Evaluation of Resistance to the Beech Scale Insect (*Cryptococcus fagisuga*) and Propagation of American Beech (*Fagus grandifolia*) by Grafting

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(Received 25th April 2006)

Abstract

Scions collected from diseased trees and from those without symptoms of beech bark disease (BBD) were cleft-grafted in 2003 and 2004 onto rootstock of unknown resistance to BBD. Grafting success varied among genotypes and year (30% in 2003 and 12% in 2004), and improved with increasing rootstock diameter. Successful grafts were used to test resistance to the beech scale insect, *Cryptococcus fagisuga* (the initiating agent of BBD) by introducing eggs onto the bark of scions and allowing time for the emergence of all developmental stages of the insects. Significantly fewer insects colonized scions collected from putatively resistant trees than those collected from diseased trees. In some cases, where egg placement overlapped a portion of the rootstock, insect colonies developed on the rootstock but not on the scion collected from resistant trees. Occasionally, scions from putatively resistant trees were colonized, whereas some of those from diseased trees were not. When scions from putatively resistant trees were heavily colonized, only adult insects were present and no eggs or other life stages of the insect were found. The findings indicate that the extent of resistance to the scale insect (hence to BBD) ranges from partial to total resistance.

Key words: Beech bark disease, disease resistance, inoculation, rootstock diameter, scion.

Introduction

American beech (*Fagus grandifolia* Ehrh.) is an important component of hardwood and mixed forest stands of eastern North America. This shade-tolerant, slow-growing tree (Farrar, 1995) is a source of food and shelter for many wildlife species and is especially important for sustaining populations of black bear (*Ursus americanus* Pallas) and marten (*Martes americana* Turton) (JAKUBAS et al., 2005).

Beech bark disease (BBD) is caused by the interaction of the woolly beech scale insect (*Cryptococcus fagisuga* Lind.) with one or two species of *Nectria* fungus, principally *Nectria coccinea* var. *faginata* Lohman, Watson & Ayers (EHRLICH, 1932). The insect and probably the most common fungal agent (MAHONEY et al., 1999) were introduced to Nova Scotia from Europe sometime before 1890 (EHRLICH, 1932), and have since been spreading through much of the natural range of American beech. Throughout New Brunswick, where the disease is well established, approximately 95% of beech trees are affected (D. McPhee, personal communication, 2004).

Scale insects feed by inserting their stylets into the bark parenchyma (WAINHOUSE et al., 1988), predisposing trees to fungal infection (SHIGO, 1972). The initial effect of infection spreading to new areas is massive mortality, and is known as the "killing front" (SHIGO, 1972). In the "aftermath forest," the insect and fungus become endemic and cause growth reduction, tree deformation, declines in wood quality and mast production, as well as premature death of affected trees (HOUSTON, 1975). The severe negative consequences of BBD have significantly reduced the ecological value and economic potential of American beech in the affected areas, caused problems for forest management, and lessened the aesthetic value of forest sites (HOUSTON, 1999).

In stands affected by BBD for many years, some trees free of BBD symptoms occur as single individuals or in small groups surrounded by diseased trees (EHRLICH, 1932; SHIGO, 1964; HOUSTON, 1982). Isozyme analyses reveal that the groups often consist of genetically identical trees for the loci examined, implying a clonal origin (root suckering). In other cases, BBD-free trees appear to be closely related, perhaps being full-sibs (HOUSTON and HOUSTON, 1987). These observations suggest genetic resistance to BBD, but the nature and extent of resistance of individual trees is unknown, as is the mode of inheritance.

Inoculation trials on BBD-free trees conducted by HOUSTON (1983) suggest that some of the symptom-free trees are truly resistant to the beech scale attack. Without the initial attack by the insect, the fungus does not cause much damage (SHIGO, 1964). When HOUSTON (1982, 1983) inoculated the bark of trees with and without disease symptoms with scale eggs, insect colonies established on susceptible trees but failed to establish or reproduce on most BBD-free trees. In a similar experiment, Houston (1982) was able to inoculate young (2-, 3-, and 4-year-old) seedlings of American beech with the scale insect and proposed that his inoculation method could be useful for screening young plant material for resistance to the attack by the scale insect.

