ABSTRACT

PETZOLDT, JANE EMILY. Nitrogen Deposition Interacts with Water Availability to Influence Herbivore Abundance and Herbivory on Red Maple (*Acer rubrum* L.). (Under the direction of Dr. Steven Frank).

Cities are hotspots of nitrogen (N) deposition arising from fossil fuel combustion. Urban trees are subject to N deposition as well as water stress due to soil compaction and impervious surfaces. Nitrogen deposition makes trees more vulnerable to water stress by lowering the root:shoot ratio, suggesting a potential interaction between water stress and N deposition. Both factors positively influence tree N available to insect herbivores, often a limiting nutrient for insects. The combination of water stress and N deposition in cities could explain why urban trees have more frequent and severe pest outbreaks relative to rural trees. To test for an interaction between N and water on tree and herbivore performance, we conducted a two year common garden experiment in which we simulated urban N deposition and lowered water availability in a factorial design. We applied N and water treatments to potted *Acer rubrum* L. of three cultivars ('October Glory', 'Autumn Flame', 'Sun Valley') versus wildtype. We hypothesized that simultaneous N deposition and water stress would cause trees to have more water stress, more insect herbivores, and more herbivory compared to either factor in isolation. Our results indicate that simulated urban N deposition and water availability interact to affect tree and herbivore performance: tree height, sap feeding and shoot feeding insects all responded to N x water interactions in at least one year of the study. We observed that trees with higher N had more growth, more insects, and more herbivory compared to low N trees, suggesting that urban N deposition is likely to elicit physiological changes in trees with consequences for herbivores in cities. However, we did not find evidence that N treatments exacerbated tree water stress as we predicted. We found that tree type was an important predictor of most variables we measured.

Intraspecific response diversity to N deposition and water availability in this study supports planting diverse tree genotypes in cities to buffer against the effects of drought, N deposition, warming, and other environmental disturbances for a robust and resilient urban canopy. The combined effects of N deposition and water stress in urban environments may be important to consider as cities strive to meet biodiversity and ecosystem service goals.

Nitrogen Deposition Interacts with Water Availability to Influence Herbivore Abundance and Herbivory on Red Maple (*Acer rubrum* L.).

by
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DEDICATION

To my dad, Curt Petzoldt. I’m glad you’re here.

BIOGRAPHY

Jane Emily Petzoldt was born to Curtis Hofer and Rixana Thode Petzoldt on December 13, 1990, in Phelps, New York. She was raised on a small farm in Phelps, New York, where she graduated from Midlakes High School in 2009. She later attended Wesleyan University where she earned B.A. degrees in Biology and Environmental Studies in 2013. In 2019, she enrolled at North Carolina State University. Under the direction of Dr. Steven Frank, she began to develop and answer questions about the influence of N deposition in urban ecosystems. She is currently employed as a lab manager in a specialty crop weed science lab at Cornell University under the direction of Dr. Lynn Sosnoskie, and in 2023 returned to the farm she grew up on.

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CHAPTER 1

1. INTRODUCTION

Urban trees improve human health, lower heat island effects via evaporative cooling and shade, and support biodiversity in cities (Bolund & Hunhammar, 1999). Despite their importance, urban trees have more pests and die sooner than rural trees (Raupp et al., 2012; Smith et al., 2019). Urban tree pest outbreaks and early death arise from many anthropogenic stressors (Hilbert et al., 2019), including heat island effects and insufficient water caused by impervious surfaces (Dale & Frank, 2017; Meineke et al., 2016). While water stress has long been a focus of urban ecology, the influence of nitrogen (N) deposition—and its interactions with water limitation—on urban tree lifespan and pest outbreaks is not well understood (Cobley & Pataki, 2019; Dale & Frank, 2018).

N deposition is the transfer of reactive N (i.e., forms of N other than inert N_2) from the atmosphere to the earth's surface. By increasing the availability of N, a limiting nutrient for primary and secondary production, N deposition alters plant growth and plant-insect interactions (Throop & Lerdau, 2004). Human activities such as fertilizer application and fossil fuel combustion have caused a 10-fold increase of atmospheric reactive N since the pre-industrial era (Fowler et al., 2013; Guerrieri et al., 2021). However, global distribution of anthropogenic N deposition is not uniform, and cities are among the hot spots. Urban areas globally are subject to more than twice as much N deposition as nearby rural areas, averaging 28.9 kg N ha^{-1} $year^{-1}$ in cities globally (Decina et al., 2020), and exceeding 100 kg N ha^{-1} $year^{-1}$ in some hotspots (Luo et al., 2013), attributed in large part to fossil fuel combustion from vehicles and industry (Li et al., 2016).

N in the atmosphere is deposited on surfaces predominately through dry and wet deposition. Dry deposition occurs when N compounds land directly on aquatic and terrestrial surfaces, while wet deposition occurs when N compounds dissolve in water and fall to earth as precipitation (Söderlund, 1981). N deposition is absorbed by trees primarily via foliage and root systems, thereby having a fertilization effect (Aber et al., 1998). Tree canopies intercept an estimated 40% of N deposition in forest ecosystems (Lovett & Lindberg, 1993). A portion of this intercepted N is consumed or transformed by lichens, epiphytes, and microbes (Guerrieri et al., 2021), and a portion is absorbed into the foliage, where it can be used in plant metabolic processes (Lovett & Lindberg, 1993). Controlled studies of N deposition in plant communities often simulate N deposition by applying N fertilizers to the soil at rates well below 100 kg N ha^{-1} $year^{-1}$. Thus, they are distinct from agronomic fertilizer studies, which apply N fertilizers at much higher rates. Croplands globally receive an average fertilizer rate of 100.9 kg N ha^{-1} $year^{-1}$, often much higher in certain crops and geographic regions (Adalibieke et al., 2023), and more than three times the average urban N deposition rate.

Nitrogen is usually a limiting nutrient for tree and herbivore growth. Supplemental N via N deposition may lead to changes in host plant chemistry that are favorable to some herbivores by reducing plant defenses or increasing nutritional value (Throop & Lerdau, 2004). Increasing plant N beyond optimal levels can induce excess plant growth and deplete photosynthetic carbon reserves that would otherwise be allocated to carbon-based defense compounds. As a result, plants are poorly defended against herbivores (growth-differentiation balance hypothesis) (Herms & Mattson, 1992). Elevated plant N concentrations benefit many herbivores, increasing survivorship, growth, and reproduction in these species (Mattson, 1980; Mattson & Scriber, 1987; Nijssen et al., 2017; Scriber & Slansky, 1981; Stevens et al., 2018). A review of 25 studies

simulating N deposition found that N deposition increased deciduous tree foliar N concentrations by an average 13% (Throop & Lerdau, 2004). In natural ecosystems, N deposition can lead to more pest outbreaks and lower arthropod diversity (Stevens et al., 2018; Throop & Lerdau, 2004). In urban ecosystems—where rates of N deposition tend to be higher than in natural ecosystems, the effects of N deposition on herbivores have rarely been studied—(but see Green et al., 2017; Zhang et al., 2024).

N deposition also makes trees vulnerable to stress caused by insufficient water through multiple mechanisms. Increasing N often induces a flush of aboveground vegetative growth and lowers absolute root biomass, thereby decreasing the root:shoot ratio and increasing water demands on the root system (Carter et al., 2017; Grulke et al., 1998; Tateno et al., 2004). Furthermore, N deposition may disrupt mycorrhizal associations with roots and reduce overall mycorrhizal diversity, limiting root system ability to scavenge water from soil (Lilleskov et al., 2019). Indeed, ponderosa pines exposed to high rates of N deposition had 6-14 times less fine and medium root biomass compared to trees in a less polluted forest (Grulke et al., 1998), as well as more aboveground growth, leading to higher rates of tree mortality during periods of drought (Grulke et al., 2009).

Like N enrichment, low water availability is a hallmark of urban street tree plantings, where impervious surfaces and compacted soils can limit root volume or water infiltration into soils (Clark & Kjelgren, 1990; Meineke & Frank, 2018). Plant stress caused by low water can also benefit certain insect herbivores, especially sap-feeders and borers (Huberty & Denno, 2004). Low water disrupts protein synthesis in vegetative tissues (Hsiao, 1973) and favors hydrolysis of structural proteins into soluble components to maintain osmotic potential (Mattson, 1980), resulting in elevated free amino acids available to herbivores (White, 1969). While

continuous water stress reduces plant turgor and limits insect access to enriched plant material, intermittent water stress replenishes turgor in plants with high levels of stress-induced free amino acids, thereby increasing sap-feeding insect density and survival and contributing to insect outbreaks (Gely et al., 2020; Huberty & Denno, 2004).

Despite the frequency with which water stress and N deposition co-occur in urban environments, the interaction between these two factors has rarely been studied in urban or rural trees (Carter et al., 2017; Throop & Lerdau, 2004) (but see Hirsch et al., 2023; McNulty & Boggs, 2010). Given that N deposition enhances the potential for tree water stress, and that N deposition and water stress individually influence tree N availability and herbivory, we predict that the combination of these factors will interact to intensify tree water stress and susceptibility to herbivores. In other words, we expect the effect of low water stress to be exacerbated under high N conditions to synergistically elevate plant N available to herbivores (Figure 1). The combination of water stress and elevated N deposition in cities could partially explain why urban trees have more frequent and severe pest outbreaks relative to rural trees (Raupp et al., 2012).

We hypothesized that simultaneous water stress and N deposition would cause trees to have more water stress, more herbivores, and more herbivory compared to either factor in isolation. We tested this hypothesis on red maple trees (*Acer rubrum* L.), which are common in urban environments throughout eastern North America (Sonti et al., 2019). Although popular with urban foresters, homeowners, and nursery growers for their rapid growth, large shady canopies, and vibrant fall color (Frank et al., 2012; Townsend & McIntosh, 1993), red maples in the urban landscape are vulnerable to a variety of stressors including prolonged drought (Bassuk et al., 2009), heat (Dale & Frank, 2014) and insect pests (Frank, 2019; Frank et al., 2013). To isolate the effects of N and water on tree and herbivore performance, we conducted a common

garden experiment in which we simulated urban N deposition and lowered water availability in a factorial design.

2. MATERIALS AND METHODS

Study species

Maple (*Acer*) is the most common genus of deciduous planted landscape tree in eastern North America (Frank et al., 2013; Raupp et al., 2006). Red maple is among the most abundant trees in eastern North America, with a native range spanning the entire East Coast as far north as southern Newfoundland and Quebec to southeastern Manitoba, as far south as Florida, and as far west as Minnesota and eastern Texas (Walters & Yawney, 1990). This study included three cultivars ('October Glory,' 'Sun Valley', and 'Autumn Flame') and wildtype. These cultivars are among the most commonly grown in NC nurseries and planted by cities and homeowners in the southeastern US (SDF personal communication). Cultivars were selected for traits such as non-fruiting, smaller stature, and tolerance to potato leafhopper feeding ('Sun Valley'), as well as the fast, symmetrical growth and brilliant fall foliage exhibited by all three cultivars (Gilman & Watson, 1993b, 1993a; US National Arboretum, 1999). 'Autumn Flame' is reported to be more tolerant of urban pollution and moderate drought relative to other cultivars in this study (Purdue University Arboretum, 2025).

