Dynamics of Root Growth in Potato Fields Affected by the Early Dying Syndrome

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ABSTRACT

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Root growth dynamics of potato cultivars Norgold Russet and Russet Burbank were studied in field plots infested with pathogens associated with the "potato early dying" (PED) syndrome. Root growth was determined from estimates of root diameter and length in 14 soil cores (5 cm in diameter) per plant in 1980 and from five soil cores (10 cm in diameter) per plant in 1981 and 1982. Treatments in 3 × 12-m field plots were: untreated, artificially infested with *Verticillium dahliae*, fumigated with methyl bromide, or fumigated and infested with *V. dahliae*. Mean root diameter decreased through the season, but root length reached a maximum at 69–105 days after planting, then declined as the plants senesced. Average total root length per plant was 502 m for Norgold Russet in 1980 and was not significantly affected by treatments. Total root length per plant of Russet Burbank in fumigated plots reached 1,248 m in 1981 and 1,154 m in 1982. Root length in fumigated plots infested with *V. dahliae* was 21% less than in fumigated, noninfested plots in 1981 ($P = 0.10$), but reductions were not statistically significant in 1982. Root surface areas and volumes were greater in fumigated plots than in unfumigated plots and were less in plots infested with *V. dahliae* than in noninfested plots.

Additional key words: plant growth, soil microbiology.

Verticillium wilt of potatoes is a major disease problem in temperate potato production areas worldwide. Symptoms of this disease, commonly referred to as the "potato early dying" (PED) syndrome have been associated with *Verticillium dahliae* (*Vd*) and a complex of other pathogens including fungi (*Colletotrichum coccodes* and *Fusarium* spp.), a bacterium (*Erwinia carotovora*), nematodes (*Meloidogyne hapla* and *Pratylenchus* spp.), and potato virus X (4,7,9,12,14,21,24,27,30,32). The symptoms of PED include wilting, chlorosis and necrosis of foliage, stunted growth, reduced yield, and premature senescence of infected plants. In addition, reduction in fresh weight, vascular discoloration, and general deterioration of the root system frequently have been reported (4,11,21,25). However, the relationship of PED and root growth dynamics has not been studied adequately.

Reliable line intercept methods for quantifying root length have become available recently (2,20,23,31). These methods are often very time consuming (3) and have not been used frequently by plant pathologists (10,18). New technological advances in automated root washing and length measurement are being developed to reduce time requirements and increase the accuracy of root growth assessments (29,33).

As part of a long term study of the effects of PED on potato growth and yield (28), field studies were initiated to quantify root growth dynamics of potatoes and to assess the impact of PED on root growth and root deterioration. Preliminary reports of this work have been published (16,17).

MATERIALS AND METHODS

Field plots, 3.6 × 12 m, were established in Plainfield loamy sand (sandy, mixed, mesic, Typic Udipsamment) at the Hancock Experiment Station in central Wisconsin. The field had been planted to potatoes continuously for 8 yr, had a history of PED, and was naturally infested with *Vd, P. penetrans, E. carotovora, C. coccodes,* and *Fusarium* spp. Methyl bromide (585 kg a.i./ha) was applied to selected plots under tarps in the fall of 1979 before soil temperature at the 15-cm depth had dropped below 10 C (50 F) and in the spring in 1981 and 1982 as soon as soil temperatures at that depth had reached 10 C (50 F). Half of the fumigated plots and the same number of unfumigated plots were artificially infested with *Vd* each year after at least 14 days aeration following fumigation and immediately prior to planting. Treatments were arranged in a completely randomized, factorial design.

Inoculum of *Vd* was grown on autoclaved rye seed, inoculated with a conidial suspension, and incubated at room temperature for 3–6 wk. After air-drying for 2 wk at room temperature, inoculum was ground in a Wiley mill with a #4 screen. Approximately 150 g of ground inoculum of *Vd* was spread over each plot with a lawn fertilizer spreader and disked into the soil to a depth of ~20 cm. Plots were hilled on 90-cm row spacings and seed tubers were hand planted to ensure a spacing of 30 cm between plants. Recommended agronomic practices for fertilization, irrigation, and pesticide application were followed throughout the season to avoid significant stress due to fertility, drought, or other pests.