WARGO (1988) proposed that a low concentration of amino-form nitrogen in some BBD-free trees limits the establishment and growth of the scale insect. Houston (2005) suggested that anatomical barriers might also contribute to the resistance (as shown for *Fagus sylvatica* by LONSDALE (1983)), but this has not been studied for American beech and the cause of resistance to BBD

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DOI:10.1515/sg-2007-0025
edited by Thünen Institute of Forest Genetics

remains unidentified. Studies are underway to determine modes of inheritance using controlled breeding (KOCH and CAREY, 2004; LOO et al., 2005).

Vegetative propagation of resistant genotypes may allow conservation of a BBD-resistant gene pool and retention or restoration of healthy beech to the forests of eastern North America. The feasibility of this approach depends on whether BBD-free trees truly demonstrate a genetically based resistance, and whether American beech can be propagated vegetatively on a large scale.

American beech is very difficult to propagate vegetatively (DIRR and HEUSER, 1987). Limited success has been achieved with rooting of cuttings and micropropagation, but the plantlets did not survive the first overwintering (BARKER et al., 1997; SIMPSON, 2001). European beech has been grafted successfully but with a low percentage of successful grafts (DIRR and HEUSER, 1987). Grafting would not be a viable method for mass production of resistant genotypes, but could be very useful for resistance screening to BBD and development of seed orchards to produce resistant seedlings.

The main objective of this study was to test if selected disease-free trees of southern New Brunswick origin are genetically resistant to the beech scale. A secondary objective was to evaluate factors affecting grafting success. The trial compared results of inoculation of scions collected from disease-free and diseased trees, and evaluated the success in grafting American beech.

Materials and methods

Plant material

Material for this study was collected from trees with diameter at breast height (DBH) of 15 cm or more. Twenty-two putatively resistant and five diseased trees were selected at nine locations in southern New Brunswick for scion collections (*Fig. 1*). Disease-free trees were selected based on accessibility (roadside), availability (only 5% of all beech trees are disease-free) and no visible signs of BBD (scale insects, cankers, or *Nectria* fruiting bodies). Diseased trees were selected randomly, and represent a control.

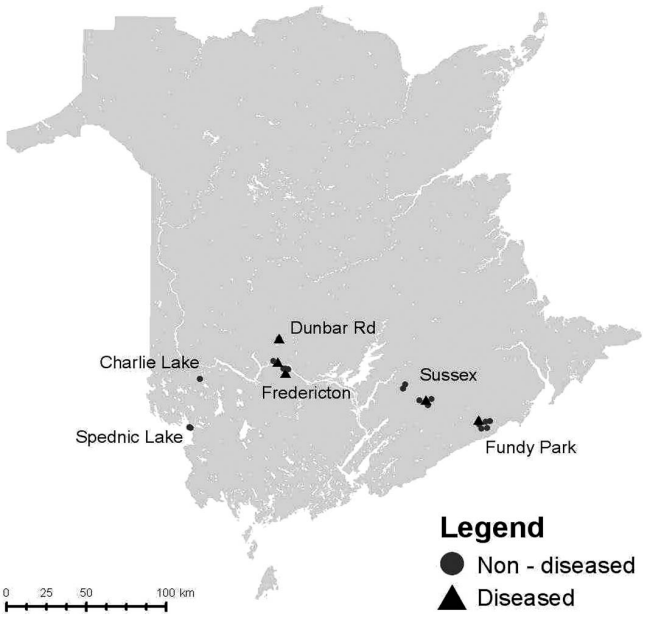

Figure 1. – New Brunswick locations of diseased and putatively resistant American beech trees from which scions were collected for challenge tests.

Grafting

Scions were collected in late February and early March of 2003 and 2004. Twigs (20 to 25 cm long) with two to three buds were cut from branches, packed into plastic bags containing snow, brought to the Atlantic Forestry Centre laboratory, and stored at 0°C for no more than 2 days before grafting. Twenty scions per tree (genotype) were grafted onto 1-year-old rootstock in 2003 and a mixture of 1- and 2-year-old rootstock in 2004 over a 2-week period each year. The rootstock was grown from seeds collected from open-pollinated trees free of disease symptoms but of unknown resistance to BBD. Seeds were germinated and potted in a mixture of peat moss, perlite, aggregate (small rock), and loam (2:2:1:1). The rootstock was carefully matched to the diameter of the scion. The grafting technique was top cleft, matching closely the cambium of the scion and rootstock. Graft unions were wrapped with rubber bands and coated with warm wax to hold the graft in place and prevent drying. Grafts were placed in a greenhouse under controlled conditions (initially, 70% humidity, 16-h photoperiod, 10–12°C, then the temperature was increased gradually to match outdoor conditions). The grafts were assessed for flushing of buds every week for 15 weeks. The diameter of the rootstock was measured in the 15th week and graft success was determined at that time. Successful grafts were kept in the greenhouse for 5 months and then placed in an outdoor shaded area until the inoculation trials began.

