An Aeroponics System for Investigating Disease Development on Soybean Taproots Infected with *Phytophthora sojae*

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ABSTRACT

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Pathogenesis on taproots of soybean (*Glycine max*) plants infected with *Phytophthora sojae* was investigated nondestructively with an aeroponics system. The main feature of the system is accessibility to the roots for direct observations, measurements, and application of inoculum. Lesion expansion on the taproots of the cultivar Corsoy was more rapid at 25 C than at 15 C. Lesion length after compatible interactions on the cultivars Corsoy, Sloan, and Agripro 26 was 8.0, 6.8, and 4.5 cm at 15 C and 13.5, 11.1, and 7.2 cm at 25 C, respectively, 9 days after inoculation. Cultivars were evaluated effectively for single-gene resistance based on the length and type of lesion formed 4 days after inoculation. Cultivars containing the genes *Rps7* or *Rps1* were susceptible, and cultivars containing the genes *Rps1-b, Rps1-c, Rps1-d, Rps2, Rps3,* or *Rps6* were resistant to race 3 of the fungus.

Phytophthora root and stem rot of soybean (*Glycine max* (L.) Merr.) is caused by the fungus *Phytophthora sojae* Kaufmann & Gerdemann. Control of the disease has focused on breeding resistant cultivars. In soybean, two types of resistance have been reported—single-gene resistance and rate-reducing resistance. Single-gene resistance is conferred by single dominant genes (*Rps*) and is characterized by a hypersensitive response after an incompatible interaction between the fungus and the plant (17). Rate-reducing resistance is quantitatively inherited and is characterized by a reduced rate of lesion expansion after a compatible interaction between the fungus and plant (18).

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Although *P. sojae* is a soilborne fungus and the root is the primary site of infection by chemotactically attracted zoospores, host resistance to the fungus is most often determined by inoculating aboveground plant parts—hypocotyls, cotyledons, or leaves (5,11,18). This is primarily for convenience, because roots grown in soil are difficult to investigate. However, resistance to *P. sojae* in aboveground plant parts and roots is not always correlated. For example, the *Rps2* gene can be identified consistently only by root inoculations (12). After hypocotyl inoculations, cultivars with *Rps2* that should be incompatible with a race of *P. sojae* often produce an intermediate response, which is characterized by a large lesion that in some cases girdles the hypocotyl and kills the plant. This is in contrast to cultivars with other *Rps* genes in which all plants produce a discernable resistant response after inoculation with an incompatible race or a susceptible response after inoculation with a compatible race.

The expression of *Rps* genes also is affected by environmental and physiological factors such as light, temperature, age of the plant, inoculum concentration, and inoculation technique, resulting in false compatible or incompatible interactions (4,10,11,14,18,21,22). Resistance in aboveground plant parts also may be affected by physiological processes not associated with the root, such as photosynthesis (18). A critical evaluation of host resistance requires a close inspection of the primary infection court—the root.

Investigations of roots in soil are usually restricted to single observations after destructive sampling. Novel techniques for the study of roots have been developed that overcome this limitation; these include hydroponics, in which the root is submerged in a nutrient solution, and aeroponics, in which the root system is suspended in a chamber and periodically misted with a nutrient solution (1). Several aeroponics systems have been described and successfully applied in nutrition, rhizobium nodulation, and pathogenicity studies (6,8,13,16).

A desirable feature of aeroponics, pertaining to root disease research, is nondestructive direct access to the root for repetitive linear measurements of lesion expansion. However, the validity of the measurements of disease progress may be challenged by infections from residual or secondary inoculum contaminating the nutrient solution. This is a limitation of recirculating the nutrient solution and a common design of most aeroponics systems. The consequences may be more severe with zoosporic fungi, as demonstrated by their ability to be formidable pathogens in hydroponic culture (12,23).

This paper describes the development and application of an aeroponics system with a noncirculating nutrient solution designed for the nondestructive investigation of disease development on soybean taproots inoculated with *P. sojae*.

MATERIALS AND METHODS

Aeroponics system: Design and operation. Components of the aeroponics system include a root misting chamber, solenoid valve, electronic time clock, stainless steel canister, oxygen regulator, and oxygen tank (Fig. 1).

