Eur J Plant Pathol (2019) 155:789–799
https://doi.org/10.1007/s10658-019-01809-9

Host range of *Peronospora belbahrii*, causal agent of basil downy mildew, in Israel

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Accepted: 9 July 2019 / Published online: 16 July 2019

Abstract Downy mildew in sweet basil (*Ocimum basilicum* L) was first recorded in Israel in late 2011. Within one year, the disease was reported all over the country, causing devastating economic damage to basil crops. The pathogen was reported to have similarly spread widely in Europe, the USA and Asia. Seed transmission and seedling trade were suggested as possible causes for rapid spread. Here, we report that some members of the *Labiatae* family beside *O. basilicum* serve as hosts of *Peronospora belbahrii* in Israel, thus possibly aiding its spread and survival. One hundred and two entries of *Labiatae* (Syn *Lamiaceae*), belonging to 22 genera and 53 species, were tested for sensitivity to *P. belbahrii* in artificial-inoculated plants in growth chambers and in field. Following artificial inoculation of potted plants in growth chambers and of field-grown plants, sporulation of *P. belbahrii* was observed in seven species: *Salvia eigii, Salvia fruticosa, Salvia pinnata, Rosmarinus officinalis, Nepeta curviflora*, *Micromeria fruticosa*, and *Agastache* spp. Six other entries (belonging to four other genera) showed small chlorotic spots but not sporulation. All other entries were symptom-free. This is the first report showing pathogenicity of *P. belbahrii* to *Salvia, Rosmarinus*, *Nepeta and Micromeria* spp. in Israel. Whether these species play a role in the epidemiology of basil downy mildew in Israel needs to be studied.

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Keywords Alternative host · Epidemiology · Green bridge: *Lamiaceae* · Ocimum: Over-seasoning · Oomycete · Sweet basil

Introduction

Basil downy mildew (BDM), caused by the oomycete *Peronospora belbahrii* (Thines), is a very destructive disease of sweet basil. It was first reported in Uganda in 1932 as *Peronospora* spp. and again in 1937 as *P. lamii*, seen as causing defoliation and death of sweet basil (Hansford 1933). The disease emerged in Switzerland in 2001 (Belbahri et al. 2005). First occurrence of the disease in Italy was next reported in 2003 (Garibaldi et al. 2004a), and in France and Belgium in 2004 (Coosemans 2004; Garibaldi et al. 2005). Since then, *P.belbahrii* has spread worldwide (Cohen et al. 2017).

Peronospora belbahrii is an obligate oomycete that attacks mainly sweet basil (*Ocimum basilicum*), producing chlorotic lesions on leaf blades and sporangia on the lower leaf surfaces. The lesions gradually turn necrotic and infected leaves abscised. Sporangia are purplish, oval, 30.4 ± 2.9 μm long × 21.4 ± 1.7 μm wide (Cohen et al. 2013a). Sporangiophores, which emerge from stomatal openings in saturated atmosphere, are hyaline, 400 to 600 μm long, dichotomously branched, with three to five branches per sporangiophore, and bear a single sporangium on each branchlet tip. Infected plants may sporulate during shipping and infected symptomless plants may turn dark upon marketing.

How *P. belbahrii* persists between growth seasons in Israel and elsewhere is still unknown. Possible routes of over-seasoning are green bridges, seed transmission, oospores in plant debris, and secondary hosts (Ben-Naim et al. 2017). Garibaldi et al. (2004b) and Farahani-Kofoet et al. (2012) both suggested transmission of the pathogen via seeds, although no direct evidence showing the pathogen inside the seed embryo of basil was presented. The fact that the pathogen is systemic suggests potential seed transmission (Falach-Block et al. 2018; Farahani-Kofoet et al. 2012). In Israel, seeds harvested from infected basil plants never developed downy mildew under confined conditions despite the presence of the pathogen's DNA on the seeds (Cohen et al. 2017; Falach-Block et al. 2018).

We know little on oospore formation of *P. belbahrii* and on their role in the epidemiology of BDM. Cohen et al. (2013b) reported on the erratic occurrence of *P. belbahrii* oospores inside the mesophyll of BDM-infected basil leaves. Microscopic examination of infected leaves revealed brown, round oospores with a diameter of 46.2 ± 2.8 µm. Attempts to induce oospore formation in the laboratory by inoculating basil plants with sporangia of paired isolates from various years, various locations, or various hosts, provided no answer on whether the pathogen is homothallic or heterothallic, since oospore formation was erratic (Cohen et al. 2017). Our repeated attempts failed to germinate oospores in vitro or in vivo (unpublished data). Oospore production in other countries has not been reported to date.