For this study, we focused on four insect herbivores of red maples. The potato leafhopper (*Empoasca fabae* Harris) feeds on more than 220 plant species, including red maples (Lamp et al., 1994), and is a frequent nursery pest (Frank et al., 2013). Mesophyll feeding of potato leafhopper via a lacerate-and-flush technique results in symptoms known as hopperburn characterized by leaf cupping, chlorosis, necrosis, and stunting (Backus et al., 2005; Bentz & Townsend, 1997; Frank et al., 2013; Potter & Spicer, 1993). Potato leafhopper responds to the

nutrient quality of its host plants and exhibits preference for N fertilized red maples (Bentz & Townsend, 2003; Prado et al., 2015).

The painted maple aphid (*Drepanaphis acerifoliae* Thomas) is a specialist of maple trees and is most often found on silver maples (*Acer saccharinum* L.) and red maples throughout North America (C. F. Smith & Dillery, 1968). The aphids occasionally reach high densities and become nuisances when they excrete honeydew that coats surfaces below the canopy and promotes sooty mold growth (Dreistadt & Flint, 1995).

Two tortricid caterpillars, *Proteoterus aesculana* (Riley) and *Episimus tyrius* (Henrich), cause superficially similar symptoms of shoot dieback, but their feeding habits and phenology are distinct. *P. aesculana* overwinters as adult moths and lays eggs on terminal buds in early spring. Caterpillars bore into growing shoot tips, causing shoot "flagging" (wilting and dieback of the shoot tip) (Seagraves et al., 2012), and are important nursery pests in maples throughout much of the US and Canada (Seagraves et al., 2008). In contrast, the lesser known *E. tyrius* is confined to the east coast of the US (Heppner, 1994), tends to be active later in summer, and feeds on shoots by tying leaves with silk and consuming foliage (Seagraves et al., 2008; JEP personal observations).

Experimental design

To determine how water and simulated N deposition interact to affect tree water stress, insect abundance, and herbivory, we conducted a common garden experiment with potted red maple trees at the Lake Wheeler Research Field Station in Raleigh, North Carolina, USA (35.737473, -78.674028). The four tree types in this study ('October Glory,' 'Sun Valley', 'Autumn Flame', and wildtype, henceforth abbreviated as OG, SV, AF, and WT, respectively) were crossed with two water treatments and three N treatments in a randomized split-split plot

design. Each block contained two main plots to which water treatment levels were assigned (high and low). Each main plot (irrigation line) was split into 12 subplots of individual trees of four types crossed with three N levels. We used a total of 192 trees with eight replicates of each tree/water/N combination.

On 26 February 2019, we obtained rooted cuttings of red maple cultivars from JLPN, Inc. (Salem, Oregon, USA), and one-year-old wildtype trees grown from seed from Lovelace Seeds (Elsberry, Missouri, USA). On 27-29 March, we planted trees in C1600 #5 pots (Nursery Supplies Inc., Chambersburg, Pennsylvania, USA) prior to budbreak in a nursery mix of aged pine bark fines (90%), sand, lime, and AMP Agri-Mag micronutrients 3-0-12 (Reese, Michigan, USA) at a rate of 8 lbs. lime and micronutrients per cubic yard, sourced from Parker Bark Co. (Rose Hill, North Carolina, USA). All trees received 86.24 g 18-4-8 slow-release fertilizer (Harrell's Inc., Lakeland, Florida, USA) at the time of planting, and received automated irrigation at a rate of approximately 174 ml/minute for 10 minutes once per day until May 1, whereupon we increased irrigation to two times per day for 10 minutes until leaves senesced.

On 13-16 March 2020, we pruned trees to establish a central leader, transplanted them into GL2800 #7 pots (Nursery Supplies, Inc., Chambersburg, Pennsylvania, USA), and arranged them into the randomized split-plot block design. On 10 February 2021, we structurally pruned trees to subordinate competing leaders and thin canopies by 20% (Gilman & Bisson, 2007).

All trees received automated irrigation three times per week for 10 minutes beginning 13 March 2020. To establish watering treatments on 13 May 2020, we programmed "high" trees to receive daily water two times per day for 10 minutes, and "low" trees to receive water three times per week, two times per day for 10 minutes. As temperatures warmed, on 26 June we increased irrigation in both treatments to three times per day on watering days until leaves

senesced. Beginning 28 May 2021, high trees received daily irrigation for 15 minutes five times per day and increased to six times per day on 6 July, while low trees received daily irrigation for 10 minutes, two times per day. On 4 September as temperatures cooled, we lowered watering times by 20% to 12 minutes and 8 minutes for high and low trees, respectively, until leaves senesced. We established these irrigation amounts in response to volumetric soil water content during the growing season, and aimed for 40-50% for high trees, and 15-20% for low trees.

N treatments

In March 2020 all trees received 9.12 g N/pot in a top-dress of 18-4-8 slow-release fertilizer (Harrell's Inc., Lakeland, Florida, USA), equivalent to ½ of the nursery recommended rate. In May 2020 we established "high," "medium," and "low" N treatments to mimic N deposition following EPA Clean Air Status and Trends Network (CASTNET) 2017 N deposition rates. According to EPA CASTNET, 50 kg N $ha^{-1}yr^{-1}$ is the maximum N deposition rate in the United States (EPA, 2020), which we used for our high N treatment, with the medium treatment being 50% of the maximum at 25 kg N $ha^{-1}yr^{-1}$. In 2020 we applied 34% aqueous ammonium nitrate to the soil surface every two weeks on seven dates between May and September 2020. Total N applied for treatments in addition to top-dress was equivalent to 0.479 g N per tree for high N, 0.239 g N per tree for medium N, and 0 g N per tree for low N, determined based on pot surface area (0.0957 m^2).

In 2021, due to relatively small differences in N treatments and lack of observed response from trees and herbivores, we adjusted N treatments and application methods. We set high and medium rates based on a global meta-analysis of urban N deposition rates (Decina et al., 2020), with high N receiving approximately twice the median rate of urban N deposition in East Asia where N deposition is highest (108 kg N $ha^{-1}yr^{-1}$), and medium N receiving ½ the high N rate (54

kg N $ha^{-1}yr^{-1}$). We also reduced the topdress rate from 9.12 g N/pot to 0.75 g N/pot applied as Harrel's 18% slow-release fertilizer. Total N applied for treatments in addition to top-dress was equivalent to 10.53 g N per tree for high N, 5.27 g N per tree for medium N, and 0 g N per tree for low N, determined based on canopy area (0.488m^2). Half of N treatment amounts were applied as 34% aqueous ammonium nitrate to soil over two applications on 6 and 13 May 2021, and the other half was applied as Harrel's 18% slow-release fertilizer on 9 May 2021. We reasoned that trees under constant N deposition would have accumulated N over the previous season, thus the ammonium nitrate represented previous accumulation, and the Harrel's slow-release fertilizer represents N deposition during the 2021 growing season.

Soil moisture and tree water stress

To verify the efficacy of watering treatments and make informed irrigation adjustments, we measured volumetric soil moisture in each tree pot on 20 June, 2-3 July, and 22 August 2020 with an SM150 Soil Moisture Kit (Delta T Devices Ltd., Cambridge, UK). We recorded three soil moisture measurements per pot from the pot soil surface and calculated an average pot soil moisture prior to analysis. On 29 April, 16 June, 7 July, and 13 August 2021, we collected a single soil moisture measurement on the pot soil surface using a FieldScout TDR 250 meter with 8" probes (Spectrum Technologies, Inc., Aurora, Illinois, USA).

To determine the extent of water stress in trees, we measured stem midday water potential across all trees in subsets of 48 trees per day on 28 and 30 August and 4 and 6 September 2020 and 29-30 June, 30 August and 14 September 2021 between 1100 and 1400 when conditions were sunny and without precipitation for the preceding 48hrs. Automated irrigation systems were deactivated on the morning of the measurement period prior to the first scheduled irrigation for consistency. We collected one shoot in full sun of approximately 10 cm

with 5-12 fully expanded leaves from the middle canopy of each tree and placed it within a pressure chamber (Model 1605D, PMS Instrument Company, Albany, OR, USA). Stem water potential was recorded in megapascals (MPa), equivalent to the amount of pressure required to reverse the flow of xylem in the stem. Under water deficit conditions, the pulling force of transpiring leaves coupled with reduced water uptake from roots intensifies water column pressure within the xylem (Fulton, 2018). Thus, a tree experiencing a more severe water deficit will require additional pressure to reverse the flow, with a more negative measurement corresponding to more water stress.

Tree growth

To determine tree growth in response to treatments, we recorded pre- and post-season tree diameters on 20 March 2020 prior to bud break and 3 December 2020 after leaf senescence, and again on 8 November 2021 after leaf senescence, using a digital caliper 10 cm above the soil surface. We calculated tree basal area as $(0.5*\text{diameter})*\pi^2$ and subtracted pre-season from post-season basal areas to calculate basal area growth over each season. We recorded the height of the tallest stem from the pot soil surface on 13 March and 3 December 2020 using a tape measurer, and again on 10 November 2021 using a height pole. We calculated change in height over each season by subtracting pre- from post-season heights in 2020 and 2021.

Insect abundance

To determine how N and water treatments affected insect abundance, we collected beat samples of arthropods from each tree on 21-23 June 2020 and 21-28 June, 12-14 July, and 9-12 August 2021. Six randomly selected shoots from each tree were beaten 10 times with a wooden dowel, and insects were collected in an 8x12” tray and rinsed and stored in 50ml vials with 70% ethanol. We recorded the number of potato leafhoppers and painted maple aphids in each sample.

Insect herbivory

To determine how N and water treatments affected insect herbivory, we recorded potato leafhopper feeding on 18 June and 1 July 2020 and 5 and 18 June 2021 as the number of shoots exhibiting hopperburn out of ten randomly selected shoots in the upper canopy of each tree, following Prado et al. (2015). On 26 May 2020 and 18-21 June 2021, we recorded *P. aesculana* herbivory as the number of flagging shoots per tree in addition to the total number of shoots per tree. On 27-30 July 2020 and 21 July 2021, we recorded *E. tyrius* herbivory as the number of shoots with leaf tying per tree, along with the total number of shoots per tree.

Statistical analyses

General overview: All analyses were performed in R version 4.0.3 (R Core Team, 2020) and RStudio version 1.4.1106 (RStudio Team, 2020). We analyzed data from 2020 and 2021 separately due to differences in N treatments between years. We modeled each response using linear models, linear mixed-effect models, generalized linear models, or generalized linear mixed-effect models, depending on the data type and model fit, using *lme4* 1.1.27.1 (Bates et al., 2015). For all models, we included tree type (OG, SV, AF, or WT), water (low, high), N (low, medium, high), and their interactions (tree type x water, tree type x N, water x N, and tree type x water x N) as fixed effects. We included a random intercept of 'block' to account for blocking, and a random intercept of 'irrigation line' to account for the split-plot design necessitated by water treatments. Random effects were omitted when they were estimated to be zero and caused a singular fit, as in Pasch et al. (2013).

We performed Wald chi-square tests to assess the significance of fixed effects using Type II ANOVA with *car* 3.0.13 (Fox & Weisberg, 2019). We plotted residuals graphically and confirmed they met model assumptions using *DHARMa* 0.4.7 (Hartig, 2024). We performed post

hoc tests using *emmeans* 1.6.0 (Lenth, 2021) to compare estimated marginal means with Tukey-adjusted *p*-values at alpha = 0.05.