The chamber was constructed from opaque polyvinyl chloride (PVC) and had dimensions of 61 × 61 × 61 cm. Strips of PVC were used to frame the box and provide structural support. Side and bottom pieces were 3 mm thick and were fastened to the frame strips with screws. All joints inside the chamber were sealed with silicon (Dow Corning, Midland, MI). A hole in the center of the box bottom provided drainage. The removable chamber top was 1.3 cm thick and supported by the frame strips. Forty-nine holes, 3.8 cm in diameter, were drilled on 10.2-cm centers in the top and served as plant ports.

Nutrient solution was applied to the suspended roots through eight stainless steel atomizing nozzles (1/4 LNN, Spraying Systems Co., Wheaton, IL) housed within the chamber. The nozzles were chosen for their efficiency based on performance specifications provided by the company (1.26 L/min [20 gal/hr], 1.138 rad [65° spray angle] at 552 kPa [80 psi]). Nozzles were spaced to provide uniform coverage of the roots at 552 kPa. The nozzles were connected by PVC pipe (0.6 cm i.d.) and arranged in an "H" pattern. Each row contained four nozzles. The nozzles within each row were spaced 15.2 cm apart; the rows were spaced 30.5 cm apart. The pipes were fastened to the bottom of the chamber.

A 0.5× Hoagland and Arnon solution (7) was applied to the roots for 1 sec at 5-min intervals. The spray duration and application interval were selected so that the roots remained moist and turgid during the time between applications, and runoff following spraying was limited to a small droplet that formed and remained on each root tip.

Spray duration and application interval were controlled by a solenoid valve (Automatic Switch Co., Florham Park, NJ) operated by an electronic timer (Chrontrol, Lindburg Enterprises, San Diego, CA). The nutrient solution was contained in a 20-L stainless steel canister (Firestone Steel Products Co., Spartanburg, SC) and pressurized with oxygen from a commercial tank fitted with a standard two-stage oxygen regulator. Inlet and outlet couplers that attach to designated valves on the canister were connected, respectively, to the oxygen regulator and solenoid valve with high-pressure rubber hose.

The aeroponics systems were housed within two environmental growth chambers. The temperature of the first chamber was maintained at 15 C (± 2.5 C), and the photon flux density per unit area was 271 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The temperature in the second chamber was maintained 25 C (± 2.5 C), and the photon flux density per unit area was 255 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Chambers were set on alternating 12-hr light and dark photoperiods.

Soybean seeds were surface-disinfested for 2 min in a 0.5% sodium hypochlorite solution, rinsed in distilled water, planted in coarse-grade vermiculite (Terra-lite #2, Florist Products, Schaumburg, IL), and stored in a growth chamber at 23 C under alternating 12-hr light and dark periods. The vermiculite was rinsed with approximately 2 L of distilled water before planting to remove fine particles that otherwise would adhere to and discolor the root. Three-day-old seedlings were pulled gently from the vermiculite and rinsed free of particulates with distilled water. Each plant was secured in a polyurethane foam plug (4.9 cm diameter, Baxter Healthcare Corp., McGaw Park, IL) and inserted into a port in the chamber top so that the root extended into the chamber. Before use, the center of the foam plug was removed with a cork borer (0.5 cm diameter). The plugs then were soaked in 1.0 M NaOH for 1 hr, rinsed in tap water, soaked in 95% ethanol for 12 hr, rinsed in tap water, and air-dried before use to remove phytotoxins (19). After treatment, the plugs were split longitudinally along a radial line to facilitate insertion of the plant into the plug.

The lights in the growth chambers were turned off for 12 hr after the plants were transplanted from vermiculite to the root misting chambers. The plants were prone to water stress during this period, particularly at 25 C.

