Resistance Against Basil Downy Mildew in *Ocimum* Species

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ABSTRACT

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Downy mildew, caused by the oomycete *Peronospora belbahrii*, is a devastating disease of sweet basil. In this study, 113 accessions of *Ocimum* species (83 Plant Introduction entries and 30 commercial entries) were tested for resistance against downy mildew at the seedling stage in growth chambers, and during three seasons, in the field. Most entries belonging to *O. basilicum* were highly susceptible whereas most entries belonging to *O. americanum*, *O. kilimanascharicum*, *O. gratissimum*, *O. campechianum*, or *O. tenuiflorum*

were highly resistant at both the seedling stage and the field. Twenty-seven highly resistant individual plants were each crossed with the susceptible sweet basil 'Peri', and the F1 progeny plants were examined for disease resistance. The F1 plants of two crosses were highly resistant, F1 plants of 24 crosses were moderately resistant, and F1 plants of one cross were susceptible, suggesting full, partial, or no dominance of the resistance gene(s), respectively. These data confirm the feasibility of producing downy mildew-resistant cultivars of sweet basil by crossing with wild *Ocimum* species.

Additional keywords: herbs, hybrids, spices, wild basil.

Common sweet basil (*Ocimum basilicum*) is an economically important spice, extensively used for culinary purposes and as a source of essential oil and oleoresin for manufacturing perfumes and food flavors (Simon et al. 1990). The chemical composition of basil is an important source of antioxidants (Koroch et al. 2010) and antimicrobial agents (Elgayyar et al. 2001; Hussain et al. 2008) with a potential use in food preservation (Suppakul et al. 2003).

Basil includes more than 50 species of herbs and shrubs (Paton et al. 1999; Simon et al. 1990). The taxonomy of *O. basilicum* is complicated by existence of numerous botanical varieties, cultivars, and chemotypes that do not differ significantly in morphology (Simon et al. 1990). Interspecific hybridization and polyploidy occurs commonly within this genus (Harley and Heywood 1992) and creates taxonomic confusion in the understanding of the genetic relationships among the multitude number of *Ocimum* spp. (Paton and Putievsky 1996). Taxonomic issues in this genus based on morphology and chromosome number were recently reviewed based on molecular markers and nuclear DNA content (Aghaei et al. 2012; Carovic-Stanko et al. 2010; Vieira and Simon 2006). Basils also vary significantly in their morphology including growth habit, size, shape, texture, leaf orientation, and color of leaf, stem, and flower (Phippen and Simon 2000), resulting in a wide variety of ornamental cultivars (Simon et al. 1990).

The demand for fresh-market basil has grown in recent years due to increased consumer demand which has led to more intensive field and greenhouse production systems (Homa et al. 2014). Downy mildew caused by the oomycete *Peronospora belbahrii* is a limiting factor in basil production (Belbahri et al. 2005) and integrated management programs for basil diseases have been proposed (Garibaldi et al. 2007).

Downy mildew of basil was first described in Uganda in 1933 (Hansford 1933). In Israel, it was first reported in 2011 (Cohen et al. 2013b). The disease occurs in Europe (Garibaldi et al. 2005; Garibaldi et al. 2004a; Thines et al. 2009), South America (Ronco et al. 2009), the United States (Roberts et al. 2009), and Africa

(McLeod et al. 2006). No reports are available on the occurrence races or pathotypes of *P. belbahrii*, except for isolates resistant to the fungicide mefenoxam (Cohen et al. 2013b).

Basil downy mildew (BDM) develops during periods of moderate temperatures, high air humidity, and prolonged leaf wetness (Garibaldi et al. 2005, 2007). Frequently, infection is found immediately after seeding, suggesting that the pathogen can also be spread through contaminated seed (Farahani-Kofoet et al. 2012; Garibaldi et al. 2004b). *P. belbahrii* is disseminated by airborne spores produced at night under moist conditions. Spores infect leaf lamina with a single germ tube that penetrates into the epidermal cell walls and produces intercellular mycelium with haustoria in the mesophyll. Chlorotic lesions appear in leaves at 6 to 10 days postinoculation (dpi), depending on temperature, with 25°C being optimal. Sporulation takes place within 7 h at 100% relative humidity, in darkness only, with 18 to 20°C being optimal (Cohen et al. 2013a). Basil plants showing symptoms are unmarketable, including those with latent symptoms that deteriorate in storage.

Only a few fungicides are registered for control of the disease in Europe (Gilardi et al. 2013) and the United States (Homa et al. 2014). In the United States, mono- and dipotassium salts of phosphorous acid provided the best control, whereas moderate disease suppression was provided by mandipropamid, cyazofamid, and fluopicolide (Homa et al. 2014). In Israel, best control was achieved with mefenoxam, mandipropamid, dimethomorph, and azoxystrobin, while moderate control was seen with mono- or dipotassium salts of phosphorous acid (Y. Cohen, M. Vaknin, and Y. Ben-Naim, *unpublished data*). However, mefenoxam became ineffective due to the appearance of resistant isolates (Cohen et al. 2013b) and some isolates show reduced sensitivity to dimethomorph and mandipropamid (*unpublished data*).

Darkness is essential for *P. belbahrii* to sporulate on infected basil leaves. When exposed to light during the sporulation period the pathogen produces sporophores but fails to produce spores. Indeed, nocturnal illumination in net-houses, which suppress spore production, was recently reported to effectively control the disease (Cohen et al. 2013a).

