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BRIEF REPORT

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Resistance of European ash (*Fraxinus excelsior*) saplings to larval feeding by the emerald ash borer (*Agrilus planipennis*)

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Societal Impact Statement

European ash is a significant tree commercially, ecologically, and culturally. It is currently threatened by two invasive species, the fungus that causes ash dieback and the emerald ash borer (EAB) beetle. We show that saplings of European ash are much less susceptible to EAB than black ash, which has suffered severe damage in North America, but have similar resistance to Manchurian ash, which coexists with EAB in East Asia. Selecting ash with stronger resistance to dieback is unlikely to decrease its resistance to EAB. As we do not know what the combined effect of ash dieback and EAB will be on European ash, biosecurity measures are needed to exclude EAB from Western Europe.

KEYWORDS

Ash dieback, emerald ash borer, European ash, forest pathology, partial resistance

1 | INTRODUCTION

The common or European ash, *Fraxinus excelsior*, is an important tree in woodland, hedgerows, riverbanks, commercial forestry and urban plantings in northern Europe, and is host to many other species (Mitchell et al., 2014). Since the early 1990s, *F. excelsior* has experienced widespread mortality from ash dieback, a disease caused by the fungus *Hymenoscyphus fraxineus* (Zhao, Hosoya, Baral, Hosaka, & Kakishima, 2012). In the worst-affected areas, up to 85% of mature trees have died (Coker et al., 2018). *Hymenoscyphus fraxineus* has affected *F. excelsior* in the UK since at least 2001 and possibly as early as 1991 (Wylder, Biddle, King, Baden, & Webber, 2018). Simultaneously, *F. excelsior* in the Moscow Region of Russia has been damaged by a buprestid beetle, the emerald ash borer (EAB; *Agrilus planipennis*), since 2003 (Musolin, Selikhovkin, Shabunin, Zviagintsev, & Baranchikov, 2017), but not as severely as green ash (*Fraxinus pennsylvanica*) has been (Baranchikov, Mozolevskaya, Yurchenko, & Kenis, 2008; Orlova-Bienkowskaja, 2014; Straw, Williams, Kulinich, & Gninenko, 2013). In North America, the accidental introduction of EAB has caused massive destruction of native ash, especially black ash (*Fraxinus nigra*) and *F. pennsylvanica* (Herms & McCullough, 2014). Both *H. fraxineus* (McMullan et al., 2018) and EAB (Haack, Jendek, Liu, Marchant, & Petrice, 2002) originated in

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north-east Asia and are invasive species in Europe. Manchurian ash (*Fraxinus mandshurica*), which is native to north-east Asia, is resistant to *H. fraxineus* (Nielsen, McKinney, Hietala, & Kjær, 2017) and EAB (Rebek, Herms, & Smitley, 2008) presumably by virtue of its coevolution with both parasites.

In *F. excelsior* accessions from Denmark, chemical signatures indicative of iridoid glycosides were associated with susceptibility to ash dieback (Sambles et al., 2017; Sollars et al., 2017). As these secondary metabolites are associated with insect deterrence, there is concern that breeding or selecting planting stock with high resistance to ash dieback might inadvertently increase susceptibility to invertebrate herbivores, including EAB (Sollars et al., 2017). In the work reported here, *F. excelsior* saplings from the UK were inoculated with EAB eggs to compare their responses to those of the EAB-susceptible *F. nigra* and the resistant *F. mandshurica*, and to test if they have genetic variation that might allow evolution of greater resistance to EAB. The three tree species are closely related, all falling within *Fraxinus* section *Fraxinus* (Wallander, 2008).