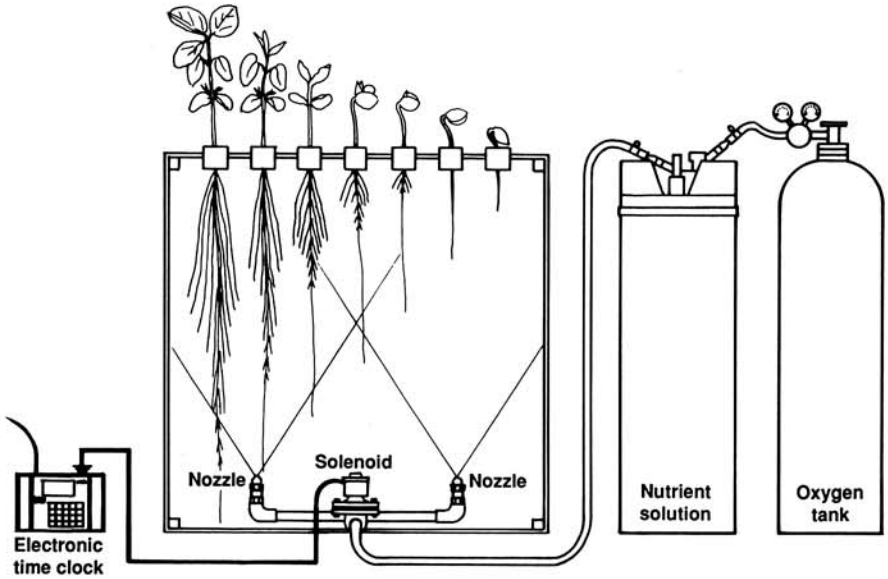

Fig. 1. Aeroponics system developed for investigating disease development on taproots of soybeans infected with *Phytophthora sojae*.

Inoculum preparation. A culture of *P. sojae* race 3 was obtained from L. E. Gray, USDA, University of Illinois, Urbana-Champaign, IL. The identity of the race was confirmed with a standard set of differential cultivars and environmental conditions (11). The fungus was maintained on 0.25× lima bean agar (LBA) (5.75 g of Difco lima bean agar supplemented with 15 g of Difco Bacto agar dissolved in deionized distilled water) and stored in an incubator at 20 C in the dark. The culture of the fungus used in all experiments originated from a single zoospore and was the fifth generation of successive, single-zoospore transfers.

Zoospores were produced by transferring four 1-cm-diameter plugs cut from the periphery of an actively growing culture of *P. sojae* to a culture plate containing 10 ml of 0.25× LBA. The culture was stored in an incubator at 20 C in the dark for 2–3 days. The culture was flooded with 10 ml of deionized distilled water (3). One-half hour later, the water was discarded and the process was repeated three times. After the water from the fourth flooding period was discarded, 10 ml of a solution that prolonged zoospore motility (13 mg of K_2HPO_4, 105 mg of KH_2PO_4, 10 mg of $MgCl_2{:}6H_2O$, and 7 mg of $CaCl_2{:}2H_2O$ per liter of deionized distilled water) was added (2). The flooded culture was stored in an incubator at 20 C in the dark.

After 7 hr, the zoospore suspension was poured into a culture plate. Zoospore concentration was determined by calculating the mean number of spores from four 2.0-μl samples drawn from the suspension. Zoospore motility was terminated by adding 0.1 μl of lactophenol cotton blue.

Taproot inoculation technique. Zoospores released by flooding were used to inoculate taproots of soybean plants. Based on the zoospore concentration, a volume of the zoospore suspension containing a desired number of zoospores was delivered to a culture tube (10 × 75 mm, Scientific Products, McGaw Park, IL) containing enough motility-prolonging solution to achieve a final volume of 500 μl. Plants were removed from the foam plugs and inserted in 1-ml capacity pipet tips (Labcraft, Curtin Matheson Scientific, TX) so that 2–3 cm of the root tip extended from the orifice (Fig. 2). Approximately 1.5 cm of the pipet tip ends were excised to increase the orifice size. Pipet tips were stacked to accommodate longer taproots. The pipet tip with the plant was reinserted into the foam plug, which was placed on top of the culture tube containing the zoospore suspension so that the pipet tip with exposed root extended into the tube. The root was lowered into the inoculum by sliding the pipet tip in the foam plug until approximately 0.5 cm of the root tip was submerged. The roots were exposed to the inoculum for 20 min, after which they were returned to the root misting chamber.

