Journal of the Torrey Botanical Society 134(1), 2007, pp. 27–33

Mycorrhizal associations in *Ailanthus altissima* (Simaroubaceae) from forested and non-forested sites[1]

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Huebner, C. D. (Northern Research Station, USDA Forest Service, 180 Canfield St. Morgantown, WV 26505), C. McQuattie and J. Rebbeck (Northern Research Station, USDA Forest Service, 359 Main Road, Delaware, OH 43015). Mycorrhizal Associations in *Ailanthus altissima* (Simaroubaceae) from Forested and Non-Forested Sites. J. Torrey Bot. Soc. 134: 27–33. 2007.—*Ailanthus altissima* tree seedlings were excavated from each of two habitats: (1) a forest adjacent to a trail and stream and (2) a non-forested steep, barren slope adjacent to a major highway. Each seedling root system was examined for colonization by mycorrhizal structures using light microscopy and transmission electron microscopy. The roots were colonized by one or more endomycorrhizal fungi with *Arum*-type colonization. Endomycorrhizal colonization of the seedlings from the non-forested site (65.2%) was significantly greater than that of the seedlings from the forested site (37.9%). Colonization by intercellular hyphae and vesicles was significantly greater in the non-forested habitat than the forested habitat. This exotic invasive species may benefit from the rapid colonization of endomycorrhizae in more extreme open environments.

Key words: *Ailanthus altissima*, *Arum*-colonization, endomycorrhizae.

Ailanthus altissima (Mill.) Swingle (Simaroubaceae; tree of heaven) is an exotic tree that proliferates in urban areas but may invade grasslands, woodlands, and mature forests in the U.S., especially after a disturbance (Hu 1979, Kowarik 1995, Knapp 2000). The distribution and spread of this species since its 1784 introduction (Hu 1979) in the U.S. suggests a preference for open sites with rich soil but an ability to colonize extreme environments in which it may be more competitive than native species (Kowarik 1995, Knapp 2000, Trifilò et al. 2004). *Ailanthus altissima* is rhizomatous and clonal with comparatively rapid growth (Hu 1979, Kowarik 1995) and thick tap and lateral roots (Pan and Bassuk 1986). Allelopathic properties (ailanthone being the primary phytotoxic, quassinoid-allelochemical; Jaziri et al. 1987) have been verified for this species (Singh et al. 2003), with the highest concentrations of ailanthone found in the roots (Heisey 1990) and in younger plants (Lawrence et al. 1991).

Several members of the Simaroubaceae family (primarily tropical to subtropical in distribution; Corbett and Manchester 2004) are known to be colonized by mycorrhizae (Torti et al. 1997, Chandra 1999, Oliveira et al. 1999); however, it is unknown if *Ailanthus altissima* is colonized. Its rapid growth and success in disturbed sites suggest it may act as a weedy, early successional or gap species in its native environment and, consequently, would be less likely to have an obligatory (if any) symbiotic relationship with mycorrhizae. This relationship between weedy, early successional species and a lack of mycorrhizae is supported by several studies (Moorman and Reeves 1979, Reeves et al. 1979, Schmidt and Scow 1986, Yamato 2004). Disturbed areas are often colonized by non-mycorrhizal plant species (Reeves et al. 1979, Rillig et al. 2003) because of low concentrations of mycorrhizae present in such soils (Moorman and Reeves 1979). In addition, we predict that any mycorrhizal association that may exist in association with *Ailanthus altissima* will be with endomycorrhizae rather than ectomycorrhizae, as is documented for several native gap and early-successional species, such as *Liriodendron tulipifera* L. and *Acer rubrum* L. (Vozzo and Hacskaylo 1964). *Ailanthus altissima*'s invasive and fast growing nature also suggests that an *Arum*-type of colonization is most likely to be present, if an endomycorrhizal association exists (Brundrett and Kendrick 1990a and b, Smith and Smith 1997, Yamato and Iwasaki 2002, Yamato 2004). In *Arum*-type coloniza-

[1] We thank Heather Smith for helping in seedling collections and Joan Jolliff for assistance with mycorrhizal structure counts.