One of the most effective measures for disease control is via genetic manipulation of the host, namely introgression of resistant genes. The objectives of this study were to expand on what others

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have reported on potential sources of resistance to BDM in some species of *Ocimum* (Farahani-Kofoet et al. 2014; Wyenandt et al. 2010) and explore additional sources of resistance genes against BDM among commercial and wild basil species. Pyne et al. (2014) developed a rapid screening approach to identify resistance to BDM at the cotyledon growth stage. Field evaluations of basil under high downy mildew pressure confirmed the applicability of their screening approach to identify resistance to basil downy mildew. We performed parallel screening for resistance in the field and growth chambers and found them highly correlative.

MATERIALS AND METHODS

Germplasm. Eighty wild and cultivated basil species (*Ocimum* spp.) were obtained from the U.S. Department of Agriculture-Agriculture Research Service Plant Introduction Station, Iowa State University, Ames, Iowa, and 33 sweet basil cultivars and ornamental basil lines were obtained from Richter's Herbs (Goodwood, Ontario, Canada), Hishitil (Petach Tikva, Israel), Flower Goddess (Beijing, China), Georgia vines, (Claxston, GA), and Frankonia Samen (Miltenberg, Germany). The origin of each entry is listed in Table 1. Leaf morphology as shown in Table 1 was assessed according to Wyenandt et al. (2010).

Plants. Seeds were sown in multicell trays (cell size 2.5 cm) filled with a potting mixture (peat: vermiculite, 1:1, vol/vol), two to three seeds per cell, and grown in the greenhouse. At the four-leaf stage, one set of plants was inoculated and another set was planted in the field in a net house covered with a 50 mesh insect-proof net. This procedure was repeated (in replicated trials) three times in 2014, in 2 to 3 months intervals.

Pathogen. Twenty-one isolates of *P. belbahrii* were collected from the major growing regions in Israel during December 2011 to October 2014. The isolates collected until late 2012 were sensitive to mefenoxam while those collected during 2013 to 2014 were mostly resistant to this fungicide (Cohen et al. 2013b). The mefenoxam-resistant isolate Knafo (collected in 2013 at Ein-Tamar, Southern Jordan Valley, Israel) was used in the experiments described below, unless stated otherwise. The isolates were maintained by repeated inoculation of sweet basil 'Peri' (Volcani Institute, Israel) at 20°C.

Inoculation and disease assessment in seedlings. To inoculate the four-leaf stage plants, fresh spores of *P. belbahrii* were collected from sporulating plants into cold distilled water, adjusted to 5,000 spores/ml, and sprayed onto the upper leaf surfaces of the test plants. Plants were placed in a dew chamber overnight at 18°C to ensure infection and thereafter at 25°C under continuous illumination (60 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for 6 days to ensure pathogen colonization. Plants were returned to the dew chamber at 7 dpi to enable sporulation of the pathogen on the inoculated plants. Sporulation intensity was visually estimated using an ordered categorical 0-to-3 scale, similar to Wyenandt et al. (2010) and Homa et al. (2014), in which 0 = no visible sporulation; 1 = scarce sporulation; 2 = moderate sporulation; and 3 = heavy sporulation.

Inoculation and disease assessment in the field. At 7 to 10 days after planting, when plants reached the six- to eight-leaf stage, they were spray-inoculated with *P. belbahrii*. Inoculation (5,000 spores/ml) was done at about 8 P.M. to ensure high humidity during infection. Starting at 1 week after inoculation, disease records were taken from the inoculated plants. Each plant was visually estimated for (i) incidence rating, the proportion of infected foliage; (ii) severity rating, the proportion of infected leaf area; and (iii) sporulation intensity. The three estimates were compiled visually using an ordered categorical 0-to-4 scale in which 0 = no visible symptoms; 0.1 to 0.9 = lesions occupy 10 to 90% of a leaf area; up to 5% of the leaves in a plant show symptoms but no sporulation is seen; 1 to 1.9 = about 6 to 25% of the leaves show symptoms, sporulation is scarce; 2 to 2.9 = about 26 to 50% of the

leaves show symptoms, sporulation is moderate; and 3 to 4 = about 51 to 100% of the leaves show symptoms, sporulation is heavy (Fig. 1).

Analysis of variance was calculated using the software JMP (SAS version 8). Means were compared using Turkey's honest significant difference test with $\alpha = 0.05$.

At the end of the first season, seeds were collected from a most resistant individual plant in each entry and used for the second field trial. During the second season, crosses were made between the most resistant individual plant in each entry and the susceptible sweet basil Peri. F1 plants (4 to 10 plants per entry) were grown in the field in the third season. The inoculation procedure performed in the first season was similarly repeated in the second and the third seasons.

RESULTS

Table 1 provides data on the 113 entries of *Ocimum* species that were grown in the field during April to May 2014, including leaf morphology, uniformity of plant morphology, and response to infection with *P. belbahrii* (BDM, basil downy mildew). The total number of plants tested per entry ranged between 7 and 20. Leaves showed various morphologies (Wyenandt et al. 2010): fold up (UP), fold down (D), flat (FL), flat-down (FL-D), or flat-up (FL-UP). Most entries were uniform in leaf shape and plant morphology except those indicated with a star. A clear difference in response to BDM was observed between the four groups of entries (A to D). All entries (except entry number 70) in group A (*O. americanum* and *O. kilimandscharicum*) were highly resistant. In group B (*O. tenuiflorum*, *O. gratissimum*, and *O. campechianum*), 11 entries were highly resistant and three entries were moderately resistant. In group C (*O. basilicum* and *Ocimum* spp.), eight entries were highly resistant and eight entries were moderately resistant. All 65 entries of group D (*O. basilicum*) were susceptible. In this group, all entries were uniform in response to BDM except 13, 37, and 58, which were susceptible except a few plants that were resistant (indicated with a double star).