2 | MATERIALS AND METHODS

Fifty *F. excelsior* accessions were studied, 20 of which were collected from Norfolk, UK, where ash dieback is especially prevalent. They were identified in October 2015 and again in February 2016 as having much less dieback than other trees nearby. A further 30 trees originated from either an existing collection at The National Institute of Agricultural Botany East Malling Research (NIAB EMR; www.emr.ac.uk) or a Forest Research (www.forestresearch.gov.uk) trial at Llandovery, Wales and were representative of the four regions of provenance within the United Kingdom (Herbert, Samuel, & Pattison, 1999). These accessions were cloned by grafting onto *F. excelsior* rootstock at EMR in April 2016, and form part of the John Innes Centre/ East Malling National Nursery for Integrated *F. excelsior* Research (JENNIFER) diversity panel. The UK-wide accessions are expected to reflect the natural frequency of ash dieback resistance in Great Britain while those from Norfolk are expected to have a higher frequency of resistance. In May 2017, three barerooted ramets per accession were sent to The Ohio State University's Biosafety Level 3 Plant and Animal Agrosecurity Research (PAAR; https://paar.cfaes.ohio-state.edu/) facility, at the Ohio Agricultural Research and Development Center, Ohio, USA. Plants were transported in compliance with a United States Department of Agriculture Animal and Plant Health Inspection Service (USDA APHIS) Plant Protection and Quarantine (PPQ) Controlled Import Permit (PCIP-17-00091_20170223). Six barerooted *F. mandshurica* seedlings were obtained from Schumacher Nursery (Heron Lake, MN, USA), and six potted *F. nigra* seedlings from Donald Cipollini, Wright State University (Dayton, Ohio, USA).

Soil was washed from *F. nigra* roots and all trees were repotted in the PAAR facility into 11.5 L pots with a steam-sterilized 9:1 mixture of pine bark fines and hardwood leaf compost (Container Mix, Kurtz Bros). *Fraxinus mandschurica* and *F. nigra* trees were cut to the same height as *F. excelsior*, approximately 20 cm. Potted trees were arranged in three randomized blocks, with two ramets each of *F. mandshurica* and *F. nigra* and one ramet of each *F. excelsior* accession per block. One ramet of one *F. excelsior* accession each from Galloway (provenance zone 108) and north-west England (zone 302) did not survive in transit while five *F. excelsior* trees, all from Norfolk, were too small to inoculate. Thus, 155 trees in total were inoculated: 55 trees of 20 *F. excelsior* accessions from Norfolk, 88 trees of 30 *F. excelsior* accessions from elsewhere in Great Britain, six *F. mandshurica*, and six *F. nigra*. Trees were grown at 23°C on a 16:8 hours light:dark cycle under 6500 K high-output fluorescent lights and watered daily to field capacity by drip irrigation.

Trees were inoculated with EAB and larval development quantified by the method of (Showalter, Villari, Herms, & Bonello 2018; Figure 1a-c). Each scion was inoculated at up to three sites at least 2 cm above the graft union. On 19 June (block 1), 26 June (block 2), and 3 July 2017 (block 3), two EAB eggs attached to coffee filter paper, obtained from the USDA-APHIS-PPQ Biological Control Rearing Facility, were placed on the bark at each site and wrapped with gauze secured by duct tape. The mean ± *SE* diameter of trees at the inoculation points was 12.6 ± 0.1 mm for *F. excelsior*, 15.0 ± 0.5 mm for *F. mandshurica*, and 12.3 ± 0.1 m for *F. nigra*. After egg hatching, *A. planipennis* larvae burrow into the phloem, forming serpentine feeding galleries and passing through four larval instars (growth stages) before pupation. Forty-two days after inoculation, trees were debarked and the presence and terminal width of feeding galleries and widths of larval peristomata were recorded. Gallery and peristomata widths were used to determine larval instars (Showalter et al., 2018).

