# **Chapter 2 Impacts of Crop Rotation and Irrigation on Soilborne Diseases and Soil Microbial Communities**

Robert P. Larkin, C. Wayne Honeycutt, O. Modesto Olanya,  **John M. Halloran, and Zhongqi He** 

**Abstract** Crop rotation provides numerous benefits to crop production, and is essential to reduce the build-up of soilborne plant pathogens and diseases that can devastate potato crops grown in multiple consecutive years. Crop rotations can reduce soilborne diseases through a variety of mechanisms, including changes in soil microbial communities, but different types of rotation crops can have very different effects. Crop rotations may be implemented as full-season harvestable crops, cover crops, or as green manures, with each approach having different impacts on soilborne diseases. In recent research in Maine, full-season rotation crops, such as barley, ryegrass, canola, and rapeseed, in 2-year and 3-year rotations with potato substantially reduced (15–50% reduction) *Rhizoctonia* and other soilborne diseases. Addition of a fall cover crop of winter rye to existing rotations further reduced *Rhizoctonia* and common scab diseases by another 5–20%. Use of specific disease-suppressive rotation crops as green manures can provide even greater reductions in soilborne diseases. In an ongoing large-scale study examining the effects of several different cropping system strategies both with and without irrigation, a disease-suppressive approach (utilizing *Brassica* and sudangrass green manures,

R.P. Larkin  $(\boxtimes) \cdot$  J.M. Halloran

C. W. Honeycutt

O.M. Olanya

Z. He

USDA-ARS, New England Plant, Soil, and Water Laboratory , Orono , ME 04469 , USA e-mail: bob.larkin@ars.usda.gov; john.halloran@ars.usda.gov

USDA, Natural Resources Conservation Service, Washington, DC 20250, USA e-mail: Wayne.Honeycutt@wdc.usda.gov

USDA-ARS, Eastern Regional Research Laboratory, Wyndmoor, PA 19038, USA e-mail: modesto.olanya@ars.usda.gov

USDA-ARS, Southern Regional Research Center, New Orleans, LA 70122, USA e-mail: zhongqi.he@ars.usda.gov

fall cover crops, and high crop diversity) reduced soilborne diseases better than any other cropping system (25–58% reduction), and both the disease-suppressive and a soil improving (with compost amendments) system substantially increased tuber yield (19–42%). Irrigation also increased yield  $(-28%)$  in most systems. Combining the disease-suppressive rotation with irrigation increased yield by 53% relative to non-irrigated continuous potato. Combining effective crop rotations with other compatible components of integrated pest management can provide more effective and sustainable disease management and crop productivity.

#### **2.1 Introduction**

 Crop rotation has been an important component of potato ( *Solanum tuberosum* L.) production since the earliest days of cultivation. Long rotations and fallow periods between potato crops were developed by the Incas in South America to increase soil fertility and reduce soilborne pests and diseases (Bridge 1996; Thurston 1990). Crop rotations, in general, provide numerous benefits to crop production, and serve multiple functions. They can help conserve, maintain, or replenish soil resources, including organic matter, nitrogen and other nutrient inputs, and physical and chemical properties (Ball et al. 2005; Karlen et al. [1992, 2006](#page-16-0); Magdoff [2000](#page-17-0); Magdoff and van Es 2000; Pankhurst et al. [1997](#page-17-0)). Crop rotations have been associated with increased soil fertility, increased soil tilth and aggregate stability, improved soil water management, and reduced erosion (Ball et al. 2005; Grandy et al. 2002). Probably most importantly, for potatoes as well as many other crops, rotations are essential to maintain crop productivity and reduce the build-up of soilborne plant pathogens and diseases, which can devastate crops grown in multiple consecutive years (Cook 1986, 2000; Krupinsky et al. 2002; Sumner 1982).

 Numerous soilborne diseases are persistent, recurrent problems in potato production, resulting in reduced plant growth and vigor, lower tuber quality, and reduced yield. Soilborne potato diseases of most concern in the Northeast U.S. and other potato-growing regions include: Rhizoctonia canker and black scurf, caused by *Rhizoctonia solani* ; common scab, caused by *Streptomyces scabiei* ; powdery scab, caused by *Spongospora subterranea* f.sp. *subterranea* ; white mold, caused by *Sclerotinia sclerotiorum* ; silver scurf, caused by *Helminthosporium solani* ; pink rot, caused by *Phytophthora erythroseptica* ; and Verticillium wilt, caused by *Verticillium dahliae*. Most of these diseases are difficult to control, and there are few effective control measures readily available.

 Potato production systems in the Northeast U.S. are characterized by short rotations, extensive tillage, minimal crop residue return, and minimal crop diversity. The overall productivity of these systems has remained constant for several decades, despite increasing inputs of pesticides, nutrients, and water (Halloran et al. 2005). Potato production faces numerous constraints to productivity and profitability, including the lack of profitable rotation crops, high potential for disease problems, high

fertilizer and pesticide requirements, degrading soil quality, and variable rainfall during the growing season. The long-term sustainability of potato production will depend on balancing the physiological production requirements of the crop with overcoming these additional constraints. Improved cropping systems that address the most important constraints should improve production.

 Current production practices in the Northeast and many other potato production areas are based on a 2-year rotation with a low maintenance grain crop (such as barley or oats). Although 2-year rotations have been shown to reduce soilborne disease levels compared to continuous potato (Honeycutt et al. [1996](#page-16-0); Specht and Leach [1987](#page-18-0)), longer rotation lengths of 3 or 4 years between potato crops are known to be more effective in controlling soilborne diseases (Carter and Sanderson 2001; Hide and Read [1991](#page-16-0); Hoekstra 1989; Peters et al. 2003, 2004; Scholte 1987). The use of crops with known disease-suppressive capabilities, such as *Brassica* spp. and Sudangrass crops, and fall cover crops may provide additional resources for reducing diseases through improved cropping systems, as shown by our previous research (Larkin and Honeycutt 2006; Larkin and Griffin 2007; Larkin et al. 2010,  $2011a$ , b). Such disease-suppressive cropping systems may suppress disease through a combination of multiple potential mechanisms, including biofumigation, manipulation of soil microbial communities, and other mechanisms. Through conserving or replenishing soil resources such as organic matter, effective cropping systems can alter soil chemical, physical, and biological properties (Ball et al. [2005](#page-15-0) ; Karlen et al. [1992, 2006](#page-16-0); Magdoff [2000](#page-17-0); Magdoff and van Es 2000; Pankhurst et al. [1997](#page-17-0)) that improve soil water management and reduce erosion (Ball et al. [2005](#page-15-0); Grandy et al. 2002). Even larger or more rapid changes in soil fertility, structure, and microbial communities can be observed by adding green manures or other organic amendments, such as compost, which provides much greater biomass and organic matter than is achieved through crop rotation alone (Abdallahi and N'Dayegamiye [2000](#page-15-0) ; Collins et al. 2006; Grandy et al. [2002](#page-16-0); Little et al. 2004; MacRae and Mehuys [1985](#page-17-0); Stark et al. 2007; Thorup-Kristensen et al. [2003](#page-18-0)).