Specific analyses: Here we note specific details of each model and any deviations or additions from the general approach described above. Full models for each analysis are available in Tables S2:S19. To analyze soil moisture percentage, we used linear mixed-effect models with plant ID (a unique identifier assigned to each tree) included as a random effect to account for repeated measures per plant, and date of measurement as a random effect to account for differences among dates. To analyze water potential, we used linear mixed-effect models and included date as a random effect to account for differences among dates since not all plants could be measured on a single day. To analyze change in tree height, we used linear mixed-effect models and omitted block from both models (2020 and 2021) due to singularity. To analyze basal area growth, we used a linear model without random effects in 2020 due to both irrigation line and block causing a singular fit. For basal area growth in 2021, we specified a linear mixed-effect model with irrigation line omitted due to a singular fit. To analyze change in tree height, we fit linear mixed-effect models with block omitted due to singularity in both years. To analyze painted maple aphid abundance, in both years we used generalized linear mixed-effect models with negative binomial distributions. To analyze potato leafhopper abundance, in 2020 once again we used a generalized linear mixed-effect model with a negative binomial distribution. In 2021 potato leafhopper count data was not overdispersed, so we used a generalized linear mixed-effect model with a Poisson distribution and irrigation line removed due to singularity. In 2020, we found that counts of shoots fed on by *P. aesculana* were particularly sparse, resulting in complete separation and a poor model fit. Therefore, we used Firth's bias-reduced logistic regression with *brglm2* 0.9.2 (Kosmidis, 2023), and included log(total shoots) as an offset

variable to account for differences in shoot numbers among trees. Block was included as a fixed effect instead of a random effect because the bias-reduced approach is incompatible with mixed models, while irrigation line was omitted due to singularity. To analyze *P. aesculana* feeding in 2021, we used a generalized linear mixed-effect model with a Poisson distribution, and once again included log(total shoots) as an offset variable and omitted block due to singularity. To analyze shoots fed upon by *E. tyrius,* in 2020 we used a generalized linear mixed-effect model with plant ID as an OLRE, log(total shoots) as an offset variable, and block and irrigation line removed due to a singular fit. We found that 2021 *E. tyrius* data were underdispersed with a generalized linear mixed-effect model with Poisson distribution, therefore, we fit a generalized Poisson regression model with *glmmTMB* 1.1.3 (Brooks et al., 2017), with log(total shoots) included as an offset variable to account for shoot number differences among trees. To analyze the ratio of shoots with vs. without hopperburn, we used generalized linear mixed-effect models with binomial distributions in both years. In 2020, we included plant ID as an OLRE due to overdispersion and omitted block due to singular fit. In 2021, we omitted irrigation line due to singular fit.

3. RESULTS

For most response variables in 2020 we recorded measurements on all 192 trees. Nine trees died between 2020 and 2021; therefore, 2021 analyses include 183 surviving trees. Dead trees resulted in 16 of 24 treatment combinations having n = 8 trees, while seven had n = 7 trees, and one combination (OG x high water x low N) had n = 6 trees (Table S1). While our comparisons were planned in a controlled experiment, we acknowledge that conducting 126 comparisons in 18 models inflates the likelihood of Type I error. The results below proceed on the basis of *p*-values, however, adjusted *q*-values derived from *qvalue* 2.22.0 (Storey et al., 2020)

are reported alongside *p*-values in ANOVA tables located in Tables S2:S19. A visual summary representation of estimated effect sizes is available in Figure S2.

Soil moisture and tree water stress

Water: Compared to the high water treatment, the low water treatment lowered soil moisture by 6.7% in 2020 ($p < 0.001$) and 10.4% in 2021 ($p < 0.001$, Figure S1a, b). This lowered water potential by an average of 0.17 MPa in 2020 and 0.12 MPa in 2021, indicating more stress in the low-water treatment ($p < 0.001$ in both years, Figure 2a, b).

Tree type: SV tended to have lower soil moisture in both years: in 2020 SV was drier than AF ($p = 0.005$), and in 2021 SV was drier than all other tree types ($p < 0.001$, Figure S1c, d). While we might expect SV to have lower water potential as a result, it did not; instead, WT trees had lower water potential than all other tree types in 2020 ($p < 0.001$) and 2021 ($p < 0.001$, Figure 2c, d).

N: High and medium N trees had less soil moisture than low N trees in 2021 ($p < 0.001$, Figure S1e). Despite this difference in soil moisture, there were no water potential differences among N treatments.

*Tree type * Water:* For soil moisture in 2020, there was an interaction between tree type and water that appears to be driven by genotypic differences in soil moisture ($p = 0.035$, Figure S1f). For water potential, there was no tree type by water interaction for water potential in either year.

*Tree type * N:* In 2020, there was a soil moisture interaction between tree type and N ($p = 0.045$, Figure S1g). This did not contribute to an interaction for water potential. WT and OG soil moisture trended negative with increasing N, while AF trended positively. SV had highest soil moisture at medium N.

Tree growth (height and basal area)

Water: Trees grew less in the low water treatment. In terms of basal area, low water trees grew on average 0.75 cm^2 less than high water trees in 2020 and 1.91 cm^2 less in 2021 ($p < 0.001$ both years, Figure 3a, b); and 23.8 cm less vertically in 2021 ($p < 0.001$, Figure 4a).

Tree type: WT exhibited less basal area growth than other tree types in both years, while OG had the most basal area growth in 2021 ($p < 0.001$ both years, Figure 3c, d). These genotypic differences in basal area growth do not completely align with vertical growth, in which SV exhibited less vertical growth in 2021 ($p < 0.001$, Figure 4b).

N: In 2021, when N treatments spanned a wider range of concentrations, trees grew more with increasing N. In terms of height, medium N trees grew an average 16.6 cm taller than low N trees, with high N trees intermediate ($p = 0.010$, Figure 4c). In terms of basal area, high and medium N trees both grew more than low N trees, with high N trees growing on average 1.92 cm^2 more than low N trees, and medium N trees growing on average 1.5 cm^2 more than low N trees ($p < 0.001$ (Figure 3e).

*N * Water:* N addition (medium or high) counteracted growth rate reductions caused by low water, while the low water * low N treatment had the least vertical growth in 2021. For high water trees, N did not influence vertical growth ($p = 0.026$, Figure 4d).

*Tree type * N:* Vertical growth was influenced by an interaction between tree type and N ($p = 0.012$, Figure 4e). OG grew taller in response to increasing N, while SV and WT height was not influenced by N. AF grew tallest in the medium N treatment.

Insect abundance

Across all trees we collected 594 individual aphids in 2020 and 727 in 2021. We found aphids on over 80% of trees, with an average of 3-4 aphids per tree in both years (range: 0-24

aphids). Leafhoppers varied between years, with 746 collected in 2020 versus 216 collected in 2021. In 2020, we found leafhoppers on 92% of trees, with an average of 3.8 leafhoppers per tree (range: 0-15). Leafhopper abundance was lower in 2021, when we found leafhoppers on 64% of trees with an average of 1.2 leafhoppers per tree (range: 0-7).

Tree type: In both years, aphid abundance varied among tree types ($p = 0.0016$ in 2020, $p < 0.001$ in 2021 Figure 5a, b). In both years, OG tended to have the fewest aphids, but other patterns varied. In 2020, AF had more aphids than WT and OG**.** Yet in 2021, SV had more aphids than all other tree types. For leafhoppers, the main effect of tree type did not predict abundance in either year, though it was involved in a three-way interaction described later.

N: In 2021, when N treatments spanned a wider range of concentrations, phloem feeders responded positively to N treatments ($p < 0.001$ for both insects). Leafhopper abundance on high N trees (mean = 1.6) was more than twice that of low N trees (mean = 0.7, Figure 6a). Similarly, we found more aphids on high N trees (mean = 5.1) compared to low N trees (mean = 3.2, Figure 5c).

*N * Water:* For leafhopper abundance in 2021, we found an interaction between N and water ($p = 0.049$). Low N * low water had the fewest leafhoppers (mean = 0.6), while high N*low water had the most leafhoppers (mean = 2.0). The positive effect of increasing N on leafhopper abundance was magnified under the low water treatment (Figure 6b).

*Tree type * N:* For aphids in 2020, there was an interaction between N and tree type ($p = 0.022$). SV aphid abundance trended negative with increasing N. AF and OG had the most aphids at medium N, while WT had the fewest aphids at medium N (Figure 5d).

*Tree type * N * Water:* In 2020, leafhopper abundance responded to a three-way interaction between tree type, N, and water ($p = 0.040$, Figure 6c). Most tree types had similar

numbers of aphids across N and water treatments. This interaction appears to be driven by SV, which tended to have fewer aphids at high N and more aphids at medium and low N when subjected to the high water treatment.

Insect herbivory

Potato leafhopper hopperburn was the most widespread insect herbivory we observed, with almost every tree exhibiting at least some hopperburn in both years. In 2020, we detected hopperburn on 82% of surveyed shoots, and 69% in 2021. *E. tyrius* feeding was also common: we detected its herbivory on a total of 314 shoots on 69% of trees in 2020, and 182 shoots on 66% of trees in 2021. In contrast, *P. aesculana* feeding was sparse in 2020: we found only 41 flagging shoots on 14% of trees. In 2021, we recorded *P. aesculana* feeding on 208 shoots across 64% of trees.

Water: In 2020, low water trees had on average 3.5x more flagging shoots caused by *P. aesculana* feeding compared to high water trees ($p < 0.001$, Figure 7a). In 2021, *E. tyrius* exhibited an opposite trend, with over 1.5x more shoots fed upon in the high vs. low water treatments ($p = 0.046$, Figure 8a).

Tree type: E. tyrius feeding varied across tree types in 2020, with SV incurring more herbivory than AF ($p = 0.008$, Figure 8b). Hopperburn followed a different pattern across tree types in both years ($p < 0.001$ both years). In 2020, SV had less hopperburn than all other tree types, while OG had more hopperburn. In 2021, SV and AF had the least hopperburn, while WT had the most and OG was intermediate (Figure 9a, b).

N: Leafhoppers responded to N treatments in 2021 ($p < 0.001$). High and medium N treatments had more hopperburn than low N (Figure 9c).

*Tree type * Water:* In 2021, we found an interaction between tree type and water for hopperburn (p = 0.035, Figure 9d). High water treatments in OG and WT had more hopperburn relative to low water treatments, whereas AF and SV had consistent hopperburn between water treatments.

*Tree type * Water * N:* In 2021 we found evidence for a three-way interaction between tree type, N, and water for herbivory by both *P. aesculana* (p = 0.031, Figure 7b) and *E. tyrius* (p = 0.046, Figure 8c), although no pairwise differences within tree type were significant for either insect. *P. aesculana* herbivory tends to decline with increasing N under low water conditions and rise with increasing N under high water conditions for most tree types except SV. The three-way interaction for *E. tyrius* appears to arise from very low herbivory in certain treatment groups, particularly WT trees under high water and low N, and in AF under low water and medium N.

4. DISCUSSION

In this study we found evidence that simulated urban N deposition and water availability interact to affect tree and herbivore performance. Change in tree height, leafhopper abundance, and shoot feeding by *E. tyrius* and *P. aesculana* all responded to N x water interactions in at least one year of the study. High N and low water led to higher than additive leafhopper abundance, but other interactions did not always follow our predictions and were often mediated by tree type. We found that tree type was an important predictor of nearly every response variable we measured. In 2021, when our simulated N deposition treatments spanned a broader range of N amounts, we observed that trees with higher N had more growth, more insects, and more herbivory compared to low N trees, indicating that urban N deposition is likely to elicit physiological changes in trees with consequences for herbivores in cities. However, we did not find evidence that N treatments exacerbated tree water stress as we predicted. Results of our

common garden experiment suggest the combined ecological effects of N deposition and water stress in urban environments may be important to consider as cities strive to meet biodiversity and ecosystem service goals.