In 1980, initial studies of root density distribution were conducted to determine efficient sampling methods. At 189 degree days (base, 10 C [50 F]) after planting (DDAP) Norgold Russet, the seedpiece, emerging sprouts, and all roots were excavated from three hills in the control and methyl bromide treatments. At 379, 595, 902, 1,265, and 1,531 DDAP, roots from two hills in each treatment were sampled by removing soil cores with a 5-cm-diameter bucket auger from depths of 0–15 and 15–30 cm below the surface of the hill. Cores were collected at 5, 15, and 38 cm from both sides of the plant and from midway between plants within the row.

Based on 1980 data, sampling procedures for 1981 and 1982 were modified to increase the number of plants and the volume of soil being sampled. Roots of Russet Burbank potatoes were sampled with a 10-cm-diameter bucket auger from depths of 0–15 and 15–30 cm, midway between plants within the row, 10 cm to one side of the plants, and 38 cm to that side of the plants (0–15 cm depth only) (Fig. 1). Cores were taken from one randomly selected plant from each of four replicate plots per treatment at 578, 1,035, 1,578, and

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1,737 DDAP in 1981 and at 554, 1,003, 1,304, 1,546, and 1,751 DDAP in 1982.

Cores were placed on a 1.7-mm (10-mesh) screen and soil was washed from the roots under a gentle flow of tap water. Total root length in each core was determined by using Newman's line intercept method (23) as modified by Marsh (20) and Tennant (31). Diameters of 10 randomly chosen root segments from each core were determined by inspection and visual comparison with measured root standards. Root density was calculated from the total root length in each core and the volume of that core. Data from individual cores were expressed on a whole-plant basis by multiplying the root densities from each core by the volume of soil in that portion of the hill and summing the root lengths from each portion to give the estimated root length per plant (Fig. 1). These estimates assumed a uniform root density throughout the portion of the hill represented by each core, and assumed that penetration of roots from adjacent plants into the volume occupied by the sampled plant is equal to the root length from the sampled plant extending beyond the sampled volume.

RESULTS

Norgold Russet potatoes showed substantial root growth prior to sprout emergence. Roots had permeated the hill and penetrated the surface layers at least 40 cm from the seedpiece by 379 DDAP.

Plants in untreated plots developed symptoms of PED and roots were colonized by *Vd*, as well as *P. penetrans, C. coccodes*, and *Fusarium* spp. Root colonization by *Vd* was greater in plots infested with additional inoculum of *Vd* than in uninfested plots by the end of the growing season in 1981, but differences were not statistically significant in 1980 or 1982 (15). Plants in fumigated noninfested plots were free of PED symptoms and exhibited increased foliage growth and yield (*unpublished*). However, no statistically significant effects on root growth were found in 1980 (Table 1). Since statistically significant effects of treatments were not found, root density data from all treatments were pooled. Root density increased from 0.15 ± 0.02 cm/cm^3 at 379 DDAP to 0.82 ± 0.05 cm/cm^3 at 1,265 DDAP and then declined to 0.71 ± 0.04 cm/cm^3 at 1,531 DDAP (mean and standard error of all samples). Root density was quite variable with results from individual cores on opposite sides of a plant occasionally differing by 10-fold or more. Root density in samples from the 0–15 cm depth in the hill was greater than in other samples ($P < 0.001$) at 379 and 595 DDAP (Fig. 2). Root density remained constant in the 0–15 cm depth through the remainder of the season (Fig. 2A) but increased steadily in samples from the 15–30 cm depth until 1,265 DDAP. Between 1,265 and 1,531 DDAP, root density in samples from the 15–30 cm depth decreased an average of 19% ($P = 0.05$) (Fig. 2B).

Total root length per plant increased from 18.5 ± 1.9 m at emergence (189 DDAP) to a maximum of 502 ± 59 m at 1,265 DDAP, but then declined to 403 ± 21 m by 1,531 DDAP (Table 1). Statistically significant effects of methyl bromide fumigation or infestation of soil with *Vd* on root length were not observed.

