

## Development of *Erysiphe pulchra*, the causal agent of powdery mildew, on leaf disks of susceptible and resistant flowering dogwood (*Cornus florida*)

Y.H. Li, M.T. Windham, R.N. Trigiano, D.C. Fare, J.M. Spiers, and W.E. Copes

**Abstract:** Understanding the relative contribution of the different resistance components is necessary to develop selection schemes and accelerate resistant-cultivar development. This study was conducted to investigate spore germination, infection-structure formation, and fungal development of *Erysiphe pulchra*, the causal agent of powdery mildew, on leaf disks of six cultivars or lines of flowering dogwood (*Cornus florida*) with different levels of resistance. The cultivars and lines tested were grouped into the following three resistance categories: highly susceptible ('Cherokee Daybreak' and MW 94-60), moderately susceptible ('Cherokee Princess' and MW 95-25), and resistant ('Cherokee Brave' and 'Karen's Appalachian Blush'). Percentages of spore germination and secondary-appressoria formation were not significantly different among the cultivars and lines. Significantly less percent germinated conidia with branched hyphae were observed on resistant cultivars than on the moderately susceptible cultivar or line, which was less than on the highly susceptible cultivar or line. Infection efficiencies were significantly different among cultivars and lines in the three resistance categories, except that there were no differences between 'Cherokee Princess' and the resistant cultivars. Resistant cultivars supported shorter latent periods than moderately and highly susceptible cultivars or lines, but no differences in latent period were detected between the later two resistance categories. The recently released 'Karen's Appalachian Blush' expressed higher levels of resistance to powdery mildew than did 'Cherokee Brave', as indicated by the longer latent period and reduced relative sporulation of the pathogen.

*Key words:* resistance, dogwood, *Cornus florida*, resistance, *Erysiphe pulchra*, *Microsphaera pulchra*.

**Résumé :** Comprendre la contribution relative des différents éléments de la résistance est nécessaire pour établir des plans de sélection et accélérer le développement de cultivars résistants. La présente recherche fut menée pour étudier la germination des spores, la formation des structures d'infection et le développement fongique de l'*Erysiphe pulchra*, agent responsable de l'oïdium, sur des rondelles de feuilles de six cultivars ou lignées de cornouiller (*Cornus florida*) en fleurs possédant différents degrés de résistance. Les cultivars et lignées testés étaient regroupés selon trois catégories de résistance : très sensibles ('Cherokee Daybreak' et MW 94-60), moyennement sensibles ('Cherokee Princess' et MW 95-25) et résistants ('Cherokee Brave' et 'Karen's Appalachian Blush'). Les pourcentages de germination des spores et la formation d'appressoria secondaires n'étaient pas significativement différents parmi les cultivars et lignées. Le pourcentage de conidies germées avec hyphes ramifiées observé chez les cultivars résistants fut significativement moins élevé que ceux du cultivar et de la lignée moyennement sensibles, eux-même moins élevés que ceux du cultivar et de la lignée très sensibles. L'efficacité de l'infection fut significativement différente parmi les cultivars et lignées dans les trois catégories de résistance, sauf entre 'Cherokee Princess' et les cultivars résistants. Les cultivars résistants ont connu des périodes de latence plus courtes que les cultivars et lignées moyennement et très sensibles, mais aucune différence dans la période de latence ne fut détectée entre ces deux dernières catégories de résistance. Le 'Karen's Appalachian Blush', récemment mis sur le marché, résiste mieux à l'oïdium que le 'Cherokee Brave', tel que révélé par la période de latence plus longue et une sporulation relativement plus faible de l'agent pathogène.

*Mots clés :* résistance, cornouiller, *Cornus florida*, *Erysiphe pulchra*, *Microsphaera pulchra*.

Accepted 28 September 2005.

**Y.H. Li, M.T. Windham,<sup>1</sup> and R.N. Trigiano.** Department of Entomology and Plant Pathology, University of Tennessee, Knoxville, TN 37996-4560, USA.

**D.C. Fare.** Floral and Nursery Plants Research Unit, Agricultural Research Service (ARS), US Department of Agriculture (USDA), McMinnville, TN 37110, USA.

**J.M. Spiers and W.E. Copes.** Small Fruit Research Unit, USDA-ARS, Poplarville, MS 39470, USA.

<sup>1</sup>Corresponding author (e-mail: mwindham@utk.edu).