Effects of water

We recorded relatively high water potential values in our trees (overall mean = -1.61 MPa in 2020, -1.55 MPa in 2021), and small average differences in stem midday water potential between our low and high water treatments in both years (mean difference = 0.17 MPa in 2020 and 0.12 MPa in 2021, Figure 2a, b). In contrast to field observations of mature urban red maples in our region, which have recorded midday water potentials spanning a broader range of values reaching -2.5 MPa or less in summer months (Dale & Frank, 2017), our treatments could be considered conservative. Yet we still observed water deficit-related declines in tree growth, both vertically (Figure 4a) and in terms of basal area (Figure 3a, b), and we found that water treatments influenced insect responses in three of the four insects we surveyed, demonstrating that even moderate reductions in water availability have consequences for red maple trees and insect herbivores.

Insect responses to water treatments in this study are consistent with guild-specific responses to plant water limitation in previous work. Our finding that the wood-boring *P. aesculana* was more prevalent in low water trees in 2020 (Figure 7a) agrees with positive responses of borers to water-deficient plants (Huberty & Denno, 2004), and with Potter et al. (1988), who found nursery-grown red maples to be more susceptible to another wood-boring insect, the flatheaded appletree borer (*Chrysobothris femorata* Oliver), during periods of drought. In 2021, we found fewer shoots affected by *E. tyrius,* a leaf-chewing insect, in the low water treatment (Figure 8a). Chewing folivores are thought not to benefit from plant water stress

because they contend with elevated allelochemicals and toughened foliage in water-stressed plants (Gely et al., 2020; Huberty & Denno, 2004; and citations therein). Other work has found that *E. tyrius* populations vary annually, and the amount of feeding per tree is associated with the number of available shoots (Dawadi et al., 2019), although we did not find a correlation between shoot number and *E. tyrius* feeding.

We hypothesized that we would observe more sap-feeding herbivory in low water trees. Unlike chewing herbivores, sap feeders avoid certain allelochemicals not present in plant sap (Raven, 1983) and often benefit from elevated plant N in vascular tissues in response to intermittent water deficit (Gely et al., 2020; Huberty & Denno, 2004). Previous work has confirmed elevated amino acid content induced by water deficit in red maples (Bissiwu et al., 2022). In 2021, we observed that sap-feeding potato leafhoppers were more prevalent on trees subjected to low water in the presence of high N (Figure 6b). However, we saw no effect of water treatments on painted maple aphid abundance in either year, and our finding that certain tree types had more hopperburn in the high water treatment (Figure 9d) is inconsistent with our prediction of more sap-feeding herbivory in low water trees.

Effects of nitrogen

The lack of response of trees and insects to differences in N treatments in 2020 can be explained by the higher top-dress rate (9.12 g N/pot) obscuring relatively small differences in N treatments. N additions in 2020 spanned 9.12 to 9.60 g N per tree between low and high N treatments. While N was involved in interactions with tree type and tree type x water in the response of aphid (Figure 5d) and leafhopper (Figure 6c) abundances in 2020, we do not see clear or consistent patterns to explain the role of N in those interactions. However, in 2021 we observed tree and insect responses to N when we lowered the overall top-dress rate to 0.75 g per

tree and recalibrated N treatment levels to span 0.75 to 11.28 g N between low and high N treatments. Other studies that have investigated N effects on red maple applied N at high rates to promote growth in nurseries and cultivated landscapes (e.g., Bentz and Townsend 2003; Day and Harris 2007; Prado et al. 2015). The 2021 high N treatment in this study (11.28 g) is equivalent to 54% of the typical N rate applied to containerized red maples in North Carolina nurseries (LeBude et al., 2012). Thus, our study is unique because we applied N at lower rates approximating urban N deposition.

In 2021, increasing N caused trees to grow taller (Figure 4c) and add more basal area (figure 2e). Medium and high N treatments also had more aphids (Figure 5c), leafhoppers (Figure 6a), and hopperburn (Figure 9c), indicating that common rates of urban N deposition are sufficient to cause changes in tree growth, insect abundance, and insect herbivory.

Studies of urban red maple responses to N deposition have demonstrated physiological changes and elevated N concentrations that could be associated with improved nutritional quality for herbivores (Hirsch et al., 2023; McDermot et al., 2020). However, the possible link between urban N deposition, urban tree host quality, and herbivory has been difficult to discern in field studies to date. While Green et al. (2017) reported elevated atmospheric NO_x along an urban gradient in North Texas, they did not find an association between atmospheric NO_x concentration and the foliar C:N ratio of post oak (*Quercus stellata* Wangenh), nor between leaf quality and chewing herbivory. Meineke et al. (2022) reported more chewing herbivory in urban areas with higher vehicle pollution, but this was not associated with changes in leaf nutritional quality for herbivores. They speculated that vehicle pollution could interfere with allelochemical synthesis pathways, thus rendering vegetation more vulnerable to herbivory. Zhang et al. (2024) confirmed a positive correlation between atmospheric NO_x, urbanization intensity, and broadleaf tree

chlorophyll content, but NO_x and chlorophyll did not predict chewing herbivory. We suggest that future investigations consider the increasing dominance of reduced (NH_x) rather than oxidized (NO_x) N as an indicator of N deposition in many urban ecosystems (Li et al., 2016). Furthermore, researchers should consider sap-feeding herbivory in response to N deposition, given the body of evidence that suggests sap-feeders are more likely to respond positively to enriched plant N. Our work demonstrates that sap-feeding herbivores may respond positively to N deposition in an urban setting.

Nitrogen-water interactions

We predicted that simulated N deposition would exacerbate water stress in our low water trees. We did not find that our trees were more water stressed (as measured by water potential) in medium or high N treatments relative to low N (Figure 2). However, we found that medium and high N trees had lower soil moisture compared to low N trees (Figure S1e), suggesting that N-fertilized trees used more water and could be vulnerable to water stress if water was further limited. Medium and high N additions induced aboveground growth, which likely increased water demand from photosynthetic tissue and could explain lower soil moisture readings in these treatments. Hirsch et al. (2023) hypothesized that N deposition in high-traffic areas would make urban trees more susceptible to drought, but they did not find N-related differences in drought tolerance among the trees they surveyed. We observed an N x water interaction in the response of vertical growth, where trees subjected to low water x low N grew less than all other water x N combinations (Figure 4d). It appears that N supplementation in medium and high N treatments enabled trees to overcome growth limitations imposed by lack of water in the low water treatment.

We also predicted N deposition would interact with water limitation to increase herbivore abundance and feeding, especially for sap-feeders. To that end, we found that high N increased potato leafhopper abundance in the presence of low water, but not in the presence of high water (Figure 6b). Our results suggest it may be important for researchers to consider water availability and N deposition together when developing models to predict herbivore abundance in urban trees. However, we did not find the same interaction in our observations of hopperburn (Figure 9), nor shoot herbivory by *P. aesculana* (Figure 7) or *E. tyrius* (Figure 8). Other studies have demonstrated that potato leafhopper abundance does not always predict hopperburn severity (Bentz & Townsend, 1997, 1999), pointing instead to genotypic differences among maple types in feeding tolerance.

Effects of tree type

Tree type was an important predictor in this study in terms of measured responses of water stress, growth, and herbivore abundance and feeding. We found that WT trees had lower average water potential relative to cultivars, indicating more water stress (Figure 1c, d) despite having comparable or elevated soil moisture (Figure S1c, d). In addition, we found that WT grew less in terms of basal area than all cultivars in 2020, and all but AF in 2021, suggesting that water limitation may have limited WT growth. Our finding that WT trees were more water stressed than cultivars was surprising in light of previous work, which found evidence for higher water use efficiency in WT trees sourced from New Jersey relative to two different red maple cultivars in a common garden experiment (Lahr et al., 2018) and unidentified cultivars in an urban landscape (Lahr et al., 2018). While we did not measure water use efficiency directly, higher water use efficiency is associated with higher midday water potential and less water stress (Lauderdale et al., 1995). WT water use efficiency and vulnerability to drought depends on seed

origin, suggesting local adaptation to water regimes across the species range (Townsend & Roberts, 1973). WT trees in this study were sourced from Missouri; thus, it is possible that different results in our study could be explained by differences in WT tree origin.

SV trees grew less vertically than all other trees (Figure 4b), which is unsurprising given that SV was selected in part for its smaller stature (US National Arboretum, 1999). We observed uneven growth responses to N across tree types: OG and AF grew more in the presence of more N in 2021 while WT and SV vertical growth remained constant (Figure 4e).

Tree type was also a strong predictor of hopperburn injury. SV incurred less hopperburn than WT or OG (Figure 8a, b), which is consistent with descriptions of potato leafhopper resistance in this cultivar (Townsend & McIntosh, 1993; US National Arboretum, 1999). Resistance to leafhopper feeding in SV does not appear to confer resistance to other herbivores in our study, as we observed higher incidence of *E. tyrius* shoot feeding (Figure 8b) and more painted maple aphids (Figure 5b) on this cultivar. WT susceptibility to potato leafhopper feeding depends strongly on the provenance of WT seedlings (Townsend, 1989). Accessions from higher latitudes and elevations tend towards earlier leaf flushing, and as a result have more hardened foliage at peak leafhopper pressure (Bentz & Townsend, 1997; Townsend, 1989). That our WT trees were sourced from Missouri, a more southern latitude, could explain why we saw relatively higher hopperburn compared to cultivars in this study.

Intraspecific response diversity to N deposition and water availability in this study supports planting diverse tree genotypes in cities to buffer against the effects of drought, N deposition, warming, and other environmental disturbances for a robust and resilient urban canopy. Urban areas are projected to more than double in extent in the next century (Gao & O'Neill, 2020) and are where most humans live (United Nations, 2018). Therefore, maintaining

urban ecological services and improving urban tree health will benefit most people. The combined ecological effects of N deposition and water stress in urban environments may be important to consider as cities strive to meet biodiversity and ecosystem service goals.

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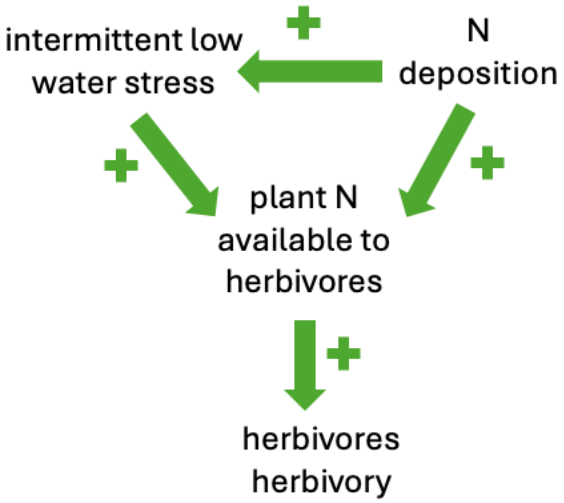

Figure 1: Schematic representation of our hypothesized interaction between intermittent low water stress and N deposition. N deposition makes plants more vulnerable to low water stress, and both factors lead to elevated plant N available to herbivores. We expect that the combination of low water stress and N deposition will result in more herbivores and herbivory than either factor in isolation.