Root systems of Russet Burbank potatoes in 1981 and 1982 were much larger than those of Norgold Russet in 1980. Mean root density in samples from Russet Burbank potatoes increased to 1.90 ± 0.10 cm/cm^3 at 1,578 DDAP in 1981 and 1.95 ± 0.16 cm/cm^3 at 1,003 DDAP in 1982. In 1981, the maximum mean root length per plant was 1,248 ± 82 m in fumigated plots (1,578 DDAP) (Fig. 3). In 1982, root length in fumigated plots peaked earlier than in 1981, reaching 1,154 m at 1,003 DDAP, but fluctuated near that level until the plants senesced at 1,751 DDAP (Fig. 4).

Total root length at 1,578 DDAP in fumigated plots infested

TABLE 1. Total root length (meters per plant) of field-grown Norgold Russet potatoes in 1980

	Degree days after planting (base, 10 C [50 F])					
Treatment	189	379	595	902	1,265	1,531
Untreated	18.3[a]	61.2	168.0	513.6	628.8	434.3
Infested	···	96.3	172.2	304.7	315.8	428.0
Fumigated	18.7	55.6	198.8	153.5	459.5	314.6
Fum + Inf	···	97.5	310.1	283.5	605.0	434.1
Mean	18.5	77.7	212.3	313.9	502.3	402.7
Std. Dev.	4.6	30.4	64.1	144.2	166.8	59.8

[a]Values represent the mean of two plants per treatment. Inoculum of *Verticillium dahliae* was applied to infested plots at planting. Methyl bromide fumigant (585 kg a.i./ha) was applied under tarps the previous fall.