## Introduction

Epidemics of powdery mildew caused by *Erysiphe pulchra* (Cooke and Peck) U. Braun & S. Takamatsu (syn. *Microsphaera pulchra* Cooke and Peck) have impeded flowering dogwood (*Cornus florida* L.) production throughout the eastern United States. Differences in levels of resistance to *E. pulchra* were identified among dogwood seedlings and cultivars. ‘Cherokee Brave’, a pink-bracted flowering dogwood cultivar, was highly resistant to powdery mildew in nurseries (Hagan et al. 1998; Windham and Witte 1998). A white-bracted flowering dogwood cultivar, ‘Karen’s Appalachian Blush’, has also been reported to have a high level of resistance to powdery mildew, and it was released by the Agricultural Experiment Station at the University of Tennessee, Knoxville, United States (Windham et al. 2003). Additionally, some dogwood seedlings have expressed partial resistance to powdery mildew, with slower disease progress than susceptible cultivars (Windham and Witte 1998).

Fungal pathogen development on plants, and within, can be affected by host resistance at many stages of the infection process (Niks and Rubiales 2002), such as spore germination (Korban and Riemer 1990), haustorium formation (Martinez et al. 2004), and hyphal growth (Carver and Carr 1978). Infection efficiency, latent period, and sporulation have been used as components to evaluate partial resistance to plant diseases (Díaz-Lago et al. 2003; Lindhout et al. 1994; Parlevliet 1989; Viljanen-Rollinson et al. 1998). The infection process of *E. pulchra* on dogwood leaves has been observed under scanning electron microscope (Li et al., 2005), but differences in spore germination, appressoria formation, hyphal growth, and reproduction of the pathogen on dogwood cultivars with different levels of resistance to powdery mildew were unclear. The objectives of the present study were to investigate the expression of resistance during the infection-structure formation and colony development of *E. pulchra* and to evaluate components of resistance to powdery mildew in flowering dogwood cultivars and lines, using leaf disks.

## Materials and methods

### Cultivars and lines

One 3- or 4-year-old tree for each of the flowering dogwood cultivars (‘Karen’s Appalachian Blush’, ‘Cherokee Brave’, ‘Cherokee Princess’, and ‘Cherokee Daybreak’) and lines (MW 95-25 and MW 94-60) were grown in containers and maintained in a greenhouse at the University of Tennessee, Knoxville. These lines were chosen because of their different levels of resistance to powdery mildew (Hagan et al. 1998; M.T. Windham, unpublished data). A fully expanded leaf was collected from each of the six cultivars or lines. Three leaf disks each, 2.0 and 0.9 cm in diameter, were acquired with cork borers, respectively for evaluation of spore germination, latent period, infection efficiency, disease severity, and sporulation and of formation of secondary appressoria and growth of branched hyphae. One leaf disk of each cultivar and line tested was randomly placed on two layers of moistened filter paper in Petri dishes, 9 or 6 cm in diameter, for inoculation.

The experiments were arranged in a randomized complete block design with three blocks and three subsamplings (leaf disks) in a block. The inoculation of one set of three Petri dishes in a settling tower was considered a block, and each block was inoculated separately. The experiments were repeated twice.

### Inoculation

Inoculum of *E. pulchra* was maintained on flowering dogwood trees of ‘Cherokee Princess’ in a greenhouse at the campus of the University of Tennessee. Foliage of infected dogwood trees was shaken by hand to remove old existing conidia 2 days before infected leaves were collected to serve as an inoculum source. Infected leaves were hung at the top of a 0.44 m high settling tower, 0.26 m in diameter, and opened Petri dishes containing leaf disks were placed on the bottom. Air discharged at a pressure of 50 psi (1 psi = 6.895 kPa) with a compressor (Gast Manufacturing Inc., Benton Harbor, Mich.) dispersed newly formed conidia from the infected leaves. To monitor conidia deposition, a glass slide was also placed in the settling tower, and the number of conidia within an area of 1 cm<sup>2</sup> of the slide was counted under a compound microscope. The spore density on leaf disks was maintained at 400–600 spores/cm<sup>2</sup> by adjusting the number of air blasts. For evaluation of infection efficiency, the precise number of conidia per square centimetre of glass slide was recorded for each run. Inoculated leaf disks in Petri dishes were incubated at 20 ± 2 °C, under a 19 h photoperiod, and water was added to filter papers, as needed, to maintain high relative humidity in the dishes.