P. belbahrii is reported as the causal agent of BDM in *O. basilicum* (sweet basil), attacking all known cultivars. It also affects other species members of the *Ocimum* genus (Ben-Naim et al. 2015; Farahani-Kofoet et al. 2014; Wyenandt et al. 2010). Only a few wild *Ocimum* species were found resistant to BDM (Ben-Naim et al. 2015, 2018; Farahani-Kofoet et al. 2014; Koroch et al. 2013). A resistant cultivar of sweet basil, Prospera, was recently released by Bar Ilan University.

In addition to *Ocimum* spp., three other species were reported as hosts of *P. belbahrii*: agastache (*Agastache* sp., Hyssops*)*, coleus *(Plectranthus scutellarioides* Syn *Solenostemon scutellarioides*) and sage (mainly *Salvia officinalis*) (see below).

P. belbahrii was first reported on *Agastache* sp. in the U.K in 2009, and was reported the following year on *O. basilicum* (Henricot et al. 2010). Webb et al. (2012) confirmed *P. belbahrii* on both sweet basil and agastache based on reciprocal cross-contaminations and molecular analyses. In the USA, downy mildew in agastache was first recorded in Missouri in 2014 (Rivera et al. 2016a). Based on morphology, ITS (rDNA internal transcribed spacer) and *cox 2*, the authors concluded that the causal agent is closely related to *P. belbahrii*, but distinct.

P. belbahrii was first reported on coleus in the UK in 2014. ITS analyses of coleus isolates showed 99% homology to *P. belbahrii* taken from *agastache* (Denton et al. 2015). Similar findings were reported in the USA (Harlan et al. 2015). Rivera et al. (2016b) reported the first occurrence of *P. belbahrii* on coleus in Tennessee in 2015. In the United States, *Peronospora* spp. on coleus has been reported since 2006 in Florida, Louisiana, and New York, and *P. belbahrii* sensu lato has been reported in Michigan. Previous records indicated the presence of *Peronospora* sp. on coleus from various landscapes of Tennessee in 2006.

The prevailing assumption describes *P. belbahrii* as a complex of species that are defined by the host plant (Thines et al. 2009). Choi et al. (2009) identified three *Peronospora* species on sages: *Peronospora swinglei*, *Peronospora salviae-plebeiae,* and *Peronospora salviae-officinalis*. Each species was restricted to a different host: *P. swinglei* to *S. reflexa*, *P. salviae-plebeiae* to *S. plebeia* and *P. salviae-officinalis* to *S. officinalis*. They suggested that speciation might be allopatric, closely linked to the geographic distributions of the host plants. In the UK, sage is attacked by *P. lamni, P. swinglei*, and others, while mint is attacked by *P. lamni* only (Wright 2014).

Thines et al. (2009) confirmed that the occurrence of downy mildew on *Solenostemon* and *Ocimum* might be attributed to a single species or two different species, but *both are unrelated* to *Peronospora lamii*, which is a common pathogen of the weed *Lamium purpureum.*

Sage, rosemary and mint are hosts of *P. lamni* in the UK (Wright 2014). *P. lamii* persists in the woody plant material of sage between growth seasons, while in mint, systemic infection of this perennial plant allows persistence of the pathogen (Wright 2014).

The *Labiatae* (Syn *Laminaceae*) family has a cosmopolitan distribution. The *Labiatae* family includes 236 genera (Harley et al. 2004), with 6,900 (Heywood et al. 2007) to 7,200 (Harley et al. 2004) species. The largest genus is *Salvia* (900 species), followed by *Clerodendrum* (400 species), *Scutellaria* (360 species) *Stachys* (300 species), *Plectranthus* (300 species), *Hyptis* (280 species), *Teucrium* (250 species), *Vitex* (250 species), *Thymus* (220 species), and *Nepeta* (200 species) (Harley et al. 2004).

In the present study, we examined the response of various members of the family *Labiatae* to inoculation with an isolate of *P. belbahrii* collected from sweet basil in Israel. We identified new host species of this pathogen that may serve as sources of inoculum or as a bridge between production seasons to infect sweet basil**.**

Materials and methods

Germplasm

One hundred and two entries of *Labiatae*, belonging to 53 species and 22 genera, were tested for susceptibility to BDM (Table 1). Seeds were obtained from the following suppliers: USDA - Agriculture Research Service Plant Introduction Station, Iowa State University, Ames, Iowa; Hishtil Ltd. (Petach Tikva, Israel); Department of Archeological Botany, Bar-Ilan University (Ramat-Gan, Israel); Genesis Seeds Ltd. (Ashalim, Israel); and Danzinger Nurseries Ltd. (Mishmar Hashiva, Israel). Potted plants of ornamental species and hybrids were obtained from Hishtil Ltd. and from other local nurseries. The obtained entries were endemic, agricultural, or ornamental. A detailed description of the entries is provided in Table 1. Seeds were sown in multi-cell trays (cell size 2.5 × 2.5 cm) filled with a potting mixture (peat: vermiculite, 1:1, *v*/v), two or three seeds per cell. Trays were kept in in the greenhouse while plants grew. At the four-leaf stage, one set of plants was transplanted into 0.5 L pots and another set of plants was transplanted to the field.

