

VARIATION AMONG STRAINS OF PSEUDOMONAS SOLANACEARUM FROM FLORIDA¹

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Abstract. The 19 collections of *Pseudomonas solanacearum* E. F. Smith from 8 counties in Florida belonged to race 1 and were pathogenic to eggplant (*Solanum melongena* L.), pepper (*Capsicum annuum* L.), potato (*Solanum tuberosum* L.), and tomato (*Lycopersicon esculentum* Mill). Some were pathogenic to sunflower (*Helianthus annuus* L.) and ginger (*Zingiber officinale* Roscoe). None was pathogenic to peanut (*Arachis hypogaea* L.). Strains from Florida were characterized as biotype I according to Hayward's classification, because they did not oxidize disaccharides, or hexose alcohols. Variation occurred in the pattern of utilization of carbon sources proposed by Harris. None fitted the 9 sub-groups of Harris.

The first report of bacterial wilt was probably made by Burrill in 1890 (30). Smith began his investigation of bacterial wilt in 1896 (18) which resulted in the first adequate description of the disease and the causal agent *Pseudomonas solanacearum*. In 1914, Smith (30) wrote "This disease has destroyed a great many fields of tomatoes and potatoes in the South and has put an end to commercial tomato growing in certain sections, e.g., Southern Mississippi, Southern Alabama and parts of Florida."

Eighty-four years have passed since Smith first described the causal agent of bacterial wilt. During those 8 decades, data have accumulated from research and observations on distribution, epidemiology, population dynamics, insect dispersal, host-pathogen interactions, virulence, exoenzymes, lysotypes, pathotypes, polysaccharides, and metabolic pathways. Even so, heavy losses (20) still occur in many parts of the world. In the developing countries this disease has limited the production of food crops at all levels, from tomatoes grown by a peasant farmer in his home garden to major agricultural crops for export, such as bananas and potatoes. The disease is widely distributed in tropical and subtropical soils with a long history of cultivation of susceptible crops.

Pathogenic variation occurs within the species. Buddenhagen (1) found 2 different strains of *P. solanacearum* in banana plantations in Costa Rica. One, isolated from *Heliconia*, caused wilt in banana, whereas the other isolated from *Physalis* and other weeds, did not. Volcani and Palti (32) reported that a strain in Israel was pathogenic only on potato, tomato, and eggplant, and was unlike a strain from the United States which wilted tobacco, tomato, chili, groundnut, and eggplant. Buddenhagen and Kelman (2) designated 3 races: race 1, pathogenic to solanaceous and other hosts; race 2, pathogenic to banana and *Heliconia*; and race 3, pathogenic to potato only. Okabe and Goto (28) divided isolates of the organisms into 13 pathotypes based on pathogenicity to tobacco, sesame, tomato, eggplant, and peanut.

Lozano and Sequeira (26) differentiated the 3 races of

Buddenhagen and Kelman on the basis of reactions in tobacco leaves infiltrated with bacterial suspensions. The race 2 isolates caused hypersensitivity (HR) on tobacco, but isolates of race 1 and race 3 did not. However, Granada and Sequeira (9) later reported that certain race 1 isolates caused HR on tobacco leaves and concluded that infiltration into tobacco leaves was not a reliable method for differentiation of races.

Isolates of *P. solanacearum* vary in physiology also. The capacity to oxidize a range of hexose alcohols and disaccharides was used by Hayward (12) to classify isolates into 3 groups; type I, II, and III. Type I included the banana pathogen from parts of Central America and West Indies; type II included the potato race, exclusively; and type III was thought to include *P. solanacearum* var. *asiaticum*. A fourth biochemical type was found later and Hayward (13) then classified the isolates into biotypes I, II, III, and IV. Isolates of biotype III oxidized both disaccharides and hexose alcohols, but those of biotype I oxidized neither. The disaccharides were oxidized, but not hexose alcohols by biotype II. Representatives of biotype IV oxidized the hexose alcohols, but not the disaccharides. Ninety-five isolates from different parts of the world were classifiable as biotype II and the optimum temperature for growth was lower than for isolates of the other biotypes.

Seneviratne (29) studied the distribution of biotypes II, III, and IV in the hill country of Sri Lanka and found them distributed according to altitude. Biotype II was isolated from potatoes, at elevations of 6200 ft and in virgin lands in the hill country wet-zone with a cool temperature climate.

