# Effects of the Invasive Shrub Lonicera maackii on Soil Water Content in Eastern Deciduous Forest

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ABSTRACT.—We quantified the fine root length density of *Lonicera maackii* (Amur honeysuckle) and native trees at two depths on transects away from individuals of this invasive shrub and tested whether the invasive shrub *L. maackii* reduced water availability for other forest plants by either of two mechanisms: (1) intercepting rainwater during light rain events or (2) absorbing large amounts of water through its fine roots. To test the two hypothesized mechanisms, we selected plots near large *L. maackii* shrubs and control plots away from any large *L. maackii* shrubs in the forest understory. Within each plot we placed a trenched and an untrenched subplot and measured soil water content in each. We also measured precipitation above and below *L. maackii* canopies. We found that within 2 m of large *L. maackii* shrubs, this shrub accounted for a large fraction (22–25%) of the fine roots in the top 12 cm of soil. Reduced throughfall and soil moisture below shrubs supported the hypothesis that *L. maackii* competes with tree seedlings by interception. Findings were inconclusive regarding the hypothesis of competition by water uptake.

## INTRODUCTION

Invasive plant species often cause deleterious effects on local communities, particularly by reducing native plant species diversity (Vila *et al.*, 2011). However, the individual mechanisms underlying these reductions in diversity have not been well studied (Levine *et al.*, 2003). While some invasive plants have been shown to be allelopathic (*e.g.*, Pisula and Meiners, 2010) and others are superior competitors for sunlight (*e.g.*, Klionsky *et al.*, 2011) or nutrients (*e.g.*, Chau *et al.*, 2013), competition for water is another mechanism by which some invasive plants achieve dominance (Cleverly *et al.*, 1997).

One of the most problematic invasive plants in many areas of eastern North America is *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), Amur honeysuckle, which is a woody shrub native to northeastern Asia (Luken and Thieret, 1996). *Lonicera maackii* reduces fecundity and survival of studied species of native annuals (Gould and Gorchov, 2000; Cipollini *et al.*, 2008) and reduces fecundity and growth of studied species of perennial herbs (Miller and Gorchov, 2004). It is correlated with reduced density and species richness of native shrubs (Medley, 1997) and canopy tree seedlings (Collier *et al.*, 2002; Hutchinson and Vankat, 1997). Gorchov and Trisel (2003) found *L. maackii* reduced the survival of native tree seedlings and Hartman and McCarthy (2004) found a higher survival of native tree seedlings when *L. maackii* was killed with herbicide.

There may be several mechanisms causing these negative impacts of *L. maackii* on native plants. There is evidence for allelopathy: extracts from the roots and leaves of *L. maackii* suppress seed germination in *Arabidopsis thaliana* (Cipollini *et al.*, 2008) and *Impatiens capensis* (Dorning and Cipollini, 2006). However, the performance of *I. capensis* in forest plots with *L. maackii* was not improved with addition of activated carbon (Cipollini *et al.*, 2008), suggesting allelopathy is not the only mechanism of *L. maackii* impact. In a factorial field experiment, Gorchov and Trisel (2003) found that *L. maackii* reduced the survival of native tree seedlings primarily through an aboveground mechanism, although belowground

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FIG. 1.—Our predictions for soil moisture in shallow soil under (left) the fine root water absorption hypothesis, (center) the interception hypothesis, and (right) both hypotheses. Abbreviations: "ctrl.tr" = control-trenched subplots; "ctrl.un" = control-untrenched subplots; "Lm.tr" = honeysuckle-trenched subplots;

effects were also detected. They reasoned interception of light by the dense *L. maackii* canopy was the most likely cause for the aboveground effects.

Lonicera maackii may compete with tree seedlings for water, a resource that can be seasonally limiting for understory plants. Southwestern Ohio, an area heavily invaded by *L. maackii*, often has high evapotranspiration (J. Rogers, Climatologist for the State of Ohio, *pers.comm.*) and low precipitation in late summer [*e.g.*, in Eaton, Ohio ( $39^{\circ}45'$ N;  $84^{\circ}38'$ W) the month of Aug. averaged fewer than 2 d with precipitation  $\geq 1.2$  cm during the 10 y period 2002–2011]. Hartman and McCarthy (2004) found that the most common cause of mortality for their planted tree seedlings was drought. They found that survival of these seedlings over 3 y was significantly lower near healthy *L. maackii* than where *L. maackii* had been treated or removed, although "drought was a greater factor of mortality in control plots than in [*L. maackii*-present] plots" (Hartman and McCarthy, 2004, p. 158). Evidence for a soil-drying effect of *L. maackii* was the higher soil water content in areas where the shrub had been killed with herbicide than in areas where the plants were alive [Carolyn Keiffer, *pers. comm.* cited in Hartman and McCarthy (2004)].