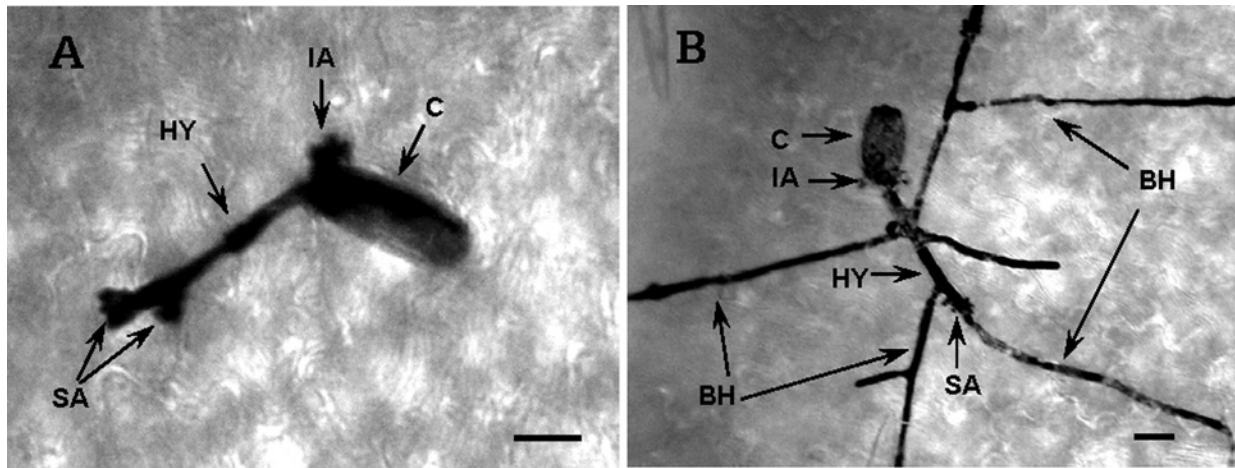
### Germination of conidia

A conidium was considered germinated when a germ tube formed an initial appressorium or when a germ-tube length was at least half the width of a conidium. At 24 h after inoculation (hai), the percentage of germinated conidia was assessed on a random sample of 100 conidia per leaf disk, 2 cm in diameter, viewed under an Olympus® SZH10 stereo microscope (magnification, × 60).

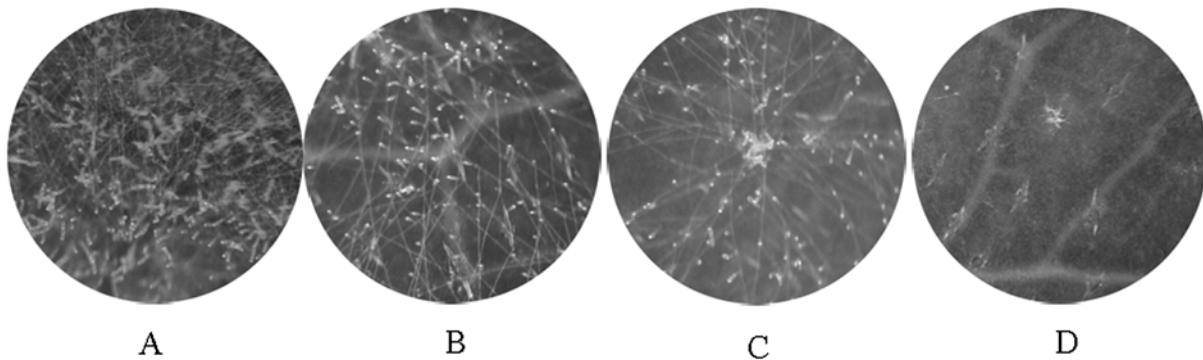
### Formation of secondary appressoria and growth of branched hyphae

To observe secondary-appressoria formation and branched hyphal growth, inoculated leaf disks, 0.9 cm in diameter, were sampled from the Petri dishes at 48 and 72 hai. The disks were cleared and stained according to the method described by Schiffer et al. (1997). Sample disks were placed on two layers of filter paper saturated with a solution of 0.15% trichloroacetic acid in chloroform–alcohol (1:4, v/v) in Petri dishes, 6 cm in diameter, at room temperature. Filter papers within the Petri dishes were changed once, at 24 h during a 48 h period. Cleared leaf disks were stained with 0.6% Coomassie Brilliant Blue R-250 in 10% trichloroacetic acid for 30 s, washed with tap water, mounted in 50% glycerol on glass slides, and examined under an Olympus BH-2 compound microscope (magnification, × 400). One hundred germinated conidia were randomly examined on each leaf disk, and the percentages of germinated conidia with secondary appressoria (48 hai) and with branching hyphae (72 hai) were recorded for each leaf disk (Fig. 1).

