Slow-Rusting Resistance in Native Spearmint to *Puccinia menthae*

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Abstract

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Rust, caused by *Puccinia menthae*, is often a serious yield-reducing problem on native and Scotch spearmint in south-central Washington State. Rust resistant mint cultivars would reduce a dependence on fungicides for disease management; however, conventional breeding practices are not possible because commercial mint plants are sterile. Mutant Scotch and native spearmint lines induced by irradiation were evaluated for partial resistance to rust. Latent period and number of uredinia per leaf from urediniospore inoculations in the greenhouse and aecial and uredinial development in the field were quantified. Length of latent period, number of uredinia per leaf, incidence of shoots with aecia, and area under the disease progress curve (AUDPC) for uredinia development all varied significantly among lines and standard cultivars. Length of latent period was significantly longer and

number of uredinia per leaf was significantly lower for native spearmint line N87-1 than for most of the other mutant lines, native spearmint, and Scotch spearmint. Line N87-1 had the lowest AUDPC values of all lines and standard cultivars for 3 years in the field. However, line N87-1 had a relatively high incidence of shoots with aecia both of two years in the field. Length of latent period was significantly and negatively correlated with AUDPC 2 of 3 years. Mean incidence of shoots with aecia was not correlated with AUDPC or with length of latent period after urediniospore infection. Rust in native spearmint in south-central Washington State could be satisfactorily managed with slow-rusting resistance when coupled with good irrigation water management and sanitation tactics that limit aecia development on early spring mint foliage.

Three mint species—*Mentha × piperita* L. (peppermint), *Mentha gracilis* Sole (*M. cardiaca* Baker) (Scotch spearmint), and *M. spicata* L. (native spearmint)—are commercially grown for their essential oils in the United States. The major production regions in North America are the U.S. states or Canadian province of Washington, Oregon, Idaho, Indiana, Alberta, California, South Dakota, Wisconsin, Nevada, and Montana (listed in order from most to least area of production; data from Mint Industry Research Council). Mint was commercially produced on more than 23,000 ha in Washington and Oregon in 2012. Verticillium wilt, caused by *Verticillium dahliae*, is the most serious disease of cultivated peppermint and Scotch spearmint worldwide. Native spearmint is highly resistant to Verticillium wilt but susceptible to rust caused by *Puccinia menthae*. Rust ranks second in importance for diseases on peppermint and Scotch spearmint and first on native spearmint (36).

Genetic resistance to disease has protected plants from pathogens throughout evolutionary time and, today, it is one of the most practical and effective tactics for controlling plant diseases (8,9,45). Disease resistance is an active process in which the host opposes, completely or to some degree, the effect of a pathogen (26). Disease resistance in plants may differ in type and degree, and several terms have been used to describe different kinds of resistance (9,26). Classification is based on signs of the pathogen and symptoms of the disease and the rate at which they appear on plants in the host populations (26).

Qualitative or race-specific resistance to rust has been identified in mint (38,43). Consequently, a high degree of physiologic specialization has been found within collections of *P. menthae* on mint hosts, suggesting variation for virulence in the pathogen and resistance in host species. A number of races of *P. menthae* have been identified from mint species in various mint regions of the world (5,6,11,13,22,38). Because of the variation for virulence and meiosis occurring annually in the population of the autoecious rust,

race-specific resistance for rust has not endured in mint cultivars grown commercially. All commercial mint (*Mentha* spp.) cultivars are susceptible to various races of *P. menthae* (22,43).

Partial resistance refers to the development of some pathogen signs or disease symptoms (other than hypersensitive reactions) on the host (2,26,47). Differences in severity of infection can be quantified and a continuum can often be observed in plant populations with partial resistance from extremely susceptible to various levels of resistance (or decreased susceptibility) (4,20,47). Partial resistance exists in a wide variety of host-pathogen combinations (1,4,12,16,28,33–35,39,47). It is characterized by one or more components that may include an extended length in latent period and reductions in lesion size, infection efficiency, spore production per unit of infection, and duration of sporulation (21,29,32,39). Components of partial resistance act cumulatively to reduce the rate of disease development in the field (2,9,15). The term “slow-rusting” has been used to describe partial resistance to rust in which the rate of disease increase is reduced.