Figure 2A provides a graphic illustration of the above results. A clear distinction in disease intensity is seen between the four groups. Mean disease intensity for the entries in groups A, B, C, and D was 0.33, 0.45, 0.96, and 3.73, respectively. Disease intensity was recorded three times during the epidemic (27 days). Values of the final score are presented in Table 1 and illustrated in Figure 2A.

The mean values (7 to 40 plants per entry) of disease intensity in four-leaf plants at 7 days after artificial inoculation in growth

Fig. 1. Symptoms on upper leaf surfaces and sporulation on lower leaf surfaces of downy mildew in basil leaves caused *Peronospora belbahrii*. Figures on top indicate the level of disease intensity on a 0 to 4 visual scale. This scale was used to assess the susceptibility/resistance to downy mildew of 113 accessions of *Ocimum* species in the field.

chambers are shown in Figure 2B. Several entries in groups A, B, and C were highly resistant to the disease, while most entries in group D were susceptible.

To verify that resistance holds against other isolates of the pathogen, 12 accessions were inoculated at the four-leaf stage with each of 11 isolates of *P. belbahrii*, four sensitive and seven resistant to mefenoxam, representing the various growing regions in the country. Accessions PI 500944, PI 500945, PI 500950, PI 500951,

PI 414201, and PI 652059 were highly resistant (disease intensity 0 to 0.5). PI 17297 and PI 172998 were resistant (disease intensity 0.5 to 0.9), Magic White and PI 652054 were moderately resistant (disease intensity 1.1 to 2.2), and the commercial cultivars Peri and Genovese were highly susceptible (disease intensity 3.5 to 4) to all isolates.

The disease intensity values obtained in seedlings in growth chambers stand in good correlation ($R = 0.73$ for all 113 entries)

TABLE 1. Response to downy mildew of 113 entries of *Ocimum* accessions under field conditions