**Fig. 1.** Light micrographs of germinated conidia of *Erysiphe pulchra*, causal agent of powdery mildew, on dogwood (*Cornus florida*) leaf disks cleared and stained with 0.6% Coomassie Brilliant Blue R-250 at 3 days after inoculation. **Fig. 1A.** Germinated conidium (C), with initial appressoria (IA), hyphae (HY), and secondary appressoria (SA). **Fig. 1B.** Germinated conidium with branched hyphae (BH). Bars, 10  $\mu$ m.



**Fig. 2.** Stereo-light micrographs representing the relative sporulation scales, from + to +++++, of colonies of *Erysiphe pulchra* on dogwood (*Cornus florida*) leaf disks. The relative sporulation scale is defined, as follows, by the percent area of dogwood leaf disks covered by chain conidia (CC) of the pathogen. **Fig. 2A.** +++++, CC > 50%. **Fig. 2B.** +++, 20%  $\leq$  CC  $\leq$  50%. **Fig. 2C.** ++, 5%  $\leq$  CC < 20%. **Fig. 2D.** +, CC < 5%.



### Infection efficiency

Infection efficiency was defined as the percentage of inoculated conidia that formed colonies on a leaf disk, 2 cm in diameter, at 8 days after inoculation (dai). A colony was defined as a germinated conidium that formed more than five branched hyphae. The numbers of powdery mildew colonies were counted under a stereo microscope (magnification,  $\times 30$ ), and the infection efficiency on each leaf disk was calculated using the equation  $IE (\%) = [C/(S \times A)] \times 100$ , where  $C$  is the number of colonies formed on a leaf disk,  $S$  is the number of conidia inoculated on 1  $\text{cm}^2$  of the leaf-disk area, and  $A$  is the total area of the leaf disk.

### Latent period

The latent period was defined as the time at which conidiophores and conidia were first observed on inoculated leaf disks. Conidiophores and conidia formation were examined on leaf disks, 2 cm in diameter, under a dissecting microscope (magnification,  $\times 60$ ), and the latent period was assessed daily after inoculation. Since preliminary experiments showed a delayed latent period for 'Karen's Appalachian Blush', the assessment lasted 6 weeks after inoculation.

### Disease severity and sporulation

Disease severity on leaf disks was rated according to a 0 to 6 scale of disease index that represented the percent diseased area (DA) as follows: DA = 0, no disease; 1,  $0 < DA < 5\%$ ; 2,  $5\% \leq DA < 15\%$ ; 3,  $15\% \leq DA < 30\%$ ; 4,  $30\% \leq DA < 50\%$ ; 5,  $50\% \leq DA < 75\%$ ; 6,  $75\% \leq DA \leq 100\%$ . Disease index was recorded, under a stereo microscope, on each of leaf disks 2 cm in diameter at 14 dai and was transformed to the midpoint of percent diseased areas of each index. At 5 weeks after inoculation, relative sporulation on dogwood leaf disks was rated as follows, on a five-points scale that represented the percent area covered by chain conidia (CC) of colonies of *E. pulchra*: -, no sporulation; +, CC < 5%; ++,  $5\% \leq CC < 20\%$ ; +++,  $20\% \leq CC \leq 50\%$ ; +++++, CC > 50% (Fig. 2).

### Data analysis

The data were analyzed as a randomized complete block design with subsamples. The experimental unit was a leaf, and the three disks from the leaf were considered as subsamples. The blocks were considered as random effects, and treatments (cultivars) were considered as fixed effects. Ef-



fects of block, cultivars or lines, and their interactions on conidia germination, secondary-appressoria formation, germinated conidia with branched hyphae, infection efficiency, latent period, and disease severity were determined by analysis of variance (ANOVA), using the general linear model (GLM) procedure of SAS, version 9.1 (SAS Institute Inc. 2004). Mean separations for each variable were conducted using the least significant difference test at  $P = 0.05$ .

## Results

### Germination of conidia and formation of secondary appressoria

Fifty to fifty-seven percent of conidia germinated at 24 hai, and 90% to 95% of germinated conidia formed secondary appressoria at 48 hai on leaf disks of all the dogwood cultivars and lines tested. There were no significant differences in percentages of spore germination ( $P = 0.1435$ ) and germinated conidia with secondary appressoria ( $P = 0.2267$ ) among any dogwood cultivars and lines.