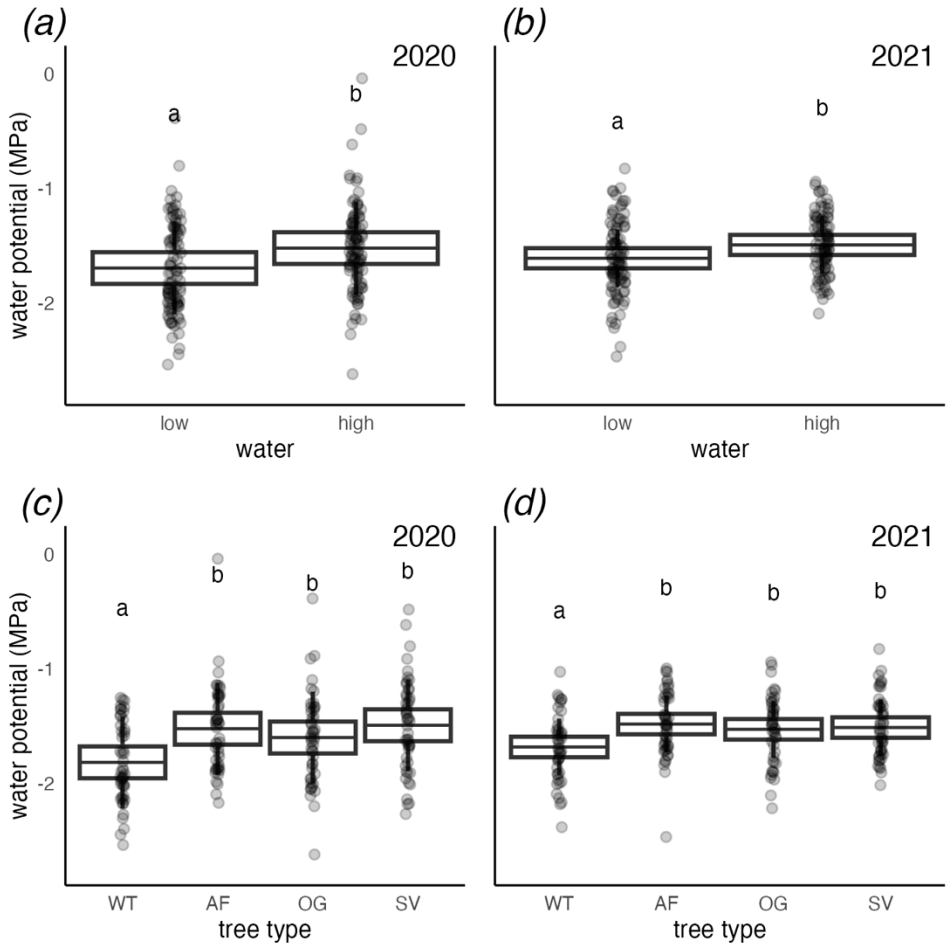

Figure 2: Water potential was lower in low water trees in 2020 (p = 0.010, a) and 2021 (p = 0.019, b), as well as in WT trees in 2020 ($p < 0.001$, c) and 2021 ($p < 0.001$, d). Box and scatter plots of stem midday water potential (MPa) on the y axis. Box plots represent linear mixed model estimates of mean +/- standard error of the mean, with whiskers indicating 95% confidence intervals. Raw data are represented by scatter plots overlayed on each box plot. Letters above box plots represent groupings based on Tukey's HSD at alpha = 0.05.

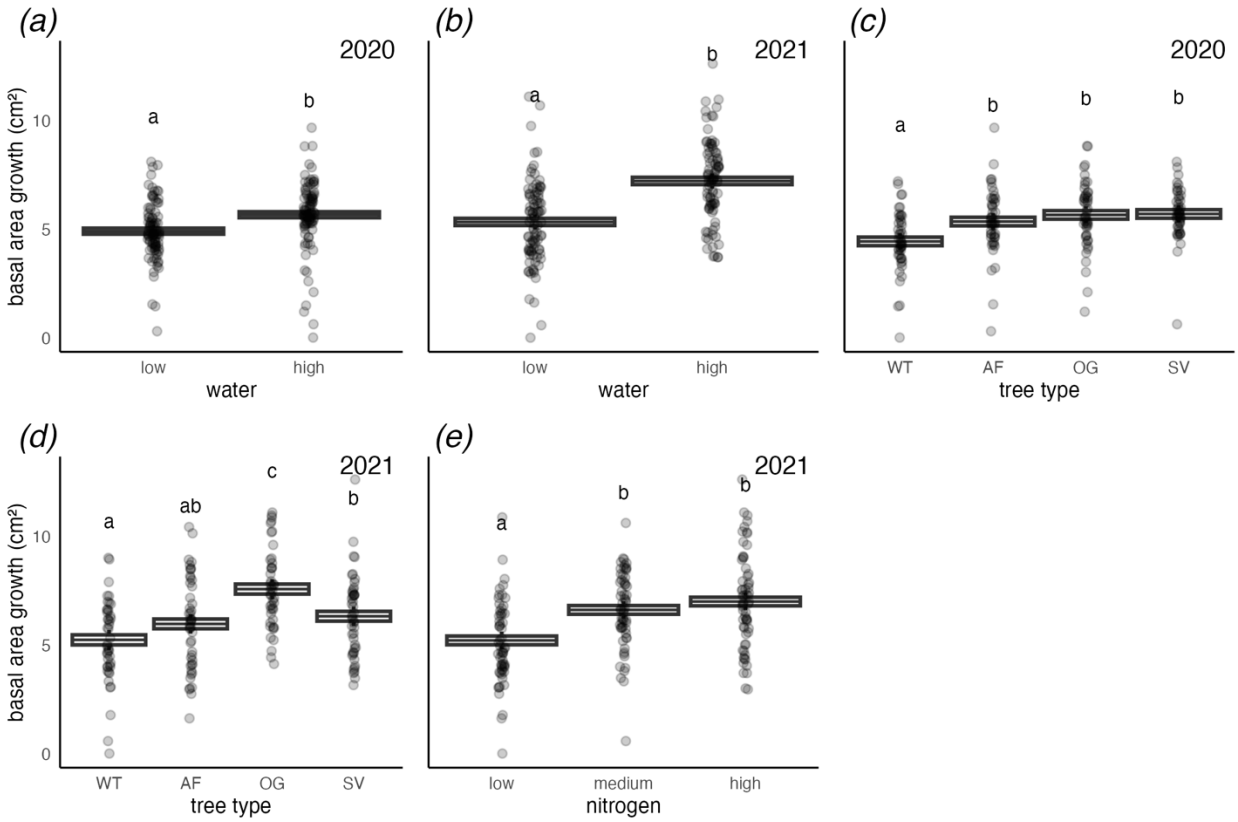

Figure 3: Basal area growth was lower in low water trees in 2020 ($p < 0.001$, a) and 2021 ($p < 0.001$, b), as well as in WT trees in 2020 ($p < 0.001$, c) and 2021 ($p < 0.001$, d). In 2021, when differences among N treatments were larger, basal area growth was lower in low N trees ($p < 0.001$, e). Box and scatter plots of basal area growth (cm^2) at 10cm above the soil surface on the y axis. Box plots represent linear mixed model estimates of mean +/- standard error of the mean, with whiskers indicating 95% confidence intervals. Raw data are represented by scatter plots overlayed on each box plot. Letters above box plots represent groupings based on Tukey's HSD at alpha = 0.05.

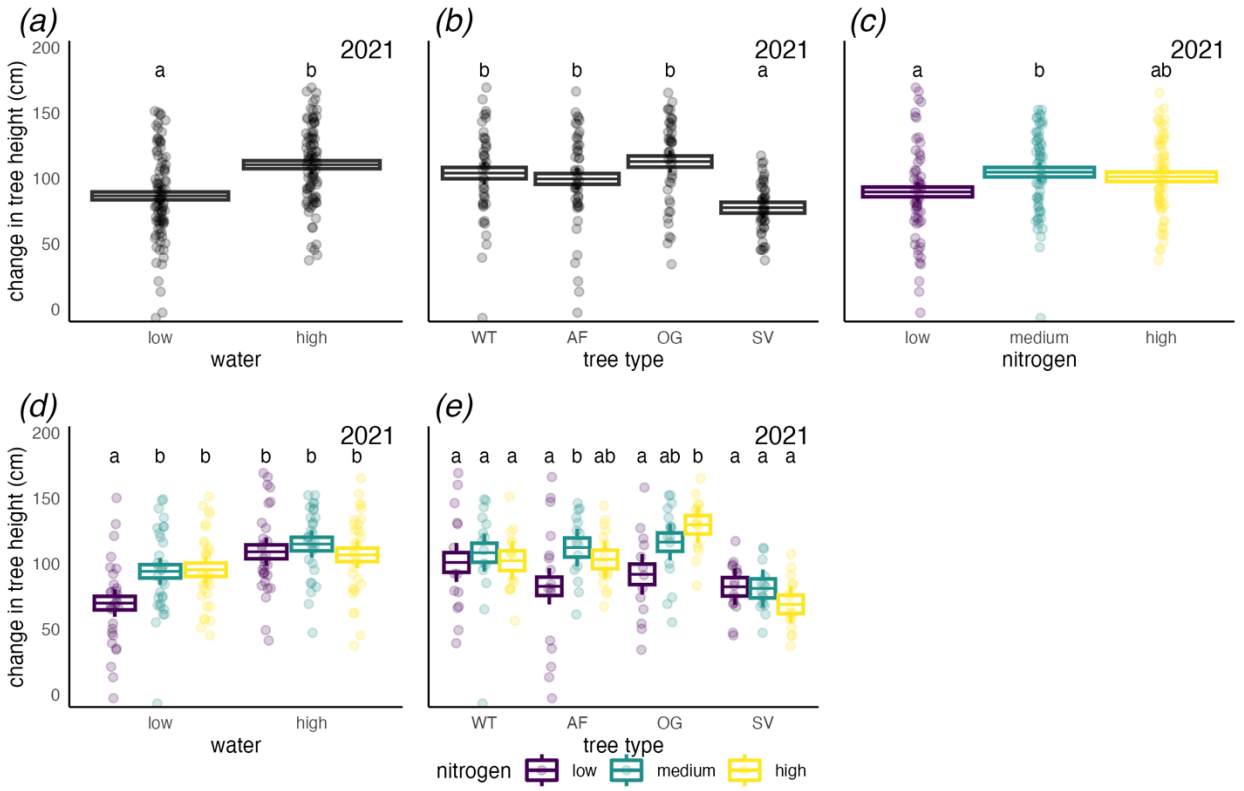

Figure 4: In 2021, change in tree height was lower in the low water treatment ($p < 0.001$, a), SV trees ($p < 0.001$, b), and in the low N treatment ($p = 0.010$, c). Trees grew less when subjected to combined low water*low N ($p = 0.026$, d), and tree types varied in their response to N ($p = 0.012$, e). Box and scatter plots of the annual change in tree height (cm) from the soil surface to tallest stem on the y axis. Box plots represent linear mixed model estimates of mean +/- standard error of the mean, with whiskers indicating 95% confidence intervals. Raw data are represented by scatter plots overlayed on each box plot. Letters above box plots represent groupings based on Tukey's HSD at alpha = 0.05. Tukey's HSD comparisons were performed within tree type in part (e).