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Received for publication December 9, 2005, and revised form November 21, 2006.

tion, hyphae grow intercellularly in the root cortex and invaginate the cortical cells as short side branches, whereas with *Paris*-type colonization, the hyphae spread directly from cortical cell to cortical cell. *Arum*-type of colonization typically occurs at a more rapid rate than *Paris*-type of colonization (Yamato and Iwasak 2002, Yamato 2004).

Habitat type or site conditions may also influence whether or not a species will be colonized by mycorrhizae and possibly the type of colonization. Plant species with facultative associations with mycorrhizae may be less likely to develop mycorrhizal associations in nutrient rich (due to no limitations on nutrient availability for the plant) or low light environments (due to a lack of photosynthates for the mycorrhizae). However, the relationship between mycorrhizae and plants with an obligatory association may be parasitic under conditions where photosynthate production is slow, such as in low light environments (Korhonen et al. 2004). *Paris*-type endomycorrhizal colonization, which is the most common type of colonization in woodland species, may help alleviate any parasitic interactions by ensuring a slower growth rate of the fungus, which is conducive to the slower growth rate of shade-tolerant plants (Brundrett and Kendrick 1990b, Cavagnaro et al. 2001b). These findings suggest that *Ailanthus altissima*, which can colonize various habitats, could exhibit differential mycorrhizal colonization (if present) based on habitat type with an *Arum*-type of colonization in an open habitat and a *Paris*-type of colonization or no colonization in a forested habitat. Differences in mycorrhizal colonization, if confirmed, may provide *A. altissima* with a competitive advantage in one or more habitat types and may help explain its success in such different environments.

We ask the following questions: 1) Is *Ailanthus altissima* colonized by mycorrhizae, if so, what type of colonization is it? 2) Does mycorrhizal colonization and type of colonization of *A. altissima* differ between forested (forest adjacent to a trail and stream; shaded) and non-forested (barren, eroded slope adjacent to a highway; open) sites?

Materials and Methods. SAMPLE COLLECTION AND PREPARATION. Ten randomly selected *Ailanthus altissima* (nomenclature follows Gleason and Cronquist 1993) seedlings less than 0.5 m in height and 5 m or more apart were excavated from each of two habitats: non-forested and forested. The non-forested site was a steep, slope corridor (approximately 200 m long), with no other associated vegetation, adjacent to a major highway (i.e., a relatively xeric site located in full sun that is likely to be nutrient-poor); the forested habitat was a mature deciduous forest corridor (approximately 200 m long) adjacent to a small stream on one side and a trail on the other with no slope (i.e., a relatively mesic site with a diverse understory in partial to full shade that is likely to be nutrient-rich). Both habitats were located in Morgantown, West Virginia (79° 57′ 22″ N, 39° 38′ 04″ W), and all excavations took place on August 24, 2004.

Each root system was separated from its stem at the root collar, washed thoroughly to remove soil, placed between two moist paper towels and into a sealed plastic bag. The 20 samples were then delivered overnight to the Delaware, OH, U.S. Forest Service Laboratory.

A fine root segment (2 mm long) randomly chosen from each of the 10 seedling root systems of each habitat type was fixed overnight in 3% phosphate-buffered glutaraldehyde at 4°C. Root segments were post-fixed in 2% osmium tetroxide, dehydrated in a graded ethanol series, and embedded in an epoxy resin mixture (Poly-Bed/Araldite). All remaining roots from each of the 20 root systems were stored in FAA (formalin-acetic acid alcohol); these roots were then cleared in 10% potassium hydroxide and stained with Trypan Blue (Phillips and Hayman 1970).