Pathogen

Isolate Knafo 3 of *P. belbahrii* was used in all experiments. It was collected in 2013 at Ein-Tamar, Southern Jordan Valley, Israel and maintained by repeated inoculation of susceptible sweet basil plants at 25 °C.

Inoculation and disease assessment

Fresh sporangia 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, including the BDM-susceptible controls 'Sweet Basil' and 'Peri'. Plants were placed in a dew chamber overnight at 18 °C to ensure infection and, thereafter, at 25 °C under continuous illumination (60 μmole m^2 s^{-1}) to ensure pathogen colonization. Plants were returned to the dew chamber at 9 days post inoculation (dpi) to enable sporulation of the pathogen on the inoculated plants. Disease symptoms and sporulation of the pathogen were visually estimated using the following ordered categorical scale (Ben-Naim et al. 2015):

- No symptoms or sporulation.
- (−) Hypersensitive response (HR) or minute chlorotic lesions with no sporulation.
- (+) Chlorotic lesions with abundant sporulation.

In the field, plant entries, including the susceptible control plants, were spray-inoculated with *P. belbahrii* at 15 days after transplanting. Disease records were taken three times during a growing period of 52 days post-inoculation, using the scale described above.

Data analysis

Experiments in growth chambers were repeated twice with 5–30 plants per entry in each experiment. Percentage of plants showing sporulation of the pathogen was calculated in each experiment. Mean values and standard deviation (SD) of the mean are presented in Table 1.

The field experiment was conducted once.

Results

Growth chamber studies

Of the 22 genera tested, sporulation occurred in plants belonging to the following six genera: *Ocimum*, *Salvia*, *Rosmarinus*, *Nepeta*, *Agastache*, and *Micromeria* (Table 1). Restricted lesions with no sporulation occurred in plants belonging to four genera: *Lamium*, *Mentha*, *Majorana*, and *Salvia* (Table 1). Plants of all other genera showed no symptoms (Table 1, Fig. 1). Not all species of a genus reacted to inoculation in the same manner, indicating that susceptibility to BDM is determined at the species rather than the genus level.

Table 1 Response of 102 *Labiatae* entries to inoculation with *Peronospora belbahrii*

Genus		Species					
Number	Name	Number	Name	Cultivar[a]	Supplier	Use/Habitat[b]	% Plants[c]
1	*Acinos*	1	*rotundifolius*	–	Bar Ilan	E	0
2	*Agastache*	2	*aurantiaca*	–	Danziger	O	100 ± 0
3	*Ballota*	3	*undulata*	–	Hishtil	E	0
4	*Hlomis*	4	*viscosa*	–	Hishtil	E	0
5	*Lamium*	5	*amplexicaule*	–	Bar Ilan	E	–
	Lamium	6	*moschatum*	–	Bar Ilan	E	0
6	*Lavandula*	7	*pinnata*	–	Hishtil	E/ A/ O	0
	Lavandula	8	*dentata*	–	Private	A/ O	0
	Lavandula	9	*dentata*	–	Private	A/ O	0
	Lavandula	10	*stoechas*	–	Hishtil	E	0
7	*Majorana*	11	*syriaca*	–	Hishtil	E	0
	Majorana	12	*syriaca*	–	Hishtil	E/ A/ O	–
	Majorana	13	*syriaca*	–	Hishtil	E	0
	Majorana	14	*syriaca*	–	Hishtil	E	0
8	*Marrubium*	15	*vulgare*	–	Hishtil	E	0
9	*Melissa*	16	*officinalis*	–	Hishtil	E	0
	Melissa	17	*officinalis*	–	Private	A/ O	0
	Melissa	18	*officinalis*	–	Hishtil	E	0
10	*Mentha*	19	*suaveolens*	"Mint"	Hishtil	A/ O	–
	Mentha	20	*spp*	"Mint" Berries and Cream"	Hishtil	A/ O	0
	Mentha	21	*suaveolens*	"Thai"	Hishtil	A/ O	0
	Mentha	22	*suaveolens*	"Basil"	Hishtil	A/ O	0
	Mentha	23	*suaveolens*	"Spanish"	Hishtil	A/ O	0
	Mentha	24	*suaveolens*	"Moroccan"	Hishtil	A/ O	0
	Mentha	25	*suaveolens*	"Apple" mint"	Private	A/ O	0
	Mentha	26	*suaveolens*	"Smithiana"	Private	A/ O	0
	Mentha	27	*pulegium*	–	Hishtil	E	–
	Mentha	28	*longifolia*	–	Hishtil	E	–
11	*Micromeria*	29	*fruticosa*	–	Hishtil	E	66.0 ± 10.2
	Micromeria	30	*fruticosa*	–	Hishtil	E	0
12	*Moluccella*	31	*laevis*	–	Bar Ilan	E	0
13	*Nepeta*	32	*curviflora*	–	Hishtil	E	66.7 ± 13.5
	Nepta	33	*curviflora*	–	Hishtil	E	39.3 ± 9.0
14	*Ocimum*	34	*basilicum var thyrsifolium*	PI 368697	USDA	A/ O	100 ± 0
	Ocimum	35	*basilicum*	"Sweet""basil"	Genesis	A/ O	100 ± 0
	Ocimum	36	*basilicum var thyrsifolium*	"Cardinal"	Genesis	A/O	100 ± 0
	Ocimum	37	*basilicum var minimum*	"Bush basil"	Hishtil	A/O	100 ± 0
	Ocimum	38	*basilicum var citrodorum*	"Mrs burnsBurns"	USDA	A/O	100 ± 0
	Ocimum	39	*kilimandscharicum*	–	USDA	A/O	96.0 ± 4.0
	Ocimum	40	*tenuiflorum*	PI 414204	USDA	A/O	94.3 ± 8.0
	Ocimum	41	*americanom var americaum*	PI 253158	USDA	A/O	100 ± 0
	Ocimum	42	*americanom var pilosum*	PI 500943	USDA	A/O	92.0 ± 5.7
	Ocimum	43	*gratissimum*	PI 211715	USDA	A/O	0