Harris (11) divided the nomenclatures into 3 main biochemical groups, which were essentially Hayward's biotypes I, II, and the combination of biotypes III and IV. Isolates within the second and third groups were found to be uniform in their biochemical characters but isolates within the first group were subdivided into a spectrum of types in which one end resembled the second group and the other end resembled the third group.

Granada and Sequeira (10) characterized Colombian isolates of *P. solanacearum* based on physiological and pathological tests. They found that the Colombian isolates differed from a standard race 1 isolate only in relatively few physiological properties. Among them were: greater ability to utilize nitrate as the sole source of N, lower tolerance to NaCl, and ability to utilize malonate, tartrate, and L-phenyl alanine as a sole source of carbon.

Most of the studies discussed above were with isolates of diverse origin in time and space. Although variation within the species is great, it is not known if such variation occurs among isolates within a specific geographical area, such as Florida. Edaphic and biological factors at different locations probably influence variation. Knowledge about this variation will be helpful in making decisions about crop rotations and selection of isolates for use in breeding programs for resistance to disease. Knowledge of the variation is essential in epidemiological studies of disease development. This research was undertaken to determine variation among isolates from different areas of Florida where many susceptible crops are grown commercially.

Materials and Methods

Isolates of *P. solanacearum* were collected from tomato, eggplant, potato, and sunflower in fields around Florida. These isolates were compared with cultures from United

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States, Panama, Honduras, and Colombia which represent races 1, 2, and 3 and were used as standards.

Isolations from diseased tissue were made following the technique of Jenkins and Kelman (17). A piece of stem away from the collar region was removed, washed in sterilized water, surface sterilized with 0.5% NaOCl, and washed again with sterilized water. Small pieces were transferred to 5 ml of sterilized distilled water for 15-30 min. The bacterial suspension obtained from the tissue after shaking well on a vortex mixer was streaked onto a tetrazolium chloride medium (TZC) in plates (19). The bacteria were incubated at 28-30°C for 48 hr. Single colonies of *P. solanacearum* were selected on the basis of appearance and suspensions of these were restreaked on the TZC agar for purification. The bacteria were stored in sterile distilled water in screw-capped tubes at room temperature for further use (22).

Bacteria were cultured in 5 ml of CPG broth (Kelman's TZC media without tetrazolium chloride) in test tubes at 27 ± 2°C for 24 hr for pathogenicity tests. The bacteria were pelleted by centrifugation of 24-hr-old cultures at 1,000 g for 15 min., washed with saline, recentrifuged, and suspended in sterilized saline. The turbidity of the suspensions was adjusted to 50% transmittance at 600 nm wavelength in a Spectronic 20 spectrophotometer. These suspensions were assumed to contain 10⁸ cells/ml and were used unless otherwise indicated.

Stem and root inoculations were carried out following the procedure of Winstead and Kelman (33). For stem inoculations an alcohol-flamed needle, or a hypodermic-syringe needle was forced into the stem through a drop of bacterial suspension placed at the axil of the second or third leaf below the stem apex. For root inoculations an alcohol-flamed scalpel was forced through the soil to cut the lateral roots along one side of the plant. About 10 ml of a bacterial suspension were poured into the cut. All the inoculations were carried out in the greenhouse at ambient temperatures ranging from 15-35°C.

Seeds of tomato ('Bonny Best'), pepper ('10R'), and eggplant ('Black Beauty') were sown in flats containing steamed soil. The seedlings, about 8 to 10 cm in height were transplanted to 10-cm pots filled with steamed soil. Stem and root inoculations were made with tomato and pepper plants and stem inoculations with eggplant. Inoculations were made 3 to 4 weeks after transplanting.

Seed of peanut ('Florunner') and sunflower ('Mammoth') were sown directly in pots containing steamed soil. Peanut plants were root-inoculated about 5 to 6 weeks after planting. Sunflower plants were stem-inoculated at the axil of the first pair of true leaves when the plants had two pairs of true leaves.

Pieces of a rhizome of ginger or a tuber of potato ('Atlantic') with a growing bud were placed in pots of steamed soil. Stem inoculations were made when the plants were about 15 to 20 cm in height.