Entry	PI/species/cultivar	Botanical name	Origin/supplier	Leaf shape ^x	Number of plants ^y			Score ^z
					Total	R (≤0.9)	S (≥1)	
Group A: <i>O. americanum</i> and <i>O. kilimandscharicum</i>								
3	PI 500945	<i>O. americanum</i> var. <i>americanum</i>	Zambia	D	9	9	0	0.00 d
67	PI 500942	<i>O. americanum</i> var. <i>pilosum</i>	Zambia	FL-D	9	9	0	0.00 d
69	PI 500944	<i>O. americanum</i> var. <i>pilosum</i>	Zambia	FL-UP*	9	9	0	0.00 d
71	PI 500948	<i>O. americanum</i> var. <i>pilosum</i>	Zambia	FL	9	9	0	0.00 d
73	PI 500950	<i>O. americanum</i> var. <i>pilosum</i>	Zambia	FL-UP*	9	9	0	0.00 d
76	PI 500954	<i>O. americanum</i> var. <i>pilosum</i>	Zambia	UP	9	9	0	0.00 d
77	PI 652052	<i>O. kilimandscharicum</i>	Zambia	F*	9	9	0	0.00 d
74	PI 500951	<i>O. americanum</i> var. <i>pilosum</i>	Zambia	D	9	9	0	0.08 c
2	PI 254352	<i>O. americanum</i> var. <i>americanum</i>	Iraq	FL	9	9	0	0.10 c
72	PI 500949	<i>O. americanum</i> var. <i>pilosum</i>	Zambia	FL-UP	9	9	0	0.13 c
54	PI 652053	<i>O. americanum</i> var. <i>americanum</i>	USA, Maryland	FL	15	15	0	0.17 c
75	PI 500953	<i>O. americanum</i> var. <i>pilosum</i>	Zambia	D	9	7	2	0.38 bc
1	PI 253158	<i>O. americanum</i> var. <i>americanum</i>	Iran	FL	9	9	0	0.43 bc
68	PI 500943	<i>O. americanum</i> var. <i>pilosum</i>	Zambia	FL-D	9	7	2	0.46 bc
6	PI 652062	<i>O. americanum</i> var. <i>americanum</i>	Tanzania	FL	9	9	0	0.50 bc
4	PI 652058	<i>O. americanum</i> var. <i>americanum</i>	Togo	FL	9	6	3	0.65 bc
5	PI 652060	<i>O. americanum</i> var. <i>americanum</i>	Pakistan	FL	9	5	4	0.96 b
70	PI 500947	<i>O. americanum</i> var. <i>pilosum</i>	Zambia	FL	9	0	9	2.03 a
Group B: <i>O. tenuiflorum</i> , <i>O. gratissimum</i> , and <i>O. campechianum</i>								
98	<i>O. tenuiflorum</i> -1	<i>O. tenuiflorum</i>	Georgia vines, USA	D	20	20	0	0.00 e
99	<i>O. gratissimum</i> -1	<i>O. gratissimum</i>	Georgia vines, USA	FL	20	20	0	0.00 e
78	PI 652066	<i>O. campechianum</i>	Brazil	FL	9	9	0	0.00 e
79	PI 652067	<i>O. gratissimum</i>	Brazil	FL	9	9	0	0.00 e
80	PI 211715	<i>O. gratissimum</i> var. <i>gratissimum</i>	Taiwan	FL	9	9	0	0.00 e
81	PI 500952	<i>O. gratissimum</i> var. <i>gratissimum</i>	Zambia	FL	9	9	0	0.00 e
82	PI 652055	<i>O. gratissimum</i> var. <i>macrophyllum</i>	Sri Lanka	FL	9	9	0	0.00 e
64	PI 414205	<i>O. tenuiflorum</i>	USA, Maryland	FL	15	15	0	0.37 de
61	PI 414202	<i>O. tenuiflorum</i>	USA, Maryland	FL	15	13	2	0.51 de
60	PI 414201	<i>O. tenuiflorum</i>	USA, Maryland	FL	15	10	5	0.60 cd
66	PI 652059	<i>O. tenuiflorum</i>	Maldives	FL	15	8	7	0.79 bcd
62	PI 414203	<i>O. tenuiflorum</i>	USA, Maryland	FL	15	6	9	1.09 bc
65	PI 652056	<i>O. tenuiflorum</i>	Denmark	FL	15	2	13	1.18 ab
63	PI 414204	<i>O. tenuiflorum</i>	USA, Maryland	FL	15	0	15	1.73 a
Group C: <i>O. basilicum</i> var. and <i>Ocimum</i> spp.								
107	Spice basil	<i>Ocimum</i> spp.	Richter's, Canada	FL	10	9	1	0.15 e
22	PI 211586	<i>O. basilicum</i> var. <i>thyrsiflorum</i>	Afghanistan	FL, UP	15	12	3	0.20 de
113	Blue Spice	<i>Ocimum</i> spp.	Richter's, Canada	FL	7	7	0	0.30 bcde
12	PI 172998	<i>O. basilicum</i> var. <i>anisatum</i>	Turkey	FL	15	15	0	0.38 cde
11	PI 172997	<i>O. basilicum</i> var. <i>anisatum</i>	Turkey	FL	20	20	0	0.50 bcde
10	PI 172996	<i>O. basilicum</i> var. <i>anisatum</i>	Turkey	FL*	20	20	0	0.57 bcde
94	Magic Mountain F1	<i>O. kilimandscharicum</i> × <i>O. basilicum</i>	Hishtil, Israel	FL-D	20	15	5	0.58 bcde
95	Magic White F1	<i>O. kilimandscharicum</i> × <i>O. basilicum</i>	Hishtil, Israel	FL-D	20	15	5	0.58 bcde
86	Wild Color F1	<i>O. basilicum</i>	Hishtil, Israel	FL	20	0	20	1.30 abcd
26	PI 296391	<i>O. basilicum</i> var. <i>citrodorum</i>	Iran	FL	15	7	8	1.30 abcd
8	PI 170579	<i>O. basilicum</i> var. <i>minimum</i>	Turkey	UP	20	0	20	1.34 abc
14	PI 174284	<i>O. basilicum</i> var. <i>anisatum</i>	Turkey	FL*	12	7	5	1.38 ab
55	PI 652054	<i>O. basilicum</i> var. <i>citrodorum</i> 'Mrs. Burns'	USA, New Mexico	FL-D	15	0	15	1.47 ab
23	PI 253157	<i>O. basilicum</i> var. <i>citrodorum</i>	Iran	FL-D	16	6	10	1.73 a
105	Lemon basil	<i>O. basilicum</i> var. <i>citrodorum</i>	Richter's, Canada	FL-D	9	1	9	1.79 a
84	Ajaka F1	<i>O. basilicum</i>	Hishtil, Israel	UP	20	0	20	1.81 a
Group D: <i>O. basilicum</i>								
102	Sweet Danni	<i>O. × Citrodonum</i>	Richter's, Canada	FL-D	12	0	12	2.15 c
83	PI 500946	<i>Ocimum</i> spp.	Zambia	F*	9	0	9	2.28 c
37	PI 368697	<i>O. basilicum</i>	Macedonia	FL**	14	1	13	2.33 c

(continued on next page)

^x Leaf shape indicates the general architecture of basil leaves: FL, flat shaped leaves; U, leaves with upward flaring margins; and D, leaves with downward flaring margins. * indicates lack of uniformity of plant morphology in the accession. ** indicates lack of uniformity of plant resistance in the accession.

^y Response to disease was classified into R (resistant, disease intensity equal or smaller than 0.9 on a 0 to 4 scale) and S (moderately resistant or susceptible, disease intensity equal or larger than 1.0).

^z Scores (mean) followed by the same letter are not significantly different according to least significant difference test at $P \leq 0.05$.

with the disease intensity values obtained in the field at 27 dpi. Twelve entries were resistant in growth chamber assays but responded susceptible in the field ($R = 0.31$) and six entries were susceptible in growth chamber assays while responding resistant in the field ($R = 0.55$). All other 95 entries were either resistant or susceptible in both the seedling stage and the field ($R = 0.83$).

At the end of the first season in the field (May 2014), seeds were collected from a single, most resistant plant of 40 entries (Table 2) and retested for BDM resistance under field conditions during June

to July 2014 (second consecutive season). Seeds were collected from a single, most resistant plant at the end the second season in July 2014 and retested in a third consecutive season for BDM resistance under field conditions during August to September 2014. From group D, eight entries were selected for the third retesting trial: Sweet Danni, which was reported resistant (Wyenandt et al. 2010), three highly resistant individuals from the segregating entries 13, 37, and 58, and four highly susceptible ones as controls.