We hypothesized two mechanisms by which *L. maackii* could exacerbate drought stress in tree seedlings. One is interception of rain. McEwan *et al.* (2012) found that, during rain events in Aug., *L. maackii* leaf canopies intercepted 7–31% of forest canopy throughfall. Second, tree seedlings might be harmed by fine root competition. *Lonicera maackii* has an extensive shallow root system (Deering and Vankat, 1999); a large amount of roots taking up water might substantially reduce soil water content.

We predicted, for the interception hypothesis, that the soil beneath *L. maackii* leaf canopies would be drier than the soil in similar areas away from *L. maackii* leaf canopies (Fig. 1). For the fine root competition hypothesis, we predicted that the soil would dry out much more slowly in areas where *L. maackii* fine roots were severed by trenching than in untrenched areas (Fig. 1). This prediction was based on the assumption that *L. maackii* fine roots are a major fraction of shallow, but not deeper, roots in these soils, an assumption that was also tested in this research.

#### Methods

Our two hypotheses were tested by a field experiment in the summer of 2012. We chose plots (see below) with and without *L. maackii*, established a trenched and an untrenched subplot within each plot, and measured the water content of the soil daily after periods of

rain. We also quantified throughfall interception and fine root density near vs. away from large (>15 cm<sup>2</sup> basal area) *L. maackii*.

Site descriptions.—We conducted the field experiment across two forest stands near Oxford, Ohio. The Fryman woodlot ('Fryman') ( $39^{\circ}31'48''N$ ,  $84^{\circ}43'48''W$ ) at the Miami University Ecology Research Center is an 11 ha secondary forest where agriculture had been abandoned at an unknown time between 1938 and 1950 (Pfeiffer, 2013). The stand density of Fryman, based on trees >10 cm diameter at breast height (DBH), was 478 trees/ha and the stand basal area was 27.5 m<sup>2</sup>/ha. The most important tree species, based on relative density and relative basal area, were white ash (*Fraxinus americana*), slippery elm (*Ulmus rubra*), sugar maple (*Acer saccharum*), and shagbark hickory (*Carya ovata*) (Pfeiffer, 2013). The density of *L. maackii* in Fryman was 77,850 stems/ha, and its basal area was 2.64 m<sup>2</sup>/ha (Pfeiffer, 2013).

Kramer Woods  $(39^{\circ}31'48''N, 84^{\circ}43'12''W)$  is a 5.2 ha secondary forest that has not been selectively cut since 1915 (Medley, 1997), with a stand density of 429 trees/ha and a basal area of  $35.1 \text{ m}^2$ /ha (Henkin *et al.*, 2013). The most important tree species were sugar maple, white ash, black walnut (*Juglans nigra*), and tulip poplar (*Liriodendron tulipifera*) (Henkin *et al.*, 2013). Forest soils are moderately eroded Russell-Miamian silt loams (Lerch *et al.*, 1980). The density of *L. maackii* in Kramer was 5472 shrubs/ha (Henkin *et al.*, 2013). Although shrubs of *L. maackii* have multiple stems, it is likely that stem density was lower in Kramer than in Fryman. However, *L. maackii* basal area was more similar between the sites; *L. maackii* basal area in Kramer was 1.89 m<sup>2</sup>/ha in 1992 (Medley 1997) and likely higher in by the time of our study, as the density of *L. maackii* shrubs >1 m tall increased 41% from 1992 to 2010 (Henkin *et al.*, 2013). These data indicate that, on average, shrubs in Kramer were sparser but larger than those in Fryman.

Lonicera maackii root profiles.—We selected 10 shrubs >15 cm<sup>2</sup> basal area (based on basal diameters of all stems) in the Fryman woodlot, each of which had a leaf canopy radius >2 m and one direction where roots of conspecifics were unlikely ( $\geq 6$  m from the nearest *L. maackii* shrub of comparable size). In a transect from the focal shrub along that direction without conspecifics, we collected one 1.8 cm diameter soil core of 24 cm depth, deep enough to include all *L. maackii* roots, at each of five distances (1.0, 1.5, 2.0, 2.5, and 3.0 m away from the focal shrub) during the 2012 growing season, with all cores for a given shrub collected on the same date. Because of the shallow root system of *L. maackii* (Deering and Vankat, 1999), we separated each soil core into top (0–12 cm) and bottom (12–24 cm) layers.