Production of tan, black, or brown pigment on potato plugs was considered diagnostic for *P. solanacearum* (14). A hypersensitive reaction in tobacco (*Nicotiana tabacum* L. cv. F₂C₁) occurred if infiltrated areas of leaves turned necrotic within 24 hr (24). Kovacs' method (25) was used to determine the oxidase reaction. The formation of alkali from arginine, anaerobically, in Thornley's arginine medium 2 (31) was used to detect arginine dihydrolase. The test for catalase was carried out according to Digat (5). Hayward's (15) method, which included a starch-iodide indicator was used to detect nitrite from nitrate. If no nitrate or nitrite occurred in media, it was assumed that all nitrate had been reduced to gas. Brown pigment formation in a modified tetrazolium chloride medium containing 0.1% tyrosine was

considered as a positive reaction for melanin (6). If bacteria moved downward in 24-48 hr in the medium of Kelman and Hruschku (21), they were considered motile. Misaghi and Grogan's technique (27) was used to determine gelatin liquefaction. Formation of an opaque halo in a medium containing Tween 80 (27) was indication of production of lipase. Crystal violet polypectate (4) and carboxymethyl cellulose (7) media were used to detect pectolytic and cellulolytic enzymes. Formation of a pit around a colony was a positive reaction. The medium described by Graham (8) was used to detect phosphatase. A pink color around colonies exposed to ammonia was a positive reaction. Approximately 10² cells of *P. solanacearum* were spread onto a CPG medium and kept at 20, 25, 30, 35, and 40°C for 96 hr to test effects of temperature on growth. Size of colonies were used to indicate rate of growth. Test tubes of nutrient both containing either 0.0, 1.0, 1.4, or 1.7% of sodium chloride were used to test effects of salt on growth. Comparisons with the control as to turbidity were used to judge growth.

The ability to oxidize the disaccharides; lactose, maltose, and cellobiose, and the hexose alcohols; mannitol, dulcitol, and sorbitol, was tested with Hayward's medium (13). A change of color from blue to yellow was considered positive. The carbon sources; trehalose, inositol, gluconate, lactate, hippurate and tryptophan were filter-sterilized and added separately to the mineral-base medium of Misaghi and Grogan (27). Presence of growth after 6 days at 30°C was considered a positive reaction according to Harris (11).

Results

Nineteen isolates of *P. solanacearum* were obtained from 8 counties in Florida. All isolates developed irregular round, fluidal, white colonies with pink centers on the TZC medium and were pathogenic to tomato. The isolates from Sri Lanka, North Carolina, Panama, Honduras, and Colombia were also typical of *P. solanacearum* in colony characteristics.

All the isolates from Florida were similar to race 1 in pathogenicity and caused wilting of eggplant, potato, and tomato within 10 to 14 days (Table 1). Pepper plants did not wilt after inoculation, but systemic necrosis extended along the stem and leaves dropped after root inoculation. With stem inoculation, a systemic necrosis on pepper developed and extended into the leaf from the point of inoculation.

Table 1. Pathogenicity of isolates from Florida compared to isolates of Races 1, 2, 3.

Host	Site of inoculation	Florida isolates	Race 1	Race 2	Race 3
Tomato	stem	19/19 ^z	1/1	0/2	3/3
	root	19/19	1/1	0/2	3/3
Potato	stem	19/19	1/1	1/2	3/3
	Pepper	19/19	1/1	0/2	0/3
Eggplant	stem	3/19	0/1	0/2	0/3
	root	19/19	1/1	2/2	0/3
Peanut	root	0/19	0/1	0/2	0/3
Ginger	stem	16/19	1/1	1/2	0/3
Sunflower	stem	17/19	1/1	0/2	2/3

^zThe number of isolates that were positive/the number of isolates tested.

The Florida isolates were variable in pathogenicity to ginger and sunflower. Some isolates caused the basal and terminal leaves of ginger to turn yellow by 7 to 10 days after inoculation, but wilt symptoms did not develop. Some isolates caused systemic necrosis along the stem of sunflower and wilting within 7 to 14 days after inoculation.

The banana isolates (race 2) were different from the

Florida isolates in pathogenicity. Eggplant was susceptible to both banana isolates, but wilt did not develop in other plants, except that a Panama isolate was pathogenic to potato and ginger.