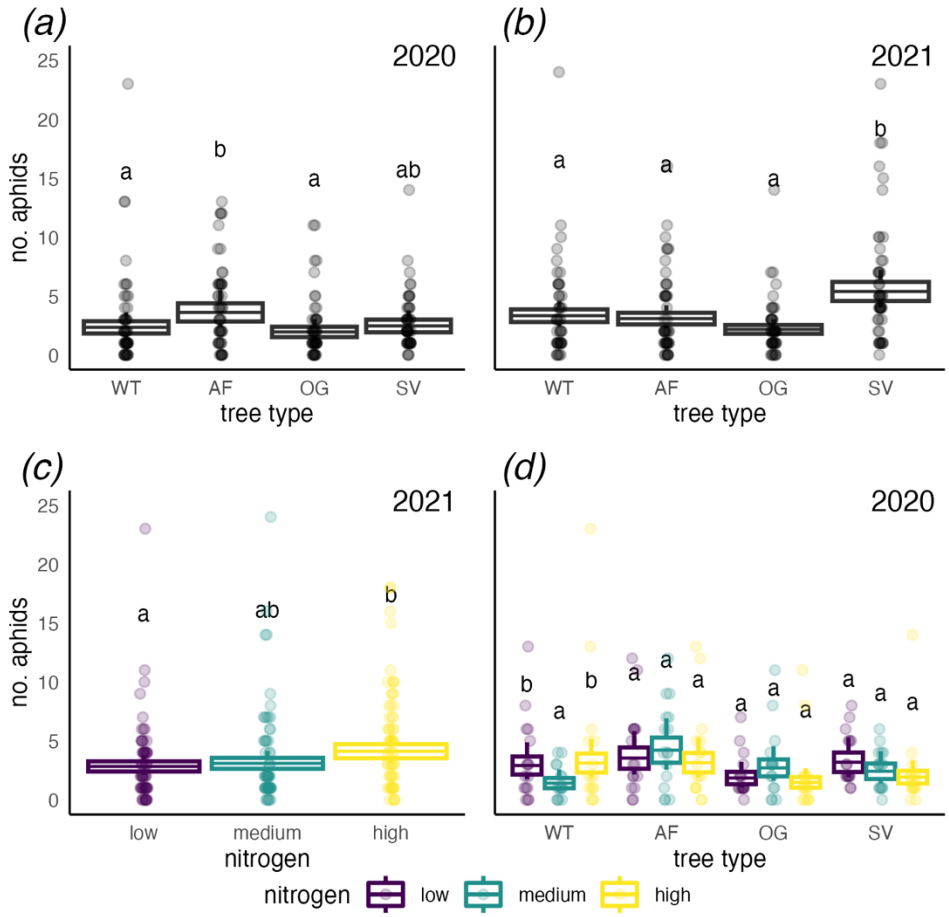

Figure 5: Painted maple aphid abundance varied among tree types in 2020 (p = 0.002, a), and 2021 (p < 0.001, b). In 2021 when differences among N treatments were larger, high N trees had more aphids (p = 0.016, c). The effect of tree type was modulated by N treatments in 2020 (p = 0.022, d). Box and scatter plots of the abundance of painted maple aphids collected from beat samples on the y axis. Box plots represent generalized linear mixed model estimates of mean +/- standard error of the mean, with whiskers indicating 95% confidence intervals. Raw data are represented by scatter plots overlayed on each box plot. Letters above box plots represent groupings based on Tukey's HSD at alpha = 0.05. Tukey's HSD comparisons were performed within tree type in part (d).

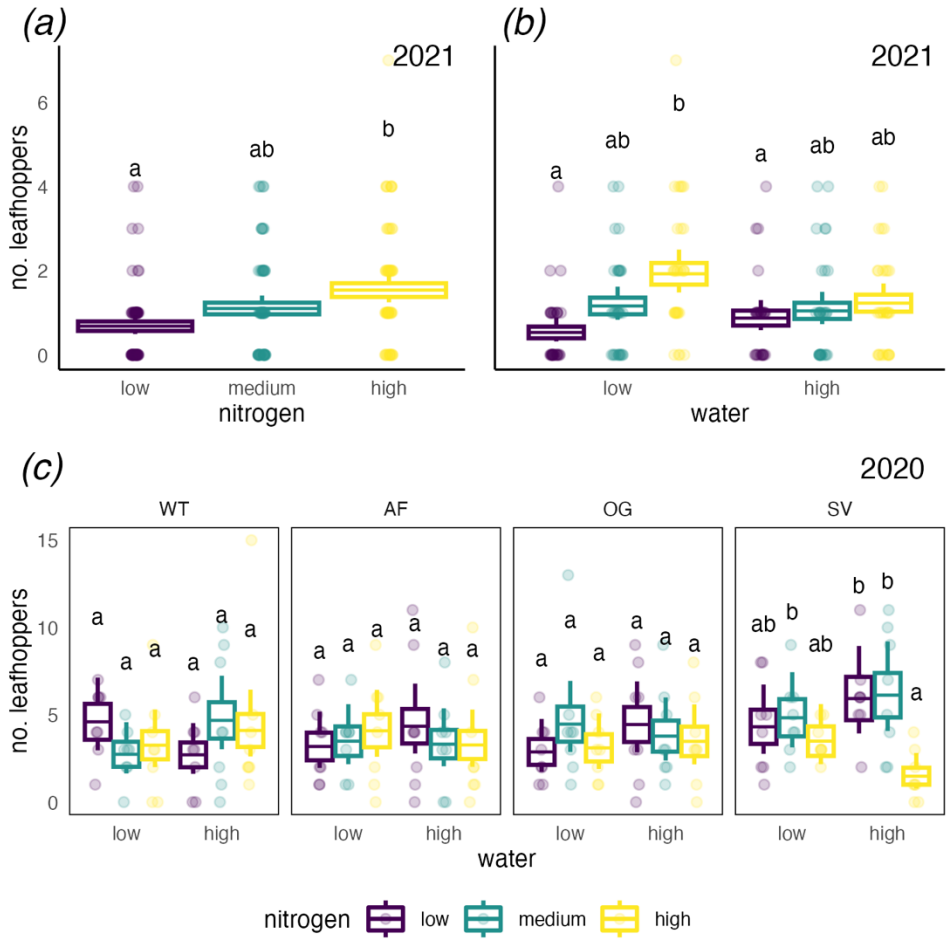

Figure 6: There were more potato leafhoppers in high N trees in 2021 ($p < 0.001$, a). The effect of high N was enhanced when combined with low water ($p = 0.049$, b). A three-way interaction appears to be driven by SV in 2020 ($p = 0.040$, c). Box and scatter plots of the abundance of potato leafhoppers collected from beat samples on the y axis. Box plots represent generalized linear mixed model estimates of mean +/- standard error of the mean, with whiskers indicating 95% confidence intervals. Raw data are represented by scatter plots overlayed on each box plot. Letters above box plots represent groupings based on Tukey's HSD at alpha = 0.05. Tukey's HSD comparisons were performed within tree type in part (c).

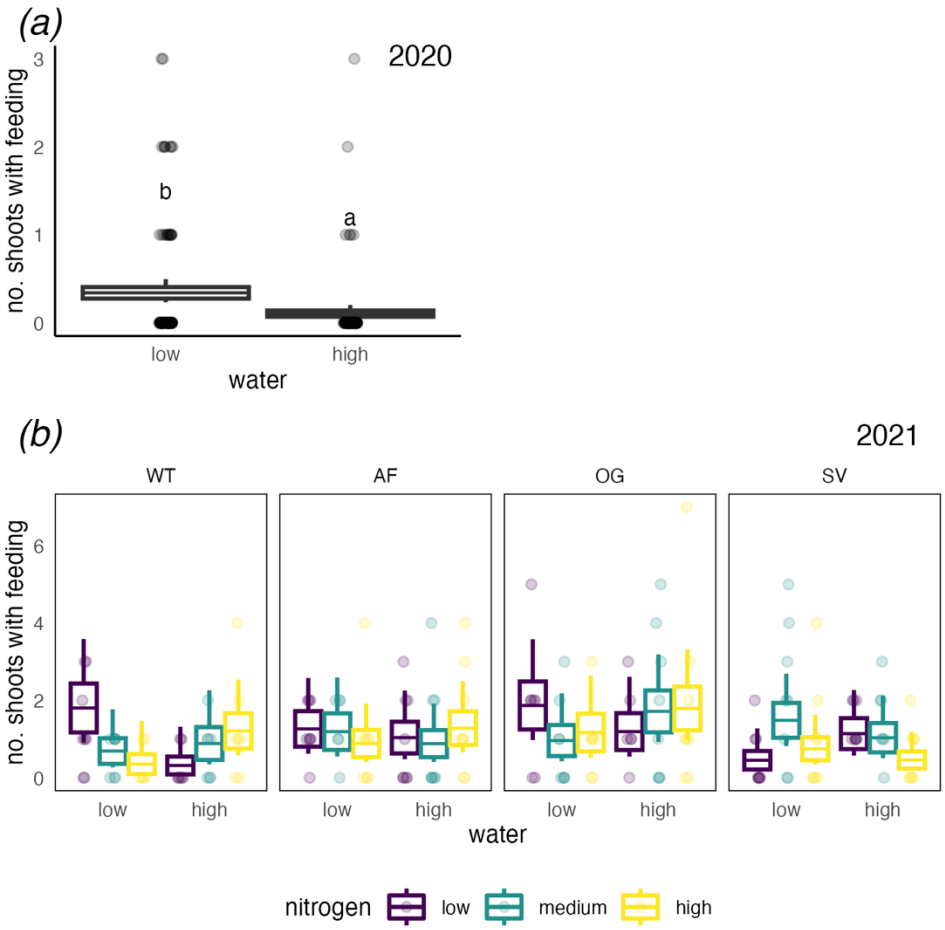

Figure 7: There were more shoots fed upon by *P. aesculana* in low water trees in 2020 ($p < 0.001$, a). We find evidence for a three-way interaction in 2021 ($p = 0.031$, b), although no pairwise differences were significant. Box and scatter plots of the incidence of tree shoots fed upon by *P. aesculana* on the y axis. Box plots represent generalized linear mixed model estimates of mean +/- standard error of the mean, with whiskers indicating 95% confidence intervals. Raw data are represented by scatter plots overlayed on each box plot. Letters above box plots represent groupings based on Tukey's HSD at alpha = 0.05.