 In the subsequent sections, recent examples of the effects of rotation, cover, and green manure crops on soilborne pathogens and diseases will be presented, highlighted by results from our own research program to show the potential for improved management of soilborne diseases using different cropping systems.

#### **2.2 Rotation Crop Effects on Soilborne Diseases**

 In previous research evaluating different rotation crops in 2- and 3-year rotations with potato over several years, Rhizoctonia diseases (stem canker and black scurf) and common scab were the soilborne diseases most commonly and consistently observed in these studies, and rotation crop significantly affected the incidence and severity of these diseases throughout the years of study (Larkin and Honeycutt 2006; Larkin et al. 2010). In the 2-year rotations, although disease levels of black scurf varied somewhat among rotations each year, canola and rapeseed rotations consistently



 **Fig. 2.1** Effects of different rotation crops on soilborne disease symptoms on potato tubers from 2-year crop rotations averaged over a 7-year study period (2000–2006) for ( **a** ) black scurf, (**b**) common scab, and (**c**) misshapen tubers.  $BA = \text{barley}, CN = \text{canola}, OP = \text{millet/rapeseed}$ , *GB* = green bean, *SC* = sweet corn, *SY* = soybean, *PP* = potato (control). Bars topped by the same letter are not significantly different according to Fisher's protected LSD test  $(P<0.05)$ 

reduced severity of black scurf over a 7-year evaluation period (2000–2006), averaging reductions of  $25-32\%$  relative to continuous potato (Fig. 2.1a). However, soybean and green bean rotations resulted in high scurf severity comparable to continuous potato. Barley/clover rotations initially were associated with lower levels of scurf through the first several years of the study (through 2002, or three full rotation cycles), but resulted in higher severity levels in subsequent years (2003–2005), and the 7-year average was not significantly lower than for continuous potato (but was lower than soybean rotations). Significant differences in common scab were also observed among rotations, with average disease severity significantly lower for canola and rapeseed rotations than continuous potato (25–31% reduction) over multiple years of study (Fig.  $2.1<sub>b</sub>$ ). However, incidence and severity of common scab increased substantially in all plots and all rotations from 2002 to 2005. Most rotations, including barley/clover, canola, rapeseed, and soybean reduced the percentage of severely misshapen tubers (55–70% reduction) relative to continuous potato (Fig. 2.1c). Misshapen tubers reduce the market value of the crop and can be an indication of soilborne disease problems. Each rotation crop was also associated with distinct changes in soil microbial community characteristics as determined by fatty acid methyl ester (FAME) and substrate utilization (SU; aka BIOLOG or CLPP) profile analyses (Larkin [2003](#page-16-0); Larkin et al. [2010](#page-16-0)).

 In addition, although not present during the early years of the study, Verticillium wilt developed to become a prominent problem in all plots, with incidence of wilt ranging from  $60\%$  to  $100\%$  in  $2005$  and  $2006$  (Larkin et al.  $2010$ ). The barley rotation resulted in the lowest levels of wilt among the rotations, but wilt symptoms were severe in all plots and rotations. Productivity (yield), in general, also declined over time in the 2-year rotations. However, most of these effects were not evident until the third or fourth rotation cycle. Thus, although some rotation crops significantly reduced soilborne disease relative to other 2-year rotations, no 2-year rotation was effective in preventing long-term increases in diseases such as Verticillium wilt and common scab (Larkin et al. [2010](#page-16-0)).

With the 3-year rotations, initial analyses following the first full rotation cycle indicated that potato crops following canola, barley, or sweet corn provided the lowest levels of Rhizoctonia disease and best tuber quality, whereas potato crops following clover or soybean resulted in disease problems (Larkin and Honeycutt 2006). Crops associated with increased disease levels, such as green bean and soybean, did not adversely affect the potato crop as long as the crop did not immediately precede potato (e.g. soybean-barley, green bean-sweet corn). With analyses of subsequent potato crops in 2003 and 2004 (second rotation cycle), effects due to cropping sequence (the specific sequence of rotation crops) became more evident, in addition to the effects of the crop preceding potato (Larkin et al., unpublished). For example, by the second cycle, rotations containing soybean and green bean (Sb-Ba, Sc-Sb, Gb-Sc) did not significantly reduce scurf severity, whereas all rotations that included canola (C-Sc, Sc-C, and Sb-C) significantly reduced scurf  $(35-50\%$  reduction), even when canola did not precede potato (Fig.  $2.2a$ ) Thus, by the second full rotation cycle, it appeared that the entire cropping sequence and not just the crop preceding potato was influential in shaping the soilborne disease characteristics. In 2004, the Ba-Cl, C-Sc, and Sb-Ba also significantly reduced severity of common scab relative to continuous potato and some of the other rotations (Fig. [2.2b](#page-5-0)). As with the 2-year rotation studies, each rotation resulted in distinctly different effects on soil microbial community characteristics (as determined by SU and FAME profile analyses) and were correlated to some degree with potato disease and yield measurements (Larkin and Honeycutt 2006). In these studies, a full year of clover preceding potato was associated with high levels of Rhizoctonia disease. However, in other studies, the 3-year barley-clover rotation emerged as a desirable rotation with low levels of disease, particularly Rhizoctonia diseases (Peters et al. [2003, 2004](#page-17-0)).