The potato isolates (race 3) also were different from Florida isolates in pathogenicity. Isolates from Sri Lanka were pathogenic only to potato and tomato. The Colombia isolates were pathogenic to sunflower as well as to potato and tomato.

The results of tests for physiological characteristics of *P. solanacearum* are in Table 2. All isolates produced tar-black, or brown pigments on sterilized potato plugs, were positive for oxidase and catalase, formed pits in polypectate and carboxymethyl cellulose media, and were negative for arginine dihydrolase and gelatin hydrolysis.

Table 2. Reactions in physiological tests with Florida isolates and isolates of Races 1, 2, and 3.

Physiological test	Florida isolates	Race 1	Race 2	Race 3
Potato plug	19/19 ^z	1/1	2/2	3/3
Hypersensitivity	19/19	0/1	2/2	0/3
Oxidase	19/19	1/1	2/2	3/3
Arginine dihydrolase	0/19	0/1	0/2	0/3
Catalase	19/19	1/1	2/2	3/3
Nitrate reduction	19/19	1/1	2/2	3/3
Gas from nitrate	0/19	0/1	2/2	0/3
Melanin	19/19	1/1	0/2	2/3
Motility	0/19	0/1	0/2	0/3
Gelatin hydrolysis	0/19	0/1	0/2	0/3
Lipase	18/19	1/1	2/2	3/3
Polypectate pitting	19/19	1/1	2/2	3/3
CMC pitting	19/19	1/1	2/2	3/3
Phosphatase	2/19	0/1	2/2	3/3

^zThe number of isolates that were positive/the number of isolates tested.

All the isolates except the race 1 isolate from North Carolina and the race 3 isolates from Sri Lanka and Colombia caused hypersensitivity on tobacco. The isolate from North Carolina was judged to give a susceptible reaction and the potato isolates induced a yellowish discoloration, which is typical of a saprophytic reaction. All isolates reduced nitrate, since blue color developed with the starch iodine indicator. The blue color was very weak with the potato isolates from Colombia, but became intense after the addition of zinc dust. Nitrates were not converted to gas with any isolate.

The isolates from Florida and the race 1 isolate gave positive reactions for melanin formation. The banana isolates (race 2) were distinct in not producing the brown coloration in the medium. Variation occurred among the race 3 isolates. All isolates were not motile and all Florida isolates except an isolate from Hastings hydrolyzed Tween 80.

The race 2 and race 3 isolates produced phosphatase and a pink color formed in the medium within 30 min. Some of the isolates from Florida eventually turned the medium pink, but the pink color was not as intense as with the race 2 and race 3 isolates. Many Florida isolates did not produce phosphatase.

All isolates except the race 3 isolates from Sri Lanka and Colombia grew best at 35°C at 36 hr of incubation. The latter grew best at 30°C. At 25°C, growth of all isolates was slow and 96 hr were required for moderate growth. The growth was very slow at 20°C and colonies of all isolates were only pinhead size after 72 hr of incubation. No growth occurred at 40°C.

All isolates were not sensitive to 1.7% NaCl, except the potato isolates from Sri Lanka and Colombia, which did

not grow. All isolates grew at 1.0% and 1.4% NaCl in the medium.

The Florida isolates of *P. solanacearum* were of biotype I, according to Hayward's (13) classification. They did not utilize the disaccharides, maltose, lactose, and cellobiose or the hexose alcohols, mannitol, dulcitol, and sorbitol. The isolate of race 1 and the race 2 isolates were also of biotype I in utilization of the carbohydrates. On the other hand, the race 3 isolates from Sri Lanka and Colombia oxidized the disaccharides and not the hexose alcohols, and thus, were of biotype II.

Utilization of the carbon sources, hippurate, tryptophan, trehalose, inositol, gluconate, and lactate was used to subdivide the isolates further (Table 3). The Florida isolates could be divided into 4 groups. The isolate from Hastings was unique in not utilizing hippurate, trehalose, and lactate. An isolate from Bradenton was different from other isolates in not utilizing hippurate. Four isolates were different from the rest of the isolates in not utilizing lactate. The other 13 isolates were similar in utilizing all the compounds as carbon sources. The race 1 isolate which is of biotype I, differed from Florida isolates in not utilizing trehalose.

Table 3. Oxidation of carbohydrates in Hayward's biotype classification.