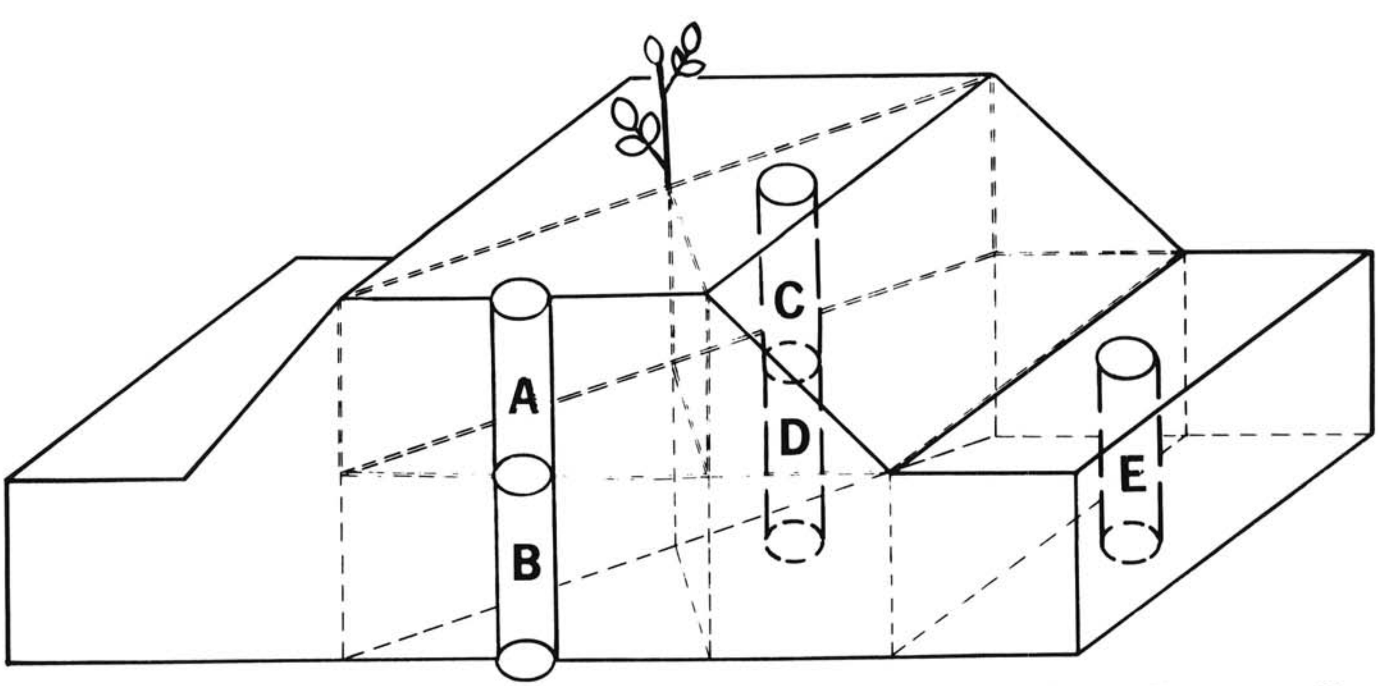

Fig. 1. Model of the potato hill and associated rooting volume. Hills are ~30 cm wide, 15 cm in height, and centered on 90-cm rows. Plants were spaced 30 cm apart. The volume of each of the five cores sampled in 1981 and 1982 was 1.18 L. The rooting volume represented by cores at each location is: A = 6.75 L, B = 6.75 L, C = 13.5 L, D = 20.25 L, and E = 13.5 L. Cores A and C are from 0–15 cm below the surface of the hill. Cores B, D, and E are 15–30 cm below the surface of the hill.

with *Vd* in 1981 was 21% less than in fumigated, uninfested plots ($P < 0.10$). Significant differences among treatments were not found on the first two sample dates nor at the final sampling when roots were senescing (Fig. 3). In 1982, there was a consistent trend for plants in fumigated plots to have the greatest root length; however, statistically significant treatment effects were not found at any sampling date (Fig. 4).

Root segments were placed in size classes (chosen to approximate the observed order of root branching) by diameter: rootlets = 0.1–0.2 mm, branch roots = 0.3–0.5 mm, and main roots ⩾0.6 mm. In both 1981 and 1982, the relative proportion of main roots and branch roots decreased through the season while the proportion of rootlets increased (Tables 2 and 3). In 1982, plants in fumigated treatments had significantly more branch roots at 1,304

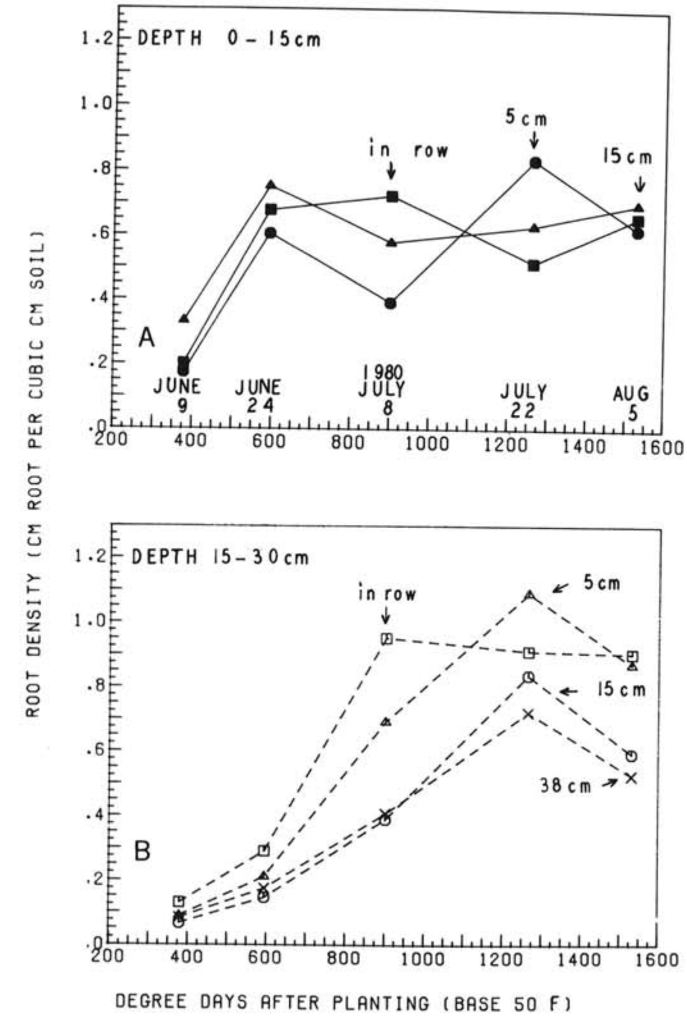

Fig. 2. Root density distribution of Norgold Russet potatoes in 1980. Points represent means of 16 cores across four treatments. The seven positions were sampled 379, 595, 902, 1,265, and 1,531 degree days (base, 10 C [50 F]) after planting. **A,** Sample cores 0–15 cm below the surface of the hill and located midway between plants in the row (■), or perpendicular to the row at 5 (●) or 15 (▲) cm from the plant. **B,** Sample cores 15–30 cm from the surface of the hill and located midway between plants in the row (□), or perpendicular to the row at 5 (O), 15 (Δ), or 38 (×) cm from the plant. Tests for statistical significance of differences are given in the text.