Testing resistance to BBD

Eggs of *C. fagisuga* were collected in mid-July 2003 and 2004 from infested trees located in southern New Brunswick (*Fig. 1*). Bark disks 5 cm in diameter were cut from the trees and placed in a moist cooler for transport to the laboratory. Masses of wax containing adult scales and eggs were removed from the disks under a dissecting microscope, placed in a fine mesh screen (1 mm^2) and gently teased with a soft brush to separate the eggs. Eggs were sieved into small plastic containers and stored at 4°C in a glass container over 20 g KOH/100 g H_2O to maintain about 85% relative humidity. The eggs were stored as long as possible to allow grafts to continue growing. Eggs were monitored regularly for viability by observing hatching response of samples placed at room temperature. There was no detectable loss of viability after 4 weeks at 4°C. Approximately 100 eggs were placed in the center of a 2 x 2 x 1 cm polyurethane foam strip previously moistened with distilled sterile water. The foam strip was wrapped around the stem above the graft union and affixed with copper wire. The grafts were kept in a greenhouse under 60% humidity, 16-h photoperiod, ventilation at 23°C, and drip irrigation directly to the soil. During winter, they were kept at 4°C in the same greenhouse. The experiment was carried out in 2003 with successful vig-

DOI:10.1515/sg-2007-0025
edited by Thünen Institute of Forest Genetics

orous grafts using 150 grafts in total from 25 genotypes. In 2004, only 54 grafts from 14 genotypes were successful; therefore, a subset of 2003 grafts from the same 14 genotypes was re-inoculated. On re-inoculated grafts, the foam was placed at a different location on the stem than for the first inoculation to avoid the possibility of counting established scale insects from the first inoculation in the counts for the second year. Twelve months after inoculation, the foam strips were removed to examine the infestation and live adult scale insects were counted up to 100. If 100 or more scales developed, it implied near 100% survival. On grafts with heavy infestations, the life stage of live insects was determined.

Statistical analysis

Data collected on numbers of scale insects were subjected to analysis of variance (ANOVA) using the General Linear Models (GLM) procedure with SAS 8.2®. Residual data were tested for departure from the normal distribution using the Univariate procedure of SAS. When data were not normally distributed, they were transformed by log (x+1) or arcsine ($\sqrt{x}$) to meet the assumption of normal distribution.

In grafting trials, the effect of diameter in grafting success was analyzed by year because of differences in the range of diameters in each year. Diameters were classified into three categories (<1.5, 1.5–2.5, and >2.5 mm in 2003; <2, 2–3, and >3 mm in 2004). Transformed data were analyzed using diameter category as a fixed factor and genotype as a random factor. Tukey's test was used for post hoc comparisons of means.

For the inoculation trials, the number of scales was analyzed using phenotype (susceptible or putatively resistant) and year of inoculation as fixed factors, and genotype as a random factor. The inoculation trials were also analyzed separately for each year of inoculation. Because some grafts died during the inoculation period, the analysis was only possible for 13 genotypes.

Results

Grafting

Most buds on grafted scions flushed 6 to 9 weeks after grafting. Scions grafted first were the last ones to flush and *vice versa.* Shoots elongated from flushed buds and a new set of buds eventually formed. Some grafts had two or three flushes of growth in the first growing season. Shoots of a few grafts that flushed did not continue elongating and the grafts failed.

In 2003, the overall graft survival was 30% and all genotypes had some successful grafts. In 2004, grafting success was only 12%, with 84% of genotypes producing some successful grafts. Most genotypes (88%) produced more successful grafts in 2003 than in 2004 (*Fig. 2*).

