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Resistance of eight species of ash trees to emerald ash borer and their mechanisms

Shixiang Zong[1], Jianqiang Lin[2], Tao Wang[3], Youqing Luo[1, *]

[1]Key Laboratory of Beijing for the Control of Forest Pests, Beijing Forestry University, Beijing 100 083, China
[2]Ao Yang Ecology and Agroforestry Limited Company, Jiangsu 215 623, China
[3]Mentougou Forestry Station, Beijing 102 300, China

Email address:
youqingl@yahoo.cn (Youqing Luo)

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Abstract: Ash tree, *Fraxinus* (Oleaceae), is a fine species of timber, shelter and scenic tree used for afforestation in China. Emerald ash borer (EAB), *Agrilus planipennis* Fairmaire, an important trunk borer of ash trees, have caused great damage to ash trees in China, the United States, Canada and other countries. First, adult EAB lays eggs in the bark crevices, then the newly hatched larvae feed on the superficial layers of the bark, and enter the xylem when approaching maturity, causing great damage. Therefore, bark is an important location for the adult oviposition, egg development and larval feeding of EAB. In order to understand the resistance of different species of ash trees and their mechanisms, eight ash trees with varying degrees of resistance to EAB were chosen to further investigate the morphological characteristics of the bark, anatomical structure of the tissue, main nutrients and secondary metabolites. The following results were observed: (1) The resistance of different tree species to EAB was not correlated with the bark color, but was inversely proportional to bark thickness, roughness, lenticel size, and compactness. The thicker, rougher and more compact the bark was, the larger the lenticels were, and in turn the greater the EAB-induced damage was. (2) In the anatomical structure of the bark tissues, the vessel size, wood cell number, wood cell area and stone cell number were shown to be the most important resistance factors, among which vessel area and wood cell area were both negatively correlated with insect resistance, and stone cell number and wood cell number were positively correlated. (3) Among the main nutrients and secondary metabolites, polyphenols, soluble sugars, reducing sugars and flavonoids were shown to be the most important resistance factors, the contents of which in tree species with high resistance were generally higher than those in susceptible tree species. These results provide a theoretical basis and practical guidance for revealing the resistance of different species of ash trees to EAB, and selecting suitable insect resistant tree species.

Keywords: Emerald Ash Borer, Ash Tree, Bark, Resistance Mechanism

1. Introduction

The emerald ash borer (EAB), *Agrilus planipennis* Fairmaire a species of *Agrilus* (Coleoptera: Buprestidae) (Jedned, 1994; Haack et al., 2002), is a devastating trunk borer of ash trees. Its larvae feed on xylem and phloem, between which an "S"-shaped tunnel is created, thus cutting off the conducting tissues of the trunk, resulting in reduced tree vigor and eventual tree death. As significant trunk borers of ash trees, EAB greatly harm the ash trees of Liaoning, Shandong, Tianjin and other locations throughout China, causing extreme economic losses. EAB were first discovered in Michigan, USA in 2002, after which it spread to 13 states of the northeastern USA, as well as Ontario and Quebec of southeastern Canada in 2010 (Kathleen et al., 2013; Marshall et al., 2010; Wei Xia, 2004; Zhao Tonghai, 2005b). In China, the host plants of EAB mainly include velvet ash (*Fraxinus velutina*), red ash (*F. pennsylvanica*) and white ash (*F. americana*) (Zhao Tonghai et al., 2005b; Wei Xia et al., 2004), all of which are important greening tree species which were imported from North America to China (Herms et al., 2004; Anulewicz et al., 2007; Zhao Tonghai, 2005a).

Plants are able to avoid and endure damage caused by the pests, and restore their original functions. Under similar environmental conditions, the level of resistance varies widely among different species or varieties of the same plant. This feature of the plant is generally determined by the biochemical or morphological characteristics of the plants. Although plants contain the nutrients that pests require, it is difficult for pests to obtain or use due to their characteristics, and they will not produce harmful effects after being used. During their long-term evolution, plants have established various external morphological characteristics and internal tissue structures which may be used to prevent pest invasion. These slight changes in morphology may change the palatability of herbivorous insects, thus affecting the behavior, growth and development of the pests (Seung et al, 2005; Bosu and Wagner, 2008; Raghu, et al., 2004; Etges and Ahrens, 2001; Ballabeni et al., 2003). After suffering, plants will generate a series of chemical modifications, and form mechanisms for pest tolerance and insect resistance. These chemical substances include nutrients, secondary metabolites and volatile secondary substances, among which nutrients and secondary metabolites are the major insect-resistant chemicals, and have different sources, natures, and actions in pest defense. Such interaction constitutes the mechanisms of chemical defense against pests in the natural environment (Cao Bing, 2004).