We separated fine roots (roots that have not undergone secondary thickening) from soil by gently manipulating soil clods with minute quantities of water when necessary to loosen soil. *Lonicera maackii* roots were distinguished from other roots primarily by their thick first-order roots and pale tan color. We quantified root length density by a line-intersect method (Tennant, 1975).

*Plot selection.*—At each of the two sites we selected 8 focal *L. maackii* shrubs that met the following criteria: beneath a closed forest canopy,  $\geq 13$  m from the forest edge, a basal area of  $\geq 15$  cm<sup>2</sup> (based on basal diameters of all stems), and a dripline  $\geq 2$  m away from the dripline of the nearest *L. maackii* shrub  $\geq 1$  m tall and from the trunk of the nearest tree with a  $\geq 10$  cm DBH. Around each of these focal shrubs we defined a 3 m-radius circular plot, hereafter referred to as a 'honeysuckle' plot. We also selected eight similarly-sized control plots meeting the same canopy and edge criteria as the honeysuckle plots, each of which was  $\geq 3$  m away from the central stem of the nearest *L. maackii* shrub  $\geq 1$  m tall. We used a 3 m threshold because soil core sampling revealed that *L. maackii* roots comprised <4% of the fine roots in the upper 12 cm of soil at this distance from the shrub's central stem (Fig. 2).



FIG. 2.—Average root length density of *Lonicera* fine roots (closed circles) and all other fine roots (open squares) at several distances from the central stem of the closest *Lonicera* shrub (n = 10 shrubs). Error bars represent standard error of the mean. (A) 0–12 cm depth; (B) 12–24 cm depth

The edge of each control plot was at least 0.5 m away from the nearest *L. maackii* dripline, in order to avoid possible increased soil water content where precipitation drips off *L. maackii* leaf canopies.

*Precipitation and throughfall.*—We placed one rain gauge in each of eight honeysuckle plots and in the eight control plots to measure rain throughfall above and below the *L. maackii* leaf canopy. Our gauges were 50 mL centrifuge tubes suspended on horizontal metal rods connected to metal fence posts with hex nuts, which inhibited tipping by wind. Tubes were placed at two heights: ca. 3 m, and 25 cm above ground level (only 25 cm in control plots). Interception was calculated as the difference in rainwater collected between the 3 m tube and the 25 cm tube in each rain gauge. Henceforth 'interception' refers to the average of the interception values obtained from the eight rain gauges in honeysuckle plots.

*Trenching.*—To test the root competition hypothesis, we compared soil moisture in trenched vs. untrenched subplots within each plot. Within each plot, we designated two 50 cm-diameter subplots between 0.5 and 1.0 m from the focal *L. maackii* stem, and randomly assigned one as trenched and the other as an untrenched control. The trenches were dug 12–19 May 2012; trenches were cut 12 cm deep, because this depth would sever most *L. maackii* fine roots but leave many tree fine roots uncut in the subplot, based on our finding that  $\geq$ 80% of *L. maackii* fine roots are in the upper 12 cm of soil, and <70% of non-*L. maackii* fine roots were in the upper 12 cm of soil in Fryman (Pfeiffer, 2013). The trenches

averaged about 5 cm wide and were lined with a sheet of polyethylene plastic and left open to prevent root growth across the trench.

Soil moisture.—We measured soil water content (% vol) with a Decagon GS3 Soil Moisture Meter between 0800 and 1000 every 1–2 d, from 2 Jul. to 22 Aug., and thereafter once per week through 1 Oct. This schedule of data collection was intended to provide frequent data collection during dry periods. The soil moisture meter was calibrated gravimetrically (Pfeiffer, 2013).

*Data analysis.*—To avoid confounding soil drying with the rapid increases in soil moisture immediately after a large rain event, soil moisture data were split into three 'time series,' each beginning after a rain event and ending before the next rain event >4 mm: early (Jul. 2–Jul. 23), middle (Jul. 24–Aug. 4), and late (Aug. 10–Aug. 22). For each of these time series, we used the program R to analyze soil moisture with a hierarchical ANOVA, using the number of days since a rain event >4 mm ('Days') as a random main factor grouped by Plot, and the presence of *L. maackii* ('honeysuckle') and the trenching treatment ('trenching') as fixed, fully crossed main factors. Non-significant interactions were dropped from the final model.