In order to confirm type of mycorrhizal colonization (*Paris* vs. *Arum*) and visually document our interpretation of the different structures (intercellular vs. intracellular hyphae, arbuscles, and vesicles), microscopical evaluation of mycorrhizal structures was conducted on the resin-embedded root segments using light microscopy (LM) and transmission electron microscopy (TEM). For LM, thick sections (2 μm) were cut from the 10 root segments from each habitat and photographed with an Olympus BH2 light microscope. Ultrathin sections (100 nm) of roots to be viewed by TEM were cut from regions adjacent to those examined by LM. An LKB Ultratome III was used for ultrathin sectioning, and root sections were stained in 4% aqueous uranyl acetate and Reynolds' lead citrate (Reynolds 1963). Thin sections were

examined and photographed using a JEOL JEM-1010 transmission electron microscope.

MYCORRHIZAE EVALUATION. Each of the 20 root systems that were cleared and stained with Trypan Blue were evaluated for the presence of mycorrhizal structures using the gridline intersect method (Giovannetti and Mosse 1980). The entire root systems (after cutting in transverse segments) from each seedling were placed in a Petri dish marked with a grid of lines forming 1 cm grid-squares. Transverse root sections at each gridline intersect were scored for the presence or absence of any mycorrhizal structures using a dissecting microscope at 40× magnification. Percent colonization was determined after scoring 50 (smaller root systems) intersections and 100 (larger root systems) intersections. Presence or absence of arbuscules, vesicles, intercellular hyphae, and intracellular hyphae were determined using 10 randomly chosen root sections (5 mm in length each) from each of the 20 root systems and examining three fields of view under a light microscope at 10× magnification. The resulting area examined was equivalent to 1 mm^2. Arbuscules were defined as any structures with multiple branching; there was no attempt to differentiate whether the originating hyphae were intercellular or intracellular (which could lead to intermediate types; Dickson 2004). This method may overestimate actual counts and should be used as a relative comparison among the different structures between habitat types (McGonigle et al. 1990).

DATA ANALYSIS. Significant differences in percent colonization vs. no colonization using both the gridline intersect and field of view methods were tested using one-tailed *t* tests within each habitat type. Habitat type was directly compared using an ANOVA (PROC GLM; SAS v. 9.1 2003). For the gridline intersect data, distributions were normal and variances were not significantly unequal. For the field of view method, distributions were also normal and variances were not significantly unequal, except for the arbuscule category (non-normal) and the summed structures category (unequal variances) even after several transformations. For these two variables, non-parametric Kolmogorov-Smirnov one-sample tests were run (Systat v. 10, SPSS Inc. 2000) and a non-parametric permutation procedure (Proc Multtest; SAS v. 9.1 2003) was used to test for significant differences between the two habitat types.

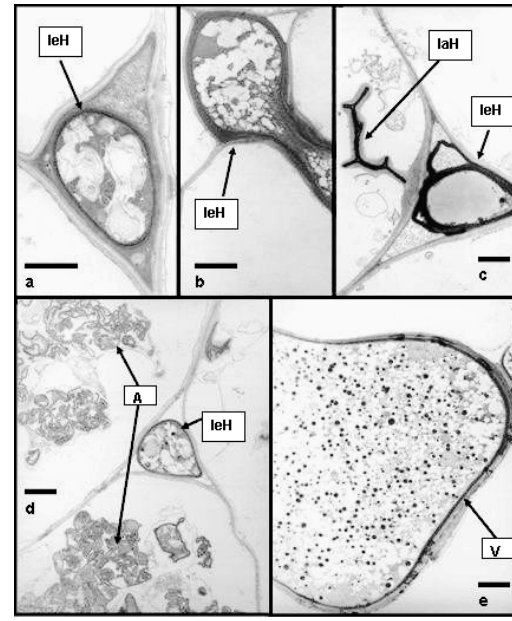

FIG. 1. a. Intercellular hypha (IeH). Scale bar = 20 μm. b. Intercellular hypha (IeH). Scale bar = 10 μm. c. Intercellular hypha (IeH) and intracellular hypha (IaH). Scale bar = 20 μm. d. Arbuscules (A) and intercellular hypha (IeH). Scale bar = 10 μm. e. Vesicle (V). Scale bar = 5 μm. All photos were taken with a JEOL JEM-1010 transmission electron microscope.