Pest resistance of plants is a preconditioned mechanism, which may be used to resist the pressure of natural selection caused by pests, and increase the opportunities for plants to survive and prosper. The pest resistance of different plants and different varieties of the same plant is of great significance for selecting excellent cultivars and understanding the mechanisms of damaged. Adult EAB first lays eggs in the bark crevices, then the newly hatched larvae feed on the superficial layers of the bark, and enter the xylem after approaching maturity, causing great harm. Therefore, bark is the main location of adult oviposition, egg development and larval feeding for EAB. At present, the EAB-resistance mechanisms of the bark of different ash trees has yet to be reported. In order to understand the features of the external morphology and internal anatomical structure of the bark of different EAB-resistant tree species, as well as the differences among nutrients and secondary metabolites, eight species of ash trees with different resistance mechanisms were chosen in this systematic study, thus providing a theoretical basis for determining the resistance mechanisms of the different species, and selecting appropriate insect resistant tree species.

2. Materials and Methods

2.1. Test Samples

From August to October, 2009, eight ash tree species with different EAB resistance levels were selected from the Beijing Botanical Garden, China. Among them were high resistance tree species, including *F. chinensis*, *F. rhynchophylla* and *F. platypoda*; low resistance species, including *F. mandshurica* and *F. excelsior*; and susceptible tree species, including *F. velutina*, *F. pennsylvanica* and *F. americana* (Zhao Tonghai et al., 2005; MacFarlane et al., 2005; Anulewicz et al., 2007). *F. mandshurica* and *F. excelsior* were 3-4 years old, and the others approximately 15 years.

2.2. Research Methods

2.2.1. Sampling Methods

From the different parts of each species, three three-year-old branches were chosen to perform close observations of the morphological characteristics of their barks. Then, from the middle of each branch, a branch segment 2 cm in length and about 2 cm in diameter was severed, and placed in a vial filled with FAA stationary liquid for sealing and storage, to observe the internal anatomical structures. Finally, the bark of each branch bark was stripped off for determination of their nutrients and secondary metabolites.

2.2.2. Determination Methods

2.2.2.1. Bark Structure

Bark thickness was measured using a vernier caliper. Bark color, roughness, compactness and lenticel size were visually observed using the contrast method.

2.2.2.2. Internal Anatomical Structure

First, after following a series of steps including fixation, extraction, softening, slicing, staining, dehydration, re-staining, color separation, and transparentizing, the slices were sealed with neutral gum and placed in dry specimen boxes to complete the sample preparation (Wang Zhizheng, 2010). Then, under an Olympus microscope, a micrometer was used to measure the internal anatomical features of the samples, including four characteristics of vessels, wood rays, wood cells and stone cell wall thickness, each of which contained different factors (Table 2). The samples were observed under 10 × 40 magnification; the number of vessels, rays, wood cells and stone cells were observed within an area of 10^3 mm^2; the measured value of each factor was the mean value of the four fields of vision.

2.2.2.3. Nutrients and Secondary Metabolites

Soluble protein content was determined with the Coomassie brilliant blue method, total sugar content with 3,5-dinitrosalicylic acid, total soluble sugar content with anthrone colorimetry, tannin content with vanillin colorimetry; total soluble phenol content with Folin colorimetry, and flavonoids with rutin colorimetry (Li Hesheng, 2000; Wu Shuqing et al., 2000).

2.3. Statistical Analysis of Data

All the test data were analyzed using SPSS 12.0 software with LSD (least significant difference), and analysis of variance and Duncan's multiple comparisons. In addition, when observing the internal anatomical structures, the observed four characteristic values of all factors and insect resistance of each of the tree species were used for correlation analysis. With serial regression and stepwise regression, the most appropriate factors, as well as those related to insect resistance level, were determined successively. At the same time, the insect resistance level was assigned for all the tree species, as shown by 0.1 for high resistance species, 0.5 for low resistance species, and 0.8 for susceptible species, in order to further determine the relationship between all of the factors and insect resistance.