TABLE 2. Proportion (percentage) of roots in three size classes[a] in samples of field-grown Russet Burbank potatoes in 1981

	Degree days after planting (base, 10 C [50 F])			
Treatment[b]	578	1,035	1,578	1,737
Rootlets				
Untreated	46.0[c]	40.0	64.0	77.0
Infested	51.0	57.0	73.0	66.0
Fumigated	43.0	36.0	78.0	78.0
Fum + Inf	48.0	38.0	68.0	75.0
Mean	47.0	46.0	70.0	74.0
Branch roots				
Untreated	37.0	45.0	32.0	16.0
Infested	34.0	29.0	24.0	26.0
Fumigated	38.0	48.0	18.0	19.0
Fum + Inf	38.0	47.0	25.0	22.0
Mean	37.0	39.0	24.0	21.0
Main roots				
Untreated	16.0	15.0	5.0	7.0
Infested	15.0	14.0	3.0	8.0
Fumigated	18.0	16.0	4.0	2.5
Fum + Inf	15.0	15.0	7.0	3.5
Mean	16.0	15.0	5.6	5.5

[a] Rootlets = 0.1–0.2 mm diameter, branch roots = 0.3–0.5 mm diameter, and main roots = >0.6 mm diameter.

[b] Inoculum of *Verticillium dahliae* was applied to infested plots at planting. Methyl bromide fumigant (585 kg a.i./ha) was applied under tarps the previous fall.

[c] Sum of rootlets, branch roots, and main roots for each treatment may not add to 100% due to rounding errors.

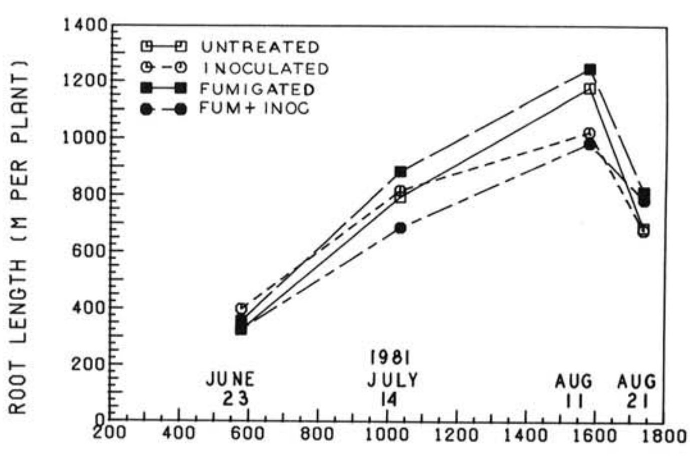

Fig. 3. Root length of Russet Burbank potatoes in 1981. Points represent means of four plants per treatment sampled at 578, 1,035, 1,578, and 1,737 degree days (base, 10 C [50 F]) after planting. Tests for statistical significance of differences are given in the text.

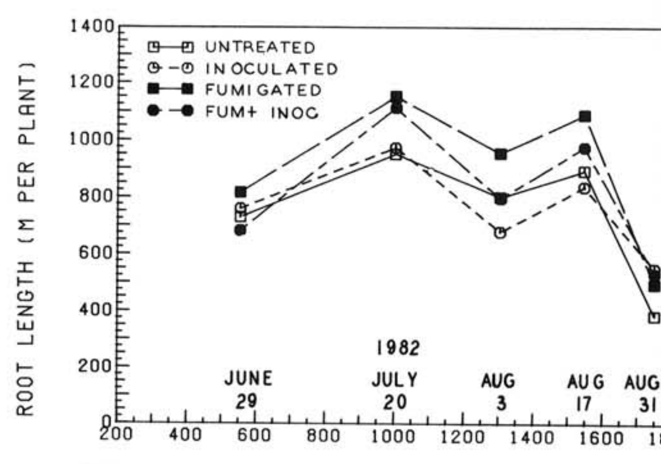

Fig. 4. Root length of Russet Burbank potatoes in 1982. Points represent means of four plants per treatment sampled 554, 1,003, 1,304, 1,546, and 1,751 degree days (base, 10 C [50 F]) after planting. Tests for statistical significance of differences are given in the text.