#### **2.3 Cover Crop Effects on Soilborne Diseases**

A cover crop is defined as a crop grown primarily to cover the soil in order to protect it from soil erosion and nutrient losses between periods of crop production (Sarrantonio and Gallandt [2003](#page-17-0)). Benefits and uses of cover crops, including reduction of water runoff and soil erosion, addition of organic matter, improved soil structure and tilth, addition and recycling of nitrogen, greater soil productivity, and weed, pest, and disease control, have been documented and summarized in numerous reviews, general references, and practical guides (Fageria et al. 2005; Hartwig and Ammon 2002; Magdoff and van Es 2000; Sustainable Agriculture Network 1998; Sarrantonio and Gallandt 2003; Snapp et al. [2005](#page-17-0); Thorup-Kristensen et al. 2003). There are numerous references to reductions of plant diseases with cover crops;

<span id="page-5-0"></span>

 **Fig. 2.2** Effects of different 3-year rotations on disease severity of potato tubers (% surface coverage) for (a) black scurf, and (b) common scab diseases after two rotation cycles (6 years). Crop rotations (crop 1 and crop 2) were: *Ba-Cl* = barley/clover-clover, *C-Sc* = canola-sweet corn, *Gb-Sc* = green bean-sweet corn, *Sb-Ba* = soybean-barley/clover, *Sb-C* = soybean-canola, *Sc-C* = sweet corn-canola, *Sc-Sb* = sweet corn-soybean, and *P-P* = consecutive potato (control), with potato the third year crop in all rotations. Bars topped by the same letter are not significantly different according to Fisher's protected LSD test  $(P<0.05)$ 

however, very few studies dealing strictly with cover crops (and not specifically green manures) have been related to potato pathogens or diseases.

In our field studies with different 2-year rotations (previous section), each rotation crop was also evaluated with and without the addition of a fall cover crop of winter rye, planted soon after harvest of the rotation and/or potato crop (Larkin et al.  $2010$ ). In the case of the barley/clover rotation, since this rotation already included a cover crop, a different cover crop (ryegrass) was substituted for the cover crop comparison. These cover/no cover comparisons were conducted from 2003 to 2006 within the long-term rotation plots established in 1997 and 1998. In these studies, modest, but significant benefits were attributed to the addition of the winter rye cover crop across all rotations. Although effects varied somewhat depending on the rotation used, overall, addition of the cover crop

reduced severity of black scurf and common scab tuber diseases by 12.5% and 7.6%, and increased tuber yield by 3.6%, when averaged over all rotations for three potato cropping seasons (Larkin et al.  $2010$ ). Black scurf severity was significantly reduced in all rotations except rapeseed (where disease was already low), with reductions due to cover crop ranging from 10% to 19%. Common scab was significantly reduced (by  $8-21\%$ ) with cover crop addition in the barley, canola, rapeseed, and potato rotations. Changing the cover crop underseeded with barley from red clover to ryegrass also resulted in significant reductions in black scurf and common scab (18.6% and 19.3%, respectively), supporting previous studies indicating that red clover can cause scurf and scab problems on potato crops (Brewer  $2003$ ; Larkin and Honeycutt  $2006$ ). Thus, ryegrass may be a preferable cover crop for underseeding with barley.

 Although reductions in soilborne disease associated with the use of cover crops were generally modest (5–20%), the combined effects of using a cover crop in conjunction with an effective rotation crop were quite substantial and greater than using either approach separately. For example, combining the winter rye cover crop with a canola or rapeseed rotation reduced black scurf and common scab by 25–41% relative to a continuous potato rotation, and 21–37% relative to the barley/clover standard rotation (Larkin et al. [2010](#page-16-0)).

#### **2.4 Green Manure Crop Effects on Soilborne Diseases**

Green manuring refers specifically to the incorporation of fresh plant material for the purpose of soil enrichment (Pieters [1927 \)](#page-17-0) . Thus, green manure crops are grown solely to be incorporated into soil as organic matter while still fresh and green. Green manuring generally results in larger organic matter inputs than traditional crop rotations or cover crops, producing improvements in soil fertility and structure (Abdallahi and N'Dayegamiye 2000; Grandy et al. [2002](#page-16-0); Little et al. [2004](#page-17-0); MacRae and Mehuys [1985](#page-17-0); Thorup-Kristensen et al. 2003), as well as significant changes in soil microbial community characteristics (Collins et al. [2006](#page-15-0); Stark et al. 2007). Green manures result in increased microbial biomass and activity, but also change microbial communities in ways that are distinctly different from other types of organic matter amendments, such as manure or sawdust (Elfstrand et al. 2007).

 Green manures of different kinds have long been associated with reductions in potato diseases, particularly common scab and Verticillium wilt, although results have been variable. Early work indicated that green manures of rye and cowpea could reduce common scab (Weinhold et al. 1964). In long-term field trials in California, soybean grown as a green manure prevented the build-up of common scab over a period of 13 years, maintaining minimal disease levels compared to a rapid increase in common scab with pea or barley green manures and in the potato control (Weinhold et al. [1964 \)](#page-18-0) . However, the soybean green manure was not effective in reducing common scab in a field with an already established high population of pathogen and high disease pressure.

 Two years of green manure treatments using sudangrass, winter pea, rapeseed, rye, oats, or corn resulted in significant reductions in the incidence of Verticillium wilt (30–80% reduction) in the subsequent potato crop, with sudangrass providing substantially greater reductions in disease and significantly greater yield than most of the other crops (Davis et al. 1996). The sudangrass, rapeseed, and oat green manure treatments also reduced wilt in a second successive potato crop the following year. In these trials, disease reduction was not necessarily associated with reduction of pathogen inoculum, but was associated with reductions in root infections, increased microbial activity, and specific changes in microbial populations (Davis et al. [1996](#page-16-0)). Multiple follow-up studies with sudangrass green manures in subsequent years also showed reduced Verticillium wilt disease and improved tuber quality and yield, and that the benefits of sudangrass treatments extended beyond disease suppression and were correlated with increases in *Fusarium* spp. populations, microbial activity, and soil fertility factors (Davis et al. 2004).

 Single season applications of green manures of sudangrass, winter pea, and broccoli at different biomass rates reduced inoculum density of *V. dahliae* and severity of wilt, but resulted only in marginal (nonsignificant) potato yield increases (Ochiai et al. [2007](#page-17-0)). Single-season green manure treatments of buckwheat or canola have resulted in significantly less Verticillium wilt and marginally less common scab as well as increased potato yield relative to fallow control plots (Wiggins and Kinkel [2005a](#page-18-0)). In these experiments, green manure treatments were also associated with an increase in the density and pathogen-inhibitory activity of indigenous Streptomycetes toward multiple soilborne potato pathogens ( *S. scabies, V. dahliae, F. oxysporum,* and *R. solani*) (Wiggins and Kinkel 2005a, b).