3. Results

3.1. Morphological Characteristics of Bark

The morphological characteristics of the barks of the different tree species are shown in Table 1. There was no significant difference shown for bark color among the tree species with insect resistance, showing its irrelevance to insect resistance. By multiple comparisons and analysis of variance, it was shown that the bark thickness of susceptible tree species was significantly more than that of other tree species (Fig. 1); in addition, the bark roughness, compactness and lenticel size were inversely proportional to resistance, i.e. the rougher and more compact the bark and the larger the lenticels were, the greater the EAB-induced harm was.

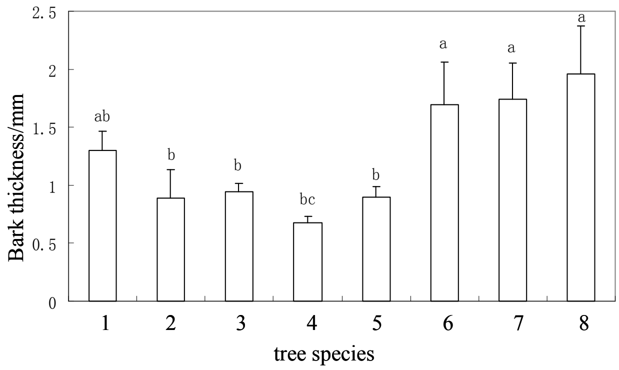


Fig. 1. *Variance analysis of the bark thickness of the eight ash tree species*

Table 1. *Morphological characteristics of the bark of the eight ash tree species*

Tree species		Bark thickness/mm	Bark color	Roughness	Compactness	Lenticel size
High resistance tree species	*F. chinensis*	1.30±0.162ab	Gray brown	Smooth	Loose	Small
	F. rhynchophylla	0.89±0.242b	Celadon	Relatively smooth	Relatively loose	Small
	F. platypoda	0.94±0.072b	Gray brown	Relatively smooth	Relatively compact	Relatively small
Low resistance tree species	*F. mandshurica*	0.68±0.053bc	Celadon	Relatively smooth	Compact	Relatively small
	F. excolsior	0.90±0.092b	Celadon	Smooth	Compact	Relatively small
Susceptible tree species	*F. americana*	1.69±0.371a	Gray brown	Rough	Compact	Large
	F. pennsylvanlca	1.74±0.310a	Gray brown	Rough	Compact	Large
	F. velutina	1.96±0.411a	Gray brown	Rough	Compact	Large

Note: different letters signify significant difference ($p < 0.05$).

3.2. Internal Anatomical Structure of Bark

The internal anatomical characteristics of the different tree species are shown in Table 2. All data were used to establish the retrogression equation of insect resistance:

$y_1=0.4465+0.0056x_1-0.0031x_2-0.3512x_3+0.0038x_4-0.0333x_5+0.2214x_6-0.0019x_7-0.0006x_8+0.0558x_9-2.0164x_{10}+0.1127x_{11}-0.0004x_{12}+0.0030x_{13}+0.4614x_{14}+0.00217x_{15}$. The coefficient of determination is shown by $R^2=0.6371$.

Table 2. *Characteristics of anatomical structure of the eight ash tree species*

Tree species		Vessels				Rays		
		Number=x_1	Radius=x_2	Thickness=x_3	Area=x_4	Number=x_5	Width=x_6	Area=x_7
High resistance tree species	*F. chinensis*	25.40	4.21	0.66	10.59	7.20	1.13	24.01
	F. rhynchophylla	20.00	4.70	0.42	15.25	5.40	0.98	20.05
	F. platypoda	31.20	6.37	0.37	23.05	7.40	0.83	21.73
Low resistance tree species	*F. mandshurica*	16.80	4.02	0.39	12.73	4.80	1.01	17.05
	F. excolsior	47.20	1.62	0.23	2.76	6.20	1.08	49.46
Susceptible tree species	*F. americana*	42.00	6.13	0.37	18.01	6.00	1.23	23.41
	F. pennsylvanlca	42.20	4.90	0.42	60.63	6.00	1.08	10.08
	F. velutina	36.70	5.64	0.40	41.84	6.70	0.96	15.91

