

VARIATION IN FIELD SUSCEPTIBILITY OF NATIVE AND EXOTIC ASH SPECIES TO ANTHRACNOSE

by Karel Jacobs¹ and Donna Danielson²

Abstract. Eight *Fraxinus* species and several cultivars of *F. americana* (white ash), *F. pennsylvanica* (green ash), *F. angustifolia* (Syrian ash), and *F. excelsior* (European ash) were evaluated for susceptibility to anthracnose disease during 1997, 1998, and 1999. Budbreak and leaf emergence rates were also recorded. The following results were found: *F. chinensis* (Chinese ash) was most susceptible followed by *F. angustifolia*, *F. pennsylvanica* and, to a lesser degree, *F. mandshurica* (Manchurian ash). The European *F. excelsior* was similar to *F. mandshurica* and appeared moderately susceptible, while the North American native *F. tomentosa* (pumpkin ash) and *F. americana* were comparatively tolerant of the disease. *Fraxinus quadrangulata* (blue ash) was resistant and showed virtually no symptoms in any year. Significant variation existed among cultivars and varieties of certain species including the widely planted green ash in which 'Patmore' and the newly available 'Cimmaron' appeared least susceptible. Despite weak statistical support, we observed a general trend in which trees that leafed out earlier developed more disease than those that leafed out later.

Key Words. Differential resistance; *Gnomoniella fraxini*; *Discula fraxinea*; phenology; *Mycosphaerella*; *Fraxinus* spp.; anthracnose.

The genus *Fraxinus* is distributed in temperate regions of Asia, Europe, and North America and consists of 62 species according to Lingelsheim (1920). Relatively few taxa are grown commonly in urban landscapes. These include green and white ash in the United States, which are favored because of their rapid growth rate, rich fall color, and tolerance to urban stresses.

A common disease of ash in urban environments is anthracnose. The disease is caused by the fungus *Gnomoniella fraxini* Redlin & Stack (anamorph = *Discula fraxinea* (Peck) Redlin & Stack) (Redlin and Stack 1988a) and while not lethal, it compromises photosynthesis and tree health by producing necrotic leaf blotches and in some cases, premature defoliation. Certain ash species are reportedly less prone to anthracnose than others (Ogawa et al. 1977; Sinclair et al. 1987), but data on comparative susceptibility of most species are lacking. The pathogen attacks foliage, petioles, and twigs via primary inoculum (conidia) originating from petioles and twig cankers (Ogawa et al. 1977; Sinclair 1987; Redlin and Stack

1988b). Spore release is dependent on spring rains and their germination on leaf wetness. Like other foliar diseases, infection is more severe when emerging, succulent leaves and shoots coincide with spore release.

In this study, we sought to compare genetic variation in anthracnose resistance among *Fraxinus* spp. as well as varieties and cultivars of four species. We also investigated whether inherent variation in budbreak and leaf emergence periods among taxa might be associated with disease susceptibility in the field.

METHODS

During three growing seasons (1997 through 1999), 161 to 256 ash trees representing 22 species were evaluated for anthracnose symptoms. Each year, trees on the grounds of The Morton Arboretum [25 mi (40 km) west of Chicago, Illinois, U.S.; USDA Hardiness Zone 5b] were rated by two individuals at the time of peak symptom expression (late June to early July). Each tree was assigned a disease severity rating (DSR) between 1 (no foliar symptoms) and 5 (greater than 75% of the canopy with necrotic blotches on leaves) (Figure 1).

Budbreak and comparative leaf emergence stages were determined by assigning each tree a number between 0 (no budbreak) and 4 (full leaf emergence) on each of two dates during May of 1998 and 1999. The accumulated degree days that coincided with the beginning of the observation periods, and a wide range of leaf emergence stages, was 252.5 degree days base 50. At slightly more degree days, most plants had fully leafed-out, precluding us from observing potential differences among taxa. Degree-day prediction of budbreak and leaf emergence is a more accurate guide than calendar date (see Herms 1999) for observing taxa differences in subsequent years.