### Germinated conidia with branched hyphae

Flowering dogwood cultivars and lines significantly contributed to total variances of germinated conidia with branched hyphae (Table 1). No significant differences in percentages of germinated conidia with branched hyphae were detected among 'Cherokee Brave', 'Karen's Appalachian Blush', and MW 95-25, which had lower levels than the other cultivars or line. 'Cherokee Daybreak' supported the greatest percentages of germinated conidia with branched hyphae among cultivars and lines tested. Percent germinated conidia with branched hyphae for MW 94-60 were less than for 'Cherokee Daybreak', but greater than for 'Cherokee Princess' (Table 1).

### Infection efficiency

Significant differences in fungal infection efficiencies were detected among dogwood cultivars and lines (Table 1). Compared with the other four cultivars or lines, 'Cherokee Brave' and 'Karen's Appalachian Blush' supported lower values of infection efficiencies, which were not significantly different from each other. The infection efficiency for 'Cherokee Daybreak' was less than for MW 94-60, and both values were significantly higher than for 'Cherokee Princess' and MW 95-25. No significant differences in infection efficiencies were detected between 'Cherokee Princess' and MW 95-25 (Table 1).

### Latent period

Flowering dogwood cultivars and lines significantly contributed to the total variance of latent period (Table 1). Latent periods of the pathogen on both 'Karen's Appalachian Blush' and 'Cherokee Brave' were longer than on the other four cultivars or lines, but the latent period on 'Karen's Appalachian Blush' was 19 days longer than on 'Cherokee Brave'. No significant differences in latent period were detected among 'Cherokee Daybreak', MW 94-60, 'Cherokee Princess', and MW 95-25, except a significantly shorter latent period on MW 94-60 than on 'Cherokee Princess' and MW 95-25 (Table 1).

### Disease severity and sporulation

Disease severity of powdery mildew was significantly different among flowering dogwood cultivars and lines tested (Table 1). 'Cherokee Brave' and 'Karen's Appalachian Blush' supported significantly lower disease severity than the other four cultivars or lines, in which, 'Cherokee Daybreak' and MW 94-60 were more susceptible than 'Cherokee Princess' and MW 95-25. Significant differences in disease severity between 'Cherokee Princess' and MW 95-25 were also detected (Table 1).

Higher relative sporulation of the pathogen was detected on 'Cherokee Daybreak' and MW 94-60 than on the other four cultivars or line. The relative sporulation on 'Cherokee Princess' and MW 95-25 was moderate among cultivars and lines tested. 'Cherokee Brave' supported little sporulation, whereas sporulation on 'Karen's Appalachian Blush' was so sparse that it was visible only microscopically (Table 1 and Fig. 2).

The flowering dogwood cultivars and lines tested were grouped into three categories of resistance to powdery mildew, according to disease severities combined with relative sporulation: highly susceptible ('Cherokee Daybreak' and MW 94-60), moderately susceptible ('Cherokee Princess' and MW 95-25), and resistant ('Cherokee Brave' and 'Karen's Appalachian Blush') (Table 1).

## Discussion

Flowering dogwood cultivars and lines tested in the present study expressed different levels of resistance to powdery mildew on leaf disks. Among them, 'Cherokee Daybreak' and MW 94-60 were highly susceptible, 'Cherokee Princess' and MW 95-25 were moderately susceptible, and 'Cherokee Brave' and 'Karen's Appalachian Blush' were resistant. Hagan et al. (1998) reported similar disease indexes for 'Cherokee Daybreak' and 'Cherokee Princess' in the field, which differed from the present data according to which 'Cherokee Daybreak' was more susceptible than 'Cherokee Princess'. This apparent difference is probably due to Hagan's et al. (1998) estimate being based on disease incidence within foliage, whereas, in the present study, the estimate was based on disease severity evaluated by diseased area. 'Cherokee Brave' was almost free of powdery mildew in the nurseries in Alabama (Hagan et al. 1995, 1998), but the incidence of diseased foliage was 10% in the nursery in Tennessee (Windham and Witte 1998; Windham et al. 2003). In the present study, 'Karen's Appalachian Blush' supported a longer latent period and smaller amount of sporulation of the pathogen than 'Cherokee Brave'. These results agree with the previous finding that 'Karen's Appalachian Blush' was more resistant to powdery mildew than 'Cherokee Brave' (Windham et al. 2003).