Table 1 (continued)

Genus		Species					
Number	Name	Number	Name	Cultivar[a]	Supplier	Use/Habitat[b]	% Plants[c]
	Ocimum	44	*campechianum*	PI 652066	USDA	A/ O	0
15	*Origanum*	45	*vulgare subsp. hritum*	"Compactu"m"	Hishtil	E	0
	Origanum	46	*vulgare*	"Origanum" Majorna"	Hishtil	A/O	0
	Origanum	47	*vulgare*	"Supreme"	Hishtil	A/ O	0
	Origanum	48	*vulgaris*	–	Private	A/ O	0
16	*Plectranthus*	49	*neochilus*	–	Bar Ilan	O	0
	Plectranthus	50	*scutellarioides*	"Wizard"	Hishtil	O	0
17	*Prasium*	51	*majus*	–	Hishtil	E	0
18	*Rosmarinus*	52	*officinalis*	"Barbecue"	Hishtil	A/ O	45.7 ± 4.6
	Rosmarinus	53	*spp*	–	Hishtil	A/ O	0
	Rosmarinus	54	*officinalis*	"Upright" Rosmarinus"	Hishtil	A/ O	0
	Rosmarinus	55	*spp*	–	Private	A/ O	0
	Rosmarinus	56	*officinalis*	–	Bar Ilan	A/ O	0
	Rosmarinus	57	*officinalis*	"Blue" lagune"	Hishtil	A/ O	57 ± 10.0
	Rosmarinus	58	*officinalis*	"Speedy"	Hishtil	A/ O	0
	Rosmarinus	59	*officinalis*	"Arp"	Hishtil	A/ O	0
	Rosmarinus	60	*officinalis*	"loweros"	Hishtil	A/ O	0
	Rosmarinus	61	*officinalis*	"Foxtail"	Hishtil	A/ O	0
	Rosmarinus	62	*officinalis*	–	Hishtil	A/ O	66.6
	Rosmarinus	63	*officinalis*	"Tuscan" Blue"	Hishtil	A/ O	40.0 ± 14.3
	Rosmarinus	64	*officinalis*	"Upright" Barbeque"	Hishtil	A/ O	0
	Rosmarinus	65	*officinalis*	"Mis Jessop"	Hishtil	A/ O	0
	Rosmarinus	66	*officinalis*	"Boule"	Hishtil	A/ O	41.5 ± 8.5
	Rosmarinus	67	*officinalis*	"Haifa falls"	Hishtil	A/ O	0
	Rosmarinus	68	*officinalis*	"Ingauno"	Hishtil	A/ O	46.6 ± 7.8
19	*Salvia*	69	*fruticosa*	–	Hishtil	E	53.0 ± 3.0
	Salvia	70	*judaica*	–	Hishtil	E	0
	Salvia	71	*dominica*	–	Hishtil	E	–
	Salvia	72	*officinalis*	"Maxima"	Hishtil	E/ A/ O	–
	Salvia	73	*purpurea*	"Purpurasce"ns"	Hishtil	A/ O	0
	Salvia	74	*officinalis*	"Tricolor"	Hishtil	A/ O	0
	Salvia	75	*spp*	"Iterina" (Bicolor)"	Hishtil	A/ O	0
	Salvia	76	*officinalis*	"Bicolor" Tricolor"	Private	E	0
	Salvia	77	*spp*	"Scarlet" pineapple"	Private	A/ O	0
	Salvia	78	*officinalis*	"Salvia" scalaria"	Genesis	A/ O	0
	Salvia	79	*hierosolymitana*	–	Genesis	A/ O	0
	Salvia	80	*hierosolymitana*	–	Hishtil	E	0
	Salvia	81	*judaica*	–	Hishtil	E	0
	Salvia	82	*fruticosa*	–	Hishtil	E	46.0 ± 13.4
	Salvia	83	*dominica*	–	Hishtil	E	0
	Salvia	84	*eigii*	–	Hishtil	E	56.5 ± 6.5
	Salvia	85	*pinnata*	–	Hishtil	E	61.6 ± 17.6
	Salvia	86	*multicaulis*	–	Bar Ilan	E	0