Effect of temperature on disease development. Taproots of the cultivars Corsoy, Sloan, and Agripro 26 were inoculated with 0 or 1,000 zoospores of *P. sojae* race 3. Seed of the cultivars were obtained from R. L. Bernard, University of Illinois, Urbana, IL, and Agripro Seed Co., Kalamazoo, MI. The relative level of rate-reducing resistance is low for Sloan and Corsoy and high for Agripro 26 (9,18,20). The cultivars do not contain an *Rps* gene that is effective against *P. sojae* race 3; therefore their interaction with the fungus is compatible after hypocotyl inoculation. The inoculated plants were maintained in the root misting chamber at 15 or 25 C. Plants were inoculated 24 hr after transplantation from vermiculite to the root misting chamber. Measurements of lesion length in centimeters were recorded at 1, 2, 3, 6, and 9 days after inoculation. Individual plants were treated as replications and each treatment was replicated seven times.

Effect of *Rps* genes on disease development. Taproots of cultivars with different *Rps* genes were inoculated with 750 zoospores of *P. sojae*. The cultivars (*Rps* gene in parentheses [15]) inoculated included L75-6141 (*Rps1*), L77-1863 (*Rps1-b*), Williams 79 (*Rps1-c*), PI 103091 (*Rps1-d*), L76-1988 (*Rps2*), L83-570 (*Rps3*), Altona (*Rps6*), and Harosoy (*Rps7*) (R. L. Buzzell, *personal communication*). The "L" lines and Williams 79 are near-isogenic lines derived by backcrossing to Williams with selection for the indicated *Rps* gene. Seeds of cultivars were obtained from R. L. Bernard. Plants were inoculated 48 hr after transplantation. The inoculated plants were maintained in the aeroponics chamber

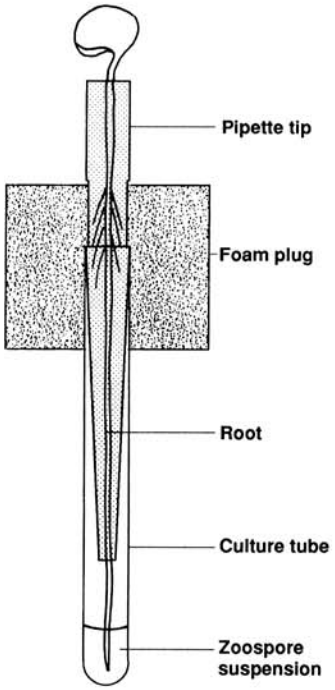

Fig. 2. Taproot inoculation technique.