To test whether control-untrenched subplots dried more slowly than honeysuckleuntrenched subplots, as predicted for the fine root hypothesis, we fit the same type of statistical model, except the honeysuckle and trenching factors were combined into a single 4-level variable. The ANOVA model parameter estimates were examined to determine if the control-untrenched subplots had a different slope, that is, whether they dried at a rate different than the honeysuckle-untrenched subplots.

## RESULTS

Lonicera maackii root distribution.—On average, L. maackii fine roots were common in the upper 12 cm of soil within 2 m of the shrub's central stem, comprising 22 to 24% of all fine roots (Fig. 2). Fewer L. maackii fine roots were found at 2.5 m from the stem, and almost none at 3.0 m from the stem. At 12 to 24 cm depth, L. maackii fine roots were sparse, comprising at most 7% of all roots (Fig. 2).

*Precipitation.*—In Jun. 2012, there were only two rain events >5 mm, with neither showing *L. maackii* interception; the rain gauges below the *L. maackii* canopy actually read higher than the rain gauges above (Fig. 3A). There were no rain events >5 mm in Jul., but three in early Aug. For these three events, *L. maackii* interception was detected and accounted for 8 to 16% of forest canopy throughfall.

*Soil moisture.*—Soil moisture in the upper 5 cm of soil declined over time following each rain event, at times becoming as low as 6% by volume (Fig. 3B). After each new large rain event, soil moisture spiked to as much as 34% by volume.

In the early time series, soil moisture declined with number of days (Table 1, Fig. 3B). Although trenching was not a significant factor, there was a significant interaction between trenching and days: the soil in trenched subplots dried more quickly than that in untrenched subplots (Table 1, Fig. 3B). There was no effect of honeysuckle or an interaction between honeysuckle and number of days. Pairwise comparison between the control-untrenched subplots and the honeysuckle-untrenched subplots revealed that they dried at the same rates (Table 1).

In both the middle and late time series, soil moisture was significantly affected by number of days, honeysuckle presence, and trenching, but there were no significant interactions (Table 1). Soil moisture declined with number of days, plots with *L. maackii* were drier than those without, and trenched subplots were wetter than untrenched



FIG. 3.—Precipitation and soil moisture in experimental plots in Fryman and Kramer from 1 Jun. to 26 Aug., 2012. (A) Precipitation measured by the rain gauges above and below the *L. maackii* canopy and away from *L. maackii.* (B) The average soil water content for each day for each treatment (n = 8 for Control-Trenched and Control-Untrenched; n = 11 for Honeysuckle-Trenched and Honeysuckle-Untrenched. Each box represents one of the "time series" into which the soil moisture data were split for statistical analysis

TABLE 1.—Final ANOVA models for soil moisture at 0–5 cm depth, for each of the three time series after rain events (Early = 2–23 Jul., Middle = 24 Jul.–4 Aug., Late = 10–26 Aug.). "Days" is the number of days since the rain event, "Honeysuckle" is the plot treatment of *L. maackii* presence v. absence, and "Trenching" is the subplot treatment of trenched v. untrenched. For each of the models, non-significant interaction terms have been dropped. Also, for each time period we report the *t*-test for the comparison of the Honeysuckle-Untrenched treatment vs. the Control-Untrenched treatment

	df	F	Р
Early			
Days	1,530	195.86	< 0.0001
Honeysuckle	1, 35	0.09	0.7714
Trenching	1, 35	2.55	0.1190
Days*Trenching	1, 530	5.01	0.0257
Pairwise comparison of untre	nched plots: $df = 34$ , $t =$	0.36, P = 0.7223	
Middle			
Days	1, 341	92.13	< 0.0001
Honeysuckle	1, 35	4.24	0.0469
Trenching	1, 35	12.77	0.0011
Pairwise comparison of untre	nched plots: $df = 34$ , $t =$	-1.86, P = 0.0722	
Late			
Days	1, 379	291.78	< 0.0001
Honeysuckle	1, 35	5.60	0.0236
Trenching	1, 35	11.28	0.0019
Pairwise comparison of untre	nched plots: $df = 34$ , $t =$	-1.24  P = 0.2245	

subplots. Control-untrenched and honeysuckle-untrenched subplots did not dry at significantly different rates.

### DISCUSSION

We predicted that, if *L. maackii* reduces soil water content by intercepting rainwater, then the soil in honeysuckle plots would be drier than the soil in control plots. Honeysuckle plots were drier than control plots in the middle and late time series, but not in the early series. This difference among the time series likely arose because the soil had experienced a different precipitation regime (*i.e.*, frequency and magnitude of rain events in the recent past) prior to the early period than it did during the middle or late periods. In contrast to the days preceding middle and late periods, local weather records showed there were only three measurable rain events during the 31 d preceding the early series. An *L. maackii* interception effect may emerge only when frequency and magnitude of rain events exceed a certain threshold.