TABLE 1. (continued from previous page)

Entry	PI/species/cultivar	Botanical name	Origin/supplier	Leaf shape ^x	Number of plants ^y			Score ^z
					Total	R (≤ 0.9)	S (≥ 1)	
9	PI 170581	<i>O. basilicum</i> var. <i>minimum</i>	Turkey	UP*	20	0	20	2.55 bc
56	PI 652061	<i>O. basilicum</i>	India	FL	14	0	14	2.67 bc
20	PI 197442	<i>O. basilicum</i>	Ethiopia	FL	15	0	15	2.83 bc
13	PI 173746	<i>O. basilicum</i>	Turkey	FL-D**	16	0	16	2.95 bc
109	Rubin	<i>O. basilicum</i>	Richter's, Canada	D	10	0	10	3.15 b
104	Bush basil	<i>O. basilicum</i> var. <i>minimum</i>	Richter's, Canada	UP	10	0	10	3.20 b
110	Globette	<i>O. basilicum</i>	Richter's, Canada	F	10	0	10	3.20 b
106	Queentte Thai	<i>O. basilicum</i>	Richter's, Canada	UP	12	0	12	3.45 b
58	PI 652070	<i>O. basilicum</i> 'Sweet basil'	USA, Pennsylvania	D**	15	1	14	3.46 b
21	PI 207498	<i>O. basilicum</i>	Afghanistan	FL	15	0	15	3.50 b
50	PI 414199	<i>O. basilicum</i>	USA, Maryland	D*	16	0	16	3.50 b
108	Spicy Globe	<i>O. basilicum</i> var. <i>minimum</i>	Richter's, Canada	UP	14	0	14	3.51 b
103	Mintte basil	<i>O. basilicum</i> var. <i>minimum</i>	Richter's, Canada	UP	10	0	10	3.67 ab
111	Corsican basil	<i>O. basilicum</i>	Richter's, Canada	D	15	0	15	3.71 ab
112	Gecofure basil	<i>O. basilicum</i> 'Genovese'	Richter's, Canada	D	12	0	12	3.73 ab
44	PI 414193	<i>O. basilicum</i>	USA, Maryland	UP*	20	0	20	3.74 ab
93	Wild Magic F1	<i>O. basilicum</i>	Hishtil, Israel	D	20	0	20	3.75 ab
91	Dark Lady F1	<i>O. basilicum</i>	Hishtil, Israel	D	20	0	20	3.80 ab
97	Sweet basil	<i>O. basilicum</i> 'Sweet basil'	F. Goddess, China	D	20	0	20	3.81 ab
25	PI 296390	<i>O. basilicum</i> var. <i>thyrsiflorum</i>	Iran	FL	16	0	16	3.83 ab
88	Habana F1	<i>O. basilicum</i>	Hishtil, Israel	D	20	0	20	3.88 ab
89	Red Ball F1	<i>O. basilicum</i>	Hishtil, Israel	D	20	0	20	3.88 ab
36	PI 368695	<i>O. basilicum</i>	Macedonia	UP*	18	0	18	3.89 ab
42	PI 379413	<i>O. basilicum</i>	Macedonia	D	20	0	20	3.90 a
34	PI 358471	<i>O. basilicum</i>	Macedonia	UP	18	0	18	3.94 a
35	PI 358472	<i>O. basilicum</i>	Macedonia	D	13	0	13	3.94 a
100	Peri	<i>O. basilicum</i> Sweet basil 'Peri'	Hishtil, Israel	D	20	0	20	3.95 a
17	PI 176646	<i>O. basilicum</i>	Turkey	UP	18	0	18	3.95 a
7	PI 170578	<i>O. basilicum</i> var. <i>minimum</i>	Turkey	UP	20	0	20	4.00 a
15	PI 174285	<i>O. basilicum</i> var. <i>purpurascens</i>	Turkey	D*	15	0	15	4.00 a
16	PI 175793	<i>O. basilicum</i>	Turkey	FL	20	0	20	4.00 a
18	PI 182246	<i>O. basilicum</i> var. <i>purpurascens</i>	Turkey	D*	14	0	14	4.00 a
19	PI 190100	<i>O. basilicum</i>	Iran	UP	15	0	15	4.00 a
24	PI 263870	<i>O. basilicum</i>	Greece	FL	15	0	15	4.00 a
27	PI 358463	<i>O. basilicum</i>	Macedonia	FL	16	0	16	4.00 a
28	PI 358464	<i>O. basilicum</i> var. <i>thyrsiflorum</i>	Serbia	FL-UP	15	0	15	4.00 a
29	PI 358465	<i>O. basilicum</i>	Macedonia	FL-UP	12	0	12	4.00 a
30	PI 358466	<i>O. basilicum</i>	Serbia	D	15	0	15	4.00 a
31	PI 358467	<i>O. basilicum</i>	Macedonia	UP	15	0	15	4.00 a
32	PI 358468	<i>O. basilicum</i>	Macedonia	UP	16	0	16	4.00 a
33	PI 358469	<i>O. basilicum</i>	Macedonia	UP*	18	0	18	4.00 a
38	PI 368698	<i>O. basilicum</i>	Macedonia	FL-D	15	0	15	4.00 a
39	PI 368699	<i>O. basilicum</i>	Macedonia	FL-D	15	0	15	4.00 a
40	PI 368700	<i>O. basilicum</i>	Macedonia	UP*	13	0	13	4.00 a
41	PI 379412	<i>O. basilicum</i>	Macedonia	D	15	0	15	4.00 a
43	PI 379414	<i>O. basilicum</i>	Macedonia	D	20	0	20	4.00 a
45	PI 414194	<i>O. basilicum</i>	USA, Maryland	FL*	20	0	20	4.00 a
46	PI 414195	<i>O. basilicum</i>	USA, Maryland	UP	15	0	15	4.00 a
47	PI 414196	<i>O. basilicum</i>	USA, Maryland	UP	15	0	15	4.00 a
48	PI 414197	<i>O. basilicum</i>	USA, Maryland	UP/D*	13	0	13	4.00 a
49	PI 414198	<i>O. basilicum</i>	USA, Maryland	UP*	14	0	14	4.00 a
51	PI 414200	<i>O. basilicum</i>	USA, Maryland	UP	17	0	17	4.00 a
52	PI 531396	<i>O. basilicum</i>	USA, Maryland	UP	15	0	15	4.00 a
53	PI 601365	<i>O. basilicum</i> 'Purple Ruffles'	USA, Maryland	D	15	0	15	4.00 a
57	PI 652065	<i>O. basilicum</i> 'Genovese'	Italy	D	12	0	12	4.00 a
59	PI 652071	<i>O. basilicum</i> var. <i>purpurascens</i> 'Dark Opal'	USA, California	D	14	0	14	4.00 a
85	Feronia	<i>O. basilicum</i> F1	Hishtil, Israel	D	20	0	20	4.00 a
87	Lhasa	<i>O. basilicum</i> F1	Hishtil, Israel	D	20	0	20	4.00 a
90	Green Ball	<i>O. basilicum</i> F1	Hishtil, Israel	D	20	0	20	4.00 a
92	Green Super Globe	<i>O. basilicum</i> F1	Hishtil, Israel	D	20	0	20	4.00 a
96	Pesto Perpetuo	<i>O. basilicum</i> F1	Hishtil, Israel	D	20	0	20	4.00 a
101	Genoveser 142	<i>O. basilicum</i> 'Genovese'	Frankonia, Germany	D	12	0	12	4.00 a