Table 1 (continued)

Genus		Species					
Number	Name	Number	Name	Cultivar[a]	Supplier	Use/Habitat[b]	% Plants[c]
20	*Satureja*	87	*thymbra*	–	Hishtil	E	0
	Satureja	88	*thymbra*	–	Hishtil	E	0
21	*Teucrium*	89	*creticum*	–	Hishtil	E	0
	Teucrium	90	*capitatum*	–	Hishtil	E	0
22	*Thymus*	91	*vulgaris*	"Gold"	Hishtil	A/ O	0
	Thymus	92	*vulgaris*	"Compactus""	Hishtil	A/ O	0
	Thymus	93	*vulgaris*	"Faustinoi"	Hishtil	A/ O	0
	Thymus	94	*citriodorus*	"Fragranntis"simus Orange"	Hishtil	A/ O	0
	Thymus	95	*vulgaris*	"Prostrate"	Hishtil	A/ O	0
	Thymus	96	*vulgaris*	"Herba" Barona"	Hishtil	A/ O	0
	Thymus	97	*citriodorus*	"Variegated"	Hishtil	A/ O	0
	Thymus	98	*thy' x pulegioides*	"Doone" valey"	Hishtil	A/ O	0
	Thymus	99	*citriodorus*	"Thymus" Citrodorus"	Hishtil	A/ O	0
	Thymus	100	*vulgaris*	"Caborn" wine" roses"	Hishtil	A/ O	0
	Thymus	101	*vulgaris*	"Tabor"	Hishtil	A/ O	0
	Thymus	102	*vulgaris*	"Wooly"	Private	A/ O	0

[a] (−) endemic entry with no cultivar designation

[b] E = endemic; A = agricultural; O = ornamental

[c] % plants showing: (0) no symptoms; (−) restricted symptoms without sporulation; (+) symptoms with sporulation. Mean and standard deviation of the mean of three independent experiments

Susceptibility of *Ocimum*

Sporulation of *P. belbahrii* on leaves of sweet basil (*Ocimum basilicum*) is shown in Fig. 2a. The following *Ocimum* species were highly susceptible to BDM: *O. basilicum*, *O. basilicum var thyrsifolium*, *O. basilicum var minimum*, *O. basilicum var citrodorum*, *O. kilimandscharicum*, *O. tenuiflorum*, *O. americanom var americaum*, and *O. americanom var pilosum*. Percentage of sporulating plants ranged between 92 and 100%. Two Ocimum species, *O. gratissimum* and *O. campechianum* were immune showing no symptoms or sporulation (Table 1).

Susceptibility of *Rosemarinus*

Six out of fifteen cultivars belonging to *Rosmarinus officinalis* were susceptible to BDM (Fig. 2b). Percentage of sporulating plants among these susceptible cultivars ranged between 41.5–66.0% (Table 1).

Susceptibility of *Salvia*

Three species of *Salvia*, *S. fruticose* (Fig. 2c), *S. pinnata* (Fig. 2d), and *S. eigii* (not shown) were susceptible to BDM. Percent plants showing sporulation of *P. belbahrii* ranged between 46.0–61.6%. *S. dominica* (Fig. 2e) showed restricted chlorotic lesions with no sporulation. Other cultivars of *S. officinalis* showed HR symptoms without sporulation. All other *Salvia* species showed no symptoms or sporulation (Table 1).

Susceptibility of other species

Two endemic entries of *Nepeta curviflora* were susceptible to BDM (Fig. 2f). One *Agastache* entry (*Agastache* spp.) was susceptible and one *Micromeria* entry, *M. fruticose,* produced symptoms with sporulation. Disease symptoms with no sporulation were observed in several species.