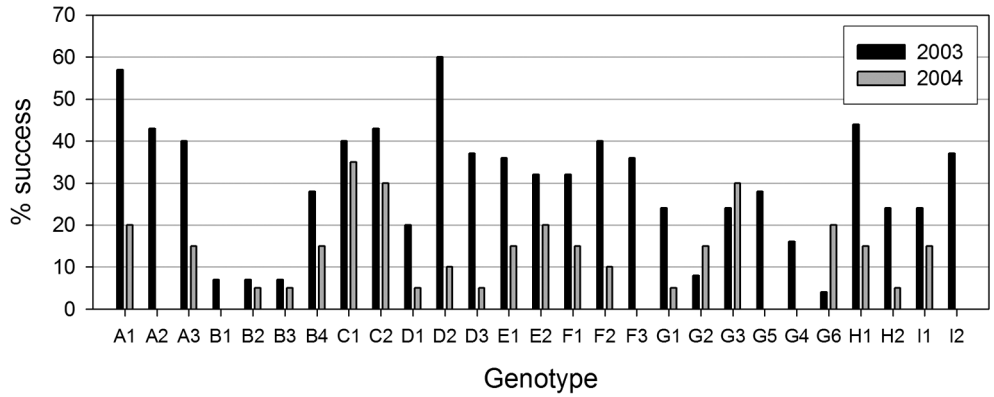

Figure 2. – Grafting success for 25 genotypes from nine locations (A-I). A3, B4, F2, G6, H1 and I2 are diseased trees, the rest are putatively resistant. In 2004, there were no successful grafts in genotypes A2, B1, F3 and G5. Genotypes G4 and I2 were not grafted in 2004.

Table 1. – Analysis of variance on percentage of grafting success in American beech scions of various genotypes, comparing effects of rootstock diameter category and genotype in 2003 and 2004; df = degrees of freedom, MS = mean square.

Sources of variation	df	MS	F	p	Post hoc comparisons* rootstock diameters (mm)
2003					
Diameter	2	0.8182	6.00	0.005	<1.5 1.5 to 2.5 >2.5
Genotype	26	0.1416	1.04	0.449	
Error	40	0.1364			
2004					
Diameter	2	1.4332	17.89	≤0.0001	<2 2 to3 >3
Genotype	24	0.1090	1.36	0.179	
Error	48	0.0801			

* In post hoc comparisons, underlined categories do not differ significantly from each other at $\alpha = 0.05$.

DOI:10.1515/sg-2007-0025
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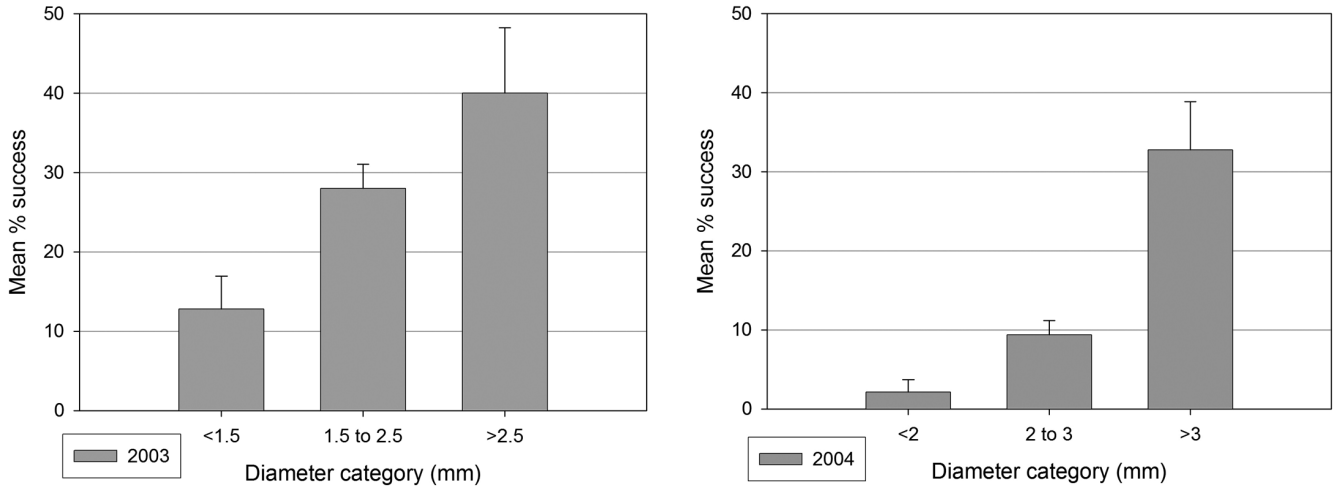

Figure 3. – Grafting success (+ S.E.) for different rootstock diameter categories. The means are of 27 genotypes in 2003 and 25 genotypes in 2004.