Variation in DSR was analyzed utilizing the General Linear Model and means separations procedures (SPSS, Inc. 1999). To test whether an association existed between leaf emergence stage and disease severity, correlation analysis using Spearman's matrix for rank order data, and Chi-square analysis were conducted (SPSS, Inc. 1999). Data are presented only for the eight species in which ten or more trees were evaluated.

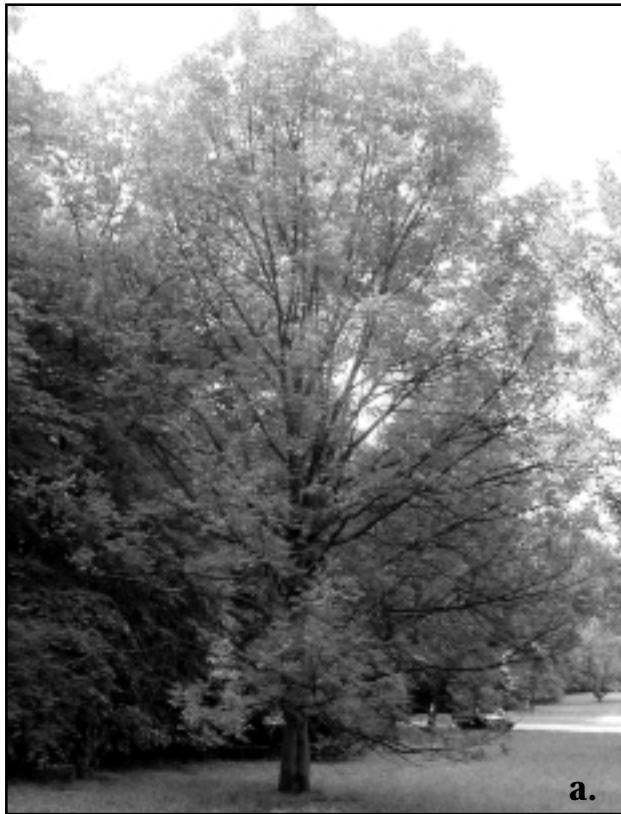


Figure 1. Ash tree showing foliar necrosis typical of anthracnose. The tree was assigned a disease severity rating of 5, indicating more than 75% of the canopy exhibited symptoms. (Note: Color photographs may be viewed online at www.mortonarb.org/plantinfo/plantclinic/phc/05-04-01.pdf)

RESULTS

Disease Susceptibility

Significant variation ($p = 0.05$) in DSR was found among the eight species represented by ten or more individuals (Table 1). The Asian species, *F. chinensis* Roxb. (Chinese ash), appeared most susceptible to anthracnose. Next was *F. pennsylvanica* Marsh (green ash—native to North America), and, to a lesser degree, *F. mandshurica* Rupr. (Manchurian ash) and *F. angustifolia* Vahl. (Eurasian species—narrowleaf or Caucasian or Syrian ash). *Fraxinus excelsior* L. (European ash) was moderately susceptible, while *F. tomentosa* Michx. (North American native—pumpkin ash) and *F. americana* L. (North American native—white ash) appeared relatively tolerant of the disease. *Fraxinus quadrangulata* Michx. (North American native—blue ash) was similar to pumpkin ash and white ash but appeared to be nearly immune as it showed no anthracnose symptoms in two of the three years despite highly conducive spring weather.

Different cultivars were evaluated in four species: *F. americana*, *F. angustifolia*, *F. excelsior*, and *F. pennsylvanica*. Although replication was sometimes small (one or two trees), significant ($p = 0.05$ – 0.10) variation in DSR was found within all species in at least one year (Table 2). The least variation was found among white ash cultivars, in-

Table 1. Anthracnose disease severity ratings for eight *Fraxinus* species. Values are means of at least ten averaged ratings per tree where 1 = healthy, no symptoms; 2 = < 25% of canopy exhibited necrotic blotching of leaves; 3 = 25%–50% of canopy with symptoms; 4 = 50%–75% of canopy with symptoms, and 5 = > 75% of canopy with symptoms. Means followed by different lowercase letters indicate a significant difference ($p \leq 0.05$) within a given year.