Results. IS *AILANTHUS ALTISSIMA* COLONIZED BY MYCORRHIZAE, IF SO, WHAT TYPE OF COLONIZATION IS IT? The root systems of *Ailanthus altissima* were colonized by one or more endomycorrhizal fungi. Significant presence of intercellular hyphae indicates that this is an *Arum*-type of colonization, showing intercellular hyphae cross sections between cortical cells (Figs. 1a) and elongating intercellular hyphae growing between cortical cell walls (Fig. 1b and 2). All four types of structures: intercellular hyphae (Figs. 1a, b and 2), intracellular hyphae (Fig. 1c), arbuscules (Fig. 1d), and vesicles (Figs. 1e and Fig. 2), were found in root systems of each habitat type. In the case of the field of view method, the forested site did not have significantly greater overall colonization than 0% due to a relatively high variance. Within each habitat type, there were significantly more intercellular hyphae than intracellular hyphae ($P <$

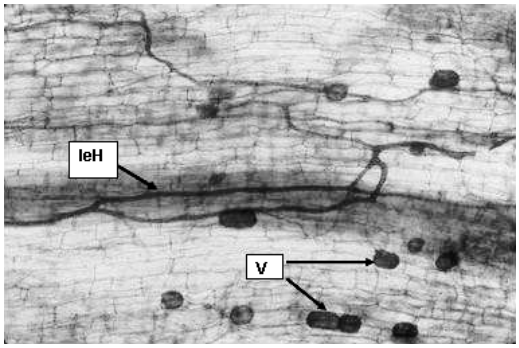

FIG. 2. Intercellular hyphae (IeH) and vesicles (V) in light microscope (Olympus BH2) transverse section. Scale bar = 0.01 μm; 10× magnification.

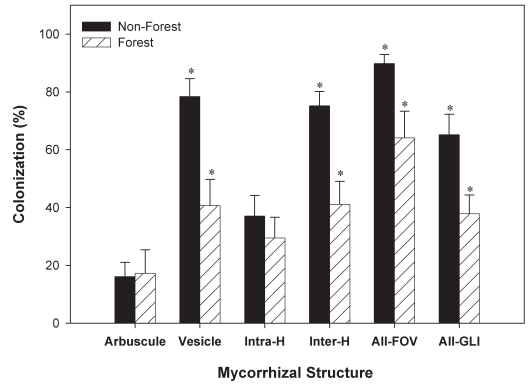

FIG. 3. Percent colonization for each of the four structure types and all types using the field of view (FOV) method as well as all structures found using the gridline intercept (GLI) method. H = hyphae. Standard error bars are provided. * indicates a significant difference between habitat type using-ANOVA.

0.001 for the non-forested site; $P = 0.039$ for the forested site), supporting the *Arum*-type colonization as the predominant type for both habitat types. As expected, the field of view method resulted in higher values of overall percent colonization than the gridline intersect method (Table 1).