For the root competition hypothesis, we predicted that: (1) trenched subplots would be wetter than untrenched ones, and (2) honeysuckle plots would be drier than control plots. Furthermore, we predicted two interaction effects: (1) trenched subplots would dry more slowly than untrenched subplots, and (2) control-untrenched subplots would dry more slowly than honeysuckle-untrenched subplots.

Results were equivocal for the root competition hypothesis. As predicted, trenched subplots were wetter than untrenched subplots in the middle and late series (Table 1). Honeysuckle plots were drier than controls in the middle and late series (Table 1), although this could have been due solely to interception. Trenched subplots did not dry more slowly than untrenched ones, suggesting that water uptake by roots in the upper 12 cm of soil was not the primary mechanism of soil drying. In fact, during the early time series, trenched subplots dried faster than untrenched subplots.

Comparison of the trenched and the untrenched subplots was confounded by two factors. First, evaporation from the soil bordering each trench may have been enhanced due to the exposure of soil surface area to the air, possibly causing the trenched subplots to dry faster than they otherwise would have. Second, water uptake by fine roots in the upper 12 cm may have continued despite the trench, due to both existing and new roots proliferating from coarse roots that passed below the trench.

Under our hypothesis of fine-root competition, the control-untrenched subplots were expected to dry more slowly than honeysuckle-untrenched subplots (Fig. 1), because the former contained fine roots of trees, but not of *L. maackii*, while the latter contained fine roots of both trees and *L. maackii* that should absorb water faster than tree roots alone. Our finding that control-untrenched subplots and honeysuckle untrenched subplots dried at similar rates could have been due to similar water uptake rates of *L. maackii* fine roots and tree fine roots, along with similar total (*L. maackii* + tree) fine root length density in honeysuckle plots and control plots. Total fine root length density did not differ among the five distances (1–3 m) from the sampled shrubs (Pfeiffer, 2013), and we observed that there were few points in the Fryman woodlot >3.0 m from the stem of a *L. maackii* shrub ≥1 m tall.

However, the prevalence of *L. maackii* fine roots in shallow soil suggested they may have had strong effects on soil moisture and perhaps nutrient uptake. Within 2 m of large (>15 cm<sup>2</sup> basal area) *L. maackii* shrubs, *L. maackii* fine roots comprised 22–25% of the total fine root length in the upper 12 cm of soil. We estimated 42% of the Fryman woodlot was within 2 m of such a shrub (Pfeiffer, 2013). Therefore about 10% of fine root length in the

upper 12 cm of soil would have been *L. maackii* roots near large *L. maackii* shrubs; this is approximately the proportion of stand basal area that was *L. maackii* (Pfeiffer, 2013). Factoring in roots from smaller *L. maackii* shrubs implies *L. maackii* comprised a greater proportion of total shallow fine root length than of basal area. Some local forest stands are in fact more heavily invaded than our stands; therefore they are likely more strongly affected by *L. maackii* roots. For example Hartman and McCarthy (2007) examined 16 forest stands in southwest Ohio (less than  $0.41^{\circ}$  latitude and  $0.65^{\circ}$  longitude from Fryman and Kramer), 12 of which had suffered *L. maackii* invasion. Of those 12 stands, six had higher *L. maackii* basal area than our stands and so probably had an even greater proportion of their area affected by *L. maackii* roots.

There is evidence that *L. maackii* contributes significantly to stand-level transpiration, equaling 5.6% of tree and vine transpiration from a wetland secondary forest in Kentucky (Boyce *et al.*, 2012). The fact that *L. maackii*'s contribution to stand transpiration exceeded its proportion of stand basal area (4.3%, Boyce *et al.*, 2012) may be due to the high density of its fine roots in shallow soil, as documented in our study.

The reduction of soil water content under *L. maackii* shrubs likely has negative impacts on tree seedlings. We found stomatal conductance of small ( $\approx$ 30 cm height) naturally-occurring *Carya* sp. and *Acer saccharum* seedlings in these plots was negligible when soil water content was below about 10% (Pfeiffer, 2013). This suggests during a dry period *L. maackii* exacerbates seedling drought stress, particularly since we observed that these tree seedlings had root systems mostly in the upper 12 cm of soil. Therefore competition for water is a mechanism, in additional to shading and allelopathy, by which *L. maackii* may suppress tree regeneration in forests.

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