Even though plants may become infected, yields of small grains and other hosts have been maintained with partial resistance when infected with rust (27,30,32). Partial resistance is considered a durable type of resistance in that it has remained effective during prolonged and widespread use in environments favorable for disease (15,16,23,47,49). Quantitative or partial resistance has not been recognized in mint infected with rust.

Rust does not generally occur on peppermint in south-central Washington, likely because of high summer temperatures (17); however, rust severity on Scotch and native spearmint can be high and varies among fields and years (48). Isolates of *P. menthae* from native spearmint do not infect peppermint and isolates from peppermint do not infect native spearmint (5,36). Isolates from both native spearmint and peppermint infect Scotch spearmint but isolates from the former are more aggressive on Scotch spearmint (22). Severe rust infection destroys photosynthetic tissue and oil glands and causes defoliation of leaves, which contain the oil glands. Mint is harvested early when rust is severe to avoid leaf defoliation, resulting in a loss in yield (48). Up to four applications of fungicides for rust management are typically made on Scotch and native spearmint per growing season in south-central Washington. Aecia and initial inoculum can be reduced by propane flaming or contact herbicide directed to the soil surface at the time of shoot emergence in early spring (18). Native spearmint can be and often

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is grown on *Verticillium*-wilt-infested soils (25) but needs to be managed for rust (46,48). Scotch and native spearmint cultivars with partial resistant would reduce a dependence on fungicides and improve rust management on mint. However, conventional breeding practices are not possible because commercial mint plants are sterile (37).

Teliospores which can be produced abundantly in the fall on native spearmint are the overwintering stage for *P. menthae* (17,48). In south-central Washington State, infection of native spearmint from basidiospores occurs in the field between October and March. Pycnia occur between October and May and aecia are most abundant between April and June. Aecia arise from primordial infections formed on the same thalli from which pycnia develop. The mycelia invade the growing points of active shoots and establish localized systemic infections in native spearmint (38,48) but remain localized in peppermint (48). Uredinia are observed between June and October.

In an effort to identify sources of *Verticillium* wilt resistance, mutant peppermint, Scotch spearmint, and native spearmint lines induced by irradiation were evaluated for resistance to *V. dahliae* in inoculation tests in the greenhouse (25) and field (24). Mutant lines originated from D. D. Roberts (Plant Technologies, Inc.), who directed an induced mutation breeding program sponsored by the Mint Industry Research Council (MIRC), an international organization of mint growers, buyers, and manufacturers. Mutant lines, in inoculation tests, varied significantly for *Verticillium* wilt resistance, and peppermint lines were selected with improved resistance to *V. dahliae* (24,25). Two mutant Scotch spearmint and six mutant native spearmint lines were evaluated for resistance to *V. dahliae* (25). The question arises of whether any of the mutant native spearmint and Scotch spearmint clones varied for resistance to *P. menthae*. The purpose of this study was to evaluate the irradiated Scotch spearmint and native spearmint lines for resistance to *P. menthae*.

Materials and Methods

Six mutant native spearmint lines and five mutant Scotch spearmint lines were selected that were received from D. D. Roberts in 1994. Lines were derived from γ -irradiated rhizomes with cobalt 60 at 8,000 to 20,000 radiation absorbed dosage units using procedures previously described (19,36,37). The six native spearmint lines and two of the five Scotch spearmint lines had been previously evaluated for resistance to *V. dahliae* (25). Lines were grown in pots and maintained in the greenhouse. Rooted cuttings of mutant lines, Scotch spearmint, and native spearmint were produced from source plants in the greenhouse.