Data recorded for larval establishment and development on each tree were the number of sites where the tree was inoculated with *A. planipennis* eggs (*S*), the number of sites where larvae successfully formed a feeding gallery (*G*), and the number of feeding galleries where larvae developed to the second or third instars (*L*). Three response variables were analyzed: (a) *G* in relation to *S* as the logit function: $\log(G/S - G)$, (b) *L* in relation to *S*, and (c) *L* in relation to *G*. The responses were analyzed by generalized linear mixed modeling using a binomial distribution with a logit link function. The statistical software used was SAS® OnDemand For Academics. The fixed effects model was Block+Species/Source. Block was treated as a fixed effect because the number of levels ($n = 3$) was insufficient to estimate the between-block variance reliably (Galway, 2006). Source was coded with four levels: *F. excelsior* from Norfolk, *F. excelsior* from elsewhere in Great Britain, *F. mandshurica*, and *F. nigra*; this treatment permits comparison of the two sources of *F. excelsior*. Accession of *F. excelsior* was modeled as a random effect, and the individual tree within *F. excelsior* accessions, *F. mandshurica* or *F. nigra* was the residual term. To analyze the effect of the purple discoloration observed in some trees (see Results), the model Block+Source+Purple (fixed) and Accession (random) was fitted to *F. excelsior* data. For all models, visual inspection of residual plots indicated that there was no obvious violation of model assumptions; in all cases, moreover, the

FIGURE 1 Inoculation procedure and symptoms of attack by emerald ash borer. (a) European ash (*Fraxinus excelsior*) tree with three inoculation sites; (b) an emerald ash borer (*Agrilus planipennis*) gallery circling through the phloem around an ash stem; (c) ash stem with three exposed inoculation sites, the lower two showing successful initiation of larval feeding galleries; (d) slight purple discoloration of phloem near an EAB gallery and; (e) superficial phloem showing strong purple color over top of an EAB gallery with (f) the color dissipating deeper in the phloem where the gallery is found

dispersion was close to 1 (range: 0.69–1.07), as expected when the choice of model is appropriate. Significance of fixed effects was assessed by *F*-tests, random effects by likelihood ratio tests, and pairwise differences between species and between the presence and absence of purple discoloration by Fisher's protected least significant difference.

3 | RESULTS

There was no evidence for significant variation between the three *Fraxinus* species in the proportions of eggs which formed galleries (22% overall; see Figure 2a for details). There were significant differences, however, between ash species in the proportions of eggs (Figure 2b) and galleries which produced later instar larvae (Figure 2c). A much higher proportion of inoculations produced later instar larvae on *F. nigra* than on *F. excelsior* or *F. mandshurica*. Slightly greater proportions of eggs and larvae produced galleries in *F. excelsior* than in *F. mandshurica* but the differences were not significant (Figure 2). There was no significant variation within *F. excelsior* for any of the three proportions, as the variance component for Accession was not significantly greater than 0 (p = 1.0 for all three tests) and there was no significant difference between the Norfolk and UK-wide groups of *F. excelsior* for any variate (Figure 2). There was significant variation between blocks in the proportion of eggs which hatched and formed galleries ($F_{2,112}$ = 10.93, p < .001) and progressed to later instars ($F_{2,112}$ = 4.71, p = .01), but not in the proportion of galleries which produced later instars ($F_{2,70}$ = 0.93, p = .4).

A deep purple discoloration developed just beneath the outer bark of 21 trees of *F. excelsior* but not in the other two species. This occurred sporadically in both the Norfolk and UK-wide sets, in one ramet of 11 accessions and two ramets of five accessions. As this was an obvious feature of the response of certain *F. excelsior* trees to EAB, we tested if it was associated with beetle development. The presence of the purple colour was associated with a higher frequency of gallery development from eggs ($F_{1,103}$ = 9.83, p = .002). The lower frequency of development of later instars from galleries in plants with discoloured bark was not statistically significant ($F_{1,65}$ = 1.75, p = .2; Figure 2b).