DDAP and main roots at 1,546 DDAP, than did plants in unfumigated treatments ($P<0.05$).

Root surface area and root volume per plant were calculated from the mean diameter of each root size class and the proportion of total root length in each size class (Fig. 5). In 1982, root biomass in fumigated, noninfested plots increased through 1,304 DDAP whereas root biomass declined in samples from all other plots taken after 1,003 DDAP (Fig. 5D). Root volume and root surface area at 1,304 and 1,546 DDAP in 1982 were significantly greater in fumigated than in nonfumigated treatments ($P<0.05$). Root volume and root surface area were reduced significantly in plots infested with *Vd* at 1,304 DDAP in 1982 ($P<0.05$) and at 1,578 DDAP in 1981 ($P<0.10$).

DISCUSSION

Root growth under field conditions is a dynamic process with the rate of both root growth and root death changing rapidly with plant ontogeny and in response to environmental conditions (10,18). While foliage growth is relatively simple, increasing to one peak in a season (18), root growth patterns are more complex, with roots proliferating at sites of increased nutrient availability (13) and being restricted in areas of high soil compaction (1,8). Because of the variability in root growth and the technical difficulty of removing roots from soil, quantitative assessment of root growth is complex, time consuming, and expensive. Lesczynski and Tanner (19) showed root density may differ at least fivefold in core samples taken from opposite sides of the same plant, and our data occasionally showed >10-fold differences. The distribution of root density is not simply a constant linear function of distance from the plant, but rather, changes with distance, depth, and time of season. In the present study, roots first proliferated near the plant in the 0–15 cm depth, and later proliferated at lower levels in the soil. Although some roots extended throughout the entire rooting volume of the hill by 379 DDAP, most increases occurred near the plant, and root density remained low in samples midway between rows.

Since localized environmental conditions can markedly affect the rate of root growth, it is apparent that a single sample cannot accurately estimate the root biomass of a given plant. The five-core samples in our experiments gave a much more comprehensive appraisal of root density distribution and root growth dynamics than that obtained from a single sample. Roots were not sampled below the 30-cm depth, and total root length per plant was therefore probably underestimated. Other workers have found at least 85% of the roots of potato located in the plow layer (5,6,19,34) suggesting that, in our calculations, the error due to lack of deeper samples is likely to be small. Errors in root density measurements from each core would be multiplied by the soil volume in that portion of the hill. However, random errors were assumed to balance within a given hill, and it was assumed that systematic errors would not affect statistical comparisons among samples.

The magnitude and time of occurrence of maximum root length varied with cultivar and year. Russet Burbank potatoes produced ~1,200 m of roots per plant in both 1981 and 1982. Norgold Russet potatoes reached a maximum of about 600 m of roots per plant. While Russet Burbank is a long-season, indeterminate cultivar, Norgold Russet is earlier maturing, determinate in growth, and, apparently, partitions less of its total biomass into root growth.

In addition to root length, quantification of root biomass production should incorporate root diameter as a variable influenced by plant ontogeny in general, and by *Vd* and/or associated PED pathogens in particular. Our data showed that the proportion of large-diameter roots decreased through the season. By comparing dates with equivalent total root lengths (eg, 1,003 and 1,546 DDAP in 1982) the decreased proportion of large diameter roots at the later date indicated that roots that had developed earlier were being replaced by equivalent lengths of roots of smaller diameter. This may be the result of root senescence and sloughing of cortical tissues, leaving only the vascular cylinder intact. Alternatively, large-diameter roots may have died and an equivalent length of fine rootlets was produced on the remaining root system. Reynolds (26) proposed that tree rootlets are determinate and that older rootlets die off under unfavorable conditions and new rootlets explore new soil when conditions favor regrowth. If potato roots were also determinate, our methods would detect only net changes in root length. Similar root lengths would reflect similar water and nutrient uptake capabilities but might not reveal significant changes in root biomass.