Table 2. – Results of nested analysis of variance on numbers of adult scale insects per graft in American beech of two phenotypes (diseased or putatively resistant), 13 genotypes, and 2 years of inoculation (2003 and 2004); df = degrees of freedom, MS = mean square.

Sources of Variation	df	MS	F	p
Phenotype	1	174.531	30.79	≤0.0001
Genotype (Phenotype)	11	5.811	9.70	≤0.0001
Year	1	0.032	0.05	0.825
Phenotype x Year	1	3.099	4.98	0.044
Genotype x Year	11	0.599	0.45	0.930
Error	170	1.325		

There was no significant difference between putatively resistant and diseased phenotypes in grafting success (p = 0.73). Rootstock diameters ranged from 0.87 to 3.35 mm and from 1.35 to 4.46 mm in 2003 and 2004, respectively. In both years, scions grafted onto rootstock with larger diameters had significantly greater success (*Table 1, Fig. 3*).

Evaluation of resistance to the scale insect

When the foam strips were removed from the inoculated scions, some insects remained attached to the bark, but most adhered to the foam. White masses of secreted wax occurred in colonies of live scales. Adults, eggs, and first-instar crawlers of the scale insect were present on successfully colonized grafts of diseased trees. Grafts of putatively resistant trees, when heavily infested, had only adult insects.

In a number of grafts from putatively resistant trees, some crawlers had moved down the stem where the foam overlapped the graft union, and had established in crevices of the union and on the rootstock. Dead insects were found on the foam covering non-colonized grafts and in some colonized grafts. They were black and shriveled, with or without wax, and of different sizes.

The difference in the numbers of adult insects that developed on diseased and putatively resistant phenotypes was significant in both years (*Table 2, Fig. 4*). There was an interaction between phenotype and year of inoculation that was marginally significant (*Table 2*). Numbers of adult insects differed significantly among genotypes and there was no significant interaction between the year and genotype (*Table 2*).

The numbers of successfully inoculated grafts per genotype varied depending on graft survival (*Tables 3* and *4*). In 2003, putatively resistant clone I2 had well-developed colonies in all its ramets. Closer examination of the source tree revealed that BBD was present in the upper crown and the tree was not used again. The same year, putatively resistant clone G3 had two ramets with more than 20 insects. In 2004, three putatively resistant clones (A1, C2, and G3) had well-established colonies in

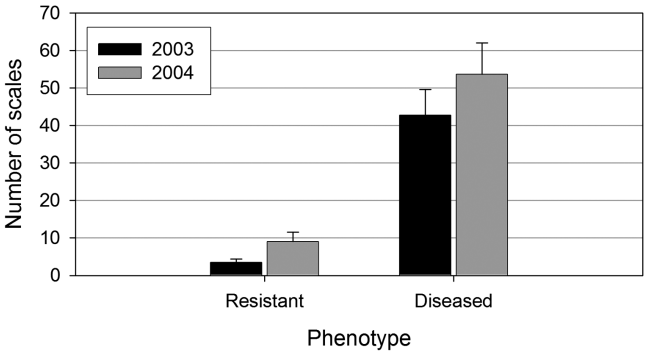

Figure 4. – Mean numbers of adult scale insects (+ S.E.) per graft for putatively resistant and diseased phenotypes in 2 years of inoculation trials.

DOI:10.1515/sg-2007-0025
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Table 3. – Number of grafts inoculated (N) and mean number of adult scale insects (Mean) per genotype in the inoculation year 2003. Genotypes B4, I2, H1, A3, and F2, are diseased phenotypes (D).

Genotype	2003	
	N	Mean
B2	2	0
B3	2	0
E2	5	0
D3	6	1
D1	4	1
C1	9	1
A2	10	2
F3	5	2
E1	8	2
C2	9	2
G5	3	3
F1	5	3
D2	16	3
B1	2	4
A1	11	4
G1	6	9
G4	4	12
G3	5	19
B4 (D)	4	26
I2 (D)	7	30
H1 (D)	9	48
A3 (D)	8	51
F2 (D)	7	72

Table 4. – Numbers of grafts (N) inoculated and re-inoculated and mean number of adult scale insects (Mean) per genotype in the inoculation year 2004. Genotypes H1, B4, G6, and A3 are diseased phenotypes (D). Genotype G6 was not re-inoculated.