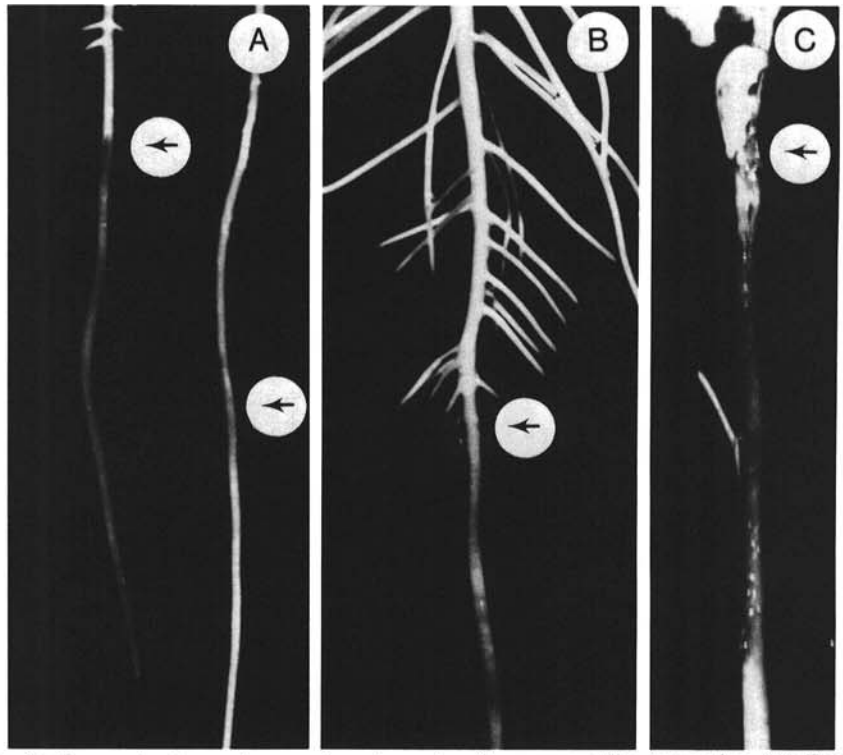

Fig. 3. Disease development on soybean taproots after a compatible interaction. **(A)** From the site of infection, a brown water-soaked lesion encircles the root (right taproot, arrow) and expands bidirectionally killing the root tip (left taproot). **(B)** The lesion expands acropetally, eventually extending from the root tip to the cotyledon **(C)**. Arrows indicate extent of lesion.

at 15 or 25 C. Measurements of lesion length were recorded 4 days after inoculation. Individual plants were treated as replications and each treatment was replicated seven times.

Data analysis. Data from measurements of lesion length were analyzed by analysis of variance and treatment means were compared by least significant difference ($P = 0.05$) using the SAS GLM procedure (SAS Institute, Cary, NC). Both experiments were repeated to confirm results. Data presented were from a single experiment.

RESULTS

Effect of temperature on disease development. The first disease symptom to appear was a single brown water-soaked lesion at the site of infection (Fig. 3). The lesion encircled the root and expanded bidirectionally. At 25 C, the lesion extended to the root tip within 48 hr and terminated taproot elongation. The lesion continued to expand acropetally, reaching the cotyledons of the cultivar Corsoy 19 days after inoculation. The roots of the noninoculated plants were white and turgid. Taproot growth averaged 6.7 cm per day. Inoculated and noninoculated plants developed secondary roots. On noninoculated plants, secondary root length increased as the distance from the root tip increased.

Disease development on Corsoy maintained at 25 C occurred in two distinct phases: an initial phase (0–3 days after inoculation), in which the rate of lesion expansion was very rapid, and a subsequent phase, in which the rate of lesion expansion was slowed (Fig. 4). At 15 C, the rapid phase of lesion expansion was delayed until 2 days after inoculation. The pattern of disease development on Sloan and Agripro 26 was similar to Corsoy at both temperatures.

Mean lesion length on the taproots of Corsoy, Sloan, and Agripro 26 was 8.0, 6.8, and 4.5 cm, respectively, when the plants were maintained at 15 C and 13.5, 11.1, and 7.2 cm, respectively, when the plants were maintained at 25 C. Lesion length on the taproots of Corsoy and Sloan was significantly longer than on Agripro 26 at 15 C (LSD = 1.92, $P = 0.05$) and 25 C (LSD = 3.66, $P = 0.05$). Lesion length on the taproots of Corsoy and Sloan was not significantly different at both temperatures. No lesions were observed on the noninoculated plants.

Effect of *Rps* genes on disease development. The interaction between *P. sojae* and cultivars containing *Rps7* or *Rps1* was compatible; the interaction between *P. sojae* and cultivars containing *Rps1-b, Rps1-c, Rps1-d, Rps2, Rps3,* or *Rps6* was incompatible (Table 1). The lengths of lesions formed after compatible interactions were significantly longer than lesions formed after incompatible interactions. Lesions of incompatible interactions were visible before lesions of compatible interactions.

Two types of lesions, referred to as types 1 and 2, formed after incompatible interactions (Fig. 5). A type 1 lesion was characterized by brown to black necrotic flecks at the site of penetration. These flecks coalesced and were considered a single lesion. Taproot elongation usually continued unimpeded. Taproot growth was terminated if the taproot tip was submerged less than 0.2 cm in the zoospore suspension during inoculation. A type 2 lesion was similar in appearance to a lesion formed after a compatible

Table 1. Lengths of lesions formed on taproots of cultivars with different *Rps* genes at 15 and 25 C 4 days after inoculation with race 3 of *Phytophthora sojae*

Cultivar	Gene	Lesion length[a] 15 C	Lesion length[a] 25 C	Interaction[b]
L75-6141	*Rpsl*	5.4	8.0	C
Harosoy	*Rps7*	5.2	8.4	C
L83-570	*Rps3*	2.4	3.0	I*
L76-1988	*Rps2*	2.3	1.7	I*
Altona	*Rps6*	1.1	0.9	I
PI 103091	*Rpsl-d*	1.1	0.9	I
Williams 79	*Rpsl-c*	1.0	1.1	I
L77-1863	*Rpsl-b*	0.8	0.5	I
LSD ($P = 0.05$)		1.64	1.21	