Species	1997	1998	1999	Overall average
<i>F. chinensis</i>	3.9 a	3.7 a	4.1 a	3.92
<i>F. pennsylvanica</i>	3.3 a	2.3 b	3.1 bc	2.88
<i>F. mandshurica</i>	3.3 a	1.5 bc	2.6 bc	2.47
<i>F. angustifolia</i>	1.4 b	2.6 ab	3.2 abc	2.42
<i>F. excelsior</i>	2.0 b	2.6 bc	2.0 cd	2.21
<i>F. tomentosa</i>	1.6 b	1.5 c	1.8 cd	1.61
<i>F. americana</i>	1.3 b	1.3 c	1.4 d	1.31
<i>F. quadrangulata</i>	1.8 b	1.0 d	1.0 d	1.27
Overall average	2.3	2.1	2.4	2.26

cluding the industry standards 'Autumn Applause' and 'Autumn Purple', which typically received DSR ratings less than or, at most, equal to 2 (no more than 25% of canopy affected). The widely available *F. excelsior* cultivar 'Hessei', along with a few other European ash cultivars, appeared to be considerably more tolerant (average DSR = 1.5) than

cultivars such as 'Pendula' (average DSR = 4.7) and, to a lesser degree, 'Nana' (average DSR = 2.9). *Fraxinus angustifolia* cultivar 'Monophylla' averaged 3 to 4 DSR points lower (less susceptible) than varieties *pannonica* and *australis* in 1999, but differences were not significant in 1998. *F. angustifolia* 'Monophylla' was not evaluated in 1997.

Several green ash cultivars were consistently rated higher than 2 and significant differences were noted in all years. The most susceptible cultivar, 'Niobrara', was rated an average of 5 (> 75 % of canopy affected). The industry standard 'Summit' averaged a moderate DSR rating of 3 when data from all three years were combined. Other popular green ash cultivars that were not included in earlier evaluations were rated in 2000. Ten trees each of 'Marshall Seedless', 'Patmore', and the newly available 'Cimmaron' were examined in several area landscapes along with 'Summit' trees growing at the arboretum. The cultivar 'Summit' was included in 2000 to allow for comparison of disease severity in all four years. Based on the 'Summit' ratings, there was less anthracnose in 2000 than the previous three years. Nonetheless, differential susceptibility was noted among green ash cultivars: Both 'Patmore' and 'Cimmaron' stood out as virtually free of disease in 2000, while 'Marshall Seedless' and 'Summit' had moderate disease with DSR values averaging 2.

Leaf Emergence

Our assessment of leaf emergence in 1999 was thwarted when hot weather hastened foliation in all species. Therefore, only data for 1998 were used in statistical analyses. Significant differences ($p = 0.05$) were found among leaf emergence rates among the principle eight species studied (Table 3). The Asian species, *F. chinensis* and *F. mandshurica*, tended to be earliest to leaf out with over 90% at stages 3

Table 2. Intraspecific variation to anthracnose for four *Fraxinus* species. Cultivars/subspecies are listed in ascending order (increasing susceptibility) based on 3-year average disease severity ratings (DSR). Each tree was assigned a DSR by two individuals where 1 = healthy, no symptoms; 2 = < 25% of canopy exhibited necrotic blotching of leaves; 3 = 25%–50% of canopy with symptoms; 4 = 50%–75% of canopy with symptoms, and 5 = > 75% of canopy with symptoms. Means followed by different lowercase letters indicate a significant difference ($p \leq 0.05$) within a given year.