Percent germination of conidia and percent formation of secondary appressoria were similar among the cultivars. Therefore, resistance to *E. pulchra* in flowering dogwood may not be expressed before secondary-appressoria formation. Similar results have been found with *Oidium lycopersicum* Cooke & Massee on *Lycopersicon* species (Huang et al. 1998), *Erysiphe pisi* DC. on sweet pea (*Pisum sativum* L.) (Poulter et al. 2003; Viljanen-Rollinson et al. 1998), *Sphaerotheca fuliginea* (Schlechtend.:Fr.) Pollacci

**Table 1.** Comparison of resistance categories to powdery mildew and disease severity (DS) in cultivars and lines of flowering dogwood (*Cornus florida*), and summary on percentage of germinated conidia with branching hyphae (GCBH), percentage of infection efficiency (IE), latent period (LP), and relative sporulation (RS) of the causal agent, *Erysiphe pulchra*.

Cultivar or line	Mean					Resistance category <sup>†</sup>
	GCBH (%) (3 dai)	IE (%) (8 dai)	LP (days)	DS (%) (14 dai)	RS (35 dai)*	
'Cherokee Daybreak'	45.7 a	6.12 b	8 cd	87 a	++++	HS
MW 94-60	33.7 b	8.00 a	7 d	87 a	++++	HS
'Cherokee Princess'	18.0 c	0.66 cd	10 c	65 b	+++	MS
MW 95-25	8.2 d	1.94 c	10 c	48 c	+++	MS
'Cherokee Brave'	5.4 d	0.01 d	16 b	8 d	++	R
'Karen's Appalachian Blush'	4.2 d	0.08 d	35 a	0 d	+	R
<i>P</i> > <i>F</i>	0.0047	0.0002	<0.0001	<0.0001		
LSD	7.6	1.61	3	10		

**Note:** Means followed by the same letter within a column, for each variable, are not significantly different from each other at the *P* = 0.05 level according to the least significant difference (LSD). dai, days after inoculation for assessment of variables.

\*Relative sporulation was rated on a five-points scale representing the percent area of dogwood leaf disks covered by chain conidia (CC) of colonies of *E. pulchra*: -, no sporulation; +, CC < 5%; ++, 5% ≤ CC < 20%; +++, 20% ≤ CC ≤ 50%; +++++, CC > 50%.

<sup>†</sup>Resistance was categorized using a combination of DS and RS. HS, highly susceptible; MS, moderately susceptible; R, resistant.

on melon (*Cucumis melo* L.) (Cohen and Eyal 1988; Floris and Alvarez 1996; Kuzuya et al. 2003; Pérez-García et al. 2001), and *Erysiphe polygoni* DC. on mungbean (*Vigna radiata* (L.) Wilczek) (Reddy et al. 2001). In contrast, differences in percentages of spore germination between susceptible and resistant cultivars were reported for *Podosphaera leucotricha* (Ellis & Everh.) Salmon in apple (*Malus domestica* Borkh.) (Korban and Riemer 1990). Huang et al. (1998) reported significant differences in the number of formations of secondary appressoria of *O. lycopersicum*, but not in the primary appressoria, between resistant and susceptible *Lycopersicon* species. Stimulation of formation of normal and mature appressoria of *Erysiphe graminis* DC. f. sp. *hordei* Ém. Marchal and *E. graminis* DC. f. sp. *tritici* Ém. Marchal by physical structure of wax layer on barley and wheat leaf surface was reported, and the physical structure was considered more important than the chemical composition of the wax layer (Ellingboe 1972). Since conidia of *E. pulchra* germinated and formed initial and secondary appressoria on glass slides (Li et al. 2005), it is not surprising that dogwood cultivars did not affect germination of *E. pulchra* in this study. Mechanisms of resistance to powdery mildew in flowering dogwood probably do not involve suppression of primary- and secondary-appressoria formation.