The maximum root length developed by Russet Burbank potato plants in plots infested with *Vd* in 1981 was 21% less than that of plants in fumigated control plots. Although similar trends were evident in 1982, no statistically significant differences occurred. In pot experiments, Burpee and Bloom (4) found *V. albo-atrum* reduced fresh weight of Katahdin and Kennebec potato roots by 70 and 72%, respectively, but had no effect on those of cultivar Abnaki. Martin et al (21) showed that an interaction between *V. dahliae* and *P. penetrans* reduced fresh root weight of plants of cultivar Superior in microplots by 60%. Morsink and Rich (22), however, did not report any effect of *V. dahliae* on roots of cultivar Katahdin in greenhouse experiments.

Our data suggest that potato plants may compensate for root loss by producing new rootlets. We found only limited effects of soil infestation with *Vd* on root length. Since the treatments also affected the rate at which large-diameter roots are lost, and since root area and volume are proportional to the frequency distribution of root diameters, the change in root area and root volume due to treatment effects is more pronounced than changes in root length. For instance, at 1,304 DDAP in 1982, there was no significant difference in root length among treatments, while root volume was reduced by as much as 40% ($P<0.05$) (Figs. 4 and 5D). A plot of root area and volume against time as measures of root growth suggested that there was an earlier peak of root growth, greater total reduction due to root senescence, and (in 1982) greater differences among treatments.

The most appropriate parameter for assessing root growth will depend on the objectives of the researcher. Measuring root weight or volume will best determine the biomass of the root system and the quantity of photosynthate being partitioned to root growth. The absorptive capacity for water and nutrients will be better

TABLE 3. Proportion (percentage) of roots in three size classes[a] in samples of field-grown Russet Burbank potatoes in 1982

	Degree days after planting (base, 10 C [50 F])				
Treatment[b]	554	1,003	1,304	1,546	1,751
Rootlets					
Untreated	52.0[c]	62.0	71.0	82.0	68.0
Infested	53.0	64.0	72.0	77.0	80.0
Fumigated	58.0	68.0	54.0	77.0	73.0
Fum + Inf	59.0	59.0	63.0	74.0	72.0
Mean	56.0	63.0	65.0	77.0	72.0
Branch roots					
Untreated	35.0	30.0	20.0	17.0	26.0
Infested	34.0	27.0	23.0	20.0	20.0
Fumigated	30.0	27.0	33.0	15.0	23.0
Fum + Inf	29.0	35.0	28.0	21.0	23.0
Mean	32.0	30.0	26.0	18.0	23.0
Main roots					
Untreated	12.2	8.5	8.5	1.6	6.0
Infested	13.0	8.5	5.3	2.5	0.0
Fumigated	11.5	4.7	13.0	7.9	4.6
Fum + Inf	12.2	6.1	9.0	4.5	5.0
Mean	12.2	6.9	9.0	4.1	4.4

[a] Rootlets = 0.1–0.2 mm diameter, branch roots = 0.3–0.5 mm diameter, and main roots = >0.6 mm diameter.

[b] Values represent the mean of two plants per treatment. Inoculum of *Verticillium dahliae* was applied to infested plots at planting. Methyl bromide fumigant (585 kg a.i./ha) was applied under tarps the previous fall.

[c] Sum of rootlets, branch roots, and main roots for each treatment may not add to 100% due to rounding errors.