Species	Cultivar/subspecies	# trees	Average DSR			Overall average DSR
			1997	1998	1999	
<i>F. americana</i>	Autumn Applause	5	1.0 ab	1.0 a	1.0 ab	1.0
	subserrata	2	na	1.0 a	1.0 ab	1.0
	Champaign County	3	1.0 ab	1.7 a	1.0 ab	1.2
	idiocarpa	2	1.0 ab	1.0 a	2.0 a	1.3
	juglandifolia	1	1.0 ab	1.0 a	2.0 a	1.3
	Autumn Purple	12	1.6 a	1.5 a	1.3 ab	1.5
<i>F. angustifolia</i>	species	5	1.5 a	2.2 ab	2.0 b	1.9
	Monophylla	2	na	2.5 ab	1.5 b	2.0
	australis	5	1.4 a	2.8 ab	4.4 a	2.9
	pannonica	2	1.5 a	3.5 a	5.0 a	3.3
<i>F. excelsior</i>	Aurea	1	na	1.0 c	1.0 b	1.0
	Diversifolia	5	1.0 b	1.2 c	1.8 b	1.0
	Hessei	7	1.6 b	1.6 c	1.3 b	1.5
	Kimberly	2	1.5 b	2.5 bc	1.5 b	1.8
	Westhof's Glorie	3	na	2.3 bc	2.3 b	2.3
	Nana	4	na	3.3 ab	2.5 b	2.9
	Pendula	1	4.0 a	5.0 a	5.0 a	4.7
<i>F. pennsylvanica</i>	Ovata	1	1.0 d	1.0 b	2.0 b	1.3
	Bosicii	1	2.0 cd	1.0 b	2.0 b	1.7
	species	17	2.2 cd	1.9 b	2.9 ab	2.3
	Honeyshade	4	3.5 b	2.0 b	2.5 ab	2.7
	Newport	1	3.0b cd	1.0 b	4.0 a	2.7
	subintegerrima	29	3.4 bc	2.4 b	3.1 ab	3.0
	Summit	8	5.0 a	1.4 b	2.6 ab	3.0
	austinii	2	na	2.5 b	4.0 a	3.3
	Niobrara	5	3.8 b	5.0 a	4.4 a	4.4

and 4 on the observation date. Somewhat slower to leaf out were *F. pennsylvanica* and *F. angustifolia* with more than 50% of these trees at stage 3 or 4 on the observation date. Extensive variability in emergence stage was noted in both *F. americana* and *F. excelsior* on the observation date. The North American natives *F. quadrangulata* and *F. tomentosa* were slowest to leaf out with no trees surpassing stage 2 on the observation date.

Analyses of DSR in 1997, 1998, and 1999 and leaf emergence stage (categories 0–4) on May 4, 1998, revealed a weak correlation between the two variables. (Spearman correlation coefficients = 0.40, 0.18, and 0.36, respectively, for each year). Chi-square analysis indicated a highly significant association ($p = 0.001$) between the

Table 3. Leaf emergence rates for eight *Fraxinus* species. Values are percentages of trees at the leaf expansion stage indicated on May 4, 1998 (252.5 degree days base 50). 0 = no budbreak, 1 = budbreak, 2 = 1 in. (2.54 cm) expansion, 3 = half expanded, and 4 = fully expanded.

Species	# trees	Leaf emergence stage				
		0	1	2	3	4
<i>F. chinensis</i>	21	0	0	9.5	38.1	52.3
<i>F. pennsylvanica</i>	69	0	5.8	34.7	40.6	18.8
<i>F. mandshurica</i>	11	0	0	0	54.5	45.5
<i>F. angustifolia</i>	14	14.3	14.3	14.3	57.1	0
<i>F. excelsior</i>	35	25.7	22.8	37.1	14.3	0
<i>F. tomentosa</i>	13	0	23	76.9	0	0
<i>F. americana</i>	30	0	30	53.3	16.7	0
<i>F. quadrangulata</i>	10	0	20	80	0	0

two variables, but the nature of the association was not clear for all taxa or in all years (Pearson Chi-square values ~ 0.5). However, in two of three years (1997 and 1999), trees that expanded rapidly, attaining leaf emergence stage 4 on the observation date, were twice as likely to have a high DSR rating (4 or 5) than low (1 or 2). Likewise, trees that had yet to break bud or were slow to leaf out (leaf emergence stage 0 or 1) were at least 2.5 times, and as much as 7 times, more likely to have a low DSR than a high DSR. This trend was not evident in the 1998 data, perhaps because fewer trees overall reached a high DSR compared to 1997 and 1999.