Greenhouse. Urediniospores were increased on infected Scotch spearmint in the greenhouse and were collected the day of inoculation with a minicyclone spore collector. The abaxial surfaces (underside) of fully expanded plant leaves of rooted cutting at least 12 weeks of age were inoculated with an oil suspension (Soltrol 170; Phillips Chemical Co.) of approximately 2 million urediniospores/ml. Urediniospores were suspended in a size 00 gelatin capsule and were applied with an atomizer (7). Plants were placed in a mist chamber, where a fine mist was provided for 1 min every 15 min for 24 h at 19 to 22°C. Plants were then returned to the greenhouse. Two leaves each of 11 lines and cultivars were inoculated. The lines and cultivars were arranged in a randomized complete block design with four replicates, with two leaves per plant as subsamples. The experiment was done in spring 1998 and repeated in spring 1999.

Natural light supplemented with sodium lamps (approximately 210 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic active radiation) provided a photoperiod of at least 15 h. Temperatures were 20 to 24°C during the day and 17 to 20°C at night.

After inoculation, uredinia were counted when the red-orange of a pustule was visible to the unaided eye on two leaves per plant every day for 12 days and then on alternate days for 8 more days. The probit model provided a good fit of the occurrence of uredinia on mint leaves as seen from scatter plots and high coefficients of

determination (usually $R^2 > 0.90$) from regression analysis. Latent period then was taken as the number of days from inoculation until 50% of uredinia appeared and was calculated from linear regression of probit percent uredinia that appeared on days after inoculation, as previously described (44).

Field nursery. Rooted cuttings, approximately 10 weeks of age, with well-developed root systems were transplanted in the field at the Washington State University Horticultural Farm on a Palouse silt loam near Pullman. Lines were grown in hill plots (plant cluster originating from a rooted cutting) on 1-m row centers arranged as randomized complete blocks, replicated four times. Three native spearmint lines, four Scotch spearmint lines, and native spearmint were planted in early June 1998. Three additional native spearmint lines, one Scotch spearmint line, and Scotch spearmint were planted in early June 1999. In total, there were 13 entries, including native spearmint and Scotch spearmint, which were used as standards. Sprinkler irrigation at night was used to irrigate plants and to encourage rust development. Plots were irrigated only when plants required water for growth.

Hill plots of native spearmint were transplanted as a border around the hill plots and were inoculated 2 weeks after transplanting in 1998 with an oil suspension of urediniospores of approximately 2 million spores/ml. Uredinia on the border hills then served as an initial source of inoculum in 1998. Telia developed on foliage toward the end of the growing season and foliage with telia was left in the field to overwinter at the end of the growing seasons in 1998 through 2000. Subsequent epidemics originated from naturally occurring inoculum.

Rust severity was estimated as the proportion of surface area of each plant covered with uredinia by using Peterson's scale for cereal rust (41). Estimations were made three times at 11- to 15-day intervals in August and early September 1998 and 1999 and in June 2000. Foliage was cut at flowering in July 2000. The area under the disease progress curve (AUDPC) was calculated for each plant hill to indicate the level of resistance to urediniospore infection (29).

Aecia developed on plants from naturally occurring telia in plots in April and early May 1999, 2000, and 2001. Shoots with aecia per hill from overwintering telia were counted in mid-May 2000 and 2001.

Data analysis. Data for length of latent period, number of uredinia per leaf, AUDPC, and incidence of shoots with aecia were analyzed by analysis of variance for a randomized complete block design with four blocks using the GLM procedure in SAS programs (version 9.1; SAS Institute, Inc.). Data for length of latent period were combined because the two trials did not differ and there was not a significant ($P > 0.05$) cultivar-trial interaction. Data for number of uredinia per leaf were transformed to the natural log and the two trials were combined because there was not a significant ($P > 0.05$) cultivar-trial interaction. Data for length of latent period, number of uredia per leaf, AUDPC in 1998, 1999, and 2000, and mean incidence of shoots with aecia in 2000 and 2001 were compared using Spearman's rank correlations with the PROC CORR procedure in SAS.

Results

Greenhouse. Length of latent period varied significantly ($P < 0.05$) among clones and standard cultivars in both inoculation tests, and it was significantly longer ($P < 0.05$) for native spearmint line N87-1 than for the other mutant lines, native spearmint, and Scotch spearmint. Length of latent period was significantly longer for lines N83-5, N83-22, and N83-23 than for native spearmint and Scotch spearmint. The latent period was also significantly longer for lines N83-21 and N83-6 than for Scotch spearmint (Table 1).