Slower disease development and slower spore production for pathogens in nonhypersensitive types of resistance may result from frequent failure of haustorium formation (Niks 1986) or from restriction of colony growth (Carver and Carr 1978). Restriction or inhibition of hyphal growth on resistant cultivars has been reported in other powdery mildew pathosystems (Floris and Alvarez 1996; Huang et al. 1998; Kuzuya et al. 2003; Poulter et al. 2003). In this study, percentages of germinated conidia with branched hyphae and colony numbers of *E. pulchra* were lower on resistant and moderately susceptible cultivars and lines than on highly susceptible cultivar and line. Furthermore, conidia production in powdery mildew colonies decreased in the order from highly susceptible to moderately susceptible, to resistant cultivars and lines. The resistance characterized by a

continuous variation in sporulation has been defined as partial resistance (Niks and Rubiales 2002; Parlevliet 1992). Therefore, the results of the present study support the previous finding that partial resistance to powdery mildew could exist in flowering dogwood (Windham et Witte 1998). Existence of functional haustoria and maintenance of a sufficient nutrient supply from the host is critical to the fungal development. Further histochemical and ultrastructure studies are needed to understand mechanisms of resistance in flowering dogwood during penetration and haustorium formation of *E. pulchra*.

Infection efficiency, latent period, and sporulation are considered major epidemiological components, and a negative effect on any one or a combination of these pathogen characteristics could represent partial resistance in the field (Parlevliet 1989). In different pathosystems, however, one component might more adequately represent partial resistance in the field than other components (Viljanen-Rollinson et al. 1998). For example, in the barley-leaf rust system, latent period was better correlated with partial resistance in the field than was infection efficiency (Parlevliet 1979). In contrast, infection efficiency was more related to partial resistance for *E. graminis* f. sp. *tritici* in wheat (Kinane and Jones 2000). Resistance to *E. pisi* in peas was expressed by a reduction of infection efficiency and lower sporulation rates, but there was no effect on latent period (Viljanen-Rollinson et al. 1998). Resistance to *O. lycopersicum* in wild tomato species was also characterized by a very low infection frequency and lack of sporulation (Lindhout et al. 1994). Longer latent period and lower sporulation rates of *S. fuliginea* were reported on moderately resistant cultivars in comparison with highly susceptible cultivars in melon (Floris and Alvarez 1996). In the present study, infection efficiency and sporulation could be used to differentiate resistant and moderately susceptible cultivars from highly susceptible cultivars, whereas latent period and sporulation could be used to differentiate resistant and moderately susceptible cultivars. Variable mechanisms of resistance, including prevention of establishing parasitic relationship, restriction of

hyphal growth, and reduction of sporulation may exist in the dogwood – powdery mildew pathosystem.

This is the first report on microscopic observation of the fungal development of *E. pulchra* on susceptible and resistant flowering dogwood leaf disks and on the evaluation of resistance components to powdery mildew in flowering dogwood. The results may be useful in developing a rapid and convenient method to screen dogwood seedlings, selections, and cultivars for resistance to powdery mildew in laboratory.

## Acknowledgements

This study was supported by funding from USDA–ARS (58-6404-2-0057).