Carbohydrates	Florida isolates	Race 1	Race 2	Race 3
Disaccharides				
Maltose	0/19 ^z	0/1	0/2	3/3
Lactose	0/19	0/1	0/2	3/3
Cellobiose	0/19	0/1	0/2	3/3
Hexose alcohols				
Mannitol	0/19	0/1	0/2	0/3
Dulcitol	0/19	0/1	0/2	0/3
Sorbitol	0/19	0/1	0/2	0/3

^zThe number of isolates that were positive/the number of isolates tested.

The race 2 isolates were also of biotype I and were similar to some of the Florida isolates according to the Harris classification. The race 2 isolate from Honduras resembled 4 isolates from Florida in not utilizing lactate. The isolate from Panama resembled the 13 isolates from Florida in utilizing all the compounds as carbon sources.

Discussion

An attempt was made to obtain representative isolates of *P. solanacearum* from Florida by isolating the organism from many hosts and locations in the state. Specific ecotypes of pathogens may occur in geographic areas as the result of environmental factors (3).

The isolates of *P. solanacearum* from Florida were remarkably similar in pathogenicity to tomato, pepper, eggplant and potato. All of the isolates belonged to race 1 (2), the tomato race. It should be noted that even the isolates from potato belonged to tomato race (race 1), not to the potato race (race 3). Others have also reported that potato plants may be wilted by the tomato race under field conditions (2). The potato race is usually found in cool climates and is pathogenic only on potato. The isolates from Florida seemed to be slightly different in pathogenicity from the standard race 1 isolate, which was isolated from North Carolina (strain K₆₀) and was reported to be pathogenic to tobacco and peanut (23).

Sunflower has not been reported previously as a host for *P. solanacearum* in Florida, or in the United States, but it

has been reported as a host in Japan (28). The disease of sunflower may be a problem for farmers in Florida, since sunflower has been suggested as a promising crop.

Ginger has been reported as a host in Hawaii (16), but not in Florida. Pathogenicity to ginger by some isolates from Florida could indicate similarity between strains that exist in Florida and Hawaii.

Some variation occurred among the Florida isolates in physiological characteristics, but this variation was not as great as the variation that occurred among the isolates used for comparison. All Florida isolates caused hypersensitivity (HR) in tobacco which was contradictory to the report of Lozano and Sequeira (26) that isolates of race 1 did not cause HR.

Results of physiological tests for oxidase, arginine dihydrolase, growth on a potato plug, gelatin hydrolysis, pitting of polypectate and carboxymethyl cellulose media, and colony appearance on TZC medium were similar for all isolates of *P. solanacearum* and can be used to characterize the species. The differences that occurred among Florida isolates in some of the physiological properties did not seem to have any taxonomic significance. The phosphatase test may differentiate the tomato race (race 1) from the banana (race 2) and potato (race 3) races.

Hayward's biotype classification (13) did not differentiate isolates from Florida. This classification may be an oversimplification of a complex situation. The data obtained indicate that biotype I includes divergent pathovars of *P. solanacearum*. This biotype includes race 2 which affects banana and strains of race 1, such as the isolates from Florida. Biotype II includes isolates that grow at low temperatures and corresponds to race 3. This was the sole biotype, usually found on potato at the most northerly and southerly limits of geographical distribution of *P. solanacearum*, in which pathogenicity corresponded to biochemical typing.

Variation occurred among isolates from Florida on the basis of utilization of carbon compounds designated by Harris (11). None of the isolates fitted into any of the 9 subgroups of biotype I given by Harris, however. With the exception of lactate utilization, which seemed to be variable, only 3 isolates were different. An isolate from Hastings did not utilize hippurate or trehalose, and an isolate from Bradenton did not utilize hippurate.

Much information has accumulated about variation of *P. solanacearum* isolates collected around the world. However, this report is the first study of the variation of the organism in Florida. Variation among the Florida isolates is not as great, when compared to the variation of isolates in a world collection. This may be because of selection by a specific environment in Florida and/or because of introduction of a limited number of strains into Florida from tropical areas.

If the isolates used in this test are typical of the population of Florida isolates, decisions could be made about crop rotations. For example, tomatoes should not be planted following potatoes in Florida but they could be planted in soils if the potato race predominated. Care should be taken in introducing new races to Florida. Infested peanut seeds from Africa or infested banana clones from South America could introduce new pathogenic types into Florida.