Number of uredinia per leaf varied significantly ($P < 0.05$) among clones and standard cultivars in both inoculation tests. Number of uredinia per leaf was significantly ($P < 0.05$) fewer for N87-1 than 9 of the other 11 lines and for native spearmint and Scotch spearmint (Table 1).

Field nursery. AUDPC varied significantly ($P < 0.05$) among clones and standard cultivars each of the 3 years. Line N87-1 had

the lowest AUDPC values of all lines and standard cultivars in 1998, 1999, and 2000 (Table 1). The AUDPC was significantly lower for N87-1 than native spearmint in 1998 and than native spearmint and Scotch spearmint in 2000. Six lines had significantly lower AUDPC values than native spearmint in 2000 (Table 1). The AUDPC was significantly greater for S90-12 than for Scotch spearmint in 1999.

Mean incidence of shoots with aecia was 0 to 20.3 in 2000 and 0 to 22.5 in 2001. Lines S90-9 and S90-6 had the lowest, N83-6 had the highest, and N87-1 the second highest incidence of shoots with aecia both years (Table 1). Native spearmint had 15 and 16% incidence in 2000 and 2001, respectively, which was greater than the median of 4.3 in 2000 and 9.4 in 2001. The incidence of shoots with aecia for Scotch spearmint was relatively low in 2000 but above the medium in 2001.

The AUDPC in 1998 was not significantly correlated with AUDPC in 1999 and 2000; however, AUDPC in 1999 and 2000 were highly correlated (Table 2). Latent period was significantly ($P < 0.01$) and negatively correlated with AUDPC in 1999 and 2000 (Table 2). Mean incidence of shoots with aecia was not correlated with AUDPC for 3 years or with latent period after urediniospore infection.

Discussion

Slow-rusting resistance to the uredinia stage of *P. menthae* was selected from native spearmint plants exposed to cobalt 60 γ -irradiation. Uredinia developed on resistant plants with slow-rusting resistance but at a slower rate than on susceptible genotypes, as is shown by lower AUDPC values. Line N87-1 had significantly lower AUDPC values than native spearmint 2 of 3 years in the field and a longer latent period when determined with inoculation tests in the greenhouse. Moderate levels of resistance to *V. dahliae* were

also selected in peppermint and Scotch spearmint lines that were treated with γ -irradiation in previous studies (24,25). The mutant native lines maintained their resistance to *V. dahliae* in inoculation tests, as was shown in a previous study (25).

Genetic variation is needed in plant populations to select for disease resistance. Variation for rust interactions in natural populations of native spearmint is difficult to assess because plants are self sterile and vegetatively propagated. In contrast, variation for rust resistance was expected and readily identified in open-pollinated and clonal hybrid populations of asparagus from heterozygous parents (20). A high degree of partial resistance as identified in line N87-1 was not fully expected to be induced by γ -irradiation of native spearmint because slow-rusting is generally associated with quantitative inheritance involving several components of resistance (9,28,39,49). However, slow-rusting resistance to *P. polysora* in a maize line appeared to be dominant and simply inherited (10). The genetic components involved with the slow-rusting resistance in native spearmint line N87-1 is not known but it is not likely to involve many genes.

Aecia give rise to an early source of spring inoculum. However, a satisfactory level of slow-rusting resistance to the uredinal stage overcame inoculum loads supplied by the aecia in this study. This was also observed in asparagus infected with *P. asparagi*, which is also autoecious. Emphasis should be placed on resistance to urediniospore over resistance to basidiospore infection for rust management in mint because of the potential of multiple infection cycles by urediniospores during a relatively long growing season.