Mentha suaveolens, *M. enthapulegium*, and *M. longifolia* exhibited small necrotic HR lesions. Similar symptoms were seen in *Lamium amplexicaule* and *Majorana syriaca*.

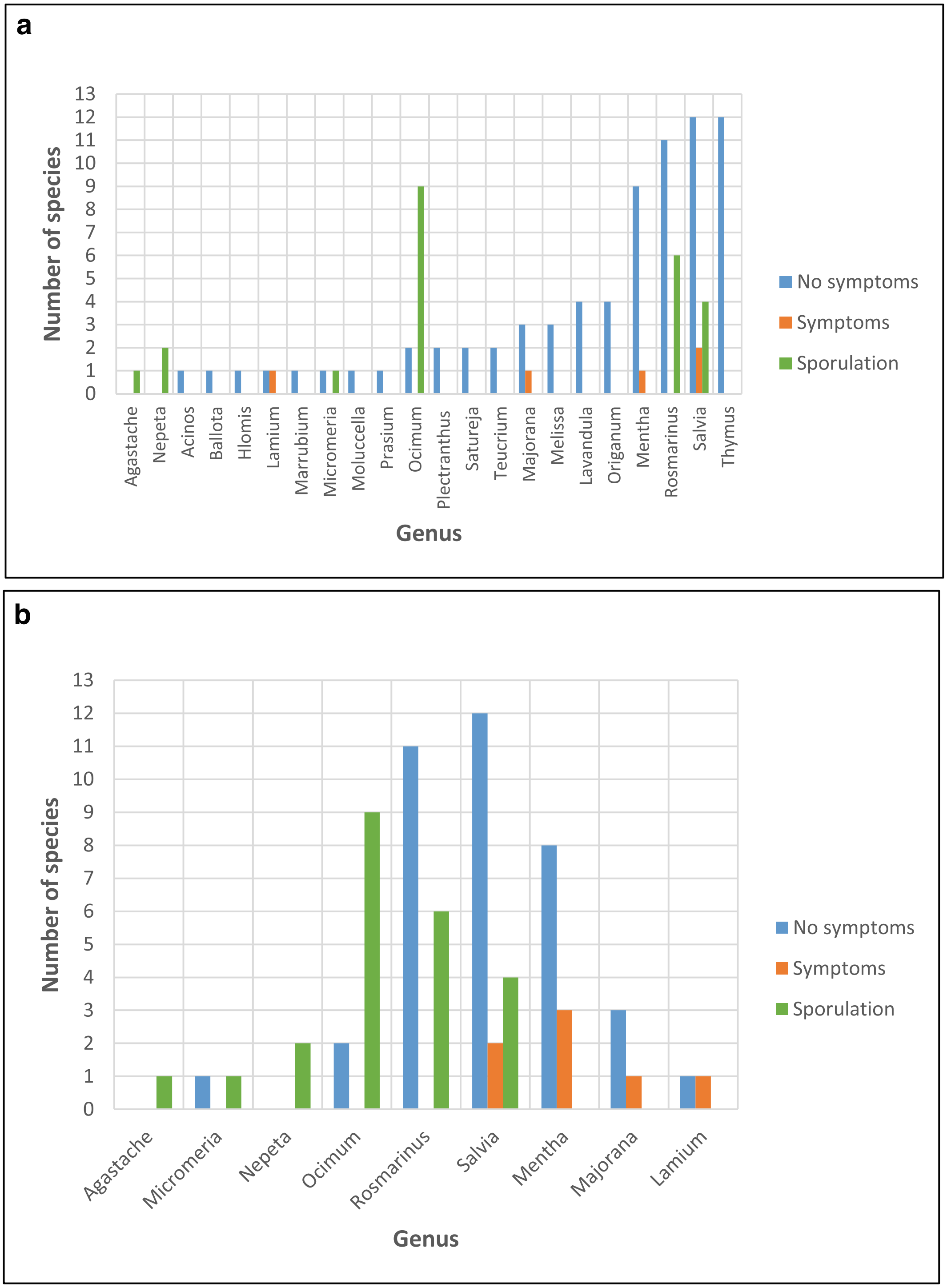

Fig. 1 Response of *Labiatae* speceies to inoculation with *Peronospora belbahrii*. **a** Response of all 102 entries; **b** Response of the nine responding genera