DOES MYCORRHIZAL COLONIZATION AND TYPE OF COLONIZATION OF *AILANTHUS ALTISSIMA* DIFFER BETWEEN THE FORESTED AND NON-FORESTED SITES? The tree seedlings of the non-forested habitat had significantly ($P_{GLI} = 0.004$; $P_{FOV} = 0.018$) more endomycorrhizal colonization ($\bar{X}_{GLI} = 65.2\%$, $SE_{GLI} = 7.06$; $\bar{X}_{FOV} = 89.8\%$, $SE_{FOV} = 3.16$) than those of the forested site ($\bar{X}_{GLI} = 37.9\%$, $SE_{GLI} = 6.46$; $\bar{X}_{FOV} = 64.1\%$, $SE_{FOV} = 9.21$). The non-forested site also had significantly more intercellular hyphae (75.5%; SE = 4.94; $P < 0.002$) and vesicles (78.5%; SE = 6.20; $P < 0.003$) than those of the forested site (41.1%; SE = 7.97 and 40.7%; SE = 9.06, respectively). Occurrence of arbuscules and intracellular hyphae did not significantly differ between the two habitat types (Fig. 3).

Discussion. IS *AILANTHUS ALTISSIMA* COLONIZED BY MYCORRHIZAE, IF SO, WHAT TYPE OF COLONIZATION IS IT? *Arum*-colonization is typically found in fast-growing plants, such as crop, gap, and early successional species (Brundrett and Kendrick 1990a and b, Smith and Smith 1997, Yamato and Iwasaki 2002, Yamato 2004), so it is not surprising to see this type of colonization in *A. altissima* based on this species' apparent preference for high-light habitats. However, *Arum*-colonization is also observed in a few shade-tolerant forest un-

Table 1. Summary mean % colonization of within habitat one-tailed *t*-tests (compared to μ = 0). Variables with a * were analyzed non-parametrically. GLI = gridline intercept method, FOV = field-of-view method, CI = confidence interval, SD = standard deviation.

Site Type	Structure	Mean	CI	SD	*t*	*P*
Non-forest	All (GLI)	65.2	49.2–81.2	22.3	9.2	<0.001
Non-forest	All (FOV)*	89.8	82.7–97.0	10.0	28.4	<0.001
Forest	All (GLI)	32.9	19.4–46.4	18.9	5.5	0.002
Forest	All (FOV)*	64.1	43.3–84.9	29.1	7.0	0.172
Non-forest	Arbuscule*	15.9	4.7–27.1	15.7	3.2	0.001
Forest	Arbuscule*	17.3	0–35.6	25.6	2.1	0.001
Non-forest	Vesicle	78.4	64.4–92.5	19.6	12.7	<0.001
Forested	Vesicle	40.7	20.2–61.2	28.6	4.5	0.001
Non-forest	Intracellular hyphae	37.1	21.1–53.1	22.3	5.2	0.001
Forest	Intracellular hyphae	29.5	13.3–45.7	22.6	4.1	0.003
Non-forest	Intercellular hyphae	75.2	64.0–86.3	15.6	15.2	<0.001
Forest	Intercellular hyphae	41.1	23.1–59.1	25.2	5.2	0.001

derstory species with longitudinal air channels, which may enable intercellular hyphal growth. Such species include *Arisaema triphyllum* (L.) Schott. (Jack in the pulpit) and *Smilacina racemosa* (L.) Desf. (false Solomon's seal). Despite having *Arum*-type colonization, these herbaceous understory species show slower rates of endomycorrhizal colonization than typically found in crop species (Brundrett and Kendrick 1990b). It is unknown if *A. altissima* has longitudinal air channels in its roots, which may be related to its *Arum*-type of colonization. *Arum*- vs. *Paris*-colonization may also depend on the fungal species present (Smith and Smith 1997, Cavagnaro et al. 2001a) and its abundance, which may differ by habitat type and site history. Without an identification of the fungus or fungi colonizing *A. altissima*, we cannot assume its root anatomy (i.e., presence of longitudinal air channels) defines the colonization type.