 Green manures of certain crops are also associated with biofumigation, which refers to the breakdown of plant metabolites in soil to produce volatile compounds that can reduce populations of weeds, nematodes, and plant pathogens (Matthiessen and Kirkegaard 2006; Sarwar et al. 1998). Crops in the *Brassicaceae* family produce glucosinolates that break down to produce isothiocyanates, whereas Sudangrass produces cyanogenic glucosides that break down to produce hydrogen cyanide, that are toxic to many soil organisms. Use of these plants as green manure crops has been shown to reduce pathogens or diseases (Brown and Morra [1997](#page-15-0); Kirkegaard et al. 1996; Muelchen et al. [1990](#page-17-0); Olivier et al. 1999; Smolinska and Horbowicz 1999), nematodes (Buskov et al. [2002](#page-15-0); Mohjtahedi et al. 1993), and weeds (Boydston and Hang [1995](#page-15-0); Brown and Morra 1995), and to improve soil characteristics and crop yield (McGuire [2003](#page-17-0) ) . Although biofumigation is the presumed mechanism of action for these crops, further research has indicated that additional mechanisms, including specific changes in soil microbial communities not related to levels of glucosinolate or other toxic metabolites, are also important in the reduction of soilborne diseases by *Brassica* crops, particularly for the control of *Rhizoctonia* (Cohen et al. 2005; Davis et al. 1996, 2004; Larkin and Griffin 2007; Mazzola et al. 2001).

 Because of the potential for biofumigation effects, interest and use of Brassica crops as rotation and green manure crops has been increasing in recent years, in various fruit, vegetable, and field crops (Mazzola and Mullinix 2005; Subbarao et al. [1999](#page-18-0); Zasada et al. 2003), as well as in potato cropping systems (Gies 2004;

McGuire [2003](#page-17-0)). In commercial applications of Brassica green manures in the Pacific Northwest, white mustard (*Sinapis alba*) and oriental mustard (*Brassica juncea*) green manures resulted in comparable tuber yield, quality, and disease control as fumigation with Metam sodium, improved certain soil properties, such as infiltration rate, and also provided an economic benefit (McGuire 2003). In our own research with Brassica green manures, a variety of Brassica crops (canola, rapeseed, Indian mustard, yellow mustard, turnip, and oilseed radish) and barley green manure treatments reduced soil inoculum levels of R. solani (20–56% reduction), and Indian mustard, rapeseed, and radish also reduced subsequent seedling diseases in greenhouse tests by  $40-83\%$  (Larkin and Griffin 2007). In on-farm field trials, Indian mustard, rapeseed, canola, and ryegrass grown as green manure rotation crops reduced powdery scab in the subsequent potato crop by 15–40%, and canola and rapeseed reduced black scurf by 70–80% relative to a standard oats rotation. At another field site, an Indian mustard green manure reduced common scab by 25%, and rapeseed, yellow mustard, and ryegrass also reduced black scurf relative to a standard rotation (Larkin and Griffin 2007). Disease reductions were not always associated with higher glucosinolate-producing crops and were also observed with non-Brassica green manures (barley and ryegrass), indicating other mechanisms and interactions were important, particularly for control of R. solani. Overall, Indian mustard (high-glucosinolate, *B. juncea* ) was most effective for reducing powdery scab and common scab diseases, but rapeseed and canola (relatively low glucosinolate-producing, *B. napus* ) were most effective in reducing *Rhizoctonia* diseases (Larkin and Griffin 2007). In recent trials in a field severely infested with Verticillium wilt, a single green manure crop of a mustard blend ('Caliente 119', a mixture of *Sinapis alba* and *Brassica juncea* ) or sorghum-sudangrass hybrid resulted in a 20–25% reduction in Verticillium wilt in the subsequent potato crop compared to a standard barley rotation (Larkin et al.  $2011a$ ). The mustard blend also reduced other soilborne diseases and increased tuber yield relative to the barley control. However, by the second rotation cycle (second potato crop), wilt was high in all treatments, and was not effectively reduced by the green manures, indicating that a 2-year green manure-potato rotation was not sustainable for disease management (Larkin et al. 2011a). Our research with Brassica green manures is continuing with evaluations of the best rotation crops for disease control, enhancing the extent of disease reduction, determining the best methods of application and implementation, and the economic consequences of these rotations.

## **2.5 Cropping System Approaches and Irrigation Effects on Soilborne Diseases: Case Study**

Beginning in 2004, large-scale field trials were established in Maine as part of a project designed to identify and establish the relative contribution of factors that limit cropping system sustainability in the Northeast. In this ongoing study, the

effects of different cropping systems designed with specific management goals were evaluated on all aspects of potato crop production, as an attempt to better understand how these various factors and interactions may be involved in constraining productivity. For this study, 3-year cropping systems designed to specifically address management issues of soil conservation, soil improvement, and disease suppression were established and their subsequent effects on crop production were determined and compared with standards representing a typical potato cropping system and a non-rotation control under both irrigated and non-irrigated conditions. In this component of the overall research project, these cropping systems were evaluated for their effects and interactions on soilborne diseases and soil microbial community characteristics. Data were collected in the potato cropping year of each system following the complete rotation cycle. To date, results have been compiled for 5 full years following the first complete rotation cycle  $(2006-2010)$ . Results regarding soilborne diseases and soil microbiology for the first 3 data years has been published thus far (Larkin et al.  $2011b$ ). Some cumulative results for the first five seasons are presented here. Subsequent reports will provide results from our interdisciplinary evaluation of these cropping systems on soil physical and chemical properties, plant nutrition, plant growth, tuber yield, economic viability, and other properties.