Line N87-1 was resistant to urediniospore infection and susceptible to basidiospore infection. The number of shoots with aecia per hill, resulting from basidiospore infection and subsequent development of pycnia, was relatively high for line N87-1. Native spearmint was susceptible to infection by both urediniospores and

Table 1. Latent period and number of uredinia per leaf in the greenhouse and area under the disease progress curve (AUDPC) and number of stems with aecia of mint lines in the field infected with *Puccinia menthae*^u

Line ^v	Latent period (days)	Uredinia/leaf (number) ^w	Uredinia AUDPC			Incidence with aecia (%)	
			1998 ^x	1999	2000	2000	2001
N87-1	11.6 a	53 d	33 a	0 a	31 a	16.5 a	21.8 ab
N83-5	10.8 b	96 abc	119 bcd	2 a	57 ab	11.0 ab	12.5 abc
N83-22	10.8 b	101 ab	166 d	1 a	48 ab	3.0 bc	8.0 abc
N83-23	10.8 b	100 ab	—	3 a	67 abc	4.3 bc	6.3 abc
N83-21	10.5 bc	96 ab	—	6 ab	68 abc	15.5 a	10.8 abc
N83-6	10.5 bc	89 abc	—	35 abc	184 de	20.3 a	22.5 a
S90-9	10.3 cd	126 a	72 ab	6 ab	113 abcd	0.0 c	5.0 bc
Native	10.3 cd	106 ab	175 d	20 abc	218 e	15.0 a	16.0 abc
S90-12	10.2 cd	67 bcd	146 cd	68 c	154 de	0.5 c	0.0 c
S90-13	10.1 cd	45 d	133 cd	12 abc	191 de	0.5 c	2.5 c
Scotch	10.0 d	146 a	—	10 ab	128 bcd	2.5 bc	15.7 abc
S90-6 ^y	10.0 d	115 ab	—	—	—	—	—
S90-7 ^z	—	—	102 bc	63 bc	—	4.3 bc	6.7 abc

^u Values with the same letter are not significantly different at $P = 0.05$ according to least significant difference. Latent period and uredinia per leaf were determined in the greenhouse, and uredinia area under the disease progress curve (AUDPC) and incidence of infected shoots with aecia were determined in the field.

^v N and S indicated native and Scotch spearmint lines, respectively.

^w Data transformed to natural log for analysis, actual values presented.

^x Symbol: — in column indicates missing data because lines were not planted until 1999.

^y Symbol: — in row indicates missing data because line S90-6 did not survive in the field.

^z Symbol: — in row indicates missing data because line did not survive 2000 summer season or in the greenhouse.

Table 2. Spearman's rank correlation coefficients and P values for relationships between latent period, area under the disease progress curve (AUDPC), and mean incidence of shoots with aecia of spearmint clones infected with *Puccinia menthae*

	Latent period	Uredinia/leaf	AUDPC 1998	AUDPC 1999	AUDPC 2000	Mean incidence ^z
Latent period	1.00	$r = -0.40, P = 0.198$	$r = -0.54, P = 0.215$	$r = -0.80, P = 0.003$	$r = -0.79, P = 0.004$	$r = 0.53, P = 0.094$
Uredinia/leaf	...	1.00	$r = 0.25, P = 0.589$	$r = 0.123, P = 0.719$	$r = 0.21, P = 0.537$	$r = 0.04, P = 0.916$
AUDPC 1998	...	...	1.00	$r = 0.36, P = 0.385$	$r = 0.57, P = 0.180$	$r = -0.17, P = 0.692$
AUDPC 1999	...	...	...	1.00	$r = 0.92, P < 0.001$	$r = -0.22, P = 0.490$
AUDPC 2000	...	...	...	...	1.00	$r = -0.12, P = 0.729$
Mean incidence ^z	...	...	...	...	...	1.00

^z Mean incidence of shoots with aecia in 2000 and 2001.

basidiospores. Resistance to urediniospore infection and susceptibility to basidiospore infection was also found in some asparagus cultivars infected with rust (21). With asparagus inoculated with rust, cultivars reacted similarly when infected with either aeciospores or urediniospores, and sometimes differently when infected with either urediniospores or basidiospores (21). Urediniospores are dikaryotic and basidiospores are haploid. Consequently, host resistance in both mint and asparagus to *Puccinia* spp. appears to depend on the type of infecting spore (21).