4 | DISCUSSION

The frequency with which larvae of EAB developed to later instars in *F. excelsior* was similar to that in the resistant *F. mandshurica* but much lower than in the highly susceptible *F. nigra*. Eggs formed galleries with similar frequencies in all three species, implying that while *F. excelsior*, like other *Fraxinus* species, is not immune to initial attack

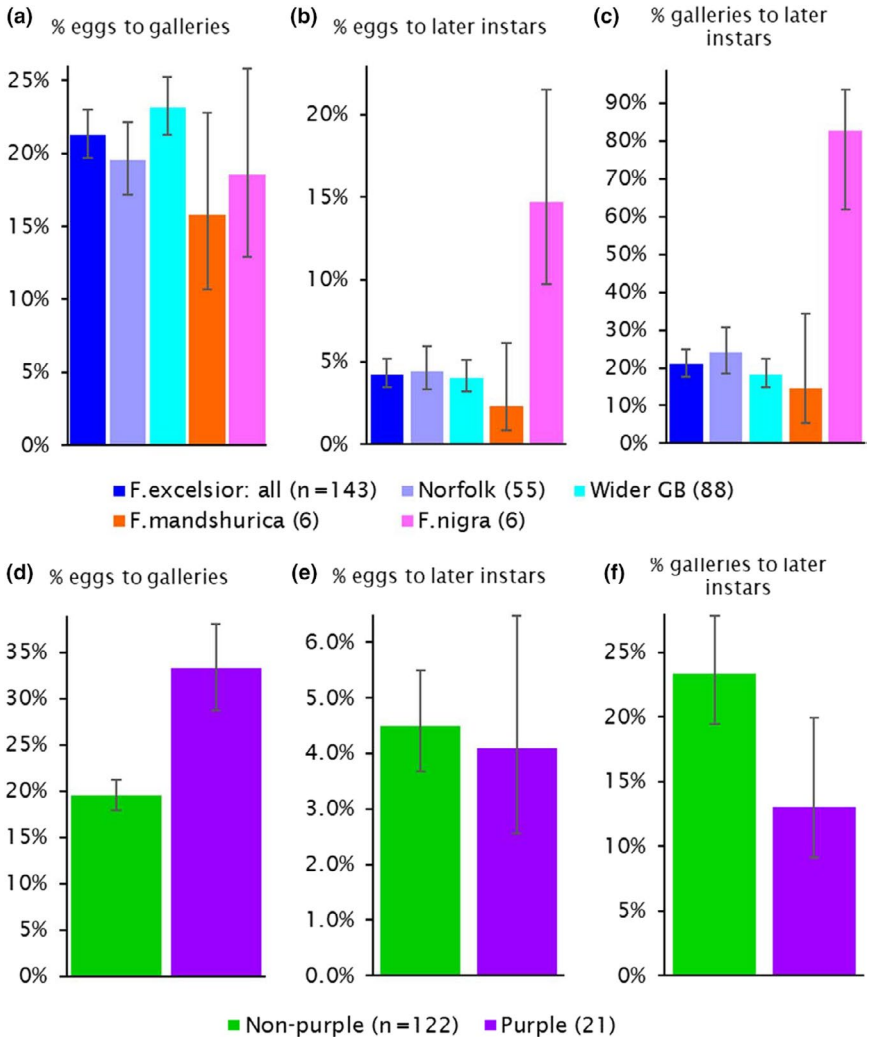

FIGURE 2 Outcomes of infestation of ash by emerald ash borer (*Agrilus planipennis*). Frequencies of sites at which (a) eggs formed larval galleries; (b) eggs produced second or third (later) instar larvae; (c) galleries produced later instar larvae, in *Fraxinus excelsior*, *Fraxinus mandshurica* and *Fraxinus nigra*; and (d–f) similar frequencies for *F. excelsior* trees in the presence or absence of purple discoloration of inner bark. *F*-tests for variation between species: (a) $F_{2,112} = 0.38$, $p = .7$; (b) $F_{2,112} = 4.11$, $p = .02$; (c) $F_{2,70} = 3.57$, $p = .03$. *t*-tests for differences between *F. excelsior* and the control species: (b) *excelsior-mandshurica* $t = 0.61$, 112 degrees of freedom (*df*), $p = .5$; *excelsior-nigra*, $t = 2.76$, 112 *df*, $p = .02$; (c) *excelsior-mandshurica* $t = 0.39$, 70 *df*, $p = .7$; *excelsior-nigra*, $t = 2.63$, 70 *df*, $p = .03$. *F*-tests for differences between *F. excelsior* from Norfolk and Great Britain as a whole: (a) $F_{1,112} = 1.28$, $p = .3$; (b) $F_{1,112} = 0.07$, $p = .8$; (c) $F_{1,70} = 0.75$, $p = .4$. *t*-tests for differences of trees with and without purple discoloration: (d) $t = 3.13$, 103 *df*, $p = .002$; (e) $t = 0.20$, 103 *df*, $p = .8$; (f) $t = 1.32$, 65 *df*, $p = .2$