## *2.5.1 Cropping Systems*

In this study, the cropping systems consisted of five different systems designed to address specific management goals of soil conservation, soil improvement, and disease suppression, as well as a system representing a typical standard rotation currently used in the Northeast US, and a non-rotation control of continuous potato ( *Solanum tuberosum* L.). The standard or 'status quo' rotation (SQ) consisted of a 2-year rotation of barley (*Hordeum vulgare* L.) underseeded with red clover ( *Trifolium pretense* L.) as a cover crop, followed by potato the following year. This system includes regular spring and fall tillage each year. The soil conserving system (SC) consisted of a 3-year rotation of barley underseeded with the forage grass timothy ( *Phleum pratense* L), and then the timothy would overwinter and be allowed to continue undisturbed for a full year (2nd year), and then followed by potato in the third year. In this system tillage was also substantially reduced, with no tillage except immediately prior to planting potato and as needed for normal maintenance and harvest of the potato crop. In addition, straw mulch was applied after potato harvest to further conserve soil resources. The soil improving system (SI) consisted of the same basic rotation as SC (3-year, barley/timothy-timothy-potato, limited tillage, straw mulch), but with yearly additions of compost, to provide C and organic matter to improve soil quality. The disease-suppressive system (DS) was designed to make use of multiple strategies for suppressing soilborne diseases, including the use of disease-suppressive rotation crops, a longer rotation period, crop diversity, green manures, and fall cover crops. The DS system consisted of a 3-year rotation with the disease-suppressive *Brassica* 'Caliente 119' Mustard Blend (blend of oriental and white mustard seeds, *Brassica juncea* L. and *Sinapis alba* L *.* ) grown as a green manure, followed by a fall cover crop of rapeseed ( *Brassica napus* L. Dwarf Essex') in the first year. In the 2nd year, a disease-suppressive Sorghum-Sudangrass hybrid ( *Sorghum bicolor* x *S. bicolor* var. *sudanense* L.) was grown as a green manure, followed by a fall cover crop of winter rye ( *Secale cereale* L.), with potato in the 3rd year. Continuous potato (PP) was the nonrotation control consisting of a potato crop planted in the same plots each year. All cropping systems were evaluated under both irrigated and rainfed management. Full experimental details and methodologies are provided elsewhere (Larkin et al.  $2011b$ .

#### *2.5.2 Effects on Soilborne Disease*

 The primary potato diseases observed throughout the study were Rhizoctonia stem and stolon canker on the potato plants, and black scurf and common scab on the tubers. Rhizoctonia diseases generally occurred at low to moderate severity levels (0.3–1.5% surface coverage) and common scab occurred at relatively high severity levels (3.0–9.0% surface coverage). Overall, all cropping systems reduced Rhizoctonia stem and stolon canker relative to continuous potato (PP) with individual yearly reductions of 10–50% and overall average reductions (all years together) of  $20-30\%$ , whereas irrigation had no significant effect on stem and stolon canker (Larkin et al. [2011b](#page-17-0)).

 Black scurf severity levels and cropping system effects varied somewhat from year to year, but average levels combined from multiple years were representative of the levels observed. Averaged over all 5 years, DS averaged significantly lower scurf severity than all other cropping systems under both irrigated and non-irrigated conditions (with reductions of 27–58%), and irrigated plots averaged 20% higher scurf severity than non-irrigated plots (Fig. 2.3a). Cropping system effects on common scab also varied somewhat from year to year, but overall consistent results were observed Overall, DS reduced scab severity better than all other cropping systems (25–40%), and irrigation tended to increase scab levels in each cropping system, averaging a  $21\%$  increase over all systems (Fig.  $2.3b$ ).

#### *2.5.3 Yield Effects*

 In all years, under non-irrigated conditions, both total and marketable yield tended to be highest in the SI system, with yield increases of up to 40–60% higher than other cropping systems. DS also increased both total and marketable yield in all years relative to PP, with increases of 13–35%. With irrigation, tuber yields for all systems (except SI) increased by 20–40%, generally bringing them comparable to

<span id="page-11-0"></span>

**Fig. 2.3** Effect of different cropping system approaches with and without irrigation on (a) severity of black scurf and ( **b** ) common scab tuber diseases, and ( **c** ) total tuber yield (combined data from 5 years of data, 2006–2010).  $SQ$  = status quo system, standard 2-year rotation (barley/clover – potato); *SC* = soil-conserving system, 3-year, limited tillage, (barley/timothy – timothy – potato);  $SI =$ soil-improving system, 3-year, system same as  $SC$  but with yearly compost amendments; *DS* = disease-suppressive, 3-year (mustard blend green manure/rapeseed cover crop – sudangrass green manure/rye cover crop – potato); *PP* = continuous potato, nonrotation control: *IRR* = irrigated; *NON* = non-irrigated (rainfed). Bars within irrigation regime topped by the same letter are not significantly different from each other based on ANOVA and Fisher's protected LSD test  $(P<0.05)$  Bars topped by an asterisk represent values that are significantly different than their corresponding value for that cropping system in the other irrigation regime  $(P<0.05)$ 

yield levels of SI without irrigation. Under irrigated conditions, DS produced the highest numerical yields, averaging slightly higher than SI in all years, and all cropping systems yielded better than PP (by 11–24%). Averaged over all 5 years, SI increased yield by 41% under rainfed conditions, and irrigation increased total yield by 18–29% in different cropping systems and 21% over all cropping systems (Fig.  $2.3c$ ). The combined effects of improved rotation and irrigation were best illustrated with the irrigated DS system, which resulted in average yields 53% higher than in non-irrigated PP, and 42% higher than the non-irrigated standard rotation (SQ) over the 5-year period.

## *2.5.4 Soil Microbial Communities*

 Soil microbial community data from soil samples collected from all plots in the spring of each year prior to planting potatoes indicated consistent and highly significant effects due to cropping system for most parameters in all years, whereas irrigation had little effect on soil microbial characteristics at this time of sampling. Combined data averaged over 3 crop years illustrated the overall effects (Larkin et al. 2011b).

 Overall average populations of culturable bacteria and fungi were higher in SI soils than all other cropping systems, with bacterial populations in DS soils next highest, and lowest microbial populations observed in PP soils. General microbial activity, as estimated by average substrate utilization across numerous carbon sources (AWCD), indicated highest activity in the SI and SQ soils, and lowest activity in the PP soils. Substrate diversity and richness tended to be higher in DS soils  $(Larkin et al. 2011b)$  $(Larkin et al. 2011b)$  $(Larkin et al. 2011b)$ . Analysis of the soil fatty acid data indicated that soil FAME profiles were distinctly different for each of the cropping systems, and that overall characteristics for each system were fairly consistent from year to year. Graphical depiction of the first two canonical variates (CV 1 and CV2) from canonical variates analysis from combined data for all 3 years illustrated that soil from each cropping system had microbial characteristics that were very distinct from each other system (Fig. [2.4 \)](#page-13-0). Irrigation also had some effects on soil microbial characteristics but these effects were minor in comparison to cropping system effects, as indicated by the greater separation among the cropping systems and closer proximity of the irrigated and not irrigated values for each cropping system. Interestingly, the SI and DS systems showed the greatest effects on soil microbiology (evident by the greater separation from the SQ and PP systems), but each showed very different effects (SI showing lower values for CV1 and DS lower values for CV2).

