Means and standard errors are shown (n＝4). Numbers in a column that are followed by different letters are significantly different as determined by contrast statements conducted under the General Linear Models program of SAS (P＜0.045).

Treatment	Dehydrogenase Activity	Saprophagus Nematodes	Collembola	Acari	Total Mesofauna
	(μg formazan/g)	(#)	(#/kg)	(#/kg)	(#/kg)
ANC	3.16±0.14a	137.00±10.2a	137.6±62.2a	66.7±6.3a	204.4±61.2a
A	3.37±0.52a	129.75±1.1a	178.9±51.6a	56.9±20.6a	235.7±40.6a
A＋175	3.25±0.26a	116.00±11.7a	180.2±54.7a	40.2±12.2a	220.4±54.4a
A＋350	3.08±0.11a	123.50±25.0a	328.7±118.8a	38.3±18.4a	367.0±134.6a

Runion et al., 1994; Zak et al., 2000). In the present study, there were no effects of CO_2 concentration on any soil organism parameter examined (Table 1). High variability contributed to lack of difference in soil mesofauna measurements, however, nematode and dehydrogenase measurements did not reflect a high degree of variability. The fact that the field site had only recently been brought back into agricultural production may also have contributed to the lack of differences in soil organism assessments; this contention is supported in that the soil was virtually devoid of parasitic nematodes (data not shown). Perhaps, had the study been exposed to the CO_2 treatments for multiple growing seasons, the changes in plant morphology, physiology, and phytochemistry from increasing levels of atmospheric CO_2 (Conn and Cochran, 2005) may have been reflected in changes in soil organism populations or activity.

In this study, CO_2 had no affect on roots and soil organisms in field grown potatoes in the subarctic region of Alaska. It is likely that the low average growing season temperature may have limited these belowground responses to CO_2. This region currently represents the northern limit of commercial agriculture in North America. However, global warming may extend the range of crop production and length of growing seasons in these northern regions (Myneni et al., 1997; Menzel and Fabian, 1999). If temperatures should increase in this region, the response of crop plants (such as potato) to rising atmospheric CO_2 could increase concomitantly.

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