Table 2. *Characteristics of anatomical structure of the eight ash tree species (continued)*

Tree species		wood cells				Stone cells			
		Number=x_8	Radius=x_9	Wall thickness=x_{10}	Area=x_{11}	Number=x_{12}	Radius=x_{13}	Wall thickness=x_{14}	Area=x_{15}
High resistance tree species	*F. chinensis*	358	1.08	0.14	1.12	37.00	2.08	0.19	3.57
	F. rhynchophylla	186	0.98	0.13	0.67	55.80	1.04	0.18	1.22
	F. platypoda	125	1.18	0.17	1.68	69.60	1.53	0.20	2.35
Low resistance tree species	*F. mandshurica*	176	0.84	0.16	0.72	22.80	0.99	0.13	1.01
	F. excolsior	270	1.03	0.12	1.32	4.20	4.61	0.25	12.73
Susceptible tree species	*F. americana*	180	0.74	0.10	1.20	80.00	1.47	0.22	2.40
	F. pennsylvanlca	80	1.18	0.11	1.56	48.00	1.37	0.20	2.21
	F. velutina	103	1.18	0.14	1.62	58.80	1.45	0.20	2.28

Note: Area is represented by mm^2. Radius, thickness, width and wall thickness are represented by μm.

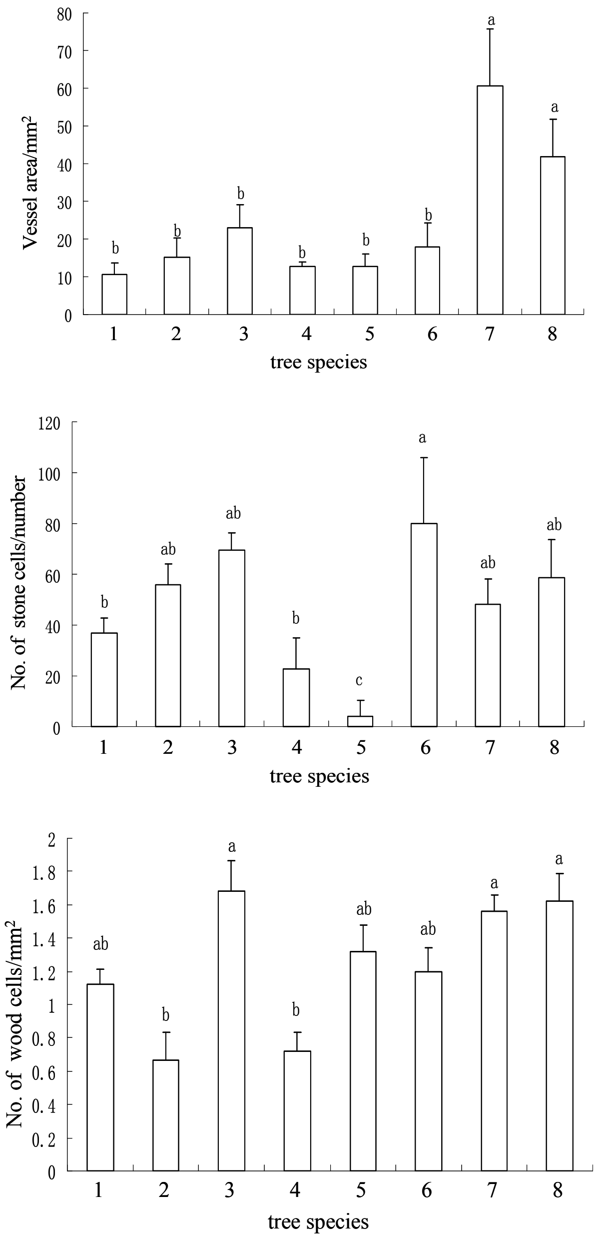
Due to the low correlation within an entire series of factors, the factors may not be interdependent among each other. In order to avoid data multicollinearity, variables having significant effects on the dependent variables are included, while those with no significant effects on the dependent variables are excluded. Finally, through further stepwise regression analysis, vessel size, wood cell area, wood cell number and stone cell number were determined as the most important factors affecting insect resistance. These four influential factors were used for analysis of variance, and the results are shown in Figure 2.