## References

- Carver, T.L.W., and Carr, A.J.H. 1978. Effects of host resistance on the development of haustoria and colonies of oat mildew. *Ann. Appl. Biol.* 88: 171–178.
- Cohen, Y., and Eyal, H. 1988. Epifluorescence microscopy of *Sphaerotheca fuliginea* race 2 on susceptible and resistant genotypes of *Cucumis melo*. *Phytopathology*, 78: 144–148.
- Díaz-Lago, J.E., Stuthman, D.D., and Leonard, K.J. 2003. Evaluation of components of partial resistance to oat crown rust using digital image analysis. *Plant Dis.* 87: 667–674.
- Ellingboe, A.H. 1972. Genetics and physiology of initial infection by *Erysiphe graminis*. *Phytopathology*, 62: 401–406.
- Floris, E., and Alvarez, J.M. 1996. Nature of resistance of seven melon lines to *Sphaerotheca fuliginea*. *Plant Pathol.* (London), 45: 155–160.
- Hagan, A.K., Gilliam, C.H., Keever, G.J., and Williams, J.D. 1995. Dogwood resist powdery mildew. *Highlights Agric. Res.* 42(4): 9–10.
- Hagan, A.K., Hardin, B., Gilliam, C.H., Keever, G.J., Williams, J.D., and Eakes, J. 1998. Susceptibility of cultivars of several dogwood taxa to powdery mildew and spot anthracnose. *J. Environ. Hortic.* 16: 147–151.
- Huang, C.C., Groot, T., Meijer-Dekens, F., Niks, R.E., and Lindhout, P. 1998. The resistance to powdery mildew (*Oidium lycopersicum*) in *Lycopersicon* species is mainly associated with hypersensitive response. *Eur. J. Plant Pathol.* 104: 399–407.
- Kinane, J.T., and Jones, P.W. 2000. Components of partial resistance to powdery mildew in wheat mutants. *Eur. J. Plant Pathol.* 106: 607–612.
- Korban, S.S., and Riemer, S.E. 1990. Genetics and histology of powdery mildew resistance in apple. *Euphytica*, 48: 261–267.
- Kuzuya, M., Hosoya, K., Tomita, K., and Ezura, H. 2003. Powdery mildew (*Sphaerotheca fuliginea*) resistance in melon is selectable at the haploid level. *J. Exp. Bot.* 54: 1069–1074.
- Li, Y.H., Windham, M.T., Trigiano, R.N., Fare, D.C., Spiers, J.M., and Copes, W.E. 2005. Spore germination, infection structure formation and colony development of *Erysiphe pulchra* on dogwood leaves and glass slides. *Plant Dis.* 89: 1301–1305.
- Lindhout, P., Pet, G., and Van der Beek, J.G. 1994. Screening wild *Lycopersicon* species for resistance to powdery mildew (*Oidium lycopersicum*). *Euphytica*, 72: 43–49.
- Martinez, F., Sillero, J.C., and Rubiales, D. 2004. Effect of host plant resistance on haustorium formation in cereal rust fungi. *J. Phytopathol.* (Berlin), 152: 381–382.
- Niks, R.E. 1986. Failure of haustorial development as factor in slow growth and development of *Puccinia hordei* in partially resistant barley seedlings. *Physiol. Mol. Plant Pathol.* 28: 309–322.
- Niks, R.E., and Rubiales, D. 2002. Potentially durable resistance mechanisms in plants to specialized fungal pathogens. *Euphytica*, 124: 201–216.
- Parlevliet, J.E. 1979. Components of resistance that reduce the rate of epidemic development. *Annu. Rev. Phytopathol.* 17: 203–222.
- Parlevliet, J.E. 1989. Identification and evaluation of quantitative resistance. *In Plant disease epidemiology*. Vol. 2. Genetics, resistance and management. Edited by K.J. Leonard and W.E. Fry. McGraw-Hill Publishing Company, London, UK. pp. 215–248.
- Parlevliet, J.E. 1992. Selecting components of partial resistance. *In Plant breeding in the 1990s*. Proceedings of the Symposium on Plant Breeding in the 1990s, March 1991, North Carolina State University, Raleigh, N.C. Edited by H.T. Stalker and J.P. Murphy. CAB International, Wallingford, Oxon, UK. pp. 281–302.
- Pérez-García, A., Olalla, L., Rivera, E., Del Pino D., Cánovas, I., De Vicente, A., and Torés, J.A. 2001. Development of *Sphaerotheca fusca* on susceptible, resistant, and temperature-sensitive resistant melon cultivars. *Mycol. Res.* 10: 1216–1222.
- Poulter, R., Harvey, L., and Burritt, D.J. 2003. Qualitative resistance to powdery mildew in hybrid sweet peas. *Euphytica*, 133: 349–358.
- Reddy, K.S., Pawar, S., and Bhatia, C.R. 2001. Host response of *Vigna radiata* genotypes to powdery mildew infection. *Indian Phytopathol.* 54: 117–120.
- SAS Institute Inc. 2004. SAS/STAT user's guide. Version 9.1. SAS Institute Inc., Cary, N.C.
- Schiffer, R., Görg, R., Jarosch, B., Beckhove, U., Bahrenberg, G., Kogel, K., and Schulze-Lefert, P. 1997. Tissue dependence and differential cordycepin sensitivity of race-specific resistance responses in the barley – powdery mildew interaction. *Mol. Plant–Microbe Interact.* 10: 830–839.
- Viljanen-Rollinson, S.L.H., Gaunt, R.E., Frampton, C.M.A., Falloon, R.E., and McNeil, D.L. 1998. Components of quantitative resistance to powdery mildew (*Erysiphe pisi*) in pea (*Pisum sativum*). *Plant Pathol.* (London), 47: 137–147.
- Windham, M.T., and Witte, W.T. 1998. Naturally occurring resistance to powdery mildew in seedlings of *Cornus florida*. *J. Environ. Hortic.* 16: 173–175.
- Windham, M.T., Witte, W.T., and Trigiano, R.N. 2003. Three white-bracted cultivars of *Cornus florida* resistant to powdery mildew. *HortScience*, 38: 1253–1255.