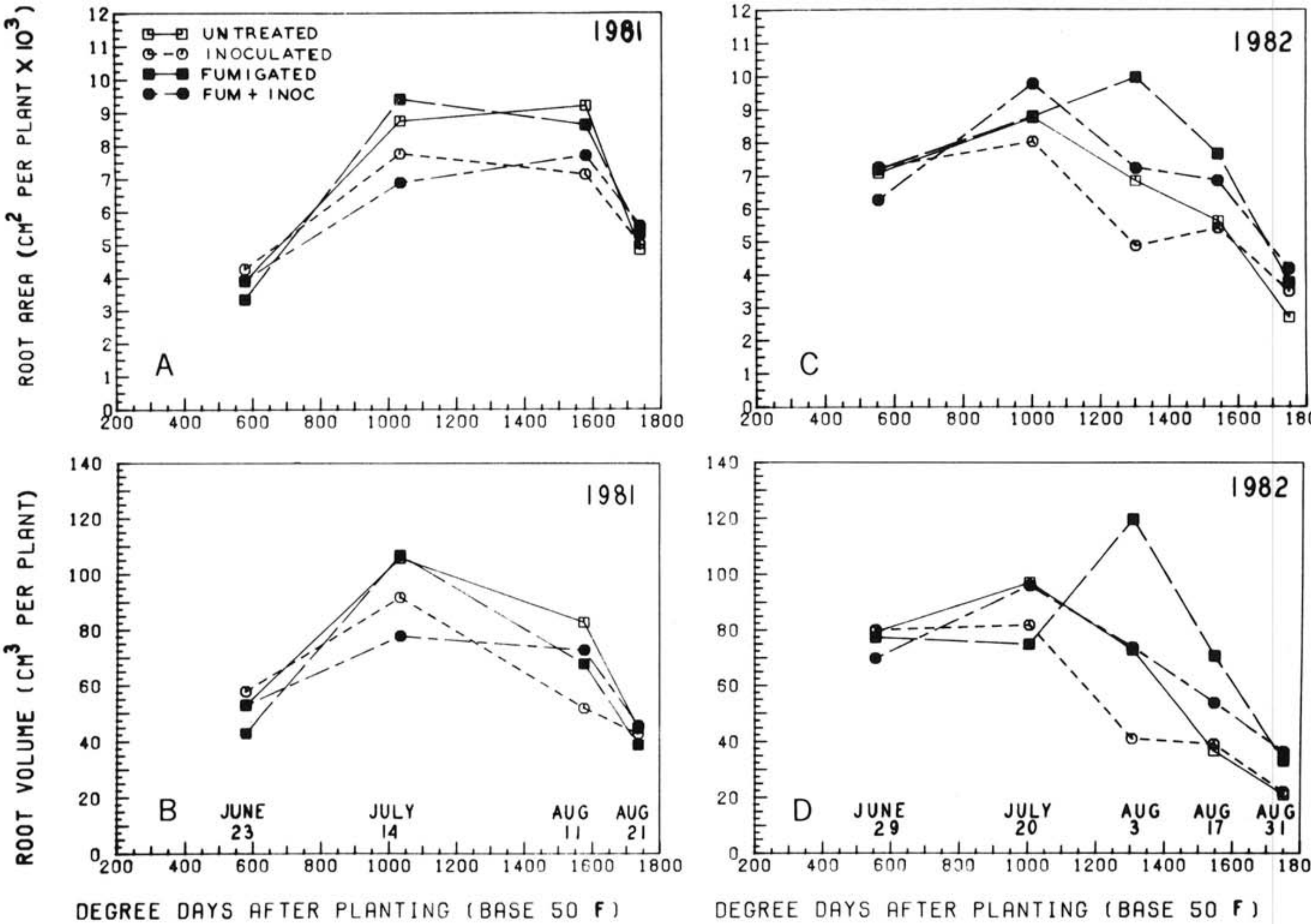

Fig. 5. A, Root surface area and **B,** root volume of Russet Burbank potatoes sampled at 578, 1,035, 1,578, and 1,737 degree days (base, 10 C [50 F]) after planting (DDAP) in 1981. **C,** Root surface area, and **D,** volume of Russet Burbank potatoes at 554, 1,003, 1,304, 1,546, and 1,737 DDAP in 1982. Points represent means of four plants per treatment and were calculated from the root length and the frequency distribution of root diameters from five core samples per plant. Tests for statistical significance of differences are given in the text.

related to root length or root surface area. In this case, root weight or root volume would overemphasize the importance of large-diameter roots and indicate a reduction in root function that is more apparent than real.

PED did not result in substantial reductions in root length of Russet Burbank potatoes in unfumigated plots. Reduction in root volume suggests that premature root deterioration, and not stunted root growth, accounts for the impact of PED on the potato root system.

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