by EAB, it is capable of restricting the beetle's development. Given that only six trees of the two control species were tested and that there was therefore limited power to test pair-wise comparisons involving these controls, it is striking that a clear difference was observed between *F. excelsior* and the susceptible species *F. nigra*. This offers some encouragement that the partial resistance to EAB observed in *F. excelsior* may be robust.

One should be cautious, however, about extrapolating these conclusions to mature trees because the only cultivar of *F. excelsior* tested in a naturally infested experiment, cv. Aureafolia, had similar long-term mortality as *F. nigra* and *F. pennsylvanica* (Herms, 2015). In previous work, however, small trees were good proxies for the relative resistance of a variety of ash species (Villari, Herms, Whitehill, Cipollini, & Bonello, 2016), and in Russia, *F. excelsior* has not been damaged by EAB as severely as *F. pennsylvanica* (Musolin et al., 2017; Orlova-Bienkowskaja, 2014; Straw et al., 2013). It should also be noted that the experiments reported here were conducted in a specific set of environmental conditions and effects of environmental variation on the responses of *Fraxinus* species or genotypes to EAB were not investigated. Nevertheless, the temperature used in the PAAR EAB testing facility is favorable for development of the beetle (Wang et al., 2010), so it is notable that *F. excelsior* showed moderate resistance to EAB attack in these conditions.

In healthy woodland, the moderate resistance of *F. excelsior* may attenuate the progress of EAB epidemics. The susceptibility of *F. mandshurica* to EAB is enhanced, however, when trees are stressed either abiotically (Chakraborty et al., 2014; Showalter et al., 2018) or biotically, for example when under attack by other parasites. In Russia, *F. excelsior* may need to suffer some form of stress before succumbing to EAB attack (Straw et al., 2013). If EAB were to arrive in the UK, it would encounter an *F. excelsior* population which has already been weakened by exposure to *H. fraxineus*. The combined effect of the two bioantagonists may prove highly destructive, at least until resistance to *H. fraxineus* becomes widespread (Plumb et al., 2019), at which point the partial resistance of *F. excelsior* to EAB may protect trees that have not been severely damaged by ash dieback.

In this study, there was no evidence for genetic variation in responses to EAB in *F. excelsior* saplings. It is not feasible to inoculate older, larger trees in a controlled environment facility but natural infestation could be studied in a much larger sample of accessions at suitable field sites, for example, where EAB has invaded the native range of *F. excelsior* in Russia. If there is indeed little or no genetic variation for EAB resistance within *F. excelsior*, selection for

resistance to *H. fraxineus* should not exacerbate susceptibility to EAB. Conversely, since the scope for selecting trees with greater resistance to EAB is limited, efforts to protect ash in the UK should focus on excluding the beetle.

The cause of the purple discoloration in shallow parts of the inner bark of some *F. excelsior* trees is unknown. Whether it occurred before or after inoculation is also unknown as it was only visible upon removal of the outer bark, but it did not result from wounding. It may have been stimulated sporadically by environmental conditions in the PAAR facility. It may repay further investigation as compounds which affect egg hatching and larval development in EAB may be involved in this host response.

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AUTHORS' CONTRIBUTIONS

All authors planned the research. R.J.S., J.K.M.B., and E.S.O. selected the *F. excelsior* trees for study. D.N.S. and P.B. designed the *A. planipennis* study and D.N.S. conducted it. J.K.M.B. and D.N.S. analyzed the data. J.K.M.B. and D.N.S. wrote the paper and all authors reviewed and approved it before submission.

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