During the second season crosses were made between the highly resistant individuals and the susceptible cultivar Peri. The F1 progeny plants were tested for resistance to BDM during the third season.

The results are given in Table 2. They confirm the high resistance of several entries in all three seasons. A correlation of 0.85 was calculated between the resistance values obtained in the first and the second seasons, and 0.89 between the second and the third seasons. In group D, three entries segregated for resistance in the first season and the selected resistant individuals expressed high levels of resistance in the next two seasons.

Twenty-seven F1 hybrids were produced and tested for resistance. Their responses to BDM in the third season are given in Figure 3 along with the responses of their parents. Resistance of most parents was inherited as a partial dominant trait. Some parents, however, had a different mode of inheritance: the resistant entries 73 (PI 500950, *O. americanum* var. *pilosum*), 3 (PI 500945, *O. americanum* var. *americanum*), and 74 (PI 500951, *O. americanum* var. *pilosum*) probably carry a dominant gene(s) for resistance while entries 55 (*O. basilicum* var. *citrodorum* 'Mrs. Burns') and 60 (PI 414201, *O. tenuiflorum*) probably carry a dominant gene(s) for partial resistance. Entry 77 (PI 500954, *O. kilimanadascharicum*) was unique. Its resistance seemed to be inherited in a recessive manner (Fig. 3).

DISCUSSION

The recent outbreak of downy mildew in sweet basil in Israel (Cohen et al. 2013b) has caused enormous economical losses to growers due to the lack of adequate knowledge on the biology and control of the disease. This study was launched to provide relief to growers by developing basil lines resistant to the mildew. For this purpose we have looked for sources of resistance genes and evaluated 113 genotypes of basil (wild, cultivated, and ornamental) for resistance against *P. belbahrii* at the four-leaf stage in growth chambers and during three consecutive seasons in the field.

The 113 accessions were divided into four groups: group A, comprised of *O. americanum* and *O. kilimandscharicum*; group B, *O. tenuiflorum*, *O. gratissimum*, and *O. campechianum*; group C, *O. basilicum* and *Ocimum* spp.; and group D, *O. basilicum*. Mean disease intensity for the entries in groups A, B, C, and D at the four-leaf stage was 0.36, 0.91, 0.71, and 2.30 (0 to 3 visual scale, data not shown) and in the field was 0.33, 0.45, 0.96, and 3.73 (0 to 4 visual scale), respectively. This suggests that genes for immunity (disease intensity = 0) or high resistance (disease intensity 0.1 to 0.9) reside mainly among wild species of *Ocimum* in groups A and B. Nevertheless, some entries of *O. basilicum* expressed high resistance (e.g., *O. basilicum* var. *anisatum*) or moderate resistance (e.g., *O. basilicum*

Fig. 2. A and B, Response to basil downy mildew of 113 accessions of *Ocimum* species. **A,** Final disease intensity score at 27 days postinoculation (dpi) under field conditions. **B,** Disease intensity in four-leaf plants at 7 dpi under growth chamber conditions. Note that accessions are arranged on the x axis in the same order in upper and lower images. The list of accessions is shown in Table 1.

var. *citrodorum*, *O. × citrodorum*, and *O. basilicum* var. *minimum*). Interestingly, in some susceptible accessions of *O. basilicum*, individual plants were resistant. Thus, among the population of sweet basil (*O. basilicum*) PI 652070, one single plant showed resistance. After self-pollination, its descendants were resistant in the field. Most commercial *O. basilicum* lines were susceptible to BDM except *O. basilicum* var. *citrodorum*, *O. × citrodorum*, and *O. basilicum* var. *minimum*, which expressed moderate resistance.