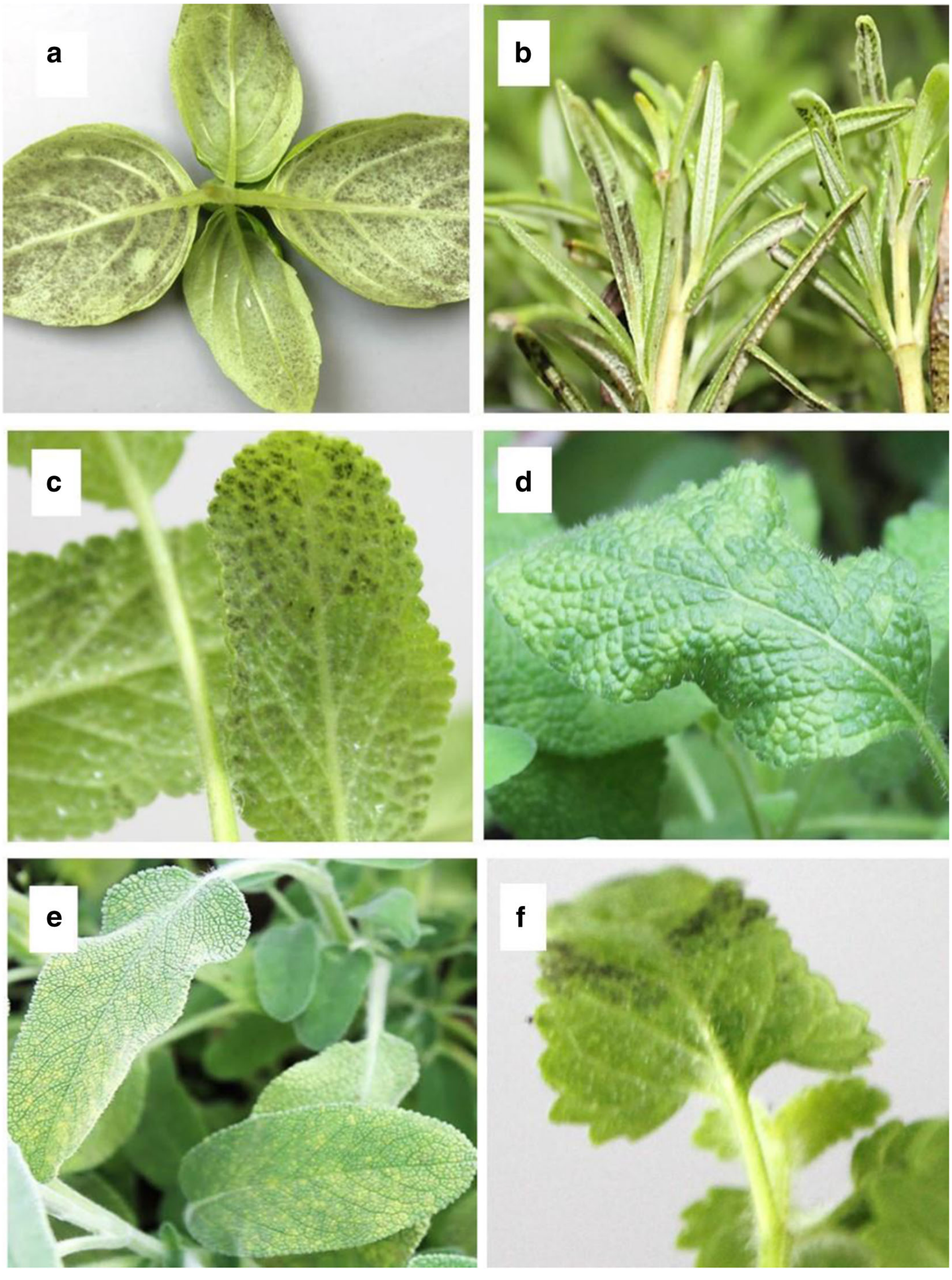

Fig. 2 The appearance of downy mildew caused by *Peronospora belbahrii* on some *Labiatae* species. **a** Sporulation on sweet basil leaves (*Ocimum basilicum* "Sweet basil"). **b** Sporulation on rosemary leaves (*Rosemarinus officinalis* "Barbecue"); **c** Sporulation on a sage leaf (*Salvia eigii*). **d** Symptoms of downy mildew on upper surface of a sage leaf (*Salvia fruticosa*). **e** Restricted chlorotic symptoms with no sporulation on sage leaf (*Salvia officinalis* "Maxiama"). **f** Sporulation on Nepeta leaf (*Nepeta curviflora*)

Koch postulates

Sporangia were collected from the sporulating *Labiatae* plants that had been inoculated with *P. belbahrii* and re-inoculated onto sweet basil plants in growth chambers. All basil plants showed BDM symptoms within a week and sporulated abundantly upon one-night of incubation in a dew chamber. Sporangia were collected from these basil plants and re-inoculated onto all *Labiatae* species in growth chambers. Again, the same six susceptible entries mentioned above became infected and subsequently sporulated under moist conditions.