Genotype	2004 Re-inoculated		2004	
	N	Mean	N	Mean
I1	4	1	5	0
D3	4	2	2	0
E2	4	2	4	0
F1	2	3	2	0
F3	3	3	3	1
E1	5	3	2	1
C1	5	7	5	0
D2	7	12	2	1
G3	4	36	6	12
C2	4	41	3	0
A1	5	41	4	3
H1 (D)	8	69	2	7
B4 (D)	3	87	4	8
G6 (D)	-	-	6	79
A3 (D)	6	100	4	0

two (out of nine), two (out of seven), and three (out of ten) ramets, respectively. The same year, two susceptible clones grafted in 2004 (A3 and B4) did not have surviving scales in three ramets each (out of ten and seven, respectively). Diseased genotypes had the greatest numbers of insects in both years (*Fig. 5*).

Although there was no statistically significant interaction between genotype and year (*Table 2*), the within-clone variation in the numbers of scales was greater in the 2004 trial due to differences in mean number of

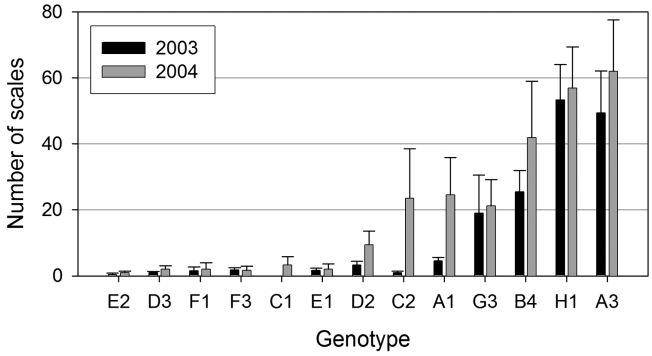

Figure 5. – Mean number of adult scale insects (+ S.E.) for ten putatively resistant genotypes and three known susceptible genotypes (B4, H1, A3) inoculated in 2003 and 2004. No colonies of the scale insect established on any scions from genotype C1 in 2003.

scales between grafts inoculated for the first time and re-inoculated ones (*Table 4*). There was considerable mortality of the 2004 grafts (16%) during the challenging trial. Significant differences were found for all genotypes between re-inoculated grafts and the ones inoculated for the first time. All genotypes that were re-inoculated had higher numbers of insects in the second year of inoculation than in the first (*Tables 3* and *4*).

Discussion

Grafting

Grafting is a useful propagation technique that can provide material for resistance trials in a short time frame, but success in grafting beech is low. Only a few studies (MEIER and REUTHER, 1994; WAINHOUSE and HOWELL, 1983) mention grafting of *Fagus* spp., and there are no published reports on different grafting methods or on the percentage of success for *F. grandifolia*. DIRR and HEUSER (1987) reported that *Fagus* spp. are very difficult to graft. They report 25%–30% success in grafting *Fagus sylvatica* L. (European beech), which is similar to the results for 2003 obtained in this study. Some genotypes had very good success and some had low success in both years, but a strong genotype effect was not observed. There was no overall consistency in the grafting success for genotypes in the two successive years.

The environment in which grafts are grown may influence the success of grafting. Temperature has been strongly related to the success or failure of grafts in many plants (DIRR and HEUSER, 1987), and different temperatures may be optimal for different species. For winter grafting of many species, HALLETT et al. (1981) recommend slowing bud flushing with cool temperatures (13–18 °C) for 3–6 weeks until the scions break bud and shoots begin to elongate. The low grafting success in 2004 may have been related to the lack of exposure to an extended period of low temperatures. That year, grafts were given only 1 week of cool temperatures and then moved to a warmer greenhouse (25 °C). Success may be improved by grafting earlier in the season when it is easier to maintain low air temperatures in the greenhouse.