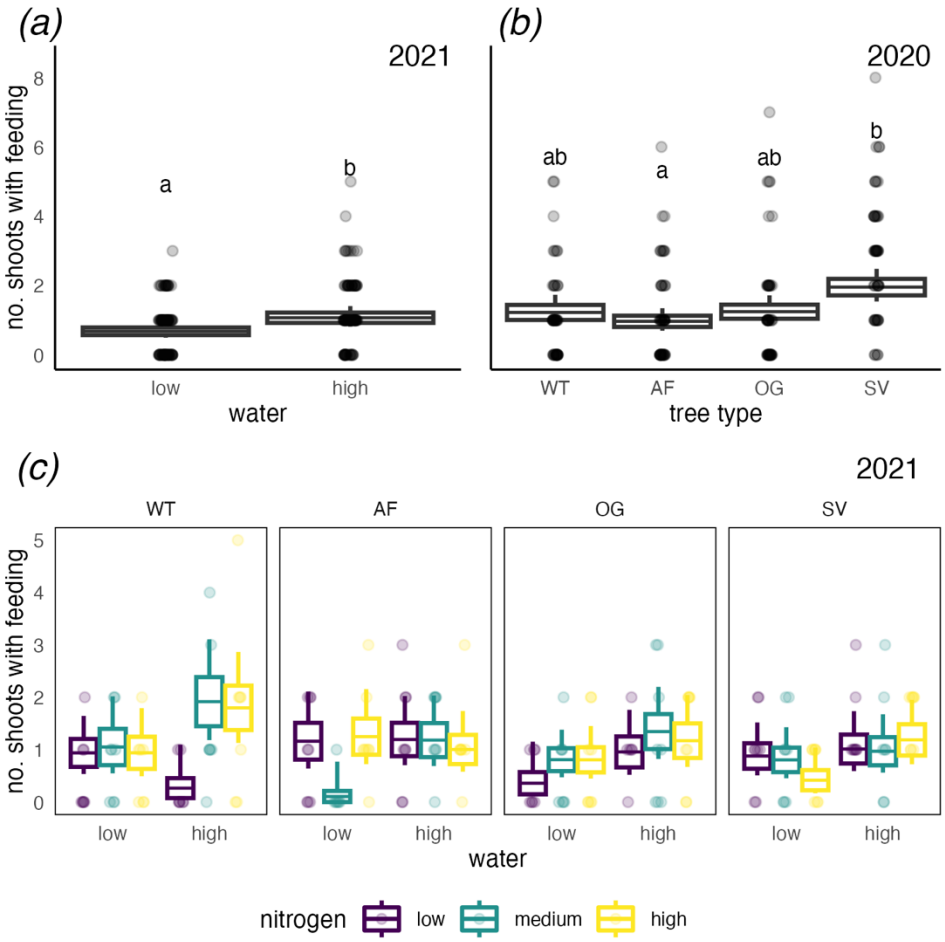

Figure 8: Fewer shoots were fed upon by *E. tyrius* in low water in 2021 ($p < 0.001$, a), and in AF relative to SV in 2020 ($p = 0.008$, b). We find evidence for a three-way interaction in 2021 ($p = 0.046$, c), although no pairwise differences were significant. Box and scatter plots of the incidence of tree shoots fed upon by *Episimus tyrius* on the y axis. Box plots represent generalized linear mixed model estimates of mean +/- standard error of the mean, with whiskers indicating 95% confidence intervals. Raw data are represented by scatter plots overlayed on each box plot. Letters above box plots represent groupings based on Tukey's HSD at alpha = 0.05.

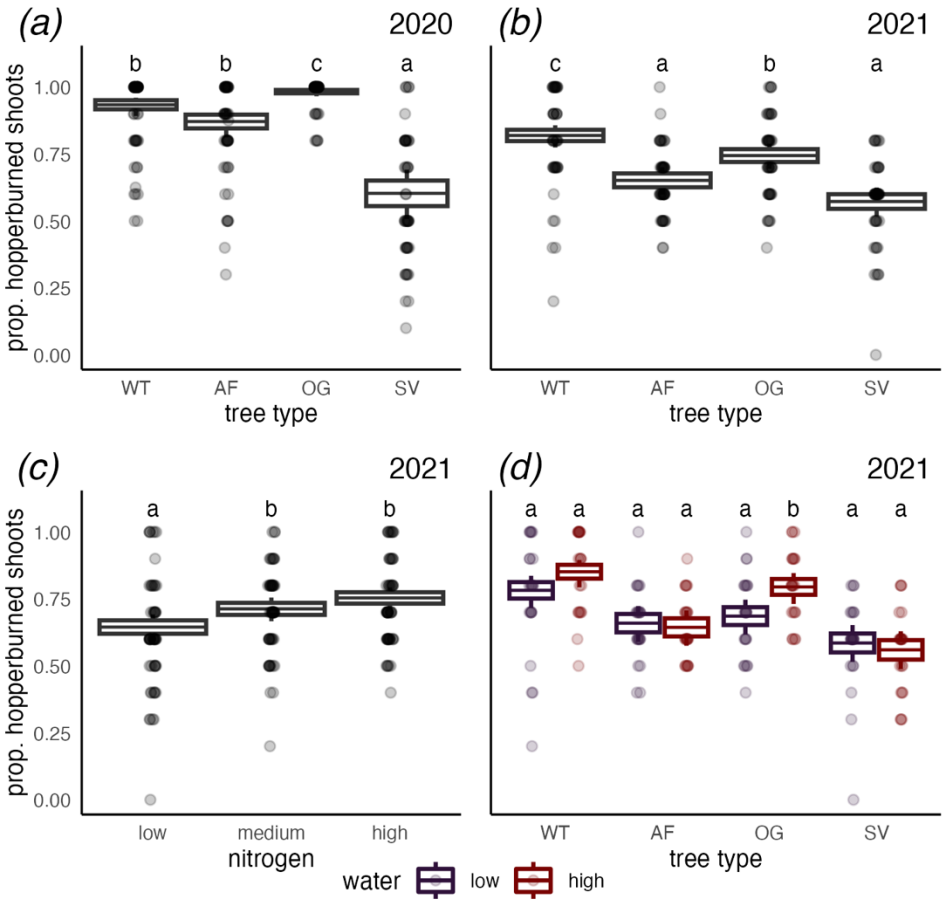

Figure 9: Potato leafhoppers fed less on SV than other tree types in 2020 ($p < 0.001$, a) and 2021 ($p < 0.001$, b). In 2021, tree type differences were influenced by water ($p = 0.035$, d). Low N trees had less potato leafhopper herbivory in 2021 ($p < 0.001$, c). Box and scatter plots of the proportion of shoots out of ten surveyed shoots per tree fed upon by potato leafhopper on the y axis. Box plots represent generalized linear mixed model estimates of mean +/- standard error of the mean, with whiskers indicating 95% confidence intervals. Raw data are represented by scatter plots overlayed on each box plot. Letters above box plots represent groupings based on Tukey's HSD at alpha = 0.05. Tukey's HSD comparisons were performed within tree type in part (d).

APPENDIX

6. SUPPLEMENTARY MATERIAL

Figure S1: Box and scatter plots of soil moisture (%) on the y axis. Box plots represent linear mixed model estimates of mean +/- standard error of the mean, with whiskers indicating 95% confidence intervals. Raw data are represented by scatter plots overlayed on each box plot. Letters above box plots represent groupings based on Tukey's HSD at alpha = 0.05. Tukey's HSD comparisons were performed within tree type in parts (f) and (g). Data are plotted separately for water treatments in 2020 ($p < 0.001$, a) and 2021 ($p < 0.001$, b), tree types in 2020 ($p = 0.005$, c) and 2021 ($p < 0.001$, d), N treatments in 2021 ($p < 0.001$, e), a two-way water*tree type interaction in 2020 ($p = 0.035$, f), and a two-way N*tree type interaction in 2020 ($p = 0.045$, g).

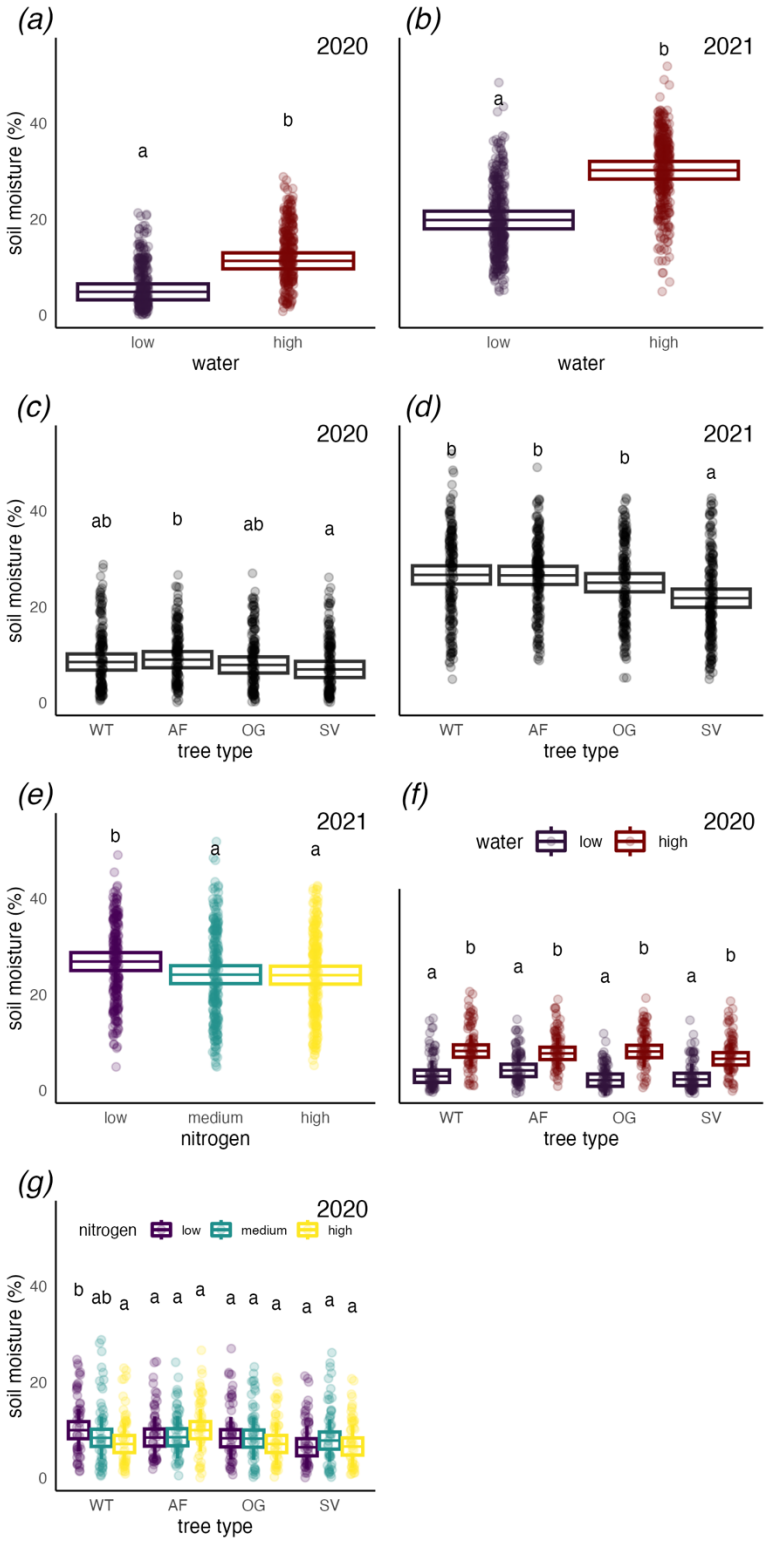
(a)
2020
soil moisture (%)
water
low
high
(b)
2021
(c)
tree type
WT
AF
OG
SV
(d)
(e)
nitrogen
low
medium
high
(f)
water
(g)

Table S1: List of trees that died in 2020-21

PlantID	tree type	N	water	block
417	AF	medium	low	5
420	OG	low	low	5
407	WT	high	low	4
302	SV	medium	high	4
115	WT	medium	high	2
128	OG	low	high	3
523	OG	low	high	8
326	WT	low	high	6
104	WT	high	high	1

Table S2: Type II Wald Chi-Squared Analysis of Variance for soil moisture (%) in 2020

Source	X^2	df	*p*	q-value
tree type	12.730	3	0.005	0.021
N	1.632	2	0.442	0.452
water	154.554	1	< 0.001	< 0.001
tree type:N	12.851	6	0.045	0.107
tree type:water	8.630	3	0.035	0.091
N:water	1.121	2	0.571	0.507
tree type:N:water	9.349	6	0.155	0.236

Full model: lmer(soil moisture ~ tree type * N * water + (1|irrigation line) + (1|date) + (1|PlantID))

Table S3: Type II Wald Chi-Squared Analysis of Variance for soil moisture (%) in 2021