[a] Lesion lengths in centimeters were the means of four replicates.
[b] Interactions were compatible (C) or incompatible (I) based on lesion length and type formed on the taproots of four plants. An asterisk after an I denotes a type 2 lesion was formed, otherwise a type 1 lesion formed. Type 1 lesions were characterized by brown necrotic flecks that collectively formed a lesion at the site of penetration by the fungus. Type 2 lesions were characterized by a restricted brown water-soaked lesion that girdled the taproot just above the site of penetration and extended to the root tip. In contrast, the brown water-soaked lesion produced following compatible interactions continued to expand acropetally.

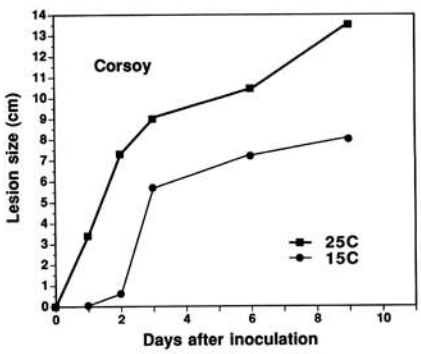

Fig. 4. Lesion expansion on the taproot of the soybean cultivar Corsoy at 15 and 25 C after inoculation with *Phytophthora sojae*.

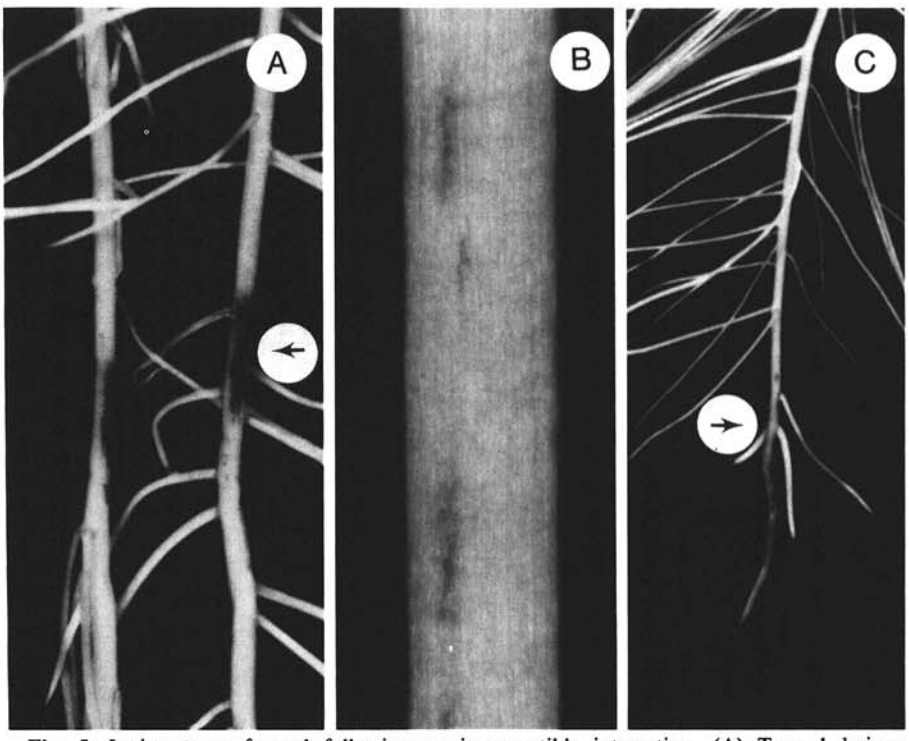

Fig. 5. Lesion types formed following an incompatible interaction. **(A)** Type 1 lesions characterized by brown necrotic flecks (arrow) formed at the site of infection. **(B)** Close-up of individual necrotic flecks. **(C)** Type 2 lesion characterized by a determinate, brown water-soaked lesion with a dark band between the healthy and diseased tissue (arrow).

interaction, except it was significantly shorter and discontinuous. No individual necrotic flecks were observed. Type 2 lesions expanded primarily from the point of penetration to the root tip. Taproot elongation was terminated. Lesion expansion above the point of penetration was restricted. A dark band usually formed between the healthy and diseased tissue at the top of the lesion. Type 2 lesions were longer than type 1 lesions.