Field observations

The response of the *Labiatae* entries to BDM in the field was similar to their response in growth chambers. Sporulation of *P. belbahrii* in field-grown plants was observed in six genera: *Ocimum*, *Salvia*, *Rosmarinus*, *Nepeta*, *Agastache*, and *Micromeria*. Symptoms of downy mildew with no sporulation of the pathogen were observed in *Mentha*, *Majorana*, *Lamium*, and two entries of *Salvia*. Plants of all other genera were free of disease symptoms. These responses were maintained all through the growing season until seed set.

Coleus downy mildew

Sporangia of *Peronospora* spp. (unidentified species) (Cohen et al. 2017) were collected from coleus and inoculated in growth chambers onto coleus, *Ocimum*, *Salvia*, *Rosmarinus*, *Nepeta*, *Agastache*, and *Micromeria*. At 10 dpi, only coleus plants showed symptoms of downy mildew with sporulation, while the other species showed neither symptoms nor sporulation.

Discussion

The present study confirms that the oomycete pathogen *Peronospora belbahrii* has additional hosts within the *Labiatae* family beside its major host, *Ocimum basilicum*. It affects endemic, ornamental, and agricultural species belonging to *Labiatae* in Israel. Symptoms of downy mildew with sporulation were observed following artificial inoculation with a *P. belbaharii* isolate in growth chambers in *Salvia eigii*, *Salvia fruticosa*, *Salvia pinnata*, *Rosmarinus officinalis*, *Nepeta curviflora*, *Micromeria fruticosa*, and *Agastache* spp. These species were also attacked by *P. belbahrii* under field conditions when artificially inoculated with the same isolate. All members of *Mentha*, *Lamium*, *Majorana*, and some *Salvia* showed symptoms but no sporulation in both growth chambers and the field.

Previous studies conducted with sweet and wild basils revealed differences in virulence among isolates in different countries. For example, in field studies resistance against BDM in the USA was reported by Wyenandt et al. (2010) in 'Spice' (*Ocimum* spp.), 'Blue Spice' (*Ocimum. americanum* × *Ocimum basilicum*) and 'Lime basil' (*O. americanum*), whereas incomplete resistance was reported in these lines against Israeli isolates (Ben-Naim et al. 2015). Similarly, resistance was reported in the USA in *O. basilicum var anisatum* accessions PI 172996, PI 172997, PI 172998, and PI 174284 (Koroch et al. 2013; Pyne et al. 2014) while disease symptoms accompanied with sporulation were observed in these accessions in Israel (Ben-Naim et al. 2015; Pyne et al. 2014).

To the best of our knowledge, this is the first report on the susceptibility of *Salvia eigii*, *S. fruticose*, and *S. pinnata* to downy mildew caused by *P. belbahrii* in Israel. Entries of the most common *Salvia* species (*S. officinalis*) were all resistant to BDM. *Salvia officinalis* was reported to also be susceptible to another downy mildew Caused by *Peronospora salviae-officinalis* (Choi et al. 2009; Thines et al. 2009).

This is also the first report in Israel on the susceptibility of three other *Labiatae* to *P. belbahrii*: rosemary (*Rosmarinus officinalis*), white leaved savory (*Micromeria fruticose*), and Syrian catnip (*Nepeta curviflora*). Rosemary is the only *Labiatae* species besides basil that was seen naturally infected with *P.belbahrii* in Israel (unpublished data). Current attempts are aimed to acertain the infection other five species in nature.

P. belbahrii from basil was infectious to *Agastache* spp. and vice versa, as reported by Denton et al. (2015), but unlike the report of Henricot et al. (2010), it was incompatible with coleus (*Plectranthus scutellarioides*). Natural infection with downy mildew of ornamental coleus was first observed in Israel in 2015 (Cohen et al. 2017). The sporangia collected from infected coleus plants were noninfectious to sweet basil and vice versa, sporangia taken from sweet basil were noninfectious to coleus. Here, we show that coleus downy mildew pathogen was neither infectious to the *Ocimum* species nor to the *Labiatae* entries found susceptible to the *P.belbahrii* isolate used in this study. These observations corroborate with Thines et al. (2009) who stated that *P.belbahhrii* is not pathogenic to coleus.

Acknowledgments We thank Eyal Klein of Hishtil Ltd. for supplying seeds and plant material.

Compliance with ethical standards

Conflict of interest This work was not submitted for publication to another journal. All authors listed have contributed to the work, have read the manuscript and declare that there are no potential conflicts of interest. This research was supported by Research Grant No. US-4947-16 R from BARD, the United States - Israel Binational Agricultural Research and Development Fund, and by a research grant from the Plant Council, Israel.

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