Does mycorrhizal colonization and type of colonization of *A. altissima* differ between the forested and non-forested sites?. The tree seedlings on the forested site were less likely to be colonized than seedlings from the non-forested site and, using the field-of-view method, mycorrhizal colonization of the seedlings from the forested site did not differ significantly from zero. Moreover, the likelihood of disturbed sites having fewer available mycorrhizae (Reeves et al. 1979, Rillig 2003) is not supported by our data. In the non-forested site, the endomycorrhizae may improve nitrogen uptake in water-stressed conditions (Tobar et al. 1994). *Ailanthus altissima* has been found to be drought-tolerant via reduced water loss from the leaves (stomatal closure) and reduced root hydraulic conductance, which may also be a response to high soil temperatures (Graves et al. 1991, Trifilò et al. 2004). If reduction of water transport is the primary mechanism which *A. altissima* uses in response to drought, this species may be able to utilize the nutrients transported by the fungus, given the mycorrhizal association is already well-established in the cortical cells. Plants under stress may also be expected to have higher rates of root senescence (Hirrel et al. 1978, Schmidt and Scow 1986). Our results do show greater numbers of vesicles (lipid-filled resting spores) in the eroded slope site, which may indicate some root senescence on these more stressed sites or possibly older root systems. Vesicle formation has been found to be plant species-specific or fungus species-specific (Brundrett and Kendrick 1990b), and our results support that habitat may play a role either by affecting host plant physiology or fungal species present. More colonization by intercellular hyphae in the non-forested site root systems suggests that colonization type (*Arum* vs. *Paris*) is environmentally defined. Indeed, *Arum*- and *Paris*-types of colonization likely follows a continuum rather than being two distinct types (Dickson 2004). Standardized definitions of mycorrhizal structures and improved methodology may eventually help separate colonization types along this continuum (Dickson 2004, McGonigle et al. 1990).

Research Implications and Future Directions. If the endomycorrhizal fungi species that colonize *Ailanthus altissima* do not have saprophytic capacities (not being wholly dependent on host plant photosynthates), the fungi may be functioning as a parasite on *A. altissima* in low-light environments due to carbon-limited nutrient uptake (Hayman 1974, Korhonen et al. 2004). If indeed arbuscules serve primarily to transport nutrients to the plant while hyphae serve primarily to transport carbon to the fungus (Smith and Smith 1997), the presence of both structures in both habitats may indicate that there is a mutualistic relationship, rather than parasitic, between *A. altissima* and the fungus or fungi. However, tests showing increased plant fitness in the presence of mycorrhizae compared to seedlings without mycorrhizae are needed in order to confirm any kind of mutualism.

Likewise, it is possible that *Ailanthus altissima*'s allelopathic exudates are more effective in the forested site compared to the non-forested site, which could negatively affect mycorrhizal colonization (Roberts and Anderson 2001). A comparison of productivity in low light environments in both sterile and non-sterile soil (controlling for allelopathic chemicals) is required before determining if any possible allelopathic effects on the fungus or fungal interactions are evident.

Sampling additional sites might have resulted in fewer differences between the two habitat types. True replicates of these habitats are difficult to find because *Ailanthus altissima* invasion dates and disturbance history of the sites are generally unknown; spatial autocor-

relation along corridors is also likely. Comparing the two habitat types directly may be considered pseudoreplication because the independence of the individual tree seedlings within each area, though quite a distance apart, may be questionable. While our study does confirm the fact that mycorrhizal colonization varies by site, it cannot confirm the potential mechanisms behind these differences. Future studies that mimic varied site conditions in controlled growth chamber experiments are needed to define the mechanisms behind the differences in colonization.

Questions that our future research will address include evaluating the root anatomy of *Ailanthus altissima* and identifying the fungal species involved. More importantly, determination of whether or not *A. altissima* benefits from the mycorrhizal colonization in relatively resource-rich or resource-poor sites will require further experimental physiological tests involving inoculations. Once these questions are answered, we will be able to define the role of mycorrhizae, if any, in terms of *A. altissima*'s competitive ability in different environments. Our results suggest that *A. altissima* may have a competitive advantage in open, stressed environments and a disadvantage in forested environments due in part to differences in *Arum*-type endomycorrhizal colonization by habitat.

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