Analysis of FAME parameters and characteristics also indicated significant differences among the cropping systems regarding FAME structural classes and indicator biomarkers. Overall, DS soil had the highest proportion of the FAME biomarker for fungi, among cropping systems, as well as a high proportion of biomarkers for actinomycetes, and a high ratio of Gram-positive:Gram-negative FAMEs. SI soil had the highest proportion of the mycorrhizae biomarker among cropping systems, whereas DS and PP had the lowest level of the mycorrhizae biomarker. PP soil also had the lowest levels of the fungi marker and the fungi:bacteria ratio (Larkin et al. 2011b). All these differences indicate that each cropping system affected microbial communities in distinct and different ways.

# *2.5.5 Cropping System Approaches Summary and Conclusions*

 Each of the designated cropping systems accomplished their respective management goals. SI, through addition of organic matter as composted dairy manure, had the greatest effects on soil properties, and improved soil quality through numerous

<span id="page-13-0"></span>

 **Fig. 2.4** Effect of different cropping system approaches with and without irrigation on soil microbial community characteristics, as represented by canonical variates (CV) 1 and 2 from CV analysis of soil fatty acid methyl-ester profiles (combined data from three field seasons, 2006–2008). *SQ* = status quo system, standard 2-year rotation (barley/clover – potato); *SC* = soil-conserving system, 3-year, limited tillage, (barley/timothy – timothy – potato); *SI* = soil-improving system, 3-year, system same as SC but with yearly compost amendments; *DS* = disease-suppressive, 3-year (mustard blend green manure/rapeseed cover crop – sudangrass green manure/rye cover crop – potato);  $PP =$  continuous potato, nonrotation control: filled shapes = irrigated; open shapes = non-irrigated

 measured parameters, and also affected plant growth characteristics. SC improved soil conservation (relative to the standard, 2-year, SQ rotation) by limiting tillage, reducing erosion, and lengthening the rotation period. However, in this study, these changes in the SC system did not result in significant effects on soil properties, diseases, yield, or most soil microbial assessments relative to the SQ rotation. Several other studies have also observed that these types of changes (limited tillage, additional year of rotation) often do not result in significant changes within the first few years of implementation (Carter and Sanderson [2001](#page-15-0); Carter et al. 2005; Griffin et al.  $2009$ ), but would be expected to show significant reductions in soilborne dis-eases over longer periods (Carter and Sanderson 2001; Peters et al. [2003, 2004](#page-17-0)). The DS system, consisting of *Brassica* and Sudangrass green manure crops, fall cover crops, and high crop diversity, resulted in the greatest reductions in stem and stolon canker, black scurf, and common scab relative to the other rotations, under both irrigated and non-irrigated conditions, thus accomplishing the disease-suppressive objective. DS also produced significant shifts in soil microbial community characteristics different from all other rotations. Thus, the strategies used for the disease suppression system, the use of disease-suppressive biofumigation rotation crops, cover crops, and crop diversity, successfully reduced disease relative to other rotations. Irrigation improved yield substantially in most cropping systems (all but SI) throughout, even in the wetter years. However, irrigation also tended to increase disease problems for both black scurf and common scab.

 Overall, soil water, soil quality, and soilborne diseases were all important factors involved in constraining productivity, and systems addressing these constraints enhanced productivity. However, for future long-term productivity, it will likely be necessary to balance the need for low disease levels with sustainable cropping practices to optimize yields. Thus, a cropping system incorporating the DS system approaches (disease-suppressive rotations, cover crops, and crop diversity), with irrigation and some of the SC/SI system soil quality inputs (limited tillage, organic amendments), and a profitable third year crop, may provide potential for enhanced sustainable production and disease management.

#### **2.6 Overall Conclusions**

 Crop rotations in all forms, whether as harvested crops, cover crops, or green manures, can have significant effects on soilborne diseases. And it is clear that the effects of crop rotations extend far beyond that of serving as a simple break in the host-pathogen cycle, with extensive influences on soil microbial community dynamics and characteristics, and potential for inhibiting, suppressing, and inactivating pathogen growth, survival, and disease development. All aspects of the rotations (rotation crop, crop genotype, rotation length, crop sequence, crop management, etc.) can significantly affect soil microorganisms and have potential effects on the development of soilborne diseases. Different uses of crop rotations (as full-season, cover, or green manure crops) also will result in different effects on soil microorganisms, and potentially different resultant effects on soilborne diseases. Overall, green manure crops may have the greatest potential for management of soilborne diseases, with their large additions of organic matter, specific effects on soil microbial communities, and potential for direct antagonism of pathogens through toxic breakdown compounds, but significant reductions in soilborne diseases can be observed with all types of rotations. In many cases, crop rotations are effective at reducing multiple diseases with a single cropping practice, although other cases exist where control of one disease results in increases in some other diseases. In general, disease control from crop rotation ranges from moderate to substantial, but will almost certainly never result in complete control of a pathogen or pathogens. Thus, crop rotations are best implemented as an important component of an integrated disease management program and not as the only control means for soilborne diseases (Lazarovits 2010). Combining crop rotations with other cultural, biological, or chemical approaches can substantially increase disease control and help achieve greater sustainability. The use of crop rotations as a crucial component in the active management of soil microbial communities to develop disease suppression and greater crop productivity

<span id="page-15-0"></span>is a viable, worthwhile, and achievable goal. However, much additional research is needed to determine the specific effects and interactions among different crop rotations and soil microorganisms, the roles and effects of the changes in soil microbial communities on soilborne diseases, and establishment and maintenance of stable disease suppression through management of soil physical, chemical, and biological attributes.

 **Acknowledgements** We thank the many people who have worked on or contributed to this research over the years, from summer workers and student aides, filed crews, technicians, colleagues, and miscellaneous expertise. In particular, we thank L. Matthiesen for her thorough and capable technical assistance on all aspects of this work; D. Cowperthwaite and D. Torrey for managing and maintaining the field sites; P. Pinette, G. Trusty, E. Champaco, B. LeGasse, and E. Mallory for additional technical support; and all the others without whom these large-scale, longterm studies could never be completed. We also thank the Maine Potato Board and USDA Potato Research Program for providing additional funding for portions of this research.