The vessel area of the susceptible tree species, i.e. *F. pennsylvanlca* and *F. velutina*, was significantly higher than that of the insect resistant tree species. Vessel area was positively correlated with insect resistance i.e. the larger the vessel was, the more susceptible the trees were, and the less effective the insect resistance was.

The stone cell numbers of *F. chinensis*, *F. mandshurica* and *F. excelsior* were significantly lower than those of the other tree species. The overall regression results showed the higher the stone cell number was, the less susceptible the trees were, and thus the more effective the insect resistance was. However, there was no significant difference between the susceptible trees, *F. pennsylvanlca* and *F. velutina*, and the resistant trees, *F. rhynchophylla* and *F. platypoda*.

Wood cell area was observed to be maximum in the susceptible trees, *F. pennsylvanlca* and *F. velutina* and resistant tree *F. platypoda*, moderate in *F. rhynchophylla* and *F. mandshurica*, and minimum in *F. excelsior*, *F. americana* and *F. chinensis*. The overall trend showed that the wood cell area was positively correlated with insect resistance, i.e. the larger the wood cell area was, the more susceptible the trees were, and thus the less effective the insect resistance was.

The wood cell numbers of high resistance tree *F. chinensis* and low resistance tree *F. excelsior* were significantly higher than those of the other tree species. The overall trend showed that the wood cell number was negatively correlated with insect resistance, i.e. the larger the wood cell number was, the less susceptible the trees were, and thus the more effective the insect resistance was.



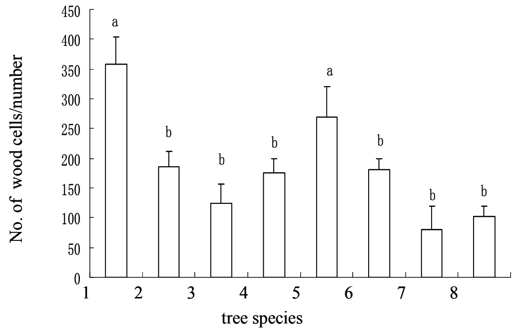


Fig. 2. *Variance analysis of the different factors of the eight ash tree species*

3.3. Nutrients and Secondary Metabolites of Bark

The nutrients and secondary metabolites of the different tree species are shown in Table 3. Serial retrogression was used to establish the relationship between contents and insect resistance: y_1=0.4250-0.00045x_1+0.0205x_2-0.0519x_3-0.02367x_4-0.0881x_5 -0.06539x_6. The coefficient of determination was shown by R^2=0.4200.

Table 3. *Contents of major nutrients and secondary metabolites of bark in the eight ash tree species*

Tree species		Protein= x_1	Soluble sugars= x_2	Reducing sugars= x_3	Tannin x_4	polyphenols= x_5	flavonoids= x_6
High resistance tree species	*F. chinensis*	42.684	204.593	105.046	12.26	48.26	31.38
	F. rhynchophylla	39.773	192.469	66.317	16.17	47.1	23.45
	F. platypoda	86.338	174.755	37.989	3.23	37.25	23.11
Low resistance tree species	*F. mandshurica*	129.629	186.008	44.186	3.52	34.29	16.45
	F. excolsior	68.149	179.909	39.76	10.41	46.46	30.1
Susceptible tree species	*F. americana*	51.051	181.071	35.776	10.43	32.78	19.02
	F. pennsylvanlca	42.32	195.155	59.235	8.02	33.55	20.94
	F. velutina	53.597	200.528	45.661	10.06	30.51	17.77

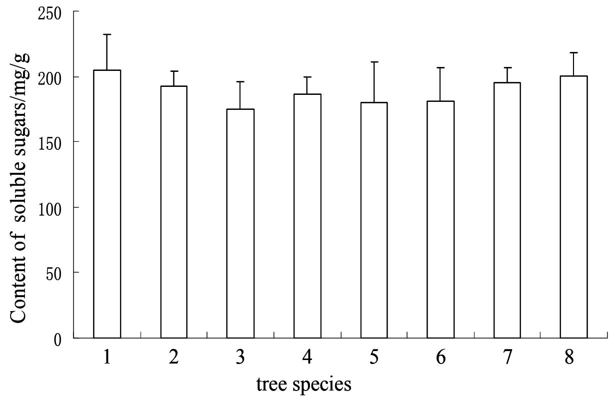
Note: The unit is represented by mg/g.