DOI:10.1515/sg-2007-0025
edited by Thünen Institute of Forest Genetics

The variation in success between rootstock diameters can be explained by the difficulty in working with very thin stems and aligning the vascular cambium of the scion with that of the rootstock. In a similar study on a tropical fruit tree, *Annona muricata* L., grafting success increased with rootstock diameters greater than 2.2 mm (KITAMURA and LEMOS, 2004). Other factors that may be associated with grafting success in beech are the number of buds on the scion, the length of the union between the scion and rootstock, and the difference in diameter between rootstock and scion (RAMIREZ et al., unpublished data).

Evaluation of resistance to the scale insect

Results from the inoculation trials indicate that the technique was useful for identifying resistance to *C. fagisuga.* To our knowledge, inoculation of grafted material of small diameter from *F. grandifolia* has not been reported. In an inoculation study with mature susceptible beech, HOUSTON (1983) found variation in colonization among different trees, and classified infestation into three groups depending on average number of colonies (low-25, medium-67, and high-198). Our results also indicated the existence of a gradient in resistance to the scale insect. Although some of the sampled disease-free trees might have been escapes and not resistant, the variation in colonization of scions collected from diseased and putatively resistant trees generally supports the notion of variable resistance. KOCH and CAREY (2004) also reported partial resistance to *C. fagisuga* in control-pollinated progeny of American beech.

HOUSTON (1982) suggested the presence of a partial anatomical barrier in some trees that appeared to be resistant, but which following inoculation, supported small colonies of insects. LONSDALE (1983) reported that the bark of *F. sylvatica* trees that supported only very low populations of the scale insect had a well-defined layer of sclerophyll cells. These cells were thicker, with a more continuous layer located closer to the surface of the bark than that observed in susceptible trees. Similar studies of the bark have not been reported for *F. grandifolia.* Another factor implicated in the resistance to BBD is the concentration of amino-form nitrogen in the bark. Bark of putatively resistant trees was found to have lower concentrations of amino nitrogen than that of susceptible trees (WARGO, 1988). It is possible that multiple factors are associated with resistance to BBD. This is supported by the observation that dead insects found on putatively resistant scions died at various stages of development.

Why few insects survived and developed on the 2004 grafts is unknown. The greater mortality and poorer growth of 2004 grafts, compared with those in 2003, suggests that the 2004 grafts were not of good quality and were perhaps less suitable for insect development. The higher colonization of re-inoculated grafts, which were a year older than the first-time inoculated grafts, suggests that the susceptibility to colonization may increase with increasing age and/or diameter of the stems. The thickening of stems may increase the cracks in the bark, which are favorable habitats for the scale establishment. In *F. sylvatica* trees, fissures in the bark have been associated with increased susceptibility to insect attack (LONSDALE, 1983).

Heavy infestations on some ramets of clones from putatively resistant genotypes have not been previously reported in challenge trials of *F. grandifolia.* HOUSTON (1982) found that in challenged resistant mature trees, some insects established, but did not continue developing after overwintering, and after 1 year, were all dead or dying. In the present study, heavily infested grafts (more than 100 insects) from putatively resistant trees had only adults present, as opposed to scions from susceptible trees where masses of eggs were also found. Hence, the insects were able to establish and develop on the bark of some resistant trees, but they were apparently unable to reproduce.

WAINHOUSE and HOWELL (1983) evaluated the adaptation of scale populations to specific hosts in *F. sylvatica* and found that scales collected from one diseased tree did not establish when inoculated onto another susceptible tree. In the present study, scale eggs used in challenging each graft were mixed from at least three different sources to reduce potential effects of host specificity. The discontinuous pattern of the disease in European forests has been related to the apparent adaptation of the insect to specific hosts only (WAINHOUSE and HOWELL, 1983). In North America, patterns of spread of the disease are continuous and more aggressive (HOUSTON et al., 1979). Nevertheless, it may be important to evaluate the host specificity of the scale regarding American beech before embarking on mass propagation of putatively resistant genotypes.

Acknowledgments

We thank DONNIE MCPHEE, KATHLEEN FORBES, LAURIE YATES, DAVE HOUSTON, JON SWEENEY, and YILL SUNG PARK for their assistance and advice. Funding for this study was provided by Parks Canada, the Fundy Model Forest, the Canadian Forest Service, the National Science and Research Council of Canada, and the Faculty of Forestry and Environmental Management of the University of New Brunswick.

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DOI:10.1515/sg-2007-0025
edited by Thünen Institute of Forest Genetics