### **References**

- Abdallahi MM, N'Dayegamiye A (2000) Effects of green manures on soil physical and biological properties and on wheat yields and N uptake. Can J Soil Sci 80:81–89
- Ball BC, Bingham I, Rees RM, Watson CA (2005) The role of crop rotations in determining soil structure and crop growth conditions. Can J Plant Sci 85:557–577
- Boydston RA, Hang HA (1995) Rapeseed ( *Brassica napus)* green manure crop suppresses weeds in potato ( *Solanum tuberosum* ). Weed Technol 9:669–675
- Brewer MT (2003) Effects of biological control and a ryegrass rotation on rhizoctonia disease of potato. Thesis (M.S.) in Plant, Soil and Environmental Sciences, University of Maine, Orono, ME
- Bridge J (1996) Nematode management in sustainable agriculture. Annu Rev Phytopathol 34:201–225
- Brown PD, Morra MJ (1995) Glucosinolate-containing plant tissues as bioherbicides. J Agric Food Chem 43:3070–3074
- Brown PD, Morra MJ (1997) Control of soilborne plant pests using glucosinolate-containing plants. Adv Agron 61:167–231
- Buskov S, Serra B, Rosa E, Sorense H, Sorensen JC (2002) Effects of intact glucosinolates and products produced from glucosinolates in myrosinase-catalyzed hydrolysis on the potato cyst nematode ( *Globodera rostichiensis* ). J Agric Food Chem 50:690–695
- Carter MR, Sanderson JB (2001) Influence of conservation tillage and rotation length on potato productivity, tuber disease and soil quality parameters on a fine sandy loam in eastern Canada. Soil Till Res 63:1–13
- Carter MR, Holmstrom D, Sanderson JB, Ivany JA, DeHaan R (2005) Comparison of conservation with conventional tillage for potato production in Atlantic Canada: crop productivity, soil physical properties and weed control. Can J Soil Sci 85:453–461
- Cohen MF, Mazzola M, Yamasaki H (2005) *Brassica napus* seed meal soil amendment modifies microbial community structure, nitric oxide production and incidence of *Rhizoctonia* root rot. Soil Biol Biochem 37:1215–1227
- Collins HP, Alva AK, Boydston RA, Cochran RL, Hamm PB, McGuire A, Riga E (2006) Soil microbial, fungal, and nematode responses to soil fumigation and cover crops under potato production. Biol Fertil Soils 42:247–257
- <span id="page-16-0"></span> Cook RJ (1986) Interrelationships of plant health and the sustainability of agriculture, with special reference to plant diseases. Am J Altern Agric 1:19–24
- Cook RJ (2000) Advances in plant health management in the twentieth century. Annu Rev Phytopathol 38:95–116
- Davis JR, Huisman OC, Westermann DT, Hafez SL, Everson DO, Sorensen LH, Schneider AT (1996) Effects of green manures on verticillium wilt of potato. Phytopathology 86:444–453
- Davis JR, Huisman OC, Westermann DT, Everson DO, Schneider A, Sorensen LH (2004) Some unique benefits with sudangrass for improved U.S.#1 yields and size of Russet Burbank potato. Am J Potato Res 81:403–413
- Elfstrand S, Hedlund K, Martensson A (2007) Soil enzyme activities, microbial community composition and function after 47 years of continuous green manuring. Appl Soil Ecol 35:610–621
- Fageria NK, Baligar VC, Bailey BA (2005) Role of cover crops in improving soil and row crop productivity. Commun Soil Sci Plant Anal 36:2733–2757
- Gies D (2004) Commercial use of mustards for green manure and biofumigation in the United States. Agroindustria 3:403–405
- Grandy AS, Porter GA, Erich MS (2002) Organic amendment and rotation crop effects on the recovery of soil organic matter and aggregation in potato cropping systems. Soil Sci Soc Am J 66:1311–1319
- Griffin TS, Larkin RP, Honeycutt CW (2009) Delayed tillage and cover crop effects in potato systems. Am J Potato Res 86:79–87
- Halloran JM, Griffin TS, Honeycutt CW (2005) An economic analysis of potential rotation crops for Maine potato cropping systems. Am J Potato Res 82:155–162
- Hartwig NL, Ammon HU (2002) Cover crops and living mulches. Weed Sci 50:688–699
- Hide GA, Read PJ (1991) Effects of rotation length, fungicide treatment of seed tubers and nematicide on diseases and the quality of potato tubers. Ann Appl Biol 119:77–87
- Hoekstra O (1989) Results of twenty-four years of crop rotation research at 'De Schreef' experimental site. In: Vos J et al (eds) Effects of crop rotation on potato production in the temperate zones. Kluwer Academic Publishers, Dordrecht, pp 37–43
- Honeycutt CW, Clapham WM, Leach SS (1996) Crop rotation and N fertilization effects on growth, yield, and disease incidence in potato. Am Potato J 73:45–61
- Karlen DL, Eash NS, Unger PW (1992) Soil and crop management effects on soil quality indicators. Am J Altern Agric 7:48–55
- Karlen DL, Hurley EG, Andrews SS, Cambardella CA, Meek DW, Duffy MD, Mallarino AP (2006) Crop rotation effects on soil quality at three northern corn/soybean belt locations. Agron J 98:484–495
- Kirkegaard JA, Wong PTW, Desmarchelier JM (1996) In vitro suppression of fungal root pathogens of cereals by Brassica tissues. Plant Pathol 45:593–603
- Krupinsky JM, Bailey KL, McMullen MM, Gossen BD, Turkington TK (2002) Managing plant disease risk in diversified cropping systems. Agron J 94:198–209
- Larkin RP (2003) Characterization of soil microbial communities under different potato cropping systems by microbial population dynamics, substrate utilization, and fatty acid profiles. Soil Biol Biochem 35:1451–1466
- Larkin RP, Griffin TS (2007) Control of soilborne diseases of potato using *Brassica* green manures. Crop Prot 26:1067–1077
- Larkin RP, Honeycutt CW (2006) Effects of different 3-year cropping systems on soil microbial communities and Rhizoctonia diseases of potato. Phytopathology 96:68–79
- Larkin RP, Griffin TS, Honeycutt CW (2010) Rotation and cover crop effects on soilborne potato diseases, tuber yield, and soil microbial communities. Plant Dis 94:1491–1502