DISCUSSION

The data presented expand upon and clarify current information available on the susceptibility of ash species to anthracnose. Previously, differential susceptibility to anthracnose was reported in only a few species in the western United States (Ogawa et al. 1977), and readily available cultivars of ash had not been rated for the disease (Santamour and McArdle 1983; Dirr 1990). Green ash is typically considered relatively resistant to anthracnose and white ash more susceptible (Sinclair et al. 1987). Others have reported high levels of disease among green ash parkway trees (Stack et al. 1990). Our findings demonstrate that variability in anthracnose susceptibility exists both among, and within, several *Fraxinus* species. Moreover, green ash appears more susceptible than white ash, although differences may be minimized in years of low disease pressure. For example, differential expression of anthracnose susceptibility among green ash cultivars was less dramatic in 2000 than in the previous years, presumably due the lower overall disease pressure in 2000.

Leaf emergence rates appear to have some association

with anthracnose susceptibility as two late emerging species, blue ash and pumpkin ash, were most resistant to the disease, while Chinese ash, the species that broke bud earliest, was most susceptible. When data from all trees were analyzed collectively, individuals that leafed out early also tended to develop more disease than those that leafed out later (data not shown). These findings suggest that ontogenic resistance may operate in ash anthracnose whereby young, succulent leaves are more susceptible to infection than fully expanded leaves. Such a scenario has been described for black spot of elm and for apple and pecan scabs, although leaf wetness, temperature, and inoculum levels are also crucial to the ultimate level of disease in any given season (McGranahan and Smalley 1984; MacHardy 1996; Turechek and Stevenson 1998). Leaf wetness and temperature are known to strongly influence development of the ash anthracnose pathogen (Ogawa et al. 1977; Redlin and Stack 1986).

The apparent leaf emergence effect noted in our study may also reflect merely a longer exposure time to inoculum for leaves that unfurl first. Longer exposure periods of susceptible tissue can expand epidemics of polycyclic diseases such as anthracnose by allowing secondary infection and spore production to occur earlier and in greater abundance (Fry 1982). Comparisons of susceptibility of leaves of different ages, from both resistant and susceptible hosts, are needed to elucidate the import of leaf phenology on disease.

It is worthwhile to note that we examined fallen ash leaves in all 22 *Fraxinus* spp. during February 2000 to determine whether the abundance of fungal fruiting bodies in leaf litter corresponded to susceptibility ratings during the growing season. We also sought to isolate the sexual stage of the anthracnose pathogen. We were successful in the latter but found no strong correlation between leaf litter colonization and field susceptibility with one exception: fallen leaves of the resistant *F. quadrangulata* were virtually free of fruiting bodies. During isolations of *G. fraxini*, another fungus, *Mycosphaerella* sp., was frequently encountered. *Mycosphaerella* species have been reported previously as causing disease and as saprophytes on ash leaves (Wolf and Davidson 1941; Heptig 1971). The species we isolated is probably the saprophytic *M. fraxinicola* (Sweinitz) House based on ascospore measurements (average length \times width = $7.7 \times 2.6 \mu$ based on 100 ascospores) (Corlett 1991). Its abundance in ash leaf litter warrants further study on the possible interaction of it and the anthracnose fungus.

CONCLUSIONS

The data presented should assist in targeting ash species for breeding programs and, in particular, suggest that the North American native blue ash would be especially promising as a source of resistance. Further, subspecific variation in susceptibility to anthracnose was identified, as was a possible link between early leafing out and increased susceptibility. This information may be noteworthy when choosing ash cultivars and varieties for nursery production and placement in the landscape.