The results of this research might mean that breeders for bacterial wilt resistance in commercial crops need not be concerned with pathogenic variation among the isolates from Florida. But they should be aware that pathogenic variation does occur in the species and resistant cultivars may succumb to new races. This organism appears to be sensitive to selection pressures and resistant cultivars have strong selection pressure for pathogenic races.

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AN ECONOMIC COMPARISON OF VEGETABLE IRRIGATION SYSTEMS¹

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Abstract. Seepage (modified furrow), subsurface tile, trickle, walking gun, and center pivot irrigation systems were evaluated to determine comparative irrigation costs (both variable and fixed) for commercial vegetable production. A sensitivity analysis based on water use and crop production (yield) was also evaluated to determine cost per unit relationships. The investment costs of the center pivot, subsurface tile and trickle irrigation systems were significantly larger than the capital requirements for the seepage and walking gun irrigation systems. The variable costs for the subsurface tile and trickle irrigation systems were less than the other systems primarily due to the lower volume of water used by these systems. Substantial variability was observed among irrigation systems for irrigation cost per unit produced, cost per irrigated acre and cost per acre inch of irrigation resulting from various levels of crop production and water use.

Vegetable production is an important segment of the Florida agricultural economy. Florida vegetable growers harvested greater than 5.7 billion lb. of vegetable products on slightly more than 400,000 acres during the 1982-83 crop year. The farm value of these vegetables accounted for approximately \$1.1 billion of Florida's agricultural income (1). A large portion of this production and income, however, would not have been realized without the aid of irrigation.

Irrigation water is an essential production input for a large majority of vegetable growers to achieve adequate yields and suitable crop quality (5, 6). Because of the importance and contribution of irrigation to vegetable production, any major adjustment in irrigation practices could have a large impact on vegetable growers and the Florida agricultural economy.

Recent increases in the investment cost of vegetable irrigation systems coupled with higher interest rates and energy costs have stimulated many vegetable growers to consider alternate irrigation systems for new installations and the replacement of traditional irrigation systems as they

either wear out or become cost prohibitive. The consideration of alternate systems requires a comprehensive economic evaluation of the possible irrigation systems.

The objectives of this study were to compare the investment costs and annual variable and fixed costs of five hypothetical vegetable irrigation systems. These systems were designed to grow tomatoes and to evaluate the cost sensitivity of pumping, level of water use and yield per cropped acre. The results should provide information that describes the potential economic advantages and disadvantages of each system to aid producers in deciding which system best complements their production setting.

Methods and Procedures

A cost analysis was performed to compare the investment, annual fixed and variable costs of five vegetable irrigation systems used to grow tomatoes. The cost analysis was based on the installation, operation, maintenance and economic life of the irrigation systems. The 5 irrigation systems included seepage, subsurface tile, travelling gun, center pivot, and trickle. Each system was designed to irrigate 160 acres.

Numerous individuals such as growers, irrigation pipe and pump suppliers, well drillers, researchers, and others who specialize in designing and installing irrigation systems provided information to design the irrigation systems. In addition, several industry representatives, area irrigation dealers and pipe distributors contributed cost data.

Irrigation costs. Costs were designated as either annual fixed (ownership) or variable (operating) costs, which when summed result in the annual total cost of the irrigation system (4). Fixed costs are unrelated to output and do not vary during the production period. The fixed costs include annual expenditures for depreciation, insurance, repairs, taxes, and interest. Variable costs describe those costs that vary during the production period and with output. These costs are related to the price and quantity of inputs used such as fuel, lubricants, electricity and labor.

The fixed costs of depreciation, insurance, repairs, taxes and interest were calculated for each irrigation system to determine the annual fixed costs of the irrigation systems. Depreciation simply allocates the loss in value over the life of the irrigation system to particular time periods. Annual depreciation, investment cost minus salvage value divided by the assets' useful life, was calculated with a straight-line depreciation schedule. Insurance, repairs, and taxes were individually estimated as a percentage (%) or flat rate of the investment costs for the system, well, pump and power unit of each irrigation system (see Table 1). Interest on investment was calculated at 14% of the average of investment cost and salvage value for each system, well, pump and power unit.

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