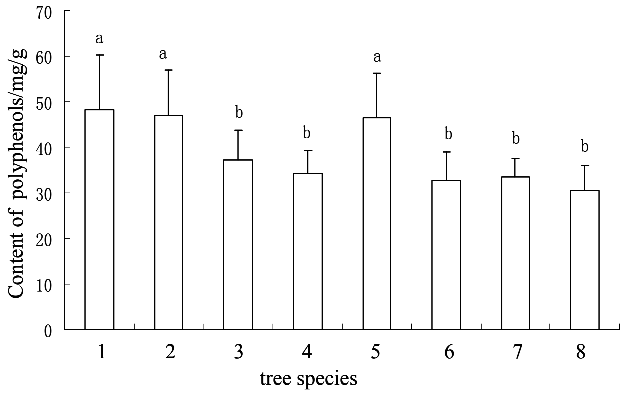
Due to the low correlation within an entire series of factors, the factors may not be interdependent among each other. In order to avoid data multicollinearity, variables with significant effects on the dependent variables were included, while those with no significant effects on the dependent variables were excluded. Through further stepwise regression analysis, polyphenols, soluble sugars, reducing sugars and flavonoids were finally determined as the most important factors affecting insect resistance. These four influential factors were used for analysis of variance, and the results are shown in Figure 3.

The contents of polyphenols in *F . chinensis*, *F. rhynchophylla* and *F. excelsior* were significantly higher than those in the other tree species. In general, the content of polyphenols was negatively correlated with insect resistance, i.e. the larger the content of polyphenols was, the less susceptible the trees were, and thus the more effective the insect resistance was. Although soluble sugar entered the model during retrogression, the differences in the contents of polyphenols among the tree species were not significant.

Multiple comparisons showed that the content of reducing sugars in *F. chinensis* was significantly higher than those in *F. rhynchophylla* and *F. pennsylvanlca*, which had significantly higher contents than other tree species. The content of reducing sugars was negatively correlated with insect resistance, i.e. the larger the content of reducing sugars was, the less susceptible the trees were, and thus the more effective the insect resistance was.

The contents of flavonoids in *F. chinensis* and *F. excelsior* were significantly higher than those in the other tree species, i.e. the larger the content of flavonoids was, the less susceptible the trees were, and thus the more effective the insect resistance was.





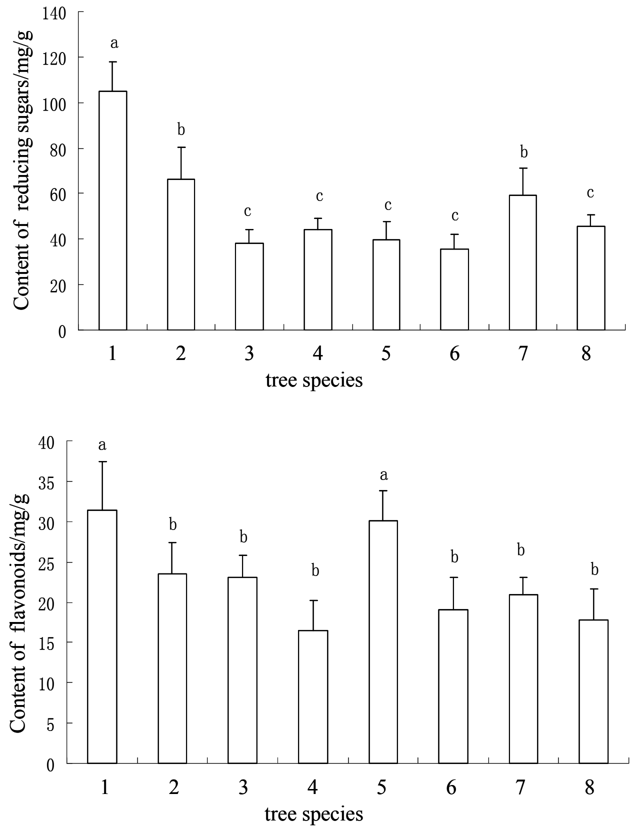


Fig. 3. Variance analysis of main nutrients and secondary metabolites of the eight ash tree species