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Résumé. Huit espèces de *Fraxinus* et plusieurs cultivars de *F. americana* (frêne blanc), *F. pennsylvanica* (frêne rouge), *F. angustifolia* (frêne de Syrie) et *F. excelsior* (frêne commun) ont été évalués pour leur susceptibilité à l'anthracnose en 1997, 1998 et 1999. Des taux d'éclosion des bourgeons et d'émergence des feuilles ont aussi été enregistrés. Les résultats suivants ont été observés: *F. chinensis* (frêne de Chine) était le plus susceptible, suivi de *F. angustifolia*, *F. pennsylvanica* et, à un moindre degré, *F. mandshurica* (frêne de mandchourie). L'espèce européenne *F. excelsior* était similaire au *F. mandshurica* et est apparue modérément susceptible, alors que les espèces *F. tomentosa* (frêne tomenteux) et *F. americana*, indigènes à l'Amérique du Nord, étaient par comparaison tolérantes à la maladie. *Fraxinus quadrangulata* (frêne anguleux) était très résistant et ne montrait virtuellement aucun symptôme à chacune des années. Des variations significatives existaient entre les cultivars et les variétés de certaines espèces, et ce incluant parmi les frênes rouges largement plantés dont les cultivars 'Patmore' et le tout nouveau 'Cimmaron' sont apparus moins susceptibles. En dépit d'un faible support statistique, on a observé une tendance générale chez les frênes qui formaient leur feuilles plus tôt à développer plus facilement la maladie que chez ceux dont la feuillaison était plus tardive.

Zusammenfassung. In den Jahren 97, 98 und 99 wurden 8 *Fraxinus*-arten und verschiedene Kultivare der *F. americana*, *pennsylvanica*, *angustifolia* und *excelsior* auf ihre Anfälligkeit gegenüber Anthracnose getestet. Die Daten der Knospung und des Blattfalls wurden auch erfasst. Folgende Ergebnisse wurden gefunden: *F. chinensis* war die anfälligste, gefolgt von *F. angustifolia*,

pennsylvanica und zu einem geringen Anteil von *F. mandshurica*. Die europäische *F. excelsior* reagierte wie *F. mandshurica* und erschien mäßig anfällig, während die nordamerikanischen *F. tomentosa* und *F. americana* relativ tolerant gegenüber der Krankheit waren. *F. quadrangulata* war sehr resistent und zeigte über die Jahre keine Symptome. Zwischen den Kultivaren und Varianten einiger Arten existieren signifikante Unterschiede inkl. der weitläufig gepflanzten *F. pennsylvanica* und ihrer Varianten ‚Patmore‘ und ‚Cimmaron‘, die als gering anfällig eingestuft wurden. Trotz der schwachen statistischen Unterstützung beobachten wir einen generellen Trend, dass Bäume mit früher Knospung anfälliger bzw. eher die Krankheit entwickelten als die Spätblüher.

Resumen. Se estudiaron ocho especies de *Fraxinus* y varios cultivares de *F. americana* (fresno blanco), *F. pennsylvanica* (fresno verde), *F. angustifolia* (fresno de Siria) y *F. excelsior* (fresno europeo), para evaluar la susceptibilidad a la enfermedad de antracnosis durante 1997, 1998 y 1999. También se registraron las tasas de

emergencia foliar y de yemas. Se encontraron los siguientes resultados: *F. chinensis* (fresno chino) fue el más susceptible seguido por *F. angustifolia*, *F. pennsylvanica* y, en menor grado, *F. mandshurica* (fresno de Manchuria). El europeo *F. excelsior* fue similar a *F. mandshurica* y apareció moderadamente susceptible, mientras que los fresnos nativos de Norte América: *F. tomentosa* y *F. Americana*, fueron comparativamente tolerantes a la enfermedad. *Fraxinus quadrangulata* (fresno azul) fue altamente resistente y no mostró virtualmente ningún síntoma en todo el tiempo. Existió variación significativa entre los cultivares y variedades de ciertas especies incluyendo los ampliamente plantados fresnos verdes, de los cuales ‚Patmore‘ y el nuevo disponible ‚Cimmaron‘, aparecieron como los menos susceptibles. A pesar del débil soporte estadístico, se observó en general una tendencia según la cual los árboles que rebrotan temprano desarrollan más enfermedad que aquellos que rebrotan más tarde.