Source	X^2	df	*p*	q-value
tree type	36.974	3	< 0.001	< 0.001
N	16.614	2	< 0.001	0.001
water	249.456	1	< 0.001	< 0.001
tree type:N	4.870	6	0.561	0.506
tree type:water	3.064	3	0.382	0.439
N:water	2.007	2	0.367	0.433
tree type:N:water	1.740	6	0.942	0.643

Full model: lmer(soil moisture ~ tree type * N * water + (1|block) + (1|irrigation line) + (1|PlantID) + (1|date))

Table S4: Type II Wald Chi-Squared Analysis of Variance for water potential (MPa) in 2020

Source	**X²**	**df**	***p***	**q-value**
tree type	36.654	3	< 0.001	< 0.001
N	5.172	2	0.075	0.162
water	6.721	1	0.010	0.035
tree type:N	8.923	6	0.178	0.253
tree type:water	1.232	3	0.745	0.570
N:water	1.827	2	0.401	0.447
tree type:N:water	4.524	6	0.606	0.509

Full model: lmer(water potential ~ tree type * N * water + (1|date) + (1|irrigation line))

Table S5: Type II Wald Chi-Squared Analysis of Variance for water potential (MPa) in 2021

Source	**X²**	**df**	***p***	**q-value**
tree type	20.729	3	< 0.001	0.001
N	4.447	2	0.108	0.206
water	5.473	1	0.019	0.060
tree type:N	6.420	6	0.378	0.439
tree type:water	5.527	3	0.137	0.233
N:water	4.372	2	0.112	0.206
tree type:N:water	8.032	6	0.236	0.314

Full model: lmer(water potential ~ tree type * N * water + (1|date) + (1|block) + (1|irrigation line))

Table S6: Type II Analysis of Variance for basal area growth (cm^2) in 2020

Source	**SS**	**df**	***p***	***q*-value**
tree type	49.583	3	< 0.001	< 0.001
N	0.321	2	0.916	0.634
water	27.465	1	< 0.001	0.001
tree type:N	9.760	6	0.506	0.491
tree type:water	10.675	3	0.125	0.218
N:water	6.638	2	0.167	0.245
tree type:N:water	11.309	6	0.409	0.447

Full model: lm(basal growth ~ tree type * N * water)

Table S7: Type II Wald Chi-Squared Analysis of Variance for basal area growth (cm^2) in 2021

Source	**X^2**	**df**	***p***	***q*-value**
tree type	57.369	3	< 0.001	< 0.001
N	50.790	2	< 0.001	< 0.001
water	74.435	1	< 0.001	< 0.001
tree type:N	9.674	6	0.139	0.233
tree type:water	1.189	3	0.756	0.570
N:water	1.237	2	0.539	0.491
tree type:N:water	6.118	6	0.410	0.447

Full model: lmer(basal growth ~ tree type * N * water + (1|block))

Table S8: Type II Wald Chi-Squared Analysis of Variance for change in tree height (cm) in 2020

Source	**X^2**	**df**	***p***	***q*-value**
tree type	0.552	3	0.907	0.634
N	1.733	2	0.420	0.449
water	0.419	1	0.517	0.491
tree type:N	5.257	6	0.511	0.491
tree type:water	2.601	3	0.457	0.457
N:water	0.643	2	0.725	0.568
tree type:N:water	5.176	6	0.521	0.491

Full model: lmer(change in height ~ tree type * N * water + (1|irrigation line))

Table S9: Type II Wald Chi-Squared Analysis of Variance for change in tree height (cm) in 2021

Source	**X^2**	**df**	***p***	***q*-value**
tree type	40.343	3	< 0.001	< 0.001
N	9.135	2	0.010	0.036
water	30.109	1	< 0.001	< 0.001
tree type:N	16.356	6	0.012	0.040
tree type:water	1.607	3	0.658	0.527
N:water	7.313	2	0.026	0.075
tree type:N:water	1.375	6	0.967	0.651

Full model: lmer(change in height ~ tree type * N * water + (1|irrigation line))

Table S10: Type II Wald Chi-Squared Analysis of Variance for painted maple aphid abundance in 2020

Source	**X^2**	**df**	***p***	***q*-value**
tree type	15.226	3	0.002	0.007
N	1.014	2	0.602	0.509
water	1.341	1	0.247	0.319
tree type:N	14.737	6	0.022	0.067
tree type:water	2.638	3	0.451	0.456
N:water	0.203	2	0.904	0.634
tree type:N:water	11.493	6	0.074	0.162

Full model: glmer.nb(aphid abundance ~ tree type * N * water + (1|block) + (1|irrigation line))

Table S11: Type II Wald Chi-Squared Analysis of Variance for painted maple aphid abundance in 2021

Source	**X^2**	**df**	***p***	***q*-value**
tree type	28.183	3	< 0.001	< 0.001
N	8.245	2	0.016	0.052
water	2.734	1	0.098	0.196
tree type:N	10.229	6	0.115	0.206
tree type:water	4.290	3	0.232	0.314
N:water	4.325	2	0.115	0.206
tree type:N:water	9.457	6	0.149	0.236

Full model: glmer.nb(aphid abundance ~ tree type * N * water + (1|block) + (1|irrigation line))

Table S12: Type II Wald Chi-Squared Analysis of Variance for potato leafhopper abundance in 2020

Source	**X^2**	**df**	***p***	***q*-value**
tree type	2.776	3	0.427	0.449
N	3.696	2	0.158	0.236
water	0.316	1	0.574	0.507
tree type:N	8.849	6	0.182	0.255
tree type:water	0.238	3	0.971	0.651
N:water	1.810	2	0.405	0.447
tree type:N:water	13.211	6	0.040	0.101

Full model: glmer.nb(leafhopper abundance ~ tree type * N * water + (1|block) + (1|irrigation line))

Table S13: Type II Wald Chi-Squared Analysis of Variance for potato leafhopper abundance in 2021

Source	**X^2**	**df**	***p***	***q*-value**
tree type	5.291	3	0.152	0.236
N	14.206	2	0.001	0.004
water	1.379	1	0.240	0.315
tree type:N	9.297	6	0.158	0.236
tree type:water	1.112	3	0.774	0.571
N:water	6.014	2	0.049	0.112
tree type:N:water	1.199	6	0.977	0.651

Full model: glmer(leafhopper abundance ~ tree type * N * water + (1|block), family = "poisson")

Table S14: Type II Wald Chi-Squared Analysis of Variance for *P. aesculana* feeding in 2020

Source	**X^2**	**df**	***p***	***q*-value**
tree type	2.179	3	0.536	0.491
N	1.698	2	0.428	0.449
water	15.686	1	< 0.001	< 0.001
tree type:N	5.112	6	0.530	0.491
tree type:water	2.724	3	0.436	0.452
N:water	0.506	2	0.776	0.571
tree type:N:water	7.535	6	0.274	0.349

Full model: glm(P. aesculana ~ tree type * N * water + block + offset(log(total shoots)), family = "poisson", method = brglmFit)

Table S15: Type II Wald Chi-Squared Analysis of Variance for *P. aesculana* feeding in 2021

Source	**X^2**	**df**	***p***	***q*-value**
tree type	6.410	3	0.093	0.191
N	0.832	2	0.660	0.527
water	0.009	1	0.922	0.634
tree type:N	4.473	6	0.613	0.509
tree type:water	0.581	3	0.901	0.634
N:water	2.093	2	0.351	0.433
tree type:N:water	13.923	6	0.031	0.085

Full model: glmer(P. aesculana ~ tree type * N * water + (1|irrigation line) + offset(log(total shoots)), family = "poisson")

Table S16: Type II Wald Chi-Squared Analysis of Variance for *E. tyrius* feeding in 2020

Source	**X^2**	**df**	***p***	***q*-value**
tree type	11.900	3	0.008	0.029
N	1.042	2	0.594	0.509
water	< 0.001	1	0.998	0.660
tree type:N	3.416	6	0.755	0.570
tree type:water	3.220	3	0.359	0.433
N:water	2.360	2	0.307	0.385
tree type:N:water	4.133	6	0.659	0.527

Full model: glmer(E. tyrius ~ tree type * N * water + (1|PlantID) + offset(log(total shoots)), family = "poisson")

Table S17: Type II Wald Chi-Squared Analysis of Variance for *E. tyrius* feeding in 2021

Source	**X^2**	**df**	***p***	***q*-value**
tree type	4.937	3	0.176	0.253
N	0.705	2	0.703	0.556
water	3.983	1	0.046	0.107
tree type:N	4.171	6	0.654	0.527
tree type:water	1.200	3	0.753	0.570
N:water	0.985	2	0.611	0.509
tree type:N:water	12.825	6	0.046	0.107

Full model: glmmTMB(E. tyrius ~ tree type * N * water + (1|irrigation line) + (1|block) + offset(log(total shoots)), family = genpois)

Table S18: Type II Wald Chi-Squared Analysis of Variance for potato leafhopper feeding in 2020

Source	**X^2**	**df**	***p***	***q*-value**
tree type	104.597	3	< 0.001	< 0.001
N	1.512	2	0.469	0.463
water	0.011	1	0.916	0.634
tree type:N	9.302	6	0.157	0.236
tree type:water	0.994	3	0.803	0.586
N:water	0.545	2	0.762	0.570
tree type:N:water	10.964	6	0.089	0.188

Full model: glmer(cbind(damaged shoots, undamaged shoots) ~ tree type * N * water + (1|irrigation line) + (1|PlantID), family = "binomial")

Table S19: Type II Wald Chi-Squared Analysis of Variance for potato leafhopper feeding in 2021

Source	**X^2**	**df**	***p***	***q*-value**
tree type	57.755	3	< 0.001	< 0.001
N	18.392	2	< 0.001	0.001
water	2.528	1	0.112	0.206
tree type:N	8.432	6	0.208	0.286
tree type:water	8.626	3	0.035	0.091
N:water	0.983	2	0.612	0.509
tree type:N:water	6.582	6	0.361	0.433

Full model: glmer(cbind(damaged shoots, undamaged shoots) ~ tree type * N * water + (1|block), family = "binomial")

		type				nitrogen			water	interaction
		WT	AF	OG	SV	low	med	high		
soil moisture %	2020	ab	a	ab	b				***	T*W, T*N
	2021	a	a	a	b	b	a	a	***	
Δ height	2020									
	2021	a	a	a	b	a	b	ab	***	N*W; T*N
Δ basal area	2020	a	b	b	b				***	
	2021	a	ab	c	b	a	b	b	***	
water potential (negative effect size = more positive value = less stressed)	2020	a	b	b	b				**	
	2021	a	b	b	b				*	
aphid abundance	2020	a	b	a	ab					T*N
	2021	a	a	a	b	a	ab	b		
leafhopper abundance	2020									T*N*W
	2021					a	ab	b		N*W
PLH hopperburn	2020	b	b	c	a					
	2021	c	a	b	a	a	b	b		T*W
E. tyrius herbivory	2020	ab	a	ab	b					
	2021								*	T*N*W
P. aesculana herbivory	2020								***	
	2021									T*N*W

est. effect size (%): -75%, -50%, -25%, 0%, 25%, 50%, 75%, 100%, 125%, 150%, 175%, 200%, 225%, 250%

Figure S2: Estimated main effect sizes for each response variable in 2020 and 2021. Letters indicate Tukey's HSD at alpha = 0.05. Estimated effect sizes were calculated from model estimates as a percentage change from control treatment values (WT, low N, and high water). Higher order interactions between model fixed effects of tree type (T), N, and/or water (W) with $p < 0.05$ are indicated in the interaction column.