Among the incompatible interactions, *P. sojae* race 3 formed only a type 1 lesion on cultivars with the genes *Rps1-b, Rps1-c, Rps1-d,* or *Rps6* at 15 and 25 C. A type 2 lesion was formed on two of four plants with the gene *Rps2*; a type 1 lesion was formed on the other two plants. A type 2 lesion was formed on four of four plants with the gene *Rps3* at 15 and 25 C. The mean lesion length of a cultivar increased as the frequency of type 2 lesions increased.

DISCUSSION

The aeroponics system provided an environment favorable for plant growth. Adequate nutrition was provided based on visual assessments for deficiency symptoms and nutrient analysis of the trifoliolate leaves (analysis performed by Cooperative Extension Service, University of Wisconsin). Roots of uninoculated plants grew vigorously and remained healthy in the same chamber with infected plants. Hence, infection by secondary inoculum was precluded by not recirculating the spent nutrient solution.

The aeroponics system provided easy, nondestructive access to the root for direct observations, measurements, and application of inoculum. The taproot inoculation technique was rapid and precise without causing injury to or desiccation of the root. Stacking the pipet tips accommodated roots of different lengths. The technique ensures that root tips of all plants are inoculated at the same relative location on the taproot, regardless of taproot length. Taproots up to 30 cm long have been inoculated using this technique. Because zoospores are chemotactically attracted to the root, it is essential that they remain motile during inoculation. Zoospores remained active and did not encyst when maintained in the solution of Cameron and Carlile (2). Zoospores appeared more sluggish and greater numbers had encysted when they were maintained in distilled water. Hence, a critical component of the inoculation technique is to initiate zoosporogenesis and maintain the zoospores in the motility-prolonging solution (2).

The aeroponics system and taproot inoculation technique for investigating pathogenesis on the taproot of soybean offered several advantages compared with inoculating aboveground plant parts. Most important, the expression of the interaction between *P. sojae* and soybean was reproducible. This reproducibility may be attributed to the fact that our system mimicked the natural infection process with the use of zoospores for inoculum and the root tip as the infection court. In addition, many of the factors reported to alter host resistance (11,14,18,21,22) were controlled or eliminated. Factors controlled with the aeroponics system included inoculum concentration and placement, plant age, nutritional and water status of the plant, humidity, temperature, and light. Keeling (11) reported that after hypocotyl inoculation, maintaining plants at temperatures below 24 C resulted in numerous false incompatible interactions, whereas maintaining plants at temperatures above 24 C resulted in numerous false compatible interactions. In contrast, interactions between the fungus and the plant were consistent at 15 and 25 C when evaluated on the taproots of aeroponically grown soybean plants. Because resistance expressed by the taproot is less influenced by environment, rate-reducing resistance and single-gene resistance can be evaluated with greater reliability with the aeroponics system.

Direct measurement of lesion length allowed quantification of the interaction between *P. sojae* and soybean. Lesion length was significantly smaller on Agripro 26 and cultivars with effective *Rps* genes, which provided an accurate assessment of rate-reducing resistance and single-gene resistance, respectively. As mentioned previously, the *Rps2* gene is difficult to identify after hypocotyl inoculations because it often produces an intermediate response as opposed to a discernable resistant response after an incompatible interaction (12). The intermediate response often is characterized by a girdling canker that can kill the plant, resulting in a misinterpretation of the interaction. The type 2 lesion that formed on the taproot of L76-1988 with the *Rps2* gene could also be classified as an intermediate response. However, whereas the type 2 resistant response resulted in a longer lesion than the lesion that formed after a type 1 resistant response, it was significantly shorter than the lesion that formed after a compatible interaction. As a result, the incompatible interaction was not misinterpreted as a compatible interaction. Hence, greater reliability in determining resistance was afforded through quantification of the interaction between *P. sojae* and soybean on the taproots of aeroponically grown plants.

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