Our results corroborate with Pyne et al. (2014) who showed that PI 652053 (*O. americanum* var. *americanum*) was resistant to BDM. PI 172996 and PI 172997 (both *O. basilicum* var. *anisatum*), which were resistant to the disease at the young plant stage in their study, were highly resistant in our study at the four-leaf stage and in the field. PI 172998 was reported resistant by Pyne et al. (2014) as well as in our study. The 30 *O. basilicum* entries reported susceptible by Pyne et al. (2014) were also susceptible in our study.

TABLE 2. Response to downy mildew of 40 *Ocimum* species in three consecutive seasons under field conditions^z

Entry	Accession	Botanical name	Disease intensity			
			First season	Second season	Third season	
			Original accessions	Progeny of a resistant individual	Progeny of a resistant individual	Resistant individual × susceptible 'Peri' (F1)
			Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
Group A						
3	PI 500945	<i>O. americanum</i> var. <i>americanum</i>	0.00	0.00	0.00	0.00 ^S
67	PI 500942	<i>O. americanum</i> var. <i>pilosum</i>	0.00		0.50 ± 0.00	1.05 ± 0.37 ^S
69	PI 500944	<i>O. americanum</i> var. <i>pilosum</i>	0.00		0.00	0.20 ± 0.00 ^S
73	PI 500950	<i>O. americanum</i> var. <i>pilosum</i>	0.00	0.00	0.00	0.00 ^S
76	PI 500954	<i>O. americanum</i> var. <i>pilosum</i>	0.00	0.00	0.25 ± 0.29	1.05 ± 0.30 ^S
77	PI 652052	<i>O. kilimandscharicum</i>	0.03 ± 0.10	0.09 ± 0.18	0.00	1.89 ± 0.22 ^S
74	PI 500951	<i>O. americanum</i> var. <i>pilosum</i>	0.80 ± 0.15	0.00	0.00	0.10 ± 0.11 ^S
2	PI 254352	<i>O. americanum</i> var. <i>americanum</i>	0.10 ± 0.17	0.00	0.04 ± 0.09	0.50 ± 0.00 ^S
72	PI 500949	<i>O. americanum</i> var. <i>pilosum</i>	0.13 ± 0.23	0.00	0.00	0.70 ± 0.00 ^S
54	PI 652053	<i>O. americanum</i> var. <i>americanum</i>	0.17 ± 0.21	0.00	0.00	
75	PI 500953	<i>O. americanum</i> var. <i>pilosum</i>	0.38 ± 0.75	0.00	0.00	1.15 ± 0.44 ^S
1	PI 253158	<i>O. americanum</i> var. <i>americanum</i>	0.43 ± 0.21	0.30 ± 0.10	0.02 ± 0.04	0.46 ± 0.09 ^S
6	PI 652062	<i>O. americanum</i> var. <i>americanum</i>	0.50 ± 0	0.50 ± 0.12		
4	PI 652058	<i>O. americanum</i> var. <i>americanum</i>	0.65 ± 0.33	0.00	0.07 ± 0.10	1.23 ± 0.13 ^S
5	PI 652060	<i>O. americanum</i> var. <i>americanum</i>	0.96 ± 0.37	1.00 ± 0.30	1.20 ± 0.18	1.59 ± 0.14 ^S
Group B						
78	PI 652066	<i>O. campechianum</i>	0.00	0.00		
79	PI 652067	<i>O. gratissimum</i>	0.00	0.00		
80	PI 211715	<i>O. gratissimum</i> var. <i>gratissimum</i>	0.00	0.00		
81	PI 500952	<i>O. gratissimum</i> var. <i>gratissimum</i>	0.00	0.00		
82	PI 652055	<i>O. gratissimum</i> var. <i>macrophyllum</i>	0.00	0.00		
64	PI 414205	<i>O. tenuiflorum</i>	0.37 ± 0.22	1.01 ± 0.49	0.60 ± 0.00	1.70 ± 0.00 ^S
60	PI 414201	<i>O. tenuiflorum</i>	0.60 ± 0.39	1.11 ± 0.31	1.50 ± 0.00	1.50 ± 0.00 ^S
66	PI 652059	<i>O. tenuiflorum</i>	0.79 ± 0.41		0.50 ± 0.00	1.30 ± 0.00 ^S
62	PI 414203	<i>O. tenuiflorum</i>	1.09 ± 0.42	1.35 ± 0.30	0.50 ± 0.00	1.40 ± 0.00 ^S
65	PI 652056	<i>O. tenuiflorum</i>	1.18 ± 0.27		0.70 ± 0.00	1.50 ± 0.00 ^S
Group C						
107	Spice basil	<i>Ocimum</i> spp.	0.15 ± 0.32	0.64 ± 0.72		
113	Blue Spice	<i>Ocimum</i> spp.	0.30 ± 0.38	1.02 ± 0.49		
12	PI 172998	<i>O. basilicum</i> var. <i>anisatum</i>	0.38 ± 0.18	0.56 ± 0.15	0.85 ± 0.14	1.35 ± 0.09 ^{LF}
11	PI 172997	<i>O. basilicum</i> var. <i>anisatum</i>	0.50 ± 0.09	0.70 ± 0.21	0.75 ± 0.20	1.50 ± 0.00 ^{LF}
10	PI 172996	<i>O. basilicum</i> var. <i>anisatum</i>	0.57 ± 0.12	1.13 ± 0.19	0.90 ± 0.00	1.32 ± 0.04 ^{LF}
94	Magic Mountain F1 ^S	<i>O. kilimandscharicum</i> × <i>O. basilicum</i>	0.58 ± 0.30	1.30 ± 0.15	1.10 ± 0.20	
95	Magic White F1 ^S	<i>O. kilimandscharicum</i> × <i>O. basilicum</i>	0.58 ± 0.42	1.25 ± 0.15	1.20 ± 0.15	
26	PI 296391	<i>O. basilicum</i> var. <i>citrodorum</i>	1.30 ± 0.77	1.86 ± 0.24	0.80 ± 0.00	1.47 ± 0.08 ^F
86	Wild Color F1 ^S	<i>O. basilicum</i>	1.30 ± 0.21	1.50 ± 0.29		
8	PI 170579	<i>O. basilicum</i> var. <i>minimum</i>	1.34 ± 0.31	1.26 ± 0.23		
14	PI 174284	<i>O. basilicum</i> var. <i>anisatum</i>	1.38 ± 1.16	0.92 ± 0.21	0.80 ± 0.00	1.56 ± 0.22 ^{LF}
55	PI 652054	<i>O. basilicum</i> var. <i>citrodorum</i> 'Mrs. Burns'	1.47 ± 0.31	1.64 ± 0.20	1.50 ± 0.00	1.50 ± 0.00 ^S
23	PI 253157	<i>O. basilicum</i> var. <i>citrodorum</i>	1.73 ± 1.04	1.11 ± 0.28	1.12 ± 0.26	1.41 ± 0.32 ^F
105	Lemon basil	<i>O. basilicum</i> var. <i>citrodorum</i>	1.79 ± 0.54	2.03 ± 0.54		
84	Ajaka F1 ^S	<i>O. basilicum</i>	1.81 ± 0.26	1.70 ± 0.21		
Group D						
102	Sweet Danni	<i>O. × citrodorum</i>	2.15 ± 0.25	2.32 ± 0.25		
37	PI 368697	<i>O. basilicum</i>	2.28 ± 1.24	1.21 ± 0.24	0.99 ± 0.21	
13	PI 173746	<i>O. basilicum</i>	2.95 ± 0.93	1.93 ± 0.34	1.50 ± 0.13	1.68 ± 0.29 ^F
109	Rubin	<i>O. basilicum</i>	3.15 ± 0.32	3.77 ± 0.63		
58	PI 652070	<i>O. basilicum</i>	3.46 ± 1.21	0.24 ± 0.46	0.92 ± 0.30	1.42 ± 0.20 ^F
112	Gecofure basil	<i>O. basilicum</i> 'Genovese'	3.73 ± 0.34	4.00 ± 0.00		
100	Peri	<i>O. basilicum</i> Sweet basil 'Peri'	3.95 ± 0.16	3.61 ± 0.53	3.08 ± 0.71	
101	Genoveser 142	<i>O. basilicum</i> 'Genovese'	4.00 ± 0.00	4.00 ± 0.00		