4. Discussion

4.1. Morphological Characteristics of Bark

EAB damage was not shown to be associated with bark color, but rather with lenticel size, roughness, compactness and crevices. The larger the bark thickness and lenticel size were, the greater the EAB-induced harm was, and thus the more serious the insect harm was. The main reasons for this were that adult EAB feeds on leaves to replenish nutrients, and large lenticel size and high roughness are favorable to adult adhesion and larvae storage (Li Huiping et al., 2004). The relationship between bark compactness and EAB harm was not evident. However, after EAB damage, the bark was easily peeled off, mainly due to the fact that larvae caused harm at the juncture of the phloem and xylem. The bark crevice size was positively correlated with EAB damage, i.e. the greater the crevice was, the greater the harm was, which was due to the fact that adult EAB laid eggs mainly in the bark crevices. The greater the crevice was, the greater the egg number held in the crevices was, thus allowing the eggs to be easily located by natural enemies.

4.2. Internal Anatomical Structure

The internal anatomical structure of bark varied among the tree species. The vessel area, stone cell number, wood cell number and wood cell area were main factors affecting insect resistance for the tree species; this differed from previous research findings which stated that the insect resistance of poplar trees was associated with vessel density, wood ray width, wood cell radius and stone cell thickness (Li Huiping et al., 2004; Liu Jinglan et al., 1999; Yang Xueyan et al., 1992). The main reason for this was that, despite the differences in vessel number among the tree species, the fitting effect was more suitable and the correlation was higher after the vessel area, rather than the vessel number, was used. All factors of wood rays did not enter during stepwise regression, but instead had collinearity with other factors, and were replaced by other factors. The stone cell thickness was originally quite thin and had little difference among the tree species, and was subject to accidental error in the observation room. Using the stone cell number instead of the stone cell thickness during retrogression may better reflect the features of the stone cells. With the exception of vessel area, the relationships among the remaining factors between insect resistant tree species and susceptible tree species were inconsistent, showing incomplete functional relationships. This signifies that although all the tree species showed certain overall trends, the differences between insect resistant and susceptible tree species were not evident during analysis of variance, possibly due to the fact that all of the factors were not interdependent, but interacting, thus resulting in the resistance of the tree species.

4.3. Nutrients and Secondary Metabolites

Plants may only be fed on and harmed by some herbivorous insects after obtaining nutrients of certain types and content (Qin Junde, 1995). After plants have been harmed by the pests, some nutrients show corresponding changes, such as increased glucose content and decreased insect resistance (Huang Jinshui, 1993). In addition, the contents of soluble sugars, total amino acids and essential amino acids have certain effects on the insect resistance (Li Jidong, 2007). The changes of soluble sugars and reducing sugars in the bark of the eight tree species simply reflected the change trends. It was found during the regression of nutrients and secondary metabolites of the eight tree species that a single species is not capable of simulating the insect resistance of plants completely. Although polyphenols showed the greatest correlation, the correlation coefficient was only 0.6979. Furthermore, although soluble sugars had insignificant differences among the species, soluble sugars with reducing sugars entered the model during the second regression, and the correlation coefficient reached 0.8437, a great increase, thus indicating that in terms of plant resistance to pests, the actions among all contents were not independent, but mutual.

Over their long-term evolution, a complex interacting relationship between plants and pests has been established, as shown by the fact that plants have a direct defense reaction in the wound site after insect feeding, and insects may also resist or adapt to plant defense through a number of methods (Kessler et al., 2004; Ge Feng, 2011). The resistance of *Fraxinus* spp. to *Agrilus planipennis* Fairmaire is influenced by various factors, all of which are mutually restrained, mutually promoting and jointly determined for insect resistance. In the present study, the morphological characteristics of bark, as well as anatomical structure of tissues, nutrients, secondary metabolites and other factors were shown to be related factors. The volatile substances of tree species, anatomical structure of the xylem tissues, nutrients and secondary metabolites were also involved, and require further investigation.

Acknowledgements

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