- Larkin RP, Honeycutt CW, Olanya OM (2011a) Management of Verticillium wilt of potato with disease-suppressive green manures and as affected by previous cropping history. Plant Dis 95:568–576
- <span id="page-17-0"></span>Larkin RP, Honeycutt CW, Griffin TS, Olanya OM, Halloran JM, He Z (2011b) Effects of different potato cropping system approaches and water management on soilborne diseases and soil microbial communities. Phytopathology 101:58–67
- Lazarovits G (2010) Managing soilborne diseases of potatoes using ecologically based approaches. Am J Potato Res 87:401–411
- Little SA, Hocking PJ, Greene RSB (2004) A preliminary study of the role of cover crops in improving soil fertility and yield for potato production. Commun Soil Sci Plant Anal 35:471–494
- MacRae RJ, Mehuys GR (1985) The effect of green manuring on the physical properties of temperate-area soils. Adv Soil Sci 3:71–94
- Magdoff F (2000) Concepts, components, and strategies of soil health in agroecosystems. J Nematol 33:169–172
- Magdoff F, van Es H (2000) Building soils for better crops, 2nd edn, Cover crops and crop rotations. Sustainable Agriculture Publications, University of Vermont, Burlington, pp 87–108
- Matthiessen JN, Kirkegaard JA (2006) Biofumigation and enhanced biodegradation: opportunity and challenge in soilborne pest and disease management. Crit Rev Plant Sci 25:235–265
- Mazzola M, Mullinix K  $(2005)$  Comparative field efficacy of management strategies containing *Brassica napus* seed meal or green manure for the control of apple replant disease. Plant Dis 89:1207–1213
- Mazzola M, Granatstein DM, Elfving DC, Mullinix K (2001) Suppression of specific apple root pathogens by *Brassica napus* seed meal amendment regardless of glucosinolate content. Phytopathology 91:673–679
- McGuire AN (2003) Mustard green manures replace fumigant and improve infiltration in potato cropping system. Crop Manage. (Online) doi:[10.1094/CM-2003-0822-01-RS](http://dx.doi.org/10.1094/CM-2003-0822-01-RS)
- Mohjtahedi H, Santo GS, Wilson JH (1993) Managing Meloidogyne chitwoodii on potato with rapeseed as green manure. Plant Dis 77:42–46
- Muelchen AM, Rand RA, Parke JL (1990) Evaluation of crucifer green manures for controlling Aphanomyces root rot of peas. Plant Dis 74:651–654
- Ochiai N, Crowe FJ, Dick RP, Powelson ML (2007) Effects of green manure type and amendment rate on Verticillium wilt severity and yield of russet burbank potato. Plant Dis 91:400–406
- Olivier C, Vaughn SF, Mizubuti EG, Loria R (1999) Variation in allyl isothiocyanate production within *Brassica* species and correlation with fungicidal activity. J Chem Ecol 25:2687–2701
- Pankhurst CE, Doube BM, Gupta VVSR (1997) Biological indicators of soil health. CAB International, Oxon
- Peters RD, Sturz AV, Carter MR, Sanderson JB (2003) Developing disease-suppressive soils through crop rotation and tillage management practices. Soil Tillage Res 72:181–192
- Peters RD, Sturz AV, Carter MR, Sanderson JB (2004) Influence of crop rotation and conservation tillage practices on the severity of soil-borne potato diseases in temperate humid agriculture. Can J Soil Sci 84:397–402
- Pieters JA (1927) Green manuring, principles and practices. Wiley, New York
- Sarrantonio M, Gallandt E (2003) The role of cover crops in North American cropping systems. J Crop Prod 8:53–74
- Sarwar M, Kirkegaard JA, Wong PTW, Desmarchelier JM (1998) Biofumigation potential of Brassicas. III. In vitro toxicity of isothiocyanates to soil-borne fungal pathogens. Plant Soil 210:103–112
- Scholte K (1987) The effect of crop rotation and granular nematicides on the incidence of *Rhizoctonia solani* in potato. Potato Res 30:187–199
- Smolinska U, Horbowicz M (1999) Fungicidal activity of volatiles from selected cruciferous plants against resting propagules of soil-borne fungal pathogens. J Phytopathol 147:119–124
- Snapp SS, Swinton SM, Labarta R, Mutch D, Black JR, Leep R, Nyiraneza J, O'Neil K (2005) Evaluating cover crops for benefits, costs, and performance within cropping system niches. Agronomy J 97:322–332
- <span id="page-18-0"></span> Specht LP, Leach SS (1987) Effects of crop rotation on Rhizoctonia disease of white potato. Plant Dis 71:433–437
- Stark C, Condron LM, Stweart A, Di HJ, O'Callaghan M (2007) Influence of organic and mineral amendments on microbial soil properties and properties. Appl Soil Ecol 35:79–93
- Subbarao KV, Hubbard JC, Koike ST (1999) Evaluation of broccoli residue incorporation into field soil for verticillium wilt control in cauliflower. Plant Dis 83:124–129
- Sustainable Agriculture Network (1998) Managing cover crops profitably, 2nd edn. Sustainable Agriculture Network, Beltsville
- Sumner DR (1982) Crop rotation and plant productivity. In: Rechcigl M (ed) CRC handbook of agricultural productivity. CRC Press, Boca Raton, pp 273–313
- Thorup-Kristensen K, Magid J, Jensen LS (2003) Catch crops and green manures as biological tools in nitrogen management in temperate zones. Adv Agron 79:227–302
- Thurston HD (1990) Plant disease management practices of traditional farmers. Plant Dis 74:96–101
- Weinhold AR, Oswald JW, Bowman T, Bishop J, Wright D (1964) Influence of green manures and crop rotation on common scab of potato. Am Potato J 41:265–273
- Wiggins BE, Kinkel LL (2005a) Green manures and crop sequences influence potato diseases and pathogen inhibitory activity of indigenous streptomycetes. Phytopathology 95:178–185
- Wiggins BE, Kinkel LL (2005b) Green manures and crop sequences influence alfalfa root rot and pathogen inhibitory activity among soil-borne streptomycetes. Plant Soil 268:271–283
- Zasada IA, Ferris H, Elmore CL, Roncoroni JA, MacDonald JD, Bolkan LR, Yakabe LE (2003) Field applications of brassicaceous amendments for control of soilborne pests and pathogens. Plant Health Prog. (Online) doi:[10.1094/PHP-2003-1120-01-RS](http://dx.doi.org/10.1094/PHP-2003-1120-01-RS)