^z First season data represent the response of a bulk population from the original accessions. Seeds were collected from a single highly resistant plant and used to test the response to basil downy mildew (BDM) at 27 days postinoculation (dpi) in a second and a third season. During the second season a cross was made between one resistant individual and the susceptible sweet basil Peri. The response to BDM of the F1 plants was recorded at 39 dpi. Final score is represented by mean ± standard deviation of the mean (SD). The uppercase letters represent sterility (S), fertility (F), or low fertility (LF) of the F1 hybrids.

Fig. 3. Response to basil downy mildew of 27 F1 hybrids of *Ocimum* species made by crossing resistant parental accessions with the susceptible cultivar Peri.

Wyenandt et al. (2010) evaluated the response to BDM of 30 basil entries in field trials in southern and northern New Jersey. The cultivars Spice, Blue Spice, and Blue Spice F1 showed neither visible symptoms nor sporulation, suggesting potential sources of resistance in *Ocimum* spp., while three *O. citrodorum* entries showed symptoms with light sporulation. In our study, Spice and Blue Spice usually showed some symptoms but no sporulation (except in the second season, Table 2), while *O. citrodorum* entries (group C) responded similarly showing symptoms with light sporulation.

The crosses we made between the highly resistant (or resistant) parents and the susceptible parent Peri provided information on the versatility of the resistance genes in the collection we have studied (Fig. 3). These data suggest that three genotypes (PI 500945, PI 500950, and PI 500951) carried dominant gene(s) for resistance while others probably carried partially dominant genes. Interestingly, one resistant genotype probably carried a recessive gene for resistance. This variety of genes may be used in breeding programs to ensure durable resistance against BDM.

The F1 offspring plants obtained from the crosses between the resistant *O. americanum* entries and the susceptible *O. basilicum* 'Peri' were infertile, and therefore could produce no F2 progeny plants. This genetic barrier, derived mainly from differential ploidy of the two species, prevents further exploitation of these important resistance genes. Current studies should be directed to overcome this genetic barrier by embryo rescue and genome duplication techniques.

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