AUDPC in 1998 was not significantly correlated with AUDPC in 1999 and 2000, possibly because initial urediniospore inoculum was not uniform throughout the nursery. Border hills were artificially inoculated in 1998 but all inoculated plants did not become infected, which resulted in a non-uniform pattern of infected border hills. Inoculum in 1999 and 2000 resulted from overwintering teliospores and was more uniform throughout the nursery. AUDPC values were highly correlated between 1999 and 2000.

A relatively long latent period is an important factor in retarding rust epidemics in the field and is highly correlated with partial rust resistance (20,28,29,39). It is a good indicator and an important component of slow rusting or partial resistance in several host–rust relationships (20,28,34). A difference in latent period of a day has been associated with substantially reduced rust development over several infection cycles (20,21,28). Certainly, the cumulative effect of several components of slow-rusting resistance is important in slowing the rate of rust development during epidemics. Line N87-1 had a significantly longer latent period than native spearmint when tested in the greenhouse.

Overwintering teliospores on mint debris (17) were the source of rust epidemics in nurseries in 1999, 2000, and 2001. Abundant pycnia and aecia developed on mint stems in early spring 1999 to 2001. This allowed the mint lines to be tested against a relatively high level of genetic diversity of the pathogen. In addition, overhead sprinkler irrigation was applied at night to favor rust development. Durable resistance to crown rust in oat was selected in irrigated nurseries in Minnesota, where the genetic diversity of *P. coronata* was increased by allowing the rust to overwinter on infected oat straw. Pycnia and aecia then developed in the spring on hawthorn, the alternate host which was maintained adjacent to oat lines (16). Thus, enhancing the diversity of the pathogen would help ensure selection for partial resistance.

The production and evaluation of rust-resistant native spearmint involves more than subjecting plant material to locally prevalent races for a few years (38). Lines should be exposed to a diversity of pathogen strains in many environments. Oil yield and quality also need to be equal to or better than the native spearmint standard. Isolate specificity in the response of partially resistant plant genotypes has been observed in controlled inoculation experiments in other pathosystems, and aggressive pathotypes may adapt to partially resistant cultivars (3,14,40). Furthermore, environmental factors such as relatively high inoculum levels and disease-favorable weather may elevate disease severity on partially resistant cultivars compared with less-favorable conditions (31,42,47). However, partially resistant cultivars have had less disease throughout epidemics than susceptible cultivars (15,16,23,47). Nevertheless, partial resistance must to be managed in agroecosystems to ensure stability (8). Reducing initial inoculum, enhancing crop diversity, and cultural practices that reduce disease rates are potential management tactics that could be coupled with partially resistant cultivars.

Slow-rusting resistance in native spearmint can be expected to be effective over many years and provide adequate protection when incorporated into an integrated disease management system employing good irrigation practices and destruction of early spring aecial inoculum. Slow-rusting resistance in small grains and other crops has been stable over a number of decades (16,23,49). Rust continues to be problematic on native spearmint in south-central Washington, and cultivars with slow-rusting resistance would be beneficial for disease management.

The mutant native lines N87-1 and N83-6 were evaluated in field plots for oil yield and quality in 1995 to 1998 and N83-22 in 1999

to 2002 in Washington, Oregon, and Indiana. Verticillium wilt resistance remained highly effective in the mutant lines. Additional data were not obtained for rust because the disease did not occur in the experimental plots. Oil quality of the mutant lines was similar to that of native spearmint but, disappointingly, oil yields were relatively low the third and fourth year of production (MIRC Research Reports, 1995 to 2002). Consequently, the mutant lines were not further pursued for consideration as commercial cultivars. However, an important finding in this study was that slow-rusting resistance was derived from induced mutation of vegetatively propagated native spearmint. In addition, resistance to *V. dahliae* and oil quality were maintained through the irradiation treatment. Obtaining disease resistance to one or more important pathogens and desirable agronomic traits in future cultivars is a daunting challenge for any crop. Induced mutation techniques may be valuable in the future in inducing partial resistance in crop species where high levels of partial resistance are not found in natural populations or where traditional breeding techniques are difficult to use because of plant